



CO₂ fluxes and ecosystem dynamics at five European treeless peatlands – merging data and process oriented modeling

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Abstract. The carbon dioxide (CO₂) exchange of five different peatland systems across Europe with a wide gradient in land use intensity, water table depth, soil fertility and climate was simulated with the process oriented CoupModel. The aim of the study was to find out whether CO₂ fluxes, measured at different sites, can be explained by common processes and parameters or to what extent a site specific configuration is needed. The model was calibrated to fit measured CO₂ fluxes, soil temperature, snow depth and leaf area index (LAI) and resulting differences in model parameters were analyzed. Finding site independent model parameters would mean that differences in the measured fluxes could be explained solely by model input data: water table, meteorological data, management and soil inventory data.

Seasonal variability in the major fluxes was well captured, when a site independent configuration was utilized for most of the parameters. Parameters that differed between sites included the rate of soil organic decomposition, photosynthetic efficiency, and regulation of the mobile carbon (C) pool from senescence to shooting in the next year.

The largest difference between sites was the rate coefficient for heterotrophic respiration. Setting it to a common value would lead to underestimation of mean total respiration by a factor of 2.8 up to an overestimation by a factor of 4. Despite testing a wide range of different responses to soil water and temperature, rate coefficients for heterotrophic respiration were consistently the lowest on formerly drained

sites and the highest on the managed sites. Substrate decomposability, pH and vegetation characteristics are possible explanations for the differences in decomposition rates.

Specific parameter values for the timing of plant shooting and senescence, the photosynthesis response to temperature, litter fall and plant respiration rates, leaf morphology and allocation fractions of new assimilates, were not needed, even though the gradient in site latitude ranged from 48° N (southern Germany) to 68° N (northern Finland) differed largely in their vegetation. This was also true for common parameters defining the moisture and temperature response for decomposition, leading to the conclusion that a site specific interpretation of these processes is not necessary. In contrast, the rate of soil organic decomposition, photosynthetic efficiency, and the regulation of the mobile carbon pool need to be estimated from available information on specific soil conditions, vegetation and management of the ecosystems, to be able to describe CO₂ fluxes under different conditions.

1 Introduction

In recent years, many data sets have been collected from a number of sites and across multiple years, containing detailed and high-resolution measurements of carbon (C) fluxes, plant and soil characteristics, meteorological and water table data (Baldocchi et al., 2001; Baldocchi, 2007).

Several of the measured sites are peatlands, which have accumulated a vast amount of C since the last deglaciation. Under drained conditions, peatlands have a high carbon dioxide (CO₂) emission potential (e.g., van den Bos, 2003; Lohila, 2004; Drösler et al., 2008; Maljanen et al., 2010). Understanding the processes driving CO₂ emissions is essential in the development of management practices to reduce greenhouse gas emissions.

Direct comparison of measured data can be used to explore the effect of single variables if the site conditions are similar or differ only in few variables, e.g., in manipulation experiments (Chivers et al., 2009; Ward et al., 2013) or different vegetation types at the same site (e.g., Chojnicki et al., 2010). However, the sites in this study have very different characteristics with respect to climate, hydrology, current and former land management, vegetation and soils. Direct site comparisons of measured flux data (e.g., Alm et al., 1999; Humphreys et al., 2006; Lund et al., 2009; Drewer et al., 2010) are often uninformative when trying to distinguish between responses of several individual factors. Typically, multiple factors are linked and interact with each other complicating the analysis. Therefore, important drivers at one site might not play a significant role on another site (e.g., Lafleur et al., 2005). Process oriented modeling provides a method to identify to what extent observations at different sites can be described by the same processes, while accounting for such interactions.

Process oriented modeling requires (1) that the model can describe the observations and (2) that the parameters used in the model to describe the observations can be estimated from available data. Typically, studies focus on demonstrating how well the model can describe a certain set of data (e.g., van Huissteden et al., 2009; Calanca et al., 2007; Frohling et al., 2001; St-Hilaire et al., 2010). In contrast, the focus of this study was exploring differences between the sites while model performance was subordinate. Process oriented models often require a large number of input parameters which are usually difficult to estimate based on available data from less intensively investigated sites (Juston et al., 2010). Parameters may interact with each other and the available information does not allow for a single or unambiguous mathematical solution (Beven and Freer; 2001, Beven, 2006; van Oijen et al., 2013). However, for all sites in this study, accurate gas flux measurements in combination with detailed measurements of soil and plant conditions were available. Such extensive measurements have been demonstrated to be useful in identifying the governing properties for specific sites. For example, the modeling of CO₂ from forest sites has shown that dynamics of CO₂ fluxes are restricted to a certain range of parameter values (Wu and Jansson, 2013; Wu et al., 2013a).

A systematic evaluation of one model against data from multiple sites with a common set of parameters will allow for a better understanding of processes not only at the individual sites but also on the site specific differences which control

the resulting fluxes (e.g., Calanca et al., 2007; van Huissteden et al., 2006; van Huissteden et al., 2009). This is a necessary precondition for accurate predictions of CO₂ fluxes under different climate scenarios or at different locations. On peatlands, some attempts have been made to consider site differences using simplified process models on national (e.g., ECOSSE; Bell et al., 2012) and global scales (e.g., InTec; Ju and Chen, 2005; McGill; St-Hilaire et al., 2010) and up to a millennial timescale (Schuldt et al., 2013). However, we are not aware of any studies comparing differences in parameter distributions of CO₂-related processes between treeless peatland sites using an uncertainty-based approach and a detailed process oriented model running on site scale.

Many carbon ecosystem models are available for site-scale application such as Biome-BC (Feng et al., 2011), DNDC (Li et al., 1992a, b; Dietiker et al., 2010), PaSim (Calanca et al., 2007), PIXGRO (Adiku et al., 2006), CANDY (Franko et al., 1997), or DAYCENT (CENTURY) (Del Grosso et al., 2005). Some models were explicitly created or adapted to peatlands such as PDM (Frohling et al., 2001), PCARS (Frohling et al., 2002), CASA (Potter et al., 2001), NASA-CASA (Del Grosso et al., 2005), ecosys (Grant et al., 2012), wetland-DNDC (Zhang et al., 2002), peatland DOS-TEM (Fan et al., 2013), PEATLAND-VU (van Huissteden et al., 2006) or GUESS-ROMUL (Yurova et al., 2007).

In this work the CoupModel was used, which is a detailed process oriented model coupling heat and mass transfer for soil–plant–atmosphere systems (Jansson and Karlberg, 2010). The CoupModel was chosen for the following reasons: the model was designed for a wide range of soil types and different ecosystems and applications (see Jansson, 2012 for review) which might be useful as some of the sites in this study are already quite degraded and might not respond like a typical, intact peatland anymore. The model has been shown to be capable of simulating all three main greenhouse gases from peatlands: CO₂ (Klemedtsson et al., 2008), nitrous oxide (N₂O) (Norman et al., 2008) and methane (CH₄) (Ravina, 2007). Furthermore, the CoupModel includes detailed submodules for the most relevant processes in the carbon cycle: it predicts plant growth, plant transpiration and autotrophic respiration, soil nitrogen (N) and C processes, energy and heat fluxes, soil temperature, soil frost and snow depth. It supports an hourly time step for input and output data and can run in even finer time resolution, which is necessary for analyzing e.g., chamber flux data. The user can select between different submodels, different equations and different complexities and easily access all parameters via a user interface. Calibration procedures with randomized parameter values and methods for visualization and detailed analysis of the model output are supported. An extensive model description can be found in Jansson and Karlberg (2010). The model and its documentation as well as several tutorials for its application can be downloaded from the CoupModel home page (CoupModel, 2014).

Table 1. Site characteristics.

Code	Lom	Amo	Hor	FsA and FsB
Country	Finland	UK	Netherlands	Germany
Site name	Lompolojänkkä	Auchencorth Moss	Horstermeer	Freisinger Moos
Area (m ²)	120 000	250 000	120 000	400
Latitude,	67°59'83" N,	55°47'34" N,	52°14'25" N,	48°22'50" N,
longitude	24°12'55" E	3°14'35" W	5°4'17" E	11°41'12" E
Peatland type	fen	bog	fen	fen
Dominant vegetation	mosses, sedges, shrubs	grasses, sedges, soft rush, mosses	grass, reeds, small shrubs	sedges, herbs, grasses (A), tall sedges (B)
Land use and management	natural mire	restored; grazed	restored; nature reserve	drained, 1 cut a ⁻¹
Mean temperature/range ^a (°C)	-1.4/-15-13	10/4-15	9.8/3-17	7.5/-2-17
Mean water table (cm)	+1.2	-12.5	~ -10	-25 (A) -20 (B)
Annual precipitation (mm)	484	1155	797	788
N deposition (kg ha ⁻¹ a ⁻¹)	8.13	1.59		7.1
Peat depth (m)	2-3	0.5-5	2	3
pH	5.5-6.0	4.4	4.8-6.0	5.5-6.7

^a Annual range of mean monthly temperatures.

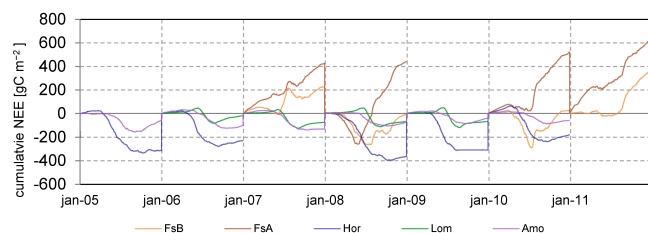


Figure 1. Measured NEE from gap-filled time series. Positive values indicate CO₂ emission, negative CO₂ uptake by the ecosystem.

The main aim of this study was to find out to what extent the large differences in measured CO₂ fluxes between five data rich European flux measurement sites can be solely explained by the differences in meteorology, water table and management. Therefore, the process oriented CoupModel was applied using an uncertainty-based Monte Carlo approach. Specific objectives were

- I. to identify differences and similarities between various sites in CO₂-related processes, corresponding parameters and responses to forcing data;
- II. to identify and discuss the impact of available data for estimating key parameters in CO₂ flux models in general;

- III. to identify problems related to the model representation of the different ecosystem processes for open peatlands.

2 Methods

2.1 Description of sites and investigations

The CoupModel was applied to five treeless peatland sites with a wide gradient in land use intensity, water level, soil nutrient status and mean annual temperature (Table 1). Together with the climatic gradient from northern Finland to southern Germany and a different growing season, this leads to great differences in amplitude and dynamics of gross primary productivity (GPP), ecosystem respiration (R_{eco}) and different amounts of biomass. This is reflected in the annual accumulated net ecosystem exchange (NEE) based on measurements, ranging from -395 to 636 g C m⁻² (Fig. 1).

Dynamic forcing data for model input (water table and meteorology) were available from measurements at all sites (Table S1). Data used for model parameter constraint included measurements of LAI, soil temperature and NEE (Table S2). Measured NEE was partitioned into R_{eco} and GPP by the use of empirical models. At sites where the eddy covariance method was used, R_{eco} was derived from nighttime NEE, otherwise it was taken from opaque chamber measurements. The empirical R_{eco} models are based on temperature (Lloyd and Taylor, 1994), while light-level-based functions

were used for GPP according to Falge et al. (2001). Corrections and gap filling at flux tower sites was done according to the methods described in Reichstein et al. (2005). A detailed description is given in the references listed in Table S2. Though R_{eco} and GPP are not explicitly measured, this will be called measured data in the following for simple distinction from the simulated fluxes by the CoupModel.

The northernmost site, Lompolojänkkä fen (Lom), located in Finland is a nutrient-rich natural mire with sedges, shrubs and mosses. Mean air temperature from 2006 to 2010 was -1.4°C and the mean groundwater table during the snow-free season was close to the peat surface. Data for model calibration were available from 2006 to 2010 and consisted of eddy covariance (EC) and automatic chamber data of CO₂ fluxes, snow depth and leaf area index (LAI) measurements. A detailed description of the site and measurement methods can be found in Aurela et al. (2009), Drewer et al. (2010) and Lohila et al. (2010).

The Scottish site, Auchencorth Moss (Amo) is an ombrotrophic bog, with vegetation consisting of grasses, sedges and soft rushes, covering a primarily Sphagnum base layer. The site is managed for low-intensity sheep grazing with less than one livestock unit per hectare, but this was not accounted for in the model. Amo encompasses a small area of peat extraction in the southwest of the catchment, which is unlikely to fall within the flux footprint of the EC system. The site was drained over a century ago, however, the drains are no longer considered to be in operation. The mean water table was -12.5 cm between 2006 and 2010. Mean temperature during this period was 10°C , CO₂ data from EC during the same period was used for model calibration. A detailed description of the site and measurements can be found in Helfter et al. (2014), Drewer et al. (2010) and Dinsmore et al. (2010).

Horstermeer fen (Hor) is located in the Netherlands in a drained natural lake. It used to be agricultural land but was abandoned more than 15 years ago. The water table was raised during restoration leading to a mean value of -10 cm during the simulation period from 2004 to 2010. It became a seminatural grassland, a nature reserve without any mowing management. The vegetation is very heterogeneous with reeds, grasses and small shrubs (Hendriks, 2009). The mean temperature during the simulation period was 10°C . CO₂ fluxes were measured half-hourly by EC and biweekly with opaque chambers between 2004 and 2010. A detailed description of the site and measurement methods can be found in Hendriks et al. (2007).

Freisinger Moos (FsA and FsB) is a drained nutrient-rich fen in the south of Germany. The two sites FsA and FsB lie next to each other in a drained sedge meadow which was cut once per year. The mean annual hay yield was 4.19 or 4.07 t dry weight $\text{ha}^{-1}\text{ a}^{-1}$ for FsA and 5.67 or 6.17 t dry weight $\text{ha}^{-1}\text{ a}^{-1}$ for FsB for the years 2010 and 2011, respectively. FsB is located in a small depression with a mean water level of -20 cm compared to -25 cm for FsA during

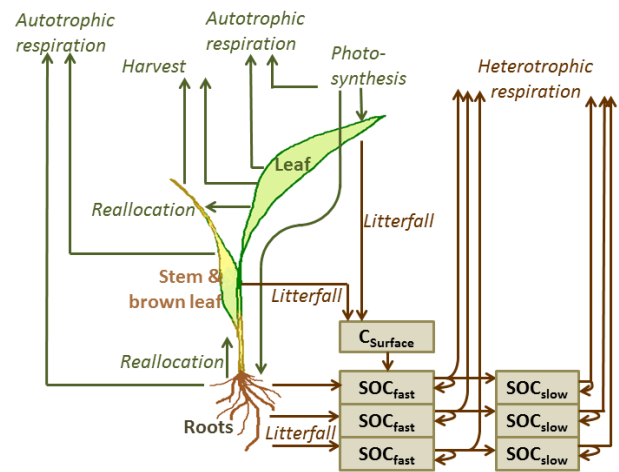


Figure 2. Scheme of carbon fluxes and pools in the current CoupModel setup.

the years 2007–2011. Mean temperature during this period was 7.5°C . FsB contains mainly tall sedges with little reed while FsA is vegetated by a mixture of sedges, grasses and herbs. Manual transparent and opaque chamber data of CO₂ fluxes ($n=3$ for each plot), measured several times a day every 3–4 weeks and half-hourly meteorological data were available for the time period of 2007–2011. A detailed description of the chamber configuration, measurement technique and empirical model approach were given in Drösler (2005), Beetz et al. (2013) and Leiber-Sauheitl et al. (2014). The measured R_{eco} and empirically modeled GPP during the measurement period of each measurement day were used for parameter constraint, empirically modeled values between measurement days were only used for visualization and comparison.

2.2 Model description

CoupModel v4 from 12 April 2013 was used for simulations. The current version can be downloaded from the CoupModel home page (CoupModel, 2014). A detailed description can be found in Jansson and Karlberg (2010). The model represents the ecosystem by a description of C and N fluxes in the soil and in the plant. It includes all main abiotic fluxes, such as soil heat and water fluxes, that represent the major drivers for regulation of the biological components of the ecosystem. The most important equations with the corresponding parameters and switches differing from the default setup in the used version can be found in Tables S3, S4, S5 and S6. The major model assumptions relating to the model application to peatlands are described below. Figure 2 shows a scheme of the main carbon fluxes and pools in the current CoupModel setup.

Table 2. Abbreviations and symbols.

Abbreviation	Description
C	carbon
CO ₂	carbon dioxide
EC	eddy covariance
GHG	greenhouse gas
GPP	gross primary production
k_{gresp}	growth respiration coefficient
k_{h}	rate coefficient for the decay of the slow C pool
k_1	rate coefficient for the decay of the fast C pool
k_{tot}	total rate of decomposition calculated from k_{h} , k_1 and SOC of the corresponding pools in the upper 30 cm
$k_{\text{mresp leaf}}$	maintenance respiration coefficient for leaves
k_{rn}	extinction coefficient in the Beer law used to calculate the partitioning of net radiation between plant canopy and soil surface
LAI	leaf area index
ME	mean error
m_{retain}	coefficient for determining allocation to mobile internal storage pool
N	nitrogen
NSE	Nash–Sutcliffe efficiency
p_{ck}	speed at which the maximum surface cover of plants is reached
$p_{\theta\text{p}}$	power coefficient in the response function of microbial activity in dependency of soil moisture
$p_{\theta\text{Satact}}$	activity under saturated conditions in the soil moisture response function for microbial activity, mineralization–immobilization, nitrification and denitrification
$p_{\theta\text{Upp}}$	water content interval in the soil moisture response function for microbial activity, mineralization–immobilization, nitrification and denitrification
R^2	coefficient of determination
R_{eco}	ecosystem respiration
SOC	soil organic carbon
T_{amean}	assumed value of mean air temperature for the lower boundary condition for heat conduction
T_{aamp}	assumed value of the amplitude of the sine curve, representing the lower boundary condition for heat conduction
$T_{\text{MatureSum}}$	temperature sum beginning from grain filling stage for plant reaching maturity stage
T_{DormTh}	critical air temperature that must be undershot for temperature sum calculation
$T_{\text{EmergeSum}}$	air temperature sum that is the threshold for start of plant development
T_{EmergeTh}	critical air temperature that must be exceeded for temperature sum calculation
t_{Q10}	response to a 10 °C soil temperature change on the microbial activity, mineralization–immobilization, nitrification, denitrification and plant respiration
t_{Q10bas}	base temperature for the microbial activity, mineralization–immobilization, nitrification and denitrification at which the response is 1
ε_{L}	radiation-use efficiency

2.2.1 Meteorological driving variables and integration time step of the model

Hourly values of global radiation, relative humidity, precipitation, wind speed, and air temperature, measured at each site were used as input. Data was gap filled by simple linear interpolation for gaps < 6 h. Larger gaps were filled by values from other adjacent climate stations. At Hor the station used for gap filling provided only daily values. Hourly values were retrieved assuming uniform distribution over 24 h for precipitation, wind speed and relative humidity and sinusoidal distribution for temperature and global radiation.

Model performance was only evaluated for the years when meteorological data was available. The simulations were started 2 years prior to the evaluation period, so the system

(in particular the plant) could adapt to the site conditions and become more independent of initial values. Data from the available years was copied to previous years if not available from an adjacent climate station.

The model's internal time step was half-hourly for abiotic processes and hourly for nitrogen- and carbon-related processes.

2.2.2 Dynamic coupled heat and water model for above soil surface conditions

An interception model for both, radiation and precipitation, a snow model and a surface pool model was used to provide boundary conditions at the soil surface. Interception and plant evaporation was dependent on the simulated leaf

area index of the plant as well as the degree of coverage, while transpiration depended additionally on the simulated water uptake of the plant. Cloud fraction was calculated from global radiation input and latitude. Incoming radiation was partitioned between one part which was absorbed by the plant canopy and another part which reached the soil. Surface temperature was simulated based on an energy balance approach, where the radiation reaching the soil equals the sum of sensible and latent heat flux to the air and heat flux to the soil. Soil evaporation was derived from an iterative solution of the soil surface energy balance of the soil surface, using an empirical parameter for estimating the vapor pressure and temperature at the soil surface. Vapor pressure deficit was calculated from the relative humidity input. Snowfall was simulated from precipitation and air temperature, snowmelt from global radiation, air temperature and simulated soil heat flux. Surface runoff was controlled by a surface pool of water that covers various fractions of the soil surface. Under oversaturated periods the flow of water in the upper soil compartment could be directed upwards, towards the surface pool. Surface runoff was calculated as a function of the amount of water in the surface pool.

2.2.3 Dynamic heat and water model for the soil

The soil profiles were divided into 12 layers with an increasing layer depth from 5 cm for the upper layer to 100 cm in the lowest layer. Heat flow between adjacent soil layers were calculated based on thermal conductivity functions accounting for the content of ice and water. The heat flow equation is based on a coupled equation accounting for the freezing and thawing in the soil (Jansson and Halldin, 1979). Convection was not accounted for. The lower boundary was calculated as temperature based on a sine variation at the soil surface and a damping depth for the whole soil profile as well as a parameter for the annual mean temperature T_{amean} and annual amplitude of temperature T_{aamp} at the site (a list of symbols and abbreviations can be found in Table 2).

Soil water depended on infiltration to the soil, soil evaporation, water uptake by plant roots and groundwater flow. Soil moisture, represented as liquid water content, was calculated based on the water storage and temperature. Water flows between adjacent soil layers were calculated according to the Richards equation (1931), considering hydraulic conductivity, water potential gradient and vapor diffusion. Soil water characteristics were described by the Brooks and Corey (1964) equation between two threshold water tensions, while a log-linear expression was applied at higher water tensions and a linear expression at water contents close to saturation. Unsaturated conductivity was simulated according to Mualem (1976), additionally accounting for the conductivity in macro pores. The groundwater level was defined by assuming a continuous zone of saturation from the water table level down to the lower boundary of the considered soil pro-

file. To force saturation at the measured groundwater level, water was added to or removed from the corresponding layer.

2.2.4 Vegetation

Vegetation was simulated according to the explicit big leaves concept (e.g., Dai et al., 2004) but only one plant canopy layer, representing the complete plant community, was defined. Albedo, LAI, vegetation height and vegetation cover were simulated. Permanent, perennial vegetation was configured with maximal plant height of 0.6 m, a lowest root depth of -0.6 m and a maximal plant cover of 100 %. Grain development was assumed to play a minor role and was therefore disabled. Plant respiration was assumed to be dependent on growth and maintenance (e.g., Hansen and Jensen, 1977).

For leaf assimilation, the light-use efficiency approach (Monteith, 1972; Monteith and Moss, 1977, see e.g., Hilker et al., 2008 for review) was used, at which total plant growth is proportional to the global radiation absorbed by canopy but limited by unfavorable temperature and limited soil water. For simplicity, plant assimilation was simulated independent of dynamics in N availability. This might be justified as none of the sites were fertilized in the recent years and the vegetation community was assumed to be adapted to the nutrient conditions at each site. Differences in N availability between sites are included in the radiation efficiency (ϵ_L). Plants were assumed to be well adapted to wet conditions (Keddy, 1992, Steed et al., 2002), including aerenchyma to tolerate water saturated soil conditions (Jackson and Armstrong, 1999). Plant stress due to high water saturation was therefore disabled.

Plant development started every spring when the accumulated sum of air temperatures above a threshold value (T_{EmergeTh}) reached the value of $T_{\text{EmergeSum}}$. Both parameters were calibrated (Table S4). The accumulation of temperatures started when the day length exceeded 10 h. Snow cover hindered shooting by reducing the radiation passing through to the plant, while low soil temperatures reduced plant water uptake.

Besides a small amount of litter fall occurring during the whole plant growth period (Robson, 1973; Duru and Ducrocq, 2000; Fulkerson and Donaghy, 2001), senescence was assumed to start after the plant reached maturity and therefore depended on growth stage (e.g., Thomas and Stoddart, 1980) and temperature sums (e.g., Davidson and Campbell, 1983). As this was not yet directly supported by the model, the stem pool was used for brown, senescent, standing biomass. Therefore new assimilates were constantly allocated to roots and leaves only, while existing leaf biomass was reallocated after maturity to the stem pool. A third stage of litter fall was configured depending on a minimum threshold temperature sum: five consecutive days in the autumn with day lengths shorter than 10 h and with temperatures below T_{DormTh} terminated the growing season and plants went into dormancy.

During litter fall part of the C is stored in a mobile pool, which can be then reused for regrowth in spring in the next year (e.g., White, 1973; Wingler, 2005).

Harvest took place at FsA and FsB. Based on observations in the field, 85 % of the aboveground plant material was removed at harvest. Harvest dates were known and implemented in the model. After harvest the growth stage was allowed to be reset to a lower value (e.g., Thomas and Stoddart, 1980). Reallocation of C from roots to leaves could take place as reported for, e.g., *Festuca pratensis* (Johansson, 1992; 1993).

2.2.5 Soil carbon and nitrogen

The organic substrate was represented by two C and N pools for each of the 12 soil layers: one with a slow and one with a high turnover rate coefficient. Decomposition products from the fast pools are partitioned into CO₂ which is released to the atmosphere and C which is partly moved to the slow pools and partly returned to the fast pools. Decomposition products from the slow pools are partly released as CO₂ and partly returned to the slow pools. The initial values for the amount of C and N per layer was given by measurements and partitioned into the two pools for each layer according to the measured C : N ratio as described in Sect. 2.2.5 and Table 3. Beside the turnover rate coefficients and amount of substrate in each pool per layer, decomposition rates depended on the response to soil moisture and temperature in the corresponding layer.

As the rate coefficients for decomposition were expected to strongly affect each other, only the coefficient for the fast decomposition pools were calibrated. The coefficient for the slow pools (k_h) was kept constant at a low value of $2 \times 10^{-8} \text{ day}^{-1}$ during the calibration runs, which might be justified as decomposition of resistant carbon is less responsible for the variation in soil respiration (e.g., Whalen et al., 2000).

Nitrogen- and methane-related processes were considered by a model including the most important pathways and fluxes. However no emphasize on the calibration of these processes was made in this study since the current objective was on CO₂ fluxes from the peatlands.

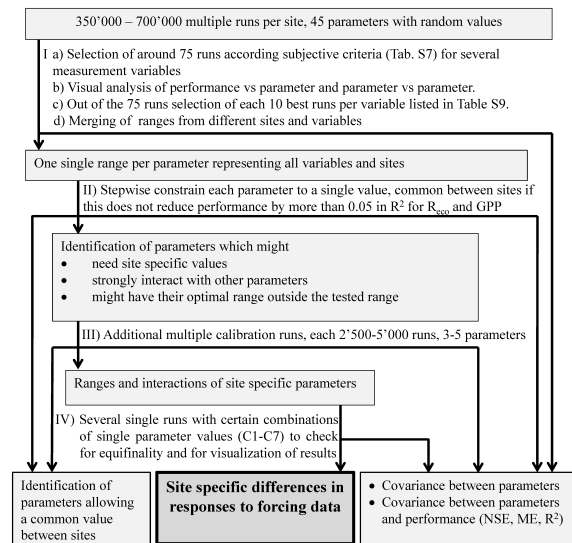


Figure 3. Stepwise parameter calibration. Boxes show the outcome of each step. Description for scenarios C1–C7 can be found in Table S8.

2.2.6 Independent approach to find values of site specific parameters

Dry and wet N deposition, latitude and thickness of the organic layer were used as constant site specific input.

Water retention parameters were assigned to each soil layer according to soil data from each site. However, at Amo and Lom, water retention and, at all sites, unsaturated conductivity was assigned from the CoupModel soil database as suggested by Lundmark (2008) for peat soils. Measured total soil organic carbon (SOC) per layer was partitioned to the two SOC pools per layer on the basis of the measured total C : N ratio per layer whereas the initial C : N ratios of the slow decomposing pools were assumed to be 10, while for the fast pool's 27.5 was chosen according to measured C : N of leaf tissues at FsA and FsB (Table 3).

2.3 Parameter calibration approach

The aim of the calibration was to find out to what extent the same parameter values could be used for all sites compared to a site specific representation. A stepwise approach was carried out starting with finding the best site specific parameter representations and then trying to merge them to common values valid for all sites. Finally, the common representation was revised to some few parameters showing great site specific effects on model performance. An overview of the different steps can be found in Fig. 3, details on the calibration procedures are presented as supplementary material.

For the basic calibration (step I, Fig. 3), 350 000–700 000 runs were performed for each site. 45 parameters, which were suspicious of eventually being site specific, were selected and calibrated with an assumed uniform random range

Table 3. Partitioning of measured SOC to the pools. The data in the table is aggregated into 3 soil layers, however 12 layers were used in the model.

	depth (m)	Lom	Amo	Hor	FsA	FsB
Measured total C (kg m ⁻³)	0–0.1	24	190	72	107	88
	0.1–0.3	30	187	79	104	90
	>0.3	51	175	156	70	61
Measured C : N (kg m ⁻³)	0–0.1	27	23	13	11	12
	0.1–0.3	20	22	13	14	13
	>0.3	20	21	22	17	17
Estimated fraction of fast pool/total C	0–0.1	95 %	72 %	18 %	3 %	9 %
	0.1–0.3	56 %	73 %	20 %	20 %	16 %
	>0.3	55 %	68 %	62 %	35 %	41 %
Dry bulk density (g cm ⁻³)	0–0.1	0.06 ^a	0.39	0.35	0.59	0.33
	0.1–0.3	0.06	0.37	0.48	0.29	0.52
	>0.3	0.10	0.37 ^b	0.50	0.18	0.17

^a No data available, value from lower layer used. ^b No data available, value from upper layer used.

(Table S4). Parameter ranges were then constrained based on selected runs (steps I and II; Fig. 3), showing acceptable performance to multiple variables (Table S7), measured at the sites.

Several additional multiple calibration runs were performed, with few selected parameters each, to unravel parameter interactions (step III; Fig. 3). A number of simulations were also made by single value representations of parameters (step IV; Fig. 3) to visualize the impact of certain parameter values on interacting parameters and on performance. These runs are called single runs in the following, numbered C1–C7 and described in Table S8.

Selection of runs and evaluation of performance was based on three indices: coefficient of determination (R^2) assesses how well the dynamics in the measurement derived values are represented by the model. Mean error (ME), also called y intercept (Willmott, 1982) indicates a lag or lead between model predictions and measured data (Moriassi et al., 2007). Nash–Sutcliffe efficiency (NSE) (Nash and Sutcliffe, 1970) accounts for both deviation of dynamics and magnitude. It ranges from $-\infty$ to 1, whereas 1 means the best fit of modeled to measured data and values <0 indicates that the mean measured value is a better predictor than the simulated value, which indicates an unacceptable performance (Moriassi et al., 2007).

3 Results

3.1 Model performance – results of basic calibration and selected common configuration

Model performance showed distinct differences between the sites, depending on the investigated variable and on the num-

ber of considered runs (Table 4). Figure 4 shows the differences between measurements and model C1.

3.1.1 Fluxes

At all sites the dynamics in R_{eco} fluxes were simulated considerably better than GPP (Table 4). Performances for NEE were worse as simulation errors in GPP and R_{eco} are summed up.

With respect to R_{eco} and GPP, the selected single runs represent a parameter configuration close to the best ones possible in the tested range: their R^2 value did not differ by more than 0.05 from the best result achieved in the multiple calibration, while ME values were smaller than $0.1 \text{ g C m}^{-2} \text{ day}^{-1}$. Clearly, the lower R^2 and higher ME values in single runs for biomass and LAI simulation indicate that none of the runs could give the best results for all variables at the same time. For example, the best values for GPP can only be achieved if poorer performance would have been accepted for other parameters such as winter R_{eco} or LAI (see criteria for accepted runs in Table S7).

The ME values in Table 4 show a clear overestimation of winter fluxes by 3.21 and $2.11 \text{ g C m}^{-2} \text{ day}^{-1}$ for the single runs at FsA and FsB, respectively, and a weaker overestimation for the accepted runs. The overestimation was less pronounced at Amo ($0.13 \text{ g C m}^{-2} \text{ day}^{-1}$) and Lom ($0.01 \text{ g C m}^{-2} \text{ day}^{-1}$). At Hor, winter fluxes were underestimated with a ME of $-0.26 \text{ g C m}^{-2} \text{ day}^{-1}$. This was reflected in the accumulated NEE (Fig. 4) leading to a much higher CO₂ loss compared to the CO₂ balance estimated by the empirical model approach at FsA and FsB. At Lom, higher accumulated NEE due to the overestimation of winter R_{eco} was visible in the first months of each year. It was nearly compensated due to the underestimated spring R_{eco}

Table 4. Highest achieved values for selected performance indices.

Variable	Index	Lom		Amo		Hor		FsA		FsB	
		all/select- ed runs	single run	all/select- ed runs	single run	all/select- ed runs	single run	all/select- ed runs	single run	all/select- ed runs	single run
NEE	R^2	0.61/0.60	0.59	0.59/0.58	0.55	0.53/0.51	0.48	0.20/0.16	0.15	0.25/0.21	0.19
	ME	0.00	0.05	0.00	0.04	0.00	0.02	0.00	1.43	0.00	−0.05
GPP	R^2	0.66/0.66	0.65	0.68/0.68	0.66	0.58/0.57	0.55	0.38/0.35	0.34	0.40/0.39	0.35
	ME	0.00	0.05	0.00	−0.09	0.00	0.04	0.00	0.06	0.00	−0.03
R_{ecoEC}	R^2	0.79/0.74	0.69	0.71/0.71	0.66	0.78/0.77	0.75	NA	NA	NA	NA
	ME	0.00	0.00	0.00	−0.05	0.00	−0.06	NA	NA	NA	NA
R_{eco} Chamber	R^2	0.73/0.71	0.64	0.67/0.57	0.38	0.52/0.48	0.45	0.73/0.66	0.69	0.87/0.81	0.85
	ME	0.00	−0.06	0.00	0.04	0.00/−4.74	−5.38	0.00	−0.01	0.00	−0.08
R_{eco} winter	R^2	0.67/0.63	0.63	0.14/0.08	0.06	0.28	0.28	0.51/0.43	0.32	0.92/0.89	0.89
	ME	0.00	0.01	0/0.04	0.13	0.00	−0.26	0/1.60	3.21	0.00/0.73	2.11
Upper soil temperature	R^2	0.88/0.87	0.87	0.86	0.84	0.92	0.91	0.88/0.86	0.84	0.88/0.86	0.84
	ME	0.00	−0.01	−0.03	−0.08	−1.37/−1.51	−1.77	0.00/0.58	0.35	0/1.20	0.35
Lower soil temperature	R^2	0.95	0.95	0.90	0.89	0.89	0.89	0.97/0.96	0.94	0.92/0.91	0.94
	ME	0.00	−0.03	0.00	0.02	0.00	−0.08	0.00	−0.15	0.00	−0.15
Snow depth	R^2	0.75	0.75	NA	NA	NA	NA	NA	NA	NA	NA
	ME	−0.1	−0.06	NA	NA	NA	NA	NA	NA	NA	NA
LAI	R^2	0.65/0.51	0.53	NA	NA	0.36/0.31	0.33	0.75/0.69	0.61	0.82/0.76	0.61
	ME	0.00	0.11	NA	NA	0.00/−0.61	−1.49	0.00	0.12	0.00	0.05
Aboveground living biomass	R^2	NA	NA	NA	NA	0.02/0.00	0.00	0.31/0.26	0.24	0.47/0.43	0.32
	ME	NA	NA	NA	NA	0	−112	0/−20	−21	0/−36	−48
Root biomass	R^2	NA	NA	NA	NA	0.28/0.07	0.01	NA	NA	NA	NA
	ME	NA	NA	NA	NA	0.00	−282	NA	NA	NA	NA

NA: not available.

or overcompensated due to GPP overestimation as, e.g., in summer 2006, which was very dry.

3.1.2 Explanatory variables

Of all variables, the highest R^2 values were achieved for soil temperature at all sites. Temperatures in deeper soil layers (−50 or −60 cm) had better fits than in upper layers with R^2 values close to 0.9 or higher and a maximum mean deviation of 0.15 °C. The fit of modeled vs. measured snow depth, which was only available at Lom, had a R^2 value of 0.75 with a mean error of less than 10 cm.

Simulation of LAI represented the measurements quite well with R^2 values of between 0.53 and 0.76 and a mean error of maximum 0.12 m² m^{−2}. An exception was Hor, where LAI was underestimated by a ME of −0.61 and −1.49 m² m^{−2} in the accepted 75 runs and in the selected single run C1, respectively. At Hor, root biomass was underestimated in the single run by a ME of −281 g C m^{−2} and living leaf biomass by −122 g C m^{−2}.

In most of the runs of the basic calibration at Hor, either GPP was overestimated or leaf biomass and LAI were underestimated. Therefore, beside the common configuration C1, a different configuration was tested where plant respiration and litter fall parameters for Hor were set to much lower values than in the tested range to fit to GPP and LAI at the same time. However, this reduced performance for R_{eco} R^2 to 0.66

compared to 0.75 in C1 and led to an overestimation of winter R_{eco} with a ME of 0.75 g C m^{−2} day^{−1}.

3.2 Parameter constraint

Site specific calibration was needed for the speed at which the maximum surface cover is reached (p_{ck}), the mean value in the analytical air temperature function (T_{amean}), temperature sum for reaching plant maturity ($T_{\text{MatureSum}}$), coefficient for determining allocation to mobile internal storage pool (m_{retain}), decomposition rate of the fast SOC pools (k_1) and radiation-use efficiency (ϵ_L).

Activity under saturated conditions ($p_{\theta\text{Satact}}$), threshold temperature for plant dormancy (T_{DormTh}), response to a 10 °C soil temperature change on the microbial activity (t_{Q10}) and base temperature for the microbial activity ($t_{Q10\text{bas}}$) covary with performance indices but showed different patterns for different validation variables and for different sites.

Most of the parameters did not show any influence on performance indices within the tested range (Fig. S1), demonstrating that either the relatively low effect of the parameter was overcompensated by the effect of more sensitive parameters, or the range used for calibration is sufficiently constraining. Each of these parameters did not reduce model performance indicated by R^2 by more than 0.05 for GPP or R_{eco} after setting them to a common value.

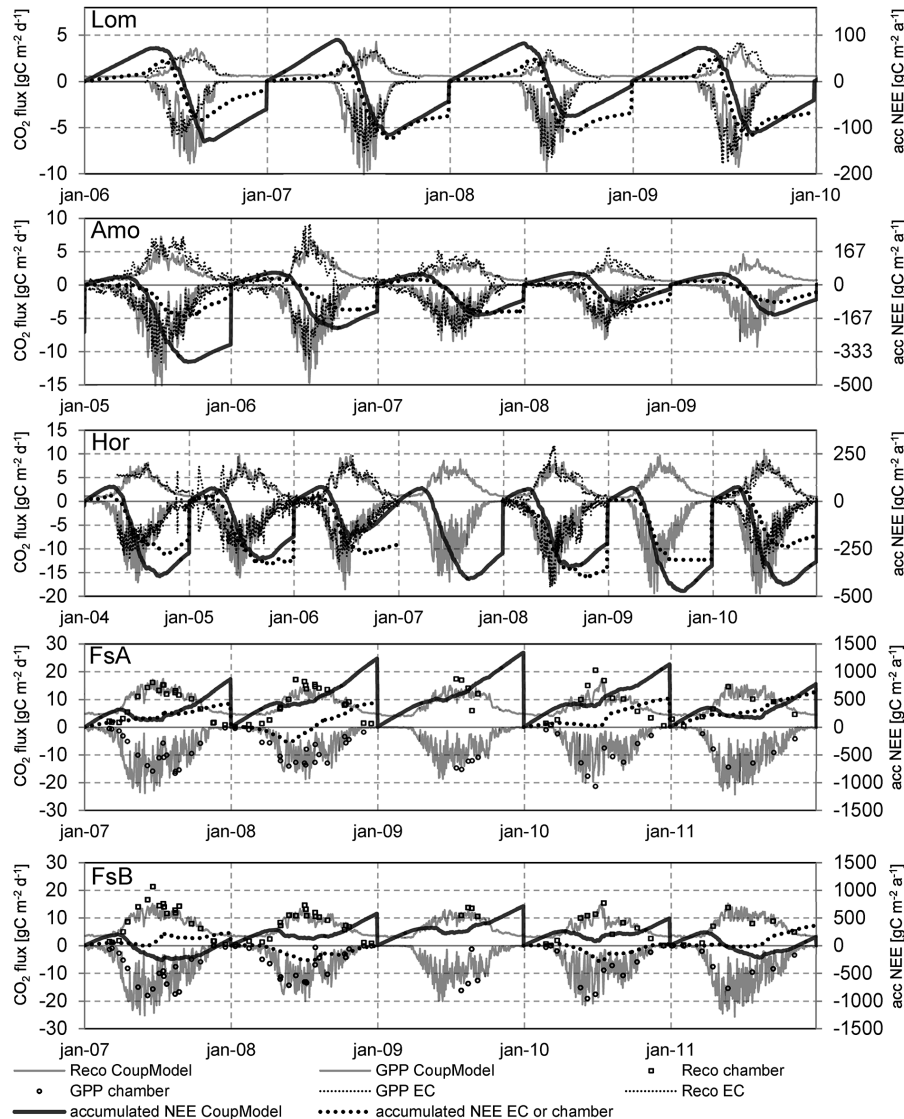


Figure 4. Simulated and measured R_{eco} (positive) and GPP (negative) fluxes and accumulated NEE for one selected set of parameter values (C1) common between all sites. Note the different scales.

3.3 Correlations between parameters

In the basic calibration, the following parameters were identified to interact with other parameters: p_{ck} covaried with the extinction coefficient in the Beer law (k_m) which is used to calculate the partitioning of net radiation between canopy and soil surface. Strong, linear, negative correlation between coefficients for growth (k_{gresp}) and maintenance respiration ($k_{mrespleaf}$) was detected.

The effect of the different parameters in the water response function, $p_{\theta Satact}$, $p_{\theta Upp}$ and $p_{\theta p}$, compensated each other. They could not be constrained without a very high measurement resolution of fluxes and water table combined with high water table fluctuation at the same time. Therefore, $p_{\theta Upp}$ and $p_{\theta p}$ were set to default values and $p_{\theta Satact}$ was con-

strained by additional multiple runs together with k_1 . Differences between sites in k_1 are reduced with higher $p_{\theta Satact}$ values (Fig. 5), however, higher $p_{\theta Satact}$ values increase overestimation of winter R_{eco} at FsA and FsB (Figs. 6, 7d). A wider range of $p_{\theta Satact}$ values was acceptable for summer R_{eco} (Fig. 6).

Besides moisture response, decomposition rate (k_1) and temperature response (t_{Q10} , t_{Q10bas}) control soil respiration. The effect on R_{eco} was cofounded by plant respiration. Different patterns for different sites and variables for each of the parameters were even more pronounced when only k_1 , t_{Q10} and $k_{mrespleaf}$ were in calibration (Fig. 6).

Single runs with different configurations (Fig. 7) revealed that higher plant respiration as well as steeper temperature response can lead to less overestimation of respiration in winter

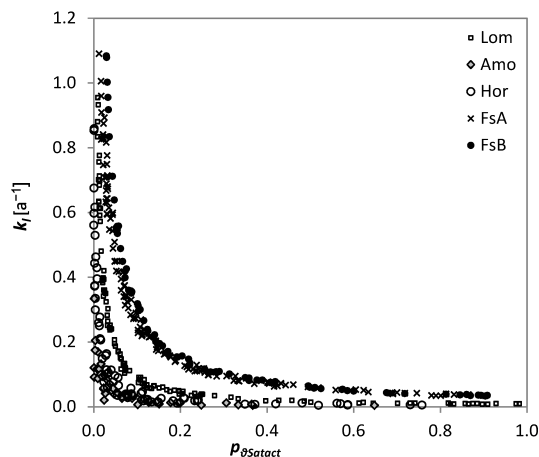


Figure 5. Dependencies between the parameters for decomposition rate and saturation activity for the different sites, based on additional multiple runs.

(Fig. 7d) but lead to reduced performance (Fig. 7c). In all single runs, despite the different configurations, FsA always showed the highest k_1 , while Amo had the lowest (Fig. 7a). A higher saturation activity reduces the difference in k_1 values, but leads to higher overestimation of winter fluxes.

4 Discussion

Despite not being specifically developed for peatlands, the CoupModel was able to simulate measured fluxes quite well. The model was run in a simple configuration with only two SOC pools per layer, no explicit representation of microbes, and only one plant layer. Even though the CoupModel was capable of adequately reproducing the measurements. Several points were identified where further peatland specific processes or more detailed representations might improve the model. Those are discussed in the following subsections.

From the 45 calibrated parameters, 8 parameters could be identified to actually need a site specific representation to achieve acceptable performance. Those parameters are discussed in Sects. 4.3–4.10. The remaining 37 parameters were not sensitive in the tested ranges, even though site specific values could have been expected; for example, it is known that grassland species differ in their assimilation and growth response to temperatures (Billings et al., 1978; Wohlfahrt et al., 1999). Plant respiration rates in graminoids differ between species (Poorter et al., 1991; Scheurwater et al., 1998; van der Werf et al., 1988) and depend, among other factors, on light (Rovira, 1969; Bahn et al., 2013), nutrient (Paterson and Sim, 2000) and moisture conditions (Crow and Wieder, 2005) as well as on cutting regime (Bokhari, 1977). Allocation fractions to different plant parts differ between species and depend on nutrient conditions (Aerts et al., 1991; Gong et al., 2014) as well as shading (Bahn et al., 2013). Values

for specific leaf areas are species specific (e.g., Poorter et al., 1990; Reich et al., 1998) and differ in response to nutrient availability (Meziane and Shipley, 1999). Leaf lifetime (e.g., Ryser and Urbas, 2000) as well as leaf and root turnover rates (Schläpfer and Ryser, 1996) vary between graminoid species.

The five peatland sites largely differed in their vegetation composition, plant life-forms and species. Nevertheless, common values for all sites could be applied for parameters related to these processes, without reducing model performance on R_{eco} and GPP in R^2 values by more than 0.05. That shows that either the studied sites on a vegetation community level did not differ much in these processes, or that the impact of those parameters is subordinate compared to the impact of other parameters, meteorological input and other site conditions.

Therefore, models with a focus on multiple-year carbon fluxes do not need a site specific interpretation of these processes.

4.1 Model initialization

Many models use spin-up routines of many years until SOC pools reach a steady state (e.g., Dimitrov et al., 2010; Smith et al., 2010; Thornton and Rosenbloom, 2005). Here, measured C:N values were used to partition the SOC between pools, while ranges for parameter values were chosen in a way that the amount of carbon in the soil pools did not change very drastically. However, no further effort was made to force the pools to be in equilibrium. It was assumed that this might not be the case in the real world either: drainage ditches at FsA and FsB are still maintained, leading to high carbon losses and changes in substrate quality. Land use at Hor was quite recently changed from a fertilized and deeply drained cropland to a nature reserve with a restored water table. Additionally, Amo used to be more intensively managed and drained, but the drainage system was not maintained. Land use history was not known and SOC measurements were available from only one date per site. The measured carbon fluxes were therefore the only indication about carbon loss or addition to the complete system, while changes in relative pool sizes were not known. The partitioning of the SOC has implications on the parameter distribution for the rate coefficient for decomposition, which is discussed in Sect. 4.10.

4.2 Model performance

The best performance achieved highly differed between the different validation variables and between the different sites. This was not only caused by the model's ability to simulate the different output parameters but also due to measurement quality, measurement uncertainty, measurement methods (temporal and spatial resolution) and heterogeneity of the sites.

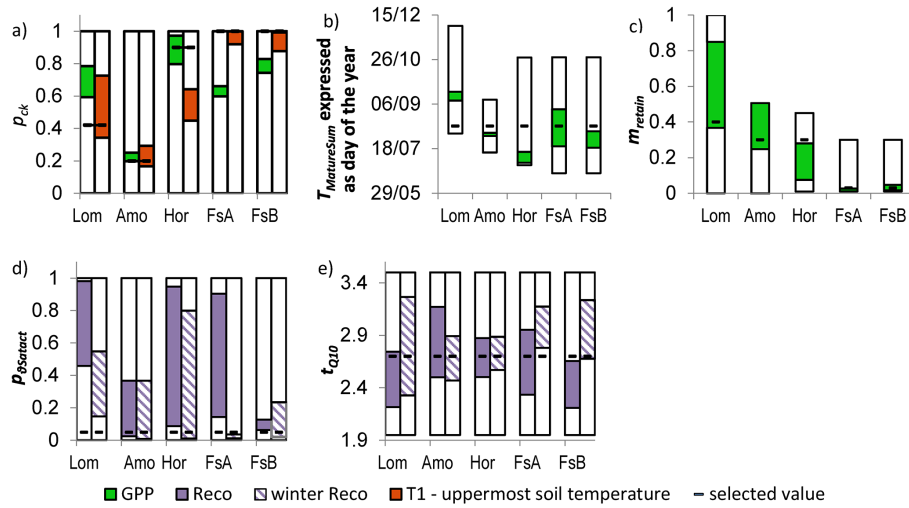


Figure 6. Obtained distributions of parameter values as constrained by additional multiple runs (calibration step III). Ranges for k_{11} and ϵ_L are not shown due to their interactions with several parameters. Colored bars show the range of the 10 runs with the best performance for each validation variable. Prior ranges are indicated by the frame around the bar. Black dash is the value chosen for the common configuration C1.

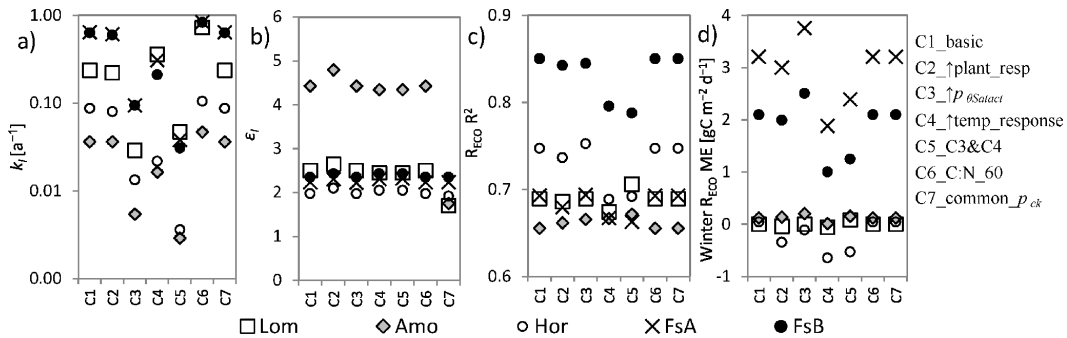


Figure 7. Values for the parameters of decomposition rate (a) light-use efficiency (b) and resulting model performance (c, d) when applying various single-value representations of parameters (C1–C7; see Table S8).

GPP was simulated markedly poorer as compared to R_{eco} at all sites and not only in the single runs, but also in the complete set of performed multiple runs. An explanation might be that in the model the whole plant community consisting of different individuals, species and even functional types, with different life cycles and adaptations to light availability and temperature was simplified to only one plant. Especially mosses, which differ largely from vascular plants in respect to their ecology and response to water, temperature and light conditions (Gaberšček and Martinčič, 1987; Harley et al., 1989; Murray et al., 1993; Turetsky, 2003), might be important at the moss-rich Lom and Amo sites. The vegetation at Hor consists of species with very different strategies and requirements for nutrients and water. At FsB, reeds, which are known for a late emergence, were well present in some of the years and hardly appeared in other years. FsA is relatively species-rich and several of these species are abundant only during parts of the vegetation period. Also, using a

more complex photosynthesis model such as in e.g., Farquhar et al. (1980, 2001) and testing a wider range of parameters might lead to a better fit. Including plant stress due to high water levels and nutrient limitation might improve the performance on some sites. For example, Sagerfors et al. (2008) found photosynthesis to be limited also by too high water levels, so that the McGill wetland model assumed reduced photosynthesis outside a water level range of -10 to -20 cm (Wu et al., 2013b). Furthermore, GPP cannot be measured directly neither by the chamber nor the EC method. Instead it was derived from NEE and R_{eco} or nighttime NEE, including the uncertainty of two different measurements and empirical modeling.

Heterogeneity of vegetation was very distinct at Hor, which might explain the difficulties to simulate the right amounts of GPP and biomass at the same time. The biomass and LAI taken into account for this study might not be fully representative of the whole EC fetch for all wind directions.

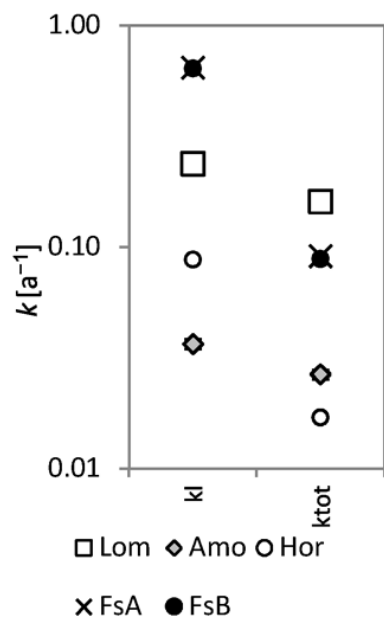


Figure 8. Decomposition rates of fast pools (k_1) and calculated rates of total organic matter decomposition if only one pool was used (k_{tot}) for each site and each layer.

Hor is also a site which deviates strongly with respect to other sites, with recent large changes in management. It is in successional transition from intensively used dairy farming meadow (approximately 20 years ago) towards reed fen with willow thickets. Soil and vegetation still show the imprint of high nutrient levels derived from manuring practices (e.g., patches with abundant *Urtica dioca*). This likely still affects GPP. These features could be a better explanation of the deviating GPP than the additionally tested configuration with strongly reduced litter fall and plant respiration rates.

Even though the winter fluxes are small compared to the summer fluxes, they have a marked role in the annual NEE balances (Fig. 4). Overestimation of winter R_{eco} in combination with slightly underestimated winter GPP leads to high overestimation of annual accumulated NEE, emphasizing the importance of winter flux dynamics in the annual balances. At all sites except Hor, winter R_{eco} was overestimated in the selected single run. For FsB and especially FsA this was also true for all multiple runs. As R_{eco} at Lom and Amo are typically relative low, the effect was less pronounced.

Several different reasons for the winter R_{eco} overestimation are possible: explanations due to model setup and parameterization are discussed in the Sects. 4.7, 4.8 and 4.9. Additionally, gases might be trapped within the snow and under the ice (Bubier et al., 2002; Maljanen et al., 2010) and therefore captured by the measurement instruments only in springtime, when they are released. A gastight ice cover was not realized in the current model setup. Frozen or ice covered soils are quite common at the boreal Lom, but also at

FsA and FsB which have a more continental climate than the other sites.

The ability of the model to simulate soil moisture could not be evaluated, as this variable was measured only at Lom, where the soil was close to saturation throughout the year. Therefore, and as groundwater level was used as input, hydraulic properties could not be constrained. Furthermore, swelling, shrinking and hysteresis effects which are important factors in hydraulic characteristics of peat soils (e.g., Kellner and Halldin, 2002) were not accounted for. This could have an effect on model performance and parameter values, especially those related to the soil moisture response.

4.3 Soil temperature dynamics

Due to the isolating impact of the snow cover (e.g., Zhang, 2005), the value of mean annual soil temperature (T_{amean}) was expected to be slightly higher than the mean annual air temperature. Constrained values of soil temperature were 1.5–5 °C higher than the mean annual air temperature at all sites. If the model was run under different conditions without further fitting, factors causing differences between mean annual soil temperatures and corresponding air temperature need to be considered.

4.4 The role of soil temperature and GPP to constrain the plant cover

Accepted fits for soil temperature in the uppermost measured soil layer led to p_{ck} values close to the measured coverage of vascular plants for each site. Therefore, the measured coverage could directly be used in the configuration C1 (Fig. 6a). Setting p_{ck} to a common value of 100 % reduced the differences in ε_L between the site's C7 (Fig. 6e), but led to underestimation of soil temperature in the uppermost soil layer by at most -0.45 °C in ME at Amo. An explanation could be that mosses are contributing to the plant coverage in respect to GPP but not to temperature, especially at sites where they are the main peat-forming material.

4.5 Start of senescence

Site specific calibration was needed for the temperature sum initiating the start of senescence ($T_{MatureSum}$). However, if the resulting day of the year was plotted instead, the differences between sites became small (Fig. 6) and setting it to the mean value of all sites did not reduce model performance in GPP R^2 by more than 0.05. Induction of senescence with graminoids is known to depend on both temperature and day length (Nuttonson, 1958; Proebsting et al., 1976; Thomas and Stoddart, 1980; Davidson and Campbell, 1983). However, the differences between the sites in this study could be explained solely by the relative day length.

4.6 Seasonal and management control of mobile plant pool for regrowth

The proportion of C in the plant which does not become litter, but instead is stored for shooting in the next year (m_{retain}), differed largely between sites. At Lom, a value of at least 40 % led to an acceptable performance while a maximum of 3 % was found for FsA and FsB; a mean value of 20 % would reduce R^2 of GPP by at least 0.04 for these sites. At Amo and Hor neither a value of 3 % nor 40 % reduced R^2 of GPP by more than 0.01. An explanation for the low m_{retain} at FsA and FsB could be that the same pool is used for regrowth after being cut and therefore not available for shooting anymore, as the regrowth rate in both early spring and after being cut depend on the carbohydrate reserve (White, 1973; Davies, 1988; Klimeš and Klimešová, 2002). Steele et al. (1984) conclude that defoliation late in the year will affect spring regrowth.

At Lom, high m_{retain} might be an adaptation to the short vegetation period (Kistritz et al., 1983). Evergreen parts of the vegetation like dwarf shrubs, lower leaf parts of graminoids and mosses were not accounted for, which also affects regrowth in spring. Saarinen (1998) found that 60–70 % of shoots and 20 % of green biomass in a *Carex rostrata* fen survived the winter and, therefore, hypothesized based on comparisons with other studies that the proportion increases with increasing latitude.

The storage pool is an important parameter needing site specific calibration but can be fitted if several measurements during spring and early summer of either GPP, biomass or LAI are available.

4.7 Radiation-use efficiency

As plants were not nutrient limited in the model setup, the lowest values for ε_L were expected under the most nutrient-poor conditions (Longstreth and Nobel, 1980; Reich et al., 1994; Haxeltine and Prentice, 1996; Gamon et al., 1997; Wohlfahrt et al., 1999). The opposite was true if site specific values were used for p_{ck} . However, a common value for p_{ck} reduced the differences in ε_L and led to low ε_L at the ombrotrophic Amo site, but to an even lower value at the minerotrophic Lom site. The nutrient status of the soil can therefore not explain the differences in ε_L . The assumption of plants being well adapted to nutrient and water stress might not be true for the restored Hor site, where parts of the vegetation still consist of species which are not typical for wetlands. This might explain the low productivity at that site, but could only be covered by a model if site specific plant responses to high water levels would be applied. Additionally, ε_L is known to be species specific (Sinclair and Horie, 1989; Reich et al., 1998; Wohlfahrt et al., 1999).

Radiation-use efficiency is an important parameter needing site specific calibration. If common values were used for ε_L , p_{ck} and m_{retain} , mean GPP would be underestimated by a

factor of 2.4 (FsB) or overestimated by a factor of 3 (Lom). If site specific values were used for p_{ck} and m_{retain} , the discrepancy would be even higher. However ε_L can easily be fitted if either GPP, biomass or LAI is known.

4.8 The control of decomposition and plant respiration by soil temperature

The annual R_{eco} , which was dominated by summer R_{eco} , could be described by a single temperature response function at all sites. However, it was not possible to find an equally good fit to both summer and winter R_{eco} using the same t_{Q10} value. Higher t_{Q10} values would decrease overestimation of winter R_{eco} especially at the southern sites FsA and FsB, but also reduce model performance for the annual R_{eco} . Different temperature responses for different sites (e.g., Jacobs et al., 2007), seasons (e.g., Lipson et al., 2002) and temperature ranges (e.g., Lloyd and Taylor, 1994; Paul, 2001; Atkin et al., 2003) are reported in the literature. This is partly explained by multiplicative effects of several temperature sensitive processes (Davidson et al., 2006; Kirschbaum, 2006) but, still, a constant t_{Q10} might be a wrong assumption (Atkin et al., 2005).

More sophisticated temperature responses like the Ratkowsky function (Ratkowsky et al., 1982) might improve the performance for individual sites. This might also be true for separate temperature response functions for plants and soil, as summer R_{eco} includes autotrophic and heterotrophic respiration, while winter R_{eco} is strongly dominated by heterotrophic respiration.

4.9 The control of decomposition by soil moisture

The activity under saturated conditions in respect to unsaturated conditions is described by $p_{\theta\text{Satact}}$ and was strongly negatively correlated with decomposition rate k_1 . Patterns for $p_{\theta\text{Satact}}$ differed between sites and variables. At all sites a minimum value of around 5 % led to the acceptable performance in annual R_{eco} , while also quite high values did not reduce the performance except at FsB. At Lom only winter R_{eco} was considered, as conditions were always saturated during summer. For acceptable winter R_{eco} , $p_{\theta\text{Satact}}$ needed to be very low. This was not true for Lom, where water in the upper soil layer partly froze in the model and led to high winter respiration.

As the soil at FsA and FsB was saturated during winter, a common lower value for $p_{\theta\text{Satact}}$ would decrease overestimation of winter fluxes. However, it would also reduce model performance at all sites and increase the site specific differences in k_1 (Fig. 7).

Permanently saturated soils contain less O₂ than temporarily saturated ones (e.g., Kettunen et al., 1999), which affects decomposition (e.g., Reddy and Patrick, 1975; DeLaune et al., 1981; Holden et al., 2004). Therefore a lower $p_{\theta\text{Satact}}$ would be justified for wetter sites. If k_1 was constant

between sites and instead $p_{\theta\text{Satact}}$ was fitted, this would lead the value of $p_{\theta\text{Satact}}$ to decrease in the order FsB > FsA > Lom > Hor > Amo (Fig. 5), which cannot be justified by the differences in water levels which increase in the order FsA < FsB << Amo < Hor <<< Lom. Therefore, a different $p_{\theta\text{Satact}}$ cannot explain differences in soil respiration between sites. However, the amount of aerenchymatous plants, leading to soil aeration (e.g., Armstrong, 1980; Bendix et al., 1994; Grosse et al., 1996) was not taken into account. It reaches its highest coverage at FsB (90 %), followed by FsA (62 %), Hor (50 %), Lom (around 10 %) and Amo (around 6 %). Modeling water response depending on soil O₂ and redox potential, including O₂ conductance from plants, might help us to analyze the differences in decomposition rate and reduce winter overestimation. For example, in the Wetland-DNDC model, the water response function depends on redox potential: decomposition under saturated condition is reduced by a factor of only 0.6 if redox potential is high, but by a factor of 0.2 if redox potential is low (Zhang et al., 2002).

4.10 The control of decomposition by substrate

The largest differences of parameters between sites appeared for the maximum decay rate of the fast C pools, k_1 . Setting it to a common value would lead to an underestimation of mean R_{eco} by a factor of 2.8 at FsB or an overestimation by a factor of 4 at Amo.

Despite different temperature and water response curves being tested, k_1 values at FsA and FsB are substantially higher than at Amo (Figs. 5, 7). Higher t_{Q10} values lead to two groups of k_1 values: similar high ones for Lom, FsA and FsB and substantially lower ones for Hor and Amo (Fig. 7).

The partitioning into SOC pools strongly effects the differences, as can be shown by calculating decomposition rates for the total SOC (k_{tot}) based on k_1 , k_h and SOC in the pools of the upper 30 cm as used in the C1 scenario (Fig. 8). However, FsB and FsA still have much higher rates than Amo. The resulting values and ranges of k_{tot} (0.02–0.16 a⁻¹) are comparable with the reported values from laboratory incubation studies of peat cores (0.03–1.66 a⁻¹, Moore and Dalva, 1997; 0.01–0.35 a⁻¹, Glatzel et al., 2004; 0.008 a⁻¹, Kechavarzi et al., 2010; a SOC content of 30 % was assumed for conversion from dry mass).

Lower decomposability is often associated with higher C:N ratios (e.g., Zeitz and Velty, 2002; Limpens and Berendse, 2003; Bragazza et al., 2006; Zhang et al., 2008), which might be important especially for the moss-rich Amo and Lom. Assuming a C:N ratio of 60 for the fast pools (Fig. 7, C6) leads to a decomposition rate at Lom which is close to those at FsA and FsB, while those of Hor and Amo remain substantially lower.

Low pH might be one reason for the low k_1 at Amo (e.g., DeLaune et al., 1981; Bergman et al., 1999). Despite being nutrient-rich and having a high pH and high biomass production, leading to large amounts of labile carbon added to

the soil, k_1 values at Hor were very low. This might be connected to land use history and the origin of the peat from partly clayey lake sediment. Most of the labile C in the parent peat in the upper, formerly drained soil layers might have been decomposed before and therefore became stabilized.

In the current setup the slow pools were almost inert. A higher decay rate for the slow pools would result in a lower k_1 for sites with high C stock in the slow pools (cf. Table 3). This would decrease the differences between FsA and FsB compared to Lom and Amo, but increase the differences between FsA compared to FsB and Hor.

Substrate quality is known to affect decomposition rates (e.g., Raich and Schleisinger, 1992; Belyea, 1996; Fang and Moncrieff, 2005; Yeloff and Mauquoy, 2006). Therefore, many other SOC models use several different SOC pools (e.g., Franko et al., 1997; Smith et al., 1997; Cui et al., 2005; Del Grosso et al., 2005; van Huissteden et al., 2006) to account for differences in substrate quality. This leads to the problem of partitioning total SOC into the pools (e.g., Helfrich et al., 2007; Zimmermann et al., 2007). In some models, the various SOC pools differ also in their response functions (e.g., Smith et al., 2010).

The highest decomposition rates occurred at sites with highest biomass production. A correlation of productivity with soil respiration was found in several comparison studies (e.g., Janssens et al., 2001; Reichstein et al., 2003). Fresh material provided by the plants might lead to higher microbial activity and priming effect (e.g., Kuzyakov, 2002; Fontaine et al., 2007). A higher plant to soil respiration ratio reduced the differences in k_1 between the sites and lowered winter R_{eco} , especially at the highly productive FsA and FsB sites, but also reduced the model performance at all sites except Amo.

Vegetation at Amo and Lom consist largely of mosses which are more resistant to decomposition than vascular plants (Rudolph and Samland, 1985; Verhoeven and Toth, 1995; Limpens and Berendse, 2003; Moore et al., 2007) and might further explain the low k_1 value at Amo. Despite the lower biomass production, higher moss cover and higher C:N ratio compared to Hor, FsA or FsB, Lom has a relatively high decomposition rate. This can be explained by the very low dry bulk density, resulting in a low amount of C in the upper soil layers (Table 3), which are most exposed to decomposition (e.g., Fang and Moncrieff, 2005). Also, a low dry bulk density accompanies the low degree of degradation and therefore high amounts of labile carbon (e.g., Grosse-Brauckmann, 1990).

Despite the large differences in accumulated NEE (Fig. 1) between FsA and FsB, these sites have nearly identical decomposition rates. This confirms the expectations that the differences in NEE between FsA and FsB can be fully explained by the differences in the water table and the biomass and carbon stocks.

5 Conclusions

Differences between sites with respect to CO₂ fluxes could be explained if, in addition to air temperature, water table and soil C and N stocks, site specific plant productivity and decomposition rates were also taken into account. Differences in nutrient availability and soil wetness could not explain the differences in plant productivity between the sites. Substrate quality and litter input, as well as pH values, are likely explanations for the differences in decomposition rates. A site specific interpretation was not needed for processes related to plant phenology, their response to temperature, allocation of new assimilates and plant respiration and litter fall rates.

The model parameters which strongly affected model performance were successfully constrained by the available long-term measurement data on NEE, partitioned into GPP and R_{eco} , LAI and biomass, including rooting depth and root biomass at one site, water table, soil temperature and soil C and N stocks, as well as meteorological data and snow data at one site. It would have been useful if additional information about root biomass, litter fall and soil water content to validate the model performance in the corresponding processes was available for all sites. A second measurement of C and N stocks, several years after the first, as well as information about the degree of decomposition on all sites would have been very helpful to constrain decomposition rates and partitioning between SOM pools.

Some improvements in the model and its configuration were identified to obtain a better performance for simulations of GHG fluxes from treeless peatlands. Examples include separate temperature responses for plant and soil heterotrophic respiration. The static response to water saturated conditions needs to be replaced by a function that considers the change of O₂ in the soil.

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The simulation files with the setup according the common configuration together with the respective version of the CoupModel can be provided upon request.

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References

- Adiku, S. G. K., Reichstein, M., Lohila, A., Dinh, N. Q., Aurela, M., Laurila, T., Lueers, J., and Tenhunen, J. D.: PIX-GRO: A model for simulating the ecosystem CO₂ exchange and growth of spring barley, *Ecol. Model.*, 190, 260–276, doi:10.1016/j.ecolmodel.2005.04.024, 2006.
- Aerts, R., Boot, R. G. A., and van der Aart, P. J. M.: The relation between above- and belowground biomass allocation patterns and competitive ability, *Oecologia*, 87, 551–559, 1991.
- Alm, J., Saarnio, S., Nykänen, H., Silvola, J., and Martikainen, P.: Winter CO₂, CH₄ and N₂O fluxes on some natural and drained boreal peatlands, *Biogeochemistry*, 44, 163–186, 1999.
- Armstrong, W.: Aeration in Higher Plants, *Adv. Bot. Res.*, 7, 225–332, doi:10.1016/S0065-2296(08)60089-0, 1980.
- Atkin, O. K., Tjoelker, M. G., and Atkin, O.: Thermal acclimation and the dynamic response of plant respiration to temperature, *Trends Plant Sci.*, 8, 343–351, doi:10.1016/S1360-1385(03)00136-5, 2003.
- Atkin, O. K., Bruhn, D., Hurry, V. M., and Tjoelker, M. G.: Evans Review No. 2: The hot and the cold: unravelling the variable response of plant respiration to temperature, 32, 87–105, doi:10.1071/FP03176, 2005.
- Aurela, M., Lohila, A., Tuovinen, J.-P., Hatakka, J. R. T., and Laurila, T.: Carbon dioxide exchange on a northern boreal fen, *Boreal Environ. Res.*, 14, 699–710, 2009.
- Bahn, M., Lattanzi, F. A., Hasibeder, R., Wild, B., Koranda, M., Danese, V., Brüggemann, N., Schmitt, M., Siegwolf, R., and Richter, A.: Responses of belowground carbon allocation dynamics to extended shading in mountain grassland, *New Phytologist*, 198, 116–126, doi:10.1111/nph.12138, 2013.
- Baldocchi, D.: Forward, *Glob. Change Biol.*, 13, 547, doi:10.1111/j.1365-2486.2007.01345.x, 2007.
- Baldocchi, D., Falge, E., Gu, L., Olson, R., Hollinger, D., Running, S., Anthoni, P., Bernhofer, C., Davis, K. J., Evans, R., Fuentes,

- J., Goldstein, A., Katul, G., Law, B., Lee, X., Malhi, Y., Meyers, T., Munger, W., Oechel, W., Paw, K. T., Pilegaard, K., Schmid, H. P., Valentini, R., Verma, S., Vesala, T., Wilson, K., and Wofsy, S.: FLUXNET: A New Tool to Study the Temporal and Spatial Variability of Ecosystem-Scale Carbon Dioxide, Water Vapor, and Energy Flux Densities, *Bull. Amer. Meteor. Soc.*, 82, 2415–2434, 2001.
- Betz, S., Liebersbach, H., Glatzel, S., Jurasinski, G., Buczko, U., and Höper, H.: Effects of land use intensity on the full greenhouse gas balance in an Atlantic peat bog, *Biogeosciences*, 10, 1067–1082, doi:10.5194/bg-10-1067-2013, 2013.
- Bell, M. J., Jones, E., Smith, J., Smith, P., Yeluripati, J. B., Augustin, J., Juszczak, R., Olejnik, J., and Sommer, M.: Simulation of soil nitrogen, nitrous oxide emissions and mitigation scenarios at 3 European cropland sites using the ECOSSE model, *Nutr. Cycl. Agroecosyst.*, 92, 161–181, doi:10.1007/s10705-011-9479-4, 2012.
- Belyea, L. R.: Separating the Effects of Litter Quality and Microenvironment on Decomposition Rates in a Patterned Peatland, *Oikos*, 77, 529–539, 1996.
- Bendix, M., Tornbjerg, T., and Brix, H.: Internal gas transport in *Typha latifolia* L. and *Typha angustifolia* L. 1. Humidity-induced pressurization and convective through flow, *Aquat. Bot.*, 49, 75–89, doi:10.1016/0304-3770(94)90030-2, 1994.
- Bergman, I., Lundberg, P., and Nilsson, M.: Microbial carbon mineralisation in an acid surface peat: effects of environmental factors in laboratory incubations, *Soil Biol. Biochem.*, 31, 1867–1877, doi:10.1016/S0038-0717(99)00117-0, 1999.
- Beven, K.: A manifesto for the equifinality thesis, *J. Hydrol.*, 320, 18–36, doi:10.1016/j.jhydrol.2005.07.007, 2006.
- Beven, K. and Freer, J.: Equifinality, data assimilation, and uncertainty estimation in mechanistic modelling of complex environmental systems using the GLUE methodology, *J. Hydrol.*, 249, 11–29, doi:10.1016/S0022-1694(01)00421-8, 2001.
- Billings, W. D., Peterson, K. M., and Shaver, G. R.: Growth, turnover, and respiration rates of roots and tillers in tundra graminoids, in: *Vegetation and production ecology of an Alaskan arctic tundra*, edited by: Tieszen, L. L., Springer-Verlag, 29, 415–434, doi:10.1007/978-1-4612-6307-4, 1978.
- Bokhari, U. G.: Regrowth of western wheatgrass utilizing ¹⁴C-labeled assimilates stored in belowground parts, *Plant Soil*, 48, 115–127, 1977.
- Bragazza, L., Freeman, C., Jones, T., Rydin, H., Limpens, J., Fenner, N., Ellis, T., Gerdol, R., Hájek, M., Tomáš, H., Lacumin, P., Kutnar, L., Tahvanainen, T., and Toberman, H.: Atmospheric nitrogen deposition promotes carbon loss from peat bogs, *PNAS*, 103, 19386–19389, 2006.
- Brooks, R. and Corey, A.: *Hydraulic Properties of Porous Media*, Hydrology Papers 3, Colorado State University, Fort Collins, 1964.
- Bubier, J., Crill, P. M., and Mosedale, A.: Net ecosystem CO₂ exchange measured by autochambers during the snow-covered season at a temperate peatland, *Hydrol. Process.*, 16, 3667–3682, doi:10.1002/hyp.1233, 2002.
- Calanca, P., Vuichard, N., Campbell, C. L., Viovy, N., Cozic, A., Fuhrer, J., and Soussana, J. F.: Simulating the fluxes of CO₂ and N₂O in European grasslands with the Pasture Simulation Model (PaSim), *Agr. Ecosyst. Environ.*, 121, 164–174, doi:10.1016/j.agee.2006.12.010, 2007.
- Chivers, M. R., Turetsky, M. R., Waddington, J. M., Harden, J. W., and McGuire, A. D.: Effects of Experimental Water Table and Temperature Manipulations on Ecosystem CO₂ Fluxes in an Alaskan Rich Fen, *Ecosystems*, 12, 1329–1342, doi:10.1007/s10021-009-9292-y, 2009.
- Chojnicki, B. H., Michalak, M., Acosta, M., Juszczak, R., Augustin, J., Drösler, M., and Olejnik, J.: Measurements of Carbon Dioxide Fluxes by Chamber Method at the Rzecin Wetland Ecosystem, Poland, *Polish J. of Environ. Stud.*, 19, 283–291, 2010.
- CoupModel: Current version of COUP model for download, available at: <http://www.coupmodel.com> (last access: 11 November 2014), 2014.
- Crow, S. E. and Wieder, R. K.: Sources of CO₂ emission from a northern peatland: root respiration, exudation and decomposition, *Ecology*, 86, 1825–1834, 2005.
- Cui, J., Li, C., and Trettin, C. C.: Analyzing the ecosystem carbon and hydrologic characteristics of forested wetland using a biogeochemical process model, *Glob. Change Biol.*, 11, 278–289, doi:10.1111/j.1365-2486.2005.00900.x, 2005.
- Dai, Y., Dickinson, R. E., and Wang, Y.-P.: A Two-Big-Leaf Model for Canopy Temperature, Photosynthesis, and Stomatal Conductance, *J. Climate*, 17, 2281–2299, doi:10.1175/1520-0442(2004)017<2281:ATMFCT>2.0.CO;2, 2004.
- Davidson, E. A., Janssens, I. A., and Luo, Y.: On the variability of respiration in terrestrial ecosystems: moving beyond Q₁₀, *Glob. Change Biol.*, 12, 154–164, doi:10.1111/j.1365-2486.2005.01065.x, 2006.
- Davidson, H. R. and Campbell, C. A.: The effect of temperature, moisture and nitrogen on the rate of development of spring wheat as measured by degree days, *Can. J. Plant Sci.*, 63, 833–846, 1983.
- Davies, A.: *The Regrowth of Grass Swards*, in: *The Grass Crop*, edited by: Jones, M. B. and Lazenby, A., The Grass Crop, Chapman and Hall, London, 85–127, UK, 1988.
- Del Grosso, S., Parton, W. J., Mosier, A., Holland, E., Pendall, E., Schimel, D., and Ojima, D.: Modeling soil CO₂ emissions from ecosystems, *Biogeochemistry*, 73, 71–91, doi:10.1007/s10533-004-0898-z, 2005.
- DeLaune, R. D., Reddy, C. N., and Patrick Jr, W. H.: Organic matter decomposition in soil as influenced by pH and redox conditions, *Soil Biol. Biochem.*, 13, 533–534, 1981.
- Dietiker, D., Buchmann, N., and Eugster, W.: Testing the ability of the DNDC model to predict CO₂ and water vapour fluxes of a Swiss cropland site, *Agr. Ecosyst. Environ.*, 139, 396–401, doi:10.1016/j.agee.2010.09.002, 2010.
- Dimitrov, D. D., Grant, R. F., Lafleur, P. M., and Humphreys, E. R.: Modeling the effects of hydrology on ecosystem respiration at Mer Bleue bog, *J. Geophys. Res.-Biogeosci.* (2005–2012), 115, G04, doi:10.1029/2010JG001312, 2010.
- Dinsmore, K. J., Billett, M. F., Skiba, U. M., Rees, R. M., Drewer, J., and Helfter, C.: Role of the aquatic pathway in the carbon and greenhouse gas budgets of a peatland catchment, *Glob. Change Biol.*, 16, 2750–2762, doi:10.1111/j.1365-2486.2009.02119.x, 2010.
- Drewer, J., Lohila, A., Aurela, M., Laurila, T., Minkkinen, K., Penttilä, T., Dinsmore, K. J., McKenzie, R. M., Helfter, C., Flechard, C., Sutton, M. A., and Skiba, U. M.: Comparison of greenhouse gas fluxes and nitrogen budgets from an ombrotrophic bog in

- Scotland and a minerotrophic sedge fen in Finland, *Eur. J. Soil Sci.*, 61, 640–650, doi:10.1111/j.1365-2389.2010.01267.x, 2010.
- Drösler, M.: Trace gas exchange and climatic relevance of bog ecosystems, Southern Germany, Ph.D. thesis, Chair of Vegetation Ecology, Department of Ecology, Technical University Munich, 179 pp., 2005.
- Drösler, M., Freibauer, A., Christensen, T. R., and Friborg, T.: Observations and Status of Peatland Greenhouse Gas Emissions in Europe, in: *The continental-scale greenhouse gas balance of Europe*, edited by: Dolman, A. J., Freibauer, A., Valentini, R., Ecological studies, 203, Springer, New York, 243–261, 2008.
- Duru, M. and Ducrocq, H.: Growth and Senescence of the Successive Grass Leaves on a Tiller, Ontogenic development and effect of temperature, *Ann. Bot.*, 85, 635–643, doi:10.1006/anbo.2000.1116, 2000.
- Falge, E., Baldocchi, D., Olson, R., Anthoni, P., Aubinet, M., Bernhofer, C., Burba, G., Ceulemans, R., Clement, R., Dolman, H., Granier, A., Gross, P., Grünwald, T., Hollinger, D. Y., Jensen, N.-O., Katul, G., Keronen, P., Kowalski, A., Lai, C. T., Law, B. E., Meyers, T., Moncrieff, J., Moors, E., Munger, W. J., Pilegaard, K., Rannik, Ü., Rebmann, C., Suyker, A., Tenhunen, J., Tu, K., Verma, S., Vesala, T., Wilson, K., and Wofsy, S.: Gap filling strategies for defensible annual sums of net ecosystem exchange, *Agr. Forest Meteorol.*, 107, 43–69, doi:10.1016/s0168-1923(00)00225-2, 2001.
- Fan, Z., David McGuire, A., Turetsky, M. R., Harden, J. W., Michael Waddington, J., and Kane, E. S.: The response of soil organic carbon of a rich fen peatland in interior Alaska to projected climate change, *Glob. Change Biol.*, 19, 604–620, doi:10.1111/gcb.12041, 2013.
- Fang, C. and Moncrieff, J. B.: The variation of soil microbial respiration with depth in relation to soil carbon composition, *Plant Soil*, 268, 243–253, doi:10.1007/s11104-004-0278-4, 2005.
- Farquhar, G. D., von Caemmerer, S. von, and Berry, J. A.: A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species, *Planta*, 149, 78–90, 1980.
- Farquhar, G. D., Caemmerer, S. von, and Berry, J. A.: Models of photosynthesis, *Plant Physiol.*, 125, 42–45, 2001.
- Feng, L., Rui, S., Tinglong, Z., Bo, H., and Tang, Y.: Simulation of carbon dioxide fluxes in agroecosystems based on BIOME-BGC model, in: *Geoscience and Remote Sensing Symposium (IGARSS)*, Vancouver, BC, Canada, 24–29 July 2011, 3327–3329, 2011.
- Fontaine, S., Barot, S., Barré, P., Bdioui, N., Mary, B., and Rumpel, C.: Stability of organic carbon in deep soil layers controlled by fresh carbon supply, *Nature*, 450, 277–280, doi:10.1038/nature06275, 2007.
- Franko, U., Crocker, G., Grace, P., Klír, J., Körschens, M., Poulton, P., and Richter, D.: Simulating trends in soil organic carbon in long-term experiments using the CANDY model, *Geoderma*, 81, 109–120, doi:10.1016/S0016-7061(97)00084-0, 1997.
- Frolking, S. E., Roulet, N. T., Moore, T. R., Richard, P. J. H., Lavoie, M., and Muller, S. D.: Modeling Northern Peatland Decomposition and Peat Accumulation, *Ecosystems*, 4, 479–498, doi:10.1007/s10021-001-0105-1, 2001.
- Frolking, S. E., Roulet, N. T., Moore, T. R., Lafleur, P. M., Bubier, J. L., and Crill, P. M.: Modeling seasonal to annual carbon balance of Mer Bleue Bog, Ontario, Canada, *Glob. Biogeochem. Cy.*, 16, 4–1–4–21, doi:10.1029/2001GB001457, 2002.
- Fulkerson, W. J. and Donaghy, D. J.: Plant-soluble carbohydrate reserves and senescence - key criteria for developing an effective grazing management system for ryegrass-based pastures: a review, *Aust. J. Exp. Agr.*, 41, 261–275, 2001.
- Gaberščik, A. and Martinčič, A.: Seasonal Dynamics of Net Photosynthesis and Productivity of *Sphagnum papillosum*, *Lindbergia*, 13, 105–110, 1987.
- Gamon, J. A., Serrano, L., and Surfus, J. S.: The photochemical reflectance index: an optical indicator of photosynthetic radiation use efficiency across species, functional types, and nutrient levels, *Oecologia*, 112, 492–501, 1997.
- Glatzel, S., Basiliko, N., and Moore, T.: Carbon dioxide and methane production potentials of peats from natural, harvested and restored sites, Eastern Quebec, Canada, *Wetlands*, 24, 261–267, 2004.
- Gong, X., Berone, G., Agnusdei, M., Rodríguez Palma, R., Schäufele, R., and Lattanzi, F.: The allocation of assimilated carbon to shoot growth: in situ assessment in natural grasslands reveals nitrogen effects and interspecific differences, *Oecologia*, 174, 1085–1095, doi:10.1007/s00442-013-2838-x, 2014.
- Grant, R. F., Desai, A. R., and Sulman, B. N.: Modelling contrasting responses of wetland productivity to changes in water table depth, *Biogeosciences*, 9, 4215–4231, doi:10.5194/bg-9-4215-2012, 2012.
- Grosse, W., Jovy, K., and Tiebel, H.: Influence of plants on redox potential and methane production in water-saturated soil, *Hydrobiol.*, 93–99, 1996.
- Grosse-Brauckmann, G.: Ablagerungen der Moore, in: *Moor-und Torfkunde*, 3rd ed., edited by: Gottlich, K., Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, 17–236, 1990.
- Hansen, G. K. and Jensen, C. R.: Growth and Maintenance Respiration in Whole Plants, Tops, and Roots of *Lolium multiflorum*, *Physiol. Plant.*, 39, 155–164, 1977.
- Harley, P. C., Tenhunen, J. D., Murray, K. J., and Beyers, J.: Irradiance and temperature effects on photosynthesis of tussock tundra *Sphagnum* mosses from the foothills of the Philip Smith Mountains, Alaska, *Oecologia*, 79, 251–259, doi:10.1007/BF00388485, 1989.
- Haxeltine, A. and Prentice, C. I.: A General Model for the Light-Use Efficiency of Primary Production, *British Ecological Society*, 10, 551–561, 1996.
- Helfrich, M., Flessa, H., Mikutta, R., Dreves, A., and Ludwig, B.: Comparison of chemical fractionation methods for isolating stable soil organic carbon pools, *Eur. J. Soil Sci.*, 58, 1316–1329, doi:10.1111/j.1365-2389.2007.00926.x, 2007.
- Helfter, C., Campbell, C., Dinsmore, K. J., Drewer, J., Coyle, M., Anderson, M., Skiba, U., Nemitz, E., Billett, M. F., and Sutton, M. A.: Drivers of long-term variability in CO₂ net ecosystem exchange in a temperate peatland, *Biogeosciences Discuss.*, 11, 14981–15018, doi:10.5194/bgd-11-14981-2014, 2014.
- Hendriks, D. M. D., van Huissteden, J., Dolman, A. J., and van der Molen, M. K.: The full greenhouse gas balance of an abandoned peat meadow, *Biogeosciences*, 4, 411–424, doi:10.5194/bg-4-411-2007, 2007.
- Hendriks, D.: Vegetation as indicator for methane emissions, carbon dioxide fluxes and greenhouse gas balances from peat land, in: *Integrated observations of greenhouse gas budgets at the ecosystem level: Changing environment and management prac-*

- tices in peat meadows, edited by: Hendriks, D., Ph.D. thesis, VU-University, Amsterdam, 133–166, 2009.
- Hilker, T., Coops, N. C., Wulder, M. A., Black, A. T., and Guy, R. D.: The use of remote sensing in light use efficiency based models of gross primary production: A review of current status and future requirements, *Sci. Total Environ.*, 404, 411–423, doi:10.1016/j.scitotenv.2007.11.007, 2008.
- Holden, J., Chapman, P. J., and Labadz, J. C.: Artificial drainage of peatlands: hydrological and hydrochemical process and wetland restoration, *Prog. Phys. Geogr.*, 28, 95–123, doi:10.1191/0309133304pp403ra, 2004.
- Humphreys, E. R., Lafleur, P. M., Flanagan, L. B., Hedstrom, N., Syed, K. H., Glenn, A. J., and Granger, R.: Summer carbon dioxide and water vapor fluxes across a range of northern peatlands, *J. Geophys. Res.*, 111, G04011, doi:10.1029/2005JG000111, 2006.
- Jackson, M. B. and Armstrong, W.: Formation of Aerenchyma and the Processes of Plant Ventilation in Relation to Soil Flooding and Submergence, *Plant Biol.*, 1, 274–287, doi:10.1111/j.1438-8677.1999.tb00253.x, 1999.
- Jacobs, C. M. J., Jacobs, A. F. G., Bosveld, F. C., Hendriks, D. M. D., Hensen, A., Kroon, P. S., Moors, E. J., Nol, L., Schrier-Uijl, A., and Veenendaal, E. M.: Variability of annual CO₂ exchange from Dutch grasslands, *Biogeosciences*, 4, 803–816, doi:10.5194/bg-4-803-2007, 2007.
- Janssens, I. A., Lankreijer, H., Matteucci, G., Kowalski, A. S., Buchmann, N., Epron, D., Pilegaard, K., Kutsch, W., Longdoz, B., Grünwald, T., Montagnani, L., Dore, S., Rebmann, C., Moors, E. J., Grelle, A., Rannik, Ü., Morgenstern, K., Oltchev, S., Clement, R., Guðmundsson, J., Minerbi, S., Berbigier, P., Ibrom, A., Moncrieff, J., Aubinet, M., Bernhofer, C., Jensen, N. O., Vesala, T., Granier, A., Schulze, E. D., Lindroth, A., Dolman, A. J., Jarvis, P. G., Ceulemans, R., and Valentini, R.: Productivity overshadows temperature in determining soil and ecosystem respiration across European forests, *Glob. Change Biol.*, 7, 269–278, 2001.
- Jansson, P. and Halldin, S.: Model for the annual water and energy flow in a layered soil. Comparison of forest and energy exchange models, *Society for Ecol. Model.*, Copenhagen, 145–163, 1979.
- Jansson, P.-E.: COUPModel: Model use, calibration and validation, *Transactions of the ASABE*, 55, 1335–1344, 2012.
- Jansson, P.-E. and Karlberg, L.: Coupled heat and mass transfer model for soil–plant–atmosphere systems, *Royal Institute of Technology, Stockholm*, 484 pp., available at: <http://www2.lwr.kth.se/VaraDatorprogram/CoupModel/coupmanual.pdf> (last access: 15 June 2012), 2010.
- Johansson, G.: Release of organic C from growing roots of meadow fescue (*Festuca pratensis* L.), *Soil Biol. Biochem.*, 24, 427–433, doi:10.1016/0038-0717(92)90205-C, 1992.
- Johansson, G.: Carbon distribution in grass (*Festuca pratensis* L.) during regrowth after cutting—utilization of stored and newly assimilated carbon, *Plant Soil*, 151, 11–20, 1993.
- Ju, W. and Chen, J. M.: Distribution of soil carbon stocks in Canada's forests and wetlands simulated based on drainage class, topography and remotely sensed vegetation parameters, *Hydrol. Process.*, 19, 77–94, doi:10.1002/hyp.5775, 2005.
- Juston, J., Andréon, O., Kätterer, T., and Jansson, P.-E.: Uncertainty analyses for calibrating a soil carbon balance model to agricultural field trial data in Sweden and Kenya, *Ecol. Model.*, 221, 1880–1888, doi:10.1016/j.ecolmodel.2010.04.019, 2010.
- Kechavarzi, C., Dawson, Q., Bartlett, M., and Leeds-Harrison, P. B.: The role of soil moisture, temperature and nutrient amendment on CO₂ efflux from agricultural peat soil microcosms, *Geoderma*, 154, 203–210, 2010.
- Keddy, P. A.: Assembly and response rules: two goals for predictive community ecology, *J. Veg. Sci.*, 3, 157–164, doi:10.2307/3235676, 1992.
- Kellner, E. and Halldin, S.: Water budget and surface layer water storage in a Sphagnum bog in central Sweden, *Hydrol. Process.*, 16, 87–103, 2002.
- Kettunen, A., Kaitala, V., Lehtinen, A., Lohila, A., Alm, J., Silvola, J., and Martikainen, P. J.: Methane production and oxidation potentials in relation to water table fluctuations in two boreal mires, *Soil Biol. Biochem.*, 31, 1741–1749, doi:10.1016/S0038-0717(99)00093-0, 1999.
- Kirschbaum, M.: The temperature dependence of organic-matter decomposition—still a topic of debate, *Soil Biol. Biochem.*, 38, 2510–2518, doi:10.1016/j.soilbio.2006.01.030, 2006.
- Kistritz, R. U., Hall, K. J., and Yesaki, I.: Productivity, detritus flux, and nutrient cycling in a *Carex lyngbyei* tidal marsh, *Estuaries*, 6, 227–236, 1983.
- Klemetsson, L., Jansson, P.-E., Gustafsson, D., Karlberg, L., Weslien, P., Arnold, K., Ernfors, M., Langvall, O., and Anders, L.: Bayesian calibration method used to elucidate carbon turnover in forest on drained organic soil, *Biogeochemistry*, 89, 61–79, doi:10.1007/s10533-007-9169-0, 2008.
- Klimeš, L. and Klimešová, J.: The effects of mowing and fertilization on carbohydrate reserves and regrowth of grasses: do they promote plant coexistence in species-rich meadows?, *Evolutionary Ecology*, 363–382, doi:10.1007/978-94-017-1345-0_8, 2002.
- Kuzyakov, Y.: Separating microbial respiration of exudates from root respiration in non-sterile soils: a comparison of four methods, *Soil Biol. Biochem.*, 34, 1621–1631, doi:10.1016/S0038-0717(02)00146-3, 2002.
- Lafleur, P., Moore, T., Roulet, N., and Frolking, S. E.: Ecosystem Respiration in a Cool Temperate Bog Depends on Peat Temperature But Not Water Table, *Ecosystems*, 8, 619–629, doi:10.1007/s10021-003-0131-2, 2005.
- Leiber-Sauheitl, K., Fuß, R., Voigt, C., and Freibauer, A.: High CO₂ fluxes from grassland on histic Gleysol along soil carbon and drainage gradients, *Biogeosciences*, 11, 749–761, doi:10.5194/bg-11-749-2014, 2014.
- Li, C., Frolking, S. E., and Frolking, T. A.: A model of nitrous oxide evolution from soil driven by rainfall events: 1. Model structure and sensitivity, *J. Geophys. Res.*, 97, 9759–9776, 1992a.
- Li, C., Frolking, S. E., and Frolking, T. A.: A model of nitrous oxide evolution from soil driven by rainfall events: 2. Model applications, *J. Geophys. Res.*, 97, 9777–9783, 1992b.
- Limpens, J. and Berendse, F.: How litter quality affects mass loss and N loss from decomposing Sphagnum, *Oikos*, 103, 537–547, 2003.
- Lipson, D., Schadt, C., and Schmidt, S.: Changes in Soil Microbial Community Structure and Function in an Alpine Dry Meadow Following Spring Snow Melt, *Microb. Ecol.*, 43, 307–314, doi:10.1007/s00248-001-1057-x, 2002.
- Lloyd, J. and Taylor, J. A.: On the temperature dependence of soil respiration, *Funct. Ecol.*, 8, 315–323, 1994.

- Lohila, A.: Annual CO₂ exchange of a peat field growing spring barley or perennial forage grass, *J. Geophys. Res.*, 109, D18166, doi:10.1029/2004JD004715, 2004.
- Lohila, A., Aurela, M., Hatakka, J., Pihlatie, M., Minkkinen, K., Penttilä, T., and Laurila, T.: Responses of N₂O fluxes to temperature, water table and N deposition in a northern boreal fen, *Eur. J. Soil Sci.*, 61, 651–661, doi:10.1111/j.1365-2389.2010.01265.x, 2010.
- Longstreth, D. J. and Nobel, P. S.: Nutrient Influences on Leaf Photosynthesis: Effects of nitrogen, phosphorus and potassium for *Gossypium hirsutum* L., *Plant Physiol.*, 65, 541–543, 1980.
- Lund, M., Lafleur, P. M., Roulet, N. T., Anders, L., Christensen, T. R., Aurela, M., Chojnicki, B. H., Lawrence, F. B., Humphreys, E. R., Laurila, T., Oechel, W. C., Olejnik, J., Rinne, J., Schubert, P. E. R., and Nilsson, M. B.: Variability in exchange of CO₂ across 12 northern peatland and tundra sites, *Glob. Change Biol.*, 16, 2436–2448, doi:10.1111/j.1365-2486.2009.02104.x, 2009.
- Lundmark, A.: Monitoring transport and fate of de-icing salt in the roadside environment: modelling and field measurements, Ph.D. thesis, KTH, Land and Water Resources Engineering, Stockholm, Sweden, 44 pp., 2008.
- Maljanen, M., Sigurdsson, B. D., Gudmundsson, J., Óskarsson, H., Huttunen, J. T., and Martikainen, P. J.: Greenhouse gas balances of managed peatlands in the Nordic countries – present knowledge and gaps, *Biogeosciences*, 7, 2711–2738, doi:10.5194/bg-7-2711-2010, 2010.
- Meziane, D. and Shipley, B.: Interacting determinants of specific leaf area in 22 herbaceous species: effects of irradiance and nutrient availability, *Plant Cell Environ.*, 22, 447–459, 1999.
- Monteith, J. L.: Solar radiation and productivity in tropical ecosystems, *J. Appl. Ecol.*, 9, 747–766, 1972.
- Monteith, J. L. and Moss, C. J.: Climate and the Efficiency of Crop Production in Britain [and Discussion], *Philos. T. Roy. Soc. B*, 281, 277–294, doi:10.1098/rstb.1977.0140, 1977.
- Moore, T. R. and Dalva, M.: Methane and carbon dioxide exchange potentials of peat soils in aerobic and anaerobic laboratory incubations, *Soil Biol. Biochem.*, 29, 1157–1164, 1997.
- Moore, T. R., Bubier, J. L., and Bledzki, L.: Litter Decomposition in Temperate Peatland Ecosystems: The Effect of Substrate and Site, *Ecosystems*, 10, 949–963, doi:10.1007/s10021-007-9064-5, 2007.
- Moriassi, D. N., Arnold G. J., van Liew, M. W., Binger R. L., Harmel, R. D., and Veith, T. L.: Model evaluation guidelines for systematic quantification of accuracy in watershed simulations, *Am. Soc. Agri. Biol. Eng.*, 50, 885–900, 2007.
- Mualem, Y.: A new model for predicting the hydraulic conductivity of unsaturated porous media, *Water Resour. Res.*, 12, 513–522, doi:10.1029/WR012i003p00513, 1976.
- Murray, K. J., Tenhunen, J. D., and Nowak, R. S.: Photoinhibition as a control on photosynthesis and production of Sphagnum mosses, *Oecologia*, 96, 200–207, doi:10.1007/BF00317733, 1993.
- Nash, J. E. and Sutcliffe, J. V.: River flow forecasting through conceptual models part I – A discussion of principles, *J. Hydrol.*, 10, 282–290, 1970.
- Norman, J., Jansson, P.-E., Farahbakhshazad, N., Butterbach-Bahl, K., Li, C., and Klemetsson, L.: Simulation of NO and N₂O emissions from a spruce forest during a freeze/thaw event using an N-flux submodel from the PnET-N-DNDC model integrated to CoupModel, *Ecol. Model.*, 216, 18–30, doi:10.1016/j.ecolmodel.2008.04.012, 2008.
- Nuttonson, M. Y.: The role of bioclimatology in agriculture with special reference to the use of thermal and photo-thermal requirements of pure-line varieties of plants as a biological indicator in ascertaining climatic analogues (Homoclimes), *Int. J. Biometeorol.*, 2, 129–148, 1958.
- Paterson, E. and Sim, A.: Effect of nitrogen supply and defoliation on loss of organic compounds from roots of *Festuca rubra*, *J. Exp. Bot.*, 51, 1449–1457, doi:10.1093/jexbot/51.349.1449, 2000.
- Paul, K.: Temperature and moisture effects on decomposition, in: Net Ecosystem Exchange Workshop proceedings, Canberra, Australia, 18–20 April 2001, 95–102, 2001.
- Poorter, H., Remkes, C., and Lambers, H.: Carbon and Nitrogen Economy of 24 Wild Species Differing in Relative Growth Rate, *Plant Physiol.*, 94, 621–627, 1990.
- Poorter, H., van der Werf, A., Atkin, O. K., and Lambers, H.: Respiratory energy requirements of roots vary with the potential growth rate of a plant species, *Physiol. Plantarum*, 83, 469–475, 1991.
- Potter, C., Bubier, J., Crill, P. M., and Lafleur, P.: Ecosystem modeling of methane and carbon dioxide fluxes for boreal forest sites, *Can. J. For. Res.*, 31, 208–223, doi:10.1139/x00-164, 2001.
- Proebsting, W. M., Davies, P. J., and Marx, G. A.: Photoperiodic control of apical senescence in a genetic line of peas, *Plant Physiol.*, 58, 800–802, 1976.
- Raich, J. W. and Schleisinger, W. H.: The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate, *Tellus*, 44B, 81–99, 1992.
- Ratkowsky, D. A., Olley, J., McMeekin, T. A., and Ball, A.: Relationship between temperature and growth rate of bacterial cultures, *J. Bacteriol.*, 149, 1–5, 1982.
- Ravina, M.: Modelling of methane emission from forest ecosystems. Implementation and test of submodel as part of the COUP-Model, Master Thesis, KTH Royal Institute of Technology, Stockholm, 54 pp., 2007.
- Reddy, K. R. and Patrick, W. H.: Effect of alternate aerobic and anaerobic conditions on redox potential, organic matter decomposition and nitrogen loss in a flooded soil, *Soil Biol. Biochem.*, 7, 87–94, doi:10.1016/0038-0717(75)90004-8, 1975.
- Reich, P. B., Walters, M. B., Ellsworth, D. S., and Uhl, C.: Photosynthesis-nitrogen relations in Amazonian tree species, *Oecologia*, 97, 62–72, 1994.
- Reich, P. B., Ellsworth, D. S., and Walters, M. B.: Leaf structure (specific leaf area) modulates photosynthesis-nitrogen relations: evidence from within and across species and functional groups, *Funct. Ecol.*, 12, 948–958, 1998.
- Reich, P., Ellsworth, D., and Walters, M.: Leaf structure (specific leaf area) modulates photosynthesis–nitrogen relations: evidence from within and across species and functional groups, *Funct. Ecol.*, 12, 948–958, 1998.
- Reichstein, M., Rey, A., Freibauer, A., Tenhunen, J. D., Valentini, R., Banza, J., Casals, P., Cheng, Y., Grünzweig, J. M., Irvine, J., Joffre, R., Law, B. E., Loustau, D., Miglietta, F., Oechel, W. C., Ourcival, J.-M., Pereira, J. S., Peressotti, A., Ponti, F., Qi, Y., Rambal, S., Rayment, M., Romanya, J., Rossi, F., Tedeschi, V., Giampiero, T., Xu, M., and Yakir, D.: Modeling temporal and large-scale spatial variability of soil respiration from soil wa-

- ter availability, temperature and vegetation productivity indices, *Glob. Biogeochem. Cy.*, 17, 1104, doi:10.1029/2003GB002035, 2003.
- Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N., Gilmanov, T. G., Granier, A., Grünwald, T., Havrankova, K., Ilvesniemi, H., Janous, D., Knohl, A., Laurila, T., Lohila, A., Loustau, D., Matteucci, G., Meyers, T., Miglietta, F., Ourcival, J.-M., Pumpanen, J., Rambal, S., Rotenberg, E., Sanz, M., Tenhunen, J. D., Seufert, G., Vaccari, F., Vesala, T., Yakir, D., and Valentini, R.: On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm, *Glob. Change Biol.*, 11, 1424–1439, doi:10.1111/j.1365-2486.2005.001002.x, 2005.
- Richards, L. A.: Capillary conduction of liquids through porous mediums, *J. Appl. Phys.*, 1, 318–333, doi:10.1063/1.1745010, 1931.
- Robson, M. J.: The Growth and Development of Simulated Swards of Perennial Ryegrass, *Ann. Bot.*, 37, 487–500, 1973.
- Rovira, A. D.: Plant root exudates, *The Botanical Review*, 35, 35–57, 1969.
- Rudolph, H. and Samland, J.: Occurrence and metabolism of sphagnum acid in the cell walls of bryophytes, *Phytochemistry*, 24, 745–749, doi:10.1016/S0031-9422(00)84888-8, 1985.
- Ryser, P. and Urbas, P.: Ecological significance of leaf life span among Central European grass species, *Oikos*, 91, 41–50, doi:10.1034/j.1600-0706.2000.910104.x, 2000.
- Saarinen, T.: Demography of *Carex rostrata* in a boreal mesotrophic fen: shoot dynamics and biomass development, *Ann. Bot. Fenn.*, 35, 203–209, 1998.
- Sagerfors, J., Lindroth, A., Grelle, A., Klemetsson, L., Weslien, P., and Nilsson, M.: Annual CO₂ exchange between a nutrient-poor, minerotrophic, boreal mire and the atmosphere, *J. Geophys. Res.-Biogeosci.*, 113, G01001, doi:10.1029/2006JG000306, 2008.
- Scheurwater, I., Cornelissen, C., Dictus, F., Welschen, R., and Lambers, H.: Why do fast- and slow-growing grass species differ so little in their rate of root respiration, considering the large differences in rate of growth and ion uptake?, *Plant, Cell and Environment*, 21, 995–1005, 1998.
- Schläpfer, B. and Ryser, P.: Leaf and Root Turnover of Three Ecologically Contrasting Grass Species in Relation to Their Performance along a Productivity Gradient, *Oikos*, 75, 398–406, 1996.
- Schuldt, R. J., Brovkin, V., Kleinen, T., and Winderlich, J.: Modelling Holocene carbon accumulation and methane emissions of boreal wetlands – an Earth system model approach, *Biogeosciences*, 10, 1659–1674, doi:10.5194/bg-10-1659-2013, 2013.
- Sinclair, T. R. and Horie, T.: Leaf Nitrogen, Photosynthesis, and Crop Radiation Use Efficiency: A Review, *Crop Science*, 29, 90–98, doi:10.2135/cropsci1989.0011183X002900010023x, 1989.
- Smith, J., Gottschalk, P., Bellarby, J., Richards, M., Nayak, D., Coleman, K., Hillier, J., Flynn, H., Wattenbach, M., Aitkenhead, M., Yeluripurti, J., Farmer, J., and Smith, P.: Model to Estimate Carbon in Organic Soils – Sequestration and Emissions (ECOSSE), User Manual, available at: <http://www.abdn.ac.uk/staffpages/uploads/soi450/ECOSSEUsermanual310810.pdf>, (last access: 05 November 2014), 2010.
- Smith, P., Smith, J., Powlson, D., McGill, W., Arah, J., Chertov, O., Coleman, K., Franko, U., Frolking, S., and Jenkinson, D.: A comparison of the performance of nine soil organic matter models using datasets from seven long-term experiments, *Geoderma*, 81, 153–225, 1997.
- Steed, J., E., De Wald, L., E., and Kolb, T., E.: Physiological and Growth Responses of Riparian Sedge Transplants to Groundwater Depth, *Int. J. Plant Sci.*, 163, 925–936, doi:10.1086/342634, 2002.
- Steele, J. M., Ratliff, R. D., and Ritenour, G. L.: Seasonal variation in total nonstructural carbohydrate levels in Nebraska sedge, *J. Range Manage.*, 37, 465–467, 1984.
- St-Hilaire, F., Wu, J., Roulet, N. T., Frolking, S. E., Lafleur, P. M., Humphreys, E. R., and Arora, V.: McGill wetland model: evaluation of a peatland carbon simulator developed for global assessments, *Biogeosciences*, 7, 3517–3530, doi:10.5194/bg-7-3517-2010, 2010.
- Thomas, H. and Stoddart, J. L.: Leaf Senescence, *Ann. Rev. Plant Physiol.*, 31, 83–111, 1980.
- Thornton, P. E. and Rosenbloom, N. A.: Ecosystem model spin-up: Estimating steady state conditions in a coupled terrestrial carbon and nitrogen cycle model, *Ecol. Model.*, 189, 25–48, doi:10.1016/j.ecolmodel.2005.04.008, 2005.
- Turetsky, M. R.: The Role of Bryophytes in Carbon and Nitrogen Cycling, *The Bryologist*, 106, 395–409, 2003.
- van den Bos, R.: Restoration of former wetlands in the Netherlands; effect on the balance between CO₂ sink and CH₄ source, *Neth. J. Geosci.*, 82, 325–332, 2003.
- van der Werf, A., Kooijman, A., Welschen, R., and Lambers, H.: Respiratory energy costs for the maintenance of biomass, for growth and for ion uptake in roots of *Carex diandra* and *Carex acutiformis*, *Physiol. Plantarum*, 72, 483–491, 1988.
- van Huissteden, J., van den Bos, R., and Alvarez, I. M.: Modelling the effect of water-table management on CO₂ and CH₄ fluxes from peat soils, *Neth. J. Geosci.*, 85, 3–18, 2006.
- van Huissteden, J., Petrescu, A. M. R., Hendriks, D. M. D., and Rebel, K. T.: Sensitivity analysis of a wetland methane emission model based on temperate and arctic wetland sites, *Biogeosciences*, 6, 3035–3051, doi:10.5194/bg-6-3035-2009, 2009.
- van Oijen, M., Reyer, C., Bohn, F. J., Cameron, D. R., Deckmyn, G., Flechsig, M., Härkönen, S., Hartig, F., Huth, A., Kiviste, A., Lasch, P., Mäkelä, A., Mette, T., Minunno, F., and Rammer, W.: Bayesian calibration, comparison and averaging of six forest models, using data from Scots pine stands across Europe, *Forest Ecology and Management*, 289, 255–268, doi:10.1016/j.foreco.2012.09.043, 2013.
- Verhoeven, J. and Toth, E.: Decomposition of *Carex* and *Sphagnum* litter in fens: Effect of litter quality and inhibition by living tissue homogenates, *Soil Biol. Biochem.*, 27, 271–275, doi:10.1016/0038-0717(94)00183-2, 1995.
- Ward, S. E., Ostle, N. J., Oakley, S., Quirk, H., Henrys, P. A., Bardgett, R. D., and van der Putten, W.: Warming effects on greenhouse gas fluxes in peatlands are modulated by vegetation composition, *Ecol Lett*, 16, 1285–1293, doi:10.1111/ele.12167, 2013.
- Whalen, J. K., Bottomley, P. J., and Myrold, D. D.: Carbon and nitrogen mineralization from light- and heavy-fraction additions to soil, *Soil Biol. Biochem.*, 32, 1345–1352, doi:10.1016/S0038-0717(00)00040-7, 2000.
- White, L. M.: Carbohydrate reserves of grasses: a review, *J. Range Manage.*, 13–18, 1973.

- Willmott, C. J.: Some Comments on the Evaluation of Model Performance, *Bull. Amer. Meteor. Soc.*, 63, 1309–1313, doi:10.1175/1520-0477(1982)063<1309:SCOTEO>2.0.CO;2, 1982.
- Wingler, A.: The role of sugars in integrating environmental signals during the regulation of leaf senescence, *J. Exp. Bot.*, 57, 391–399, doi:10.1093/jxb/eri279, 2005.
- Wohlfahrt, G., Bahn, M., Haubner, E., Horak, I., Michaeler, W., Rottmar, K., Tappeiner, U., and Cernusca, A.: Inter-specific variation of the biochemical limitation to photosynthesis and related leaf traits of 30 species from mountain grassland ecosystems under different land use, *Plant Cell Environ.*, 22, 1281–1296, 1999.
- Wu, J., Jansson, P.-E., van der Linden, L., Pilegaard, K., Beier, C., and Ibrom, A.: Modelling the decadal trend of ecosystem carbon fluxes demonstrates the important role of functional changes in a temperate deciduous forest, *Ecol. Model.*, 260, 50–61, doi:10.1016/j.ecolmodel.2013.03.015, 2013a.
- Wu, J., Roulet, N. T., Sagerfors, J., and Nilsson, M. B.: Simulation of six years of carbon fluxes for a sedge-dominated oligotrophic minerogenic peatland in Northern Sweden using the McGill Wetland Model (MWM), *J. Geophys. Res.-Biogeosci.*, 118, 795–807, doi:10.1002/jgrg.20045, 2013b.
- Wu, S. H. and Jansson, P.-E.: Modelling soil temperature and moisture and corresponding seasonality of photosynthesis and transpiration in a boreal spruce ecosystem, *Hydrol. Earth Syst. Sci.*, 17, 735–749, doi:10.5194/hess-17-735-2013, 2013.
- Yeloff, D. and Mauquoy, D.: The influence of vegetation composition on peat humification: implications for palaeoclimatic studies, *Boreas*, 35, 662–673, doi:10.1080/03009480600690860, 2006.
- Yurova, A., Wolf, A., Sagerfors, J., and Nilsson, M.: Variations in net ecosystem exchange of carbon dioxide in a boreal mire: Modeling mechanisms linked to water table position, *J. Geophys. Res.*, 112, doi:10.1029/2006JG000342, 2007.
- Zeitz, J. and Vely, S.: Soil properties of drained and rewetted fen soils, *Soil Sci. Soc. Am. J.*, 165, 618–626, 2002.
- Zhang, D., Hui, D., Luo, Y., and Zhou, G.: Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors, *J. Plant Ecol.*, 1, 85–93, doi:10.1093/jpe/rtn002, 2008.
- Zhang, T.: Influence of the seasonal snow cover on the ground thermal regime: An overview, *Rev. Geophys.*, 43, RG4002, doi:10.1029/2004RG000157, 2005.
- Zhang, Y., Li, C., Trettin, C. C., Li, H., and Sun, G.: An integrated model of soil, hydrology, and vegetation for carbon dynamics in wetland ecosystems, *Glob. Biogeochem. Cy.*, 16, 9-1–9-17, doi:10.1029/2001GB001838, 2002.
- Zimmermann, M., Leifeld, J., Schmidt, M. W. I., Smith, P., and Fuhrer, J.: Measured soil organic matter fractions can be related to pools in the RothC model, *Eur. J. Soil Science*, 58, 658–667, doi:10.1111/j.1365-2389.2006.00855.x, 2007.