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Bayesian calibration method used to elucidate carbon turnover in forest on drained organic soil

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Abstract Depending on the balance between sink and source processes for C, drained organic forest soil ecosystems can be in balance or act as net sinks or sources of CO_2 to the atmosphere. In order to study the effect of groundwater level and soil temperature on C-flux, the CoupModel was calibrated (climate data, groundwater levels, soil CO_2 flux, net ecosystem fluxes of CO_2-exchange, sensible heat flux and latent heat flux, forest production etc.) for a drained forest in Sweden. Bayesian calibration techniques were used to elucidate how different parameters and variables were interlinked in C-circulation. The calibrated model reproduced abiotic and biotic variables reasonably well except for root respiration, which was largely underestimated. Bayesian calibration reduced the uncertainties in the model and highlighted the fact that calibrations should be performed with a high number of parameters instead of specific parameter values.

Keywords Spruce forest · Drained soils · Net ecosystem exchange · Respiration · Latent heat flux · Sensible heat flux · Simulations · Eddy covariance · Chambers · Biomass

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Introduction

Drained organic forest soils have been found to be large sources of CO_2 flux (Laine et al. 1996; Silvola et al. 1996; Widén et al. 2001; von Arnold et al. 2005a, b). These high fluxes are due to organic matter that accumulated when the soil was water-saturated becoming available for aerobic decomposition after drainage. During saturated conditions, organic matter decomposition is limited by oxygen deficiency, low temperatures in deeper peat layers and possibly also by phenol toxicity (Minkkinen et al. 1999, 2007; Freeman et al. 2001). After drainage, soil respiration

is increased not only by an oxygen and temperature increase, but also by the gradual addition to the soil profile of above-ground and below-ground plant litter, which constitutes more readily decomposable organic matter than the old lignin-enriched material (Minkkinen et al. 2007). Furthermore, the fresh, readily decomposable organic matter from plants stimulates the degradation of old peat material, through the so-called priming effect (Kuzyakov 2006). Thus, CO_2 emissions from the soil increase after drainage due to a complex interaction of variables affecting decomposition by changing both physical conditions and the activity of the plant community in the post-drainage ecosystem.

Depending on the balance between sink and source processes, the drained sites can either achieve a balance or act as a net sink or a net source of CO_2 flux, as has been demonstrated for sites where flux estimates have been conducted. At some sites, the net primary production (NPP) of trees and forest floor vegetation can compensate for the soil CO_2 release and the forest becomes a net sink (Hargreaves et al. 2003; von Arnold 2005a, b), while other sites become net sources (Lindroth et al. 1998, in this volume; Lohila et al. 2004; von Arnold 2005b).

Nowadays detailed investigations of ecosystem behaviour make it possible to test and calibrate process-based models that can be used to describe both the short- and long-term dynamics of forest ecosystems. For example the CoupModel (Jansson and Karlberg 2004) has recently been used to describe the short-term dynamics (Berggren Kleja et al. in this volume) and regional patterns with long-term behaviour (Svensson et al. in this volume), as well as demonstrating the effects of climate change (Jansson et al. in this volume). A major problem with model applications is the uncertainty in parameter values and calibration procedures. The CoupModel is based on a large number of equations and parameters, generating multiple outputs, but at the same time is operated with a relatively small number of driving data. For a more detailed description, see Jansson and Karlberg (2004) or Svensson et al. (in this volume) for a more basic description of equations for forest conditions. This hampers the calibration and parameterisation of the model. However, the Bayesian calibration technique can offer a solution to the calibration process by bridging the gap between model and data, since it combines various measurements and their uncertainties with the corresponding uncertainties among the parameters in the model (Van Oijen et al. 2005). This method can also easily quantify the correlations between the different parameters and between parameters and different model variables.

The overall objective of the present study was to use Bayesian calibration techniques to elucidate how different parameters and variables are interlinked in the CoupModel applied to a forest site and with special focus on the effect of groundwater level on net CO_2 flux from a drained soil. The CoupModel (Jansson and Karlberg 2004) was therefore applied to a drained forest site at Asa (Berggren Kleja et al. in this volume). Data to calibrate the model were derived from a database on C-circulation at the site developed within the Lustra project (a multi disciplinary project "Land Use Strategies for reducing net greenhouse gas emissions"). The soil C flux from the site has been measured by von Arnold et al. (2005a, b) and the net ecosystem fluxes (CO_2-exchange, sensible heat flux, latent heat flux) and forest production at the site have been reported by Lindroth et al. (in this volume). Furthermore, driving variable data to run the model were available for a period of 5 years, together with measurements of soil temperature and groundwater level. A trenching technique was used to separate the soil respiration from root (autotrophic) respiration (Klemedtsson unpublished data), which allowed us to investigate how well the model could handle these two components of the soil C flux. The Lustra database for the drained forest site at Asa formed a unique dataset to conduct a Bayesian calibration and analyse the importance of different parameters and variables on individual sub-fluxes, as well as on the net ecosystem flux (NEE). Specific objectives were to demonstrate the potential of a Bayesian-style calibration procedure to reduce the uncertainties in the model; to establish a first set of parameter estimates for a forested, drained peat soil; and to discuss the dependencies between parameter values and different model components.

Methods

Site description

The site is located near the Asa Experimental Forest, in southern Sweden (57°10′ N, 14°48′ E). According

to the Köppen classification, the climate at Asa is cold temperate humid, with a 30-year (1961–1990) mean annual temperature of 5.6°C and a 30-year mean annual precipitation of 662 mm measured at Berg, about 15 km from Asa (Alexandersson and Eggertsson Karlström 2001).

Norway spruce (*Picea abies*) is the dominant tree species, mixed with some Scots pine (*Pinus sylvestris*) and silver birch (*Betula pendula*). The field layer mainly comprises *Vaccinium vitis-idaea*, *V. myrtillus*, *Poa* ssp., *Deschampsia* spp., *Oxalis acetosella* and *Lycopodiaceae* spp.

The soil at the site is a histosol (FAO classification) with more than 92 ± 9% organic matter and the peat depth is approx. 90 cm. At the time of measurement the soil had dry bulk density 0.17 g cm^{-3}, porosity 86 ± 4.7%, pH 3.2 ± 0.1 and the organic matter had a C:N ratio of 27.2. The site is described in more detail by von Arnold et al. (2005a).

Modelling

Simulations were carried out using the CoupModel (Jansson and Karlberg 2004), an ecosystem process model that has previously been used for similar forest ecosystems (e.g. Svensson et al. in this volume; Karlberg et al. 2006; Gustafsson et al. 2004). The CoupModel simulates one-dimensional, vertical fluxes of water, heat, carbon and nitrogen in a soil-plant-atmosphere system, including a layered soil/snow profile, covered by one or several plant layers above. Two coupled partial differential equations calculate water and heat flows in the soil, namely the Richard's equation for water flows and the Fourier law of diffusion for heat including convective flows (Jansson and Halldin 1979). Soil evapotranspiration, soil surface temperature and snow melt are based on energy balance calculations where net radiation of the respective surface is balanced by turbulent fluxes of sensible and latent heat and surface heat flux (Alvenäs and Jansson 1997; Gustafsson et al. 2004). Plant water uptake is based on a soil-plant-atmosphere-continuum approach, using the Penman–Monteith equation (Penman 1953; Monteith 1965; Lindroth 1985). Snow accumulation and melt are described, as is the partitioning between infiltration to the soil or surface runoff at the uppermost soil boundary. Carbon and nitrogen turnover is calculated in the plant and in the soil (Johnsson et al. 1987; Eckersten et al. 1998; Eckersten and Bier 1998). Biomass is partitioned into several above-ground and below-ground pools of carbon and nitrogen. Gross production of carbon (GPP) is driven by solar radiation (Monteith 1977) and regulated by water uptake, leaf temperature and plant nitrogen stress. The latter is given as a static parameter and is thus not affected by the possible dynamic variation nitrogen status of the leaf. This simplification is normally valid during shorter periods of simulations where the general CN-ratio of the soil is not expected to change with time. Assimilates are allocated to different compartments of the plant; leaves, stem, coarse roots and fine roots, according to pre-specified patterns. Plant respiration is partitioned between growth and maintenance respiration from all plant compartments (Karlberg et al. 2005). Daily litter fall is calculated as fractions of above-ground and below-ground parts of the plant entering the soil organic pools. Two pools, litter and humus, with different turnover rates are used to represent the soil organic matter. The model is described in more detail in Svensson et al. (in this volume).

In order to study the impact of drainage on ecosystem carbon balance, we used the same methodology as Berggren et al. (in this volume) and Svensson et al. (in this volume) when possible. The basic parameter settings of the model are presented in Table 1. In addition, a number of crucial parameters selected for calibration were given a uniform range between minimum and maximum values (Table 2), see further details in the calibration procedure below.

Bayesian calibration

The model was calibrated using an automated calibration procedure based on Bayesian principles, which quantifies parameter uncertainty and correlation rather than maximising fit (Van Oijen et al. 2005). Parameter uncertainties are initially estimated by subjectively chosen uniform ranges, the so-called prior probability distributions functions (pdfs). These prior pdfs are iteratively updated by means of a version of the Markov Chain Monte Carlo (MCMC) method called the Metropolis-Hastings random walk (Metropolis et al. 1953). The resulting pdfs for parameters are called the posterior distributions.

Table 1 List of parameters common to all simulations

Property	Value	Unit	Source
Plant biotic processes			
Temperature response Q_{10} value, t_{Q10}	2	–	Penning de Vries and van Laar 1982
Temperature response Q_{10} function reference temperature, t_{Q10bas}	25	°C	Penning de Vries and van Laar 1982
Shoot coefficient, m_{shoot}	0.1	–	Assumed
Fraction of soil mineral N available for plant uptake, f_{Nupt}	0.12	day^{-1}	Johnsson et al. 1987
Soil nitrogen and carbon processes			
Nitrogen deposition dry rate, p_{dry}	0.001225	g N m^{-2} day^{-1}	IVL 2006 (adjust for Asa)
Nitrogen deposition wet conc., p_{cwet}	0.1225	mg N l^{-1}	IVL 2006 (adjust for Asa)
NH_4 frac. dry deposition, $p_{fNH4,Dry}$	0.5	–	Assumed
NH_4 frac. wet deposition, $p_{fNH4,Wet}$	0.5	–	Assumed
Decomposition rate litter, k_l	0.0135	day^{-1}	Gustafsson and Svensson unpublished
Decomposition efficiency litter, $f_{e,l}$	0.5	–	Johnsson et al. 1987
Decomposition efficiency humus, $f_{e,h}$	0.5	–	Assumed same as litter
Humification fraction litter, $f_{h,l}$	0.2	–	Default
Temperature max value Ratkovsky function, t_{max}	25	°C	Seyferth 1998
Temperature min value Ratkovsky function, t_{min}	−8	°C	Seyferth 1998
Saturation activity, $p_{\theta satact}$	0	–	No activation at saturation

The basic assumption of the method, originating from the Bayes theorem, is that the probability of a candidate parameter set being part of the posterior distribution is equal to the product of its prior probability and its corresponding data likelihood. It is further assumed that the data likelihood function can be chosen such that the difference between the model output and the data can be attributed to additive measurement errors. This assumption is useful, since it allows the procedure to take into account observations of different output variables and error estimates. The following function was used to calculate the logarithm of the data likelihood L:

$$\log L = \sum_{i=1}^{n} \left(-0.5 \left(\frac{O_i - S_i}{M_i} \right)^2 - 0.5 \log(2\pi) - \log(M_i) \right) \quad (1)$$

where O_i is the observed data, S_i the simulated data, M_i the measurement error or uncertainty and n is the number of data points. Calculations were made using logarithms to avoid rounding errors, since the data likelihood value easily becomes small as the number of data points increases. Information on measurement error is often scarce, and in such situations a standard estimate of 30% for all data points is recommended (Van Oijen et al. 2005). However, in order to reduce the weight of values close to zero on behalf of large peaks, a minimum absolute error, which was subjectively defined for each variable, was introduced in the present study. In addition, differences in errors between different data were chosen both to account for errors due to different spatial representations and because of our subjective assessment of the importance of different variables for the overall model of the system. The addition of many different type of measurements are straight forward from a mathematical point of view since the Log L thus not have any unit. It is important to clarify that the addition will be related to the number of different observations and that the possible auto correlation between time series of observations means that the log of L thus not reflect a precise estimation of the real likelihood. However, for the purpose of demonstrating the reduction of uncertainty we still believe that the Log L is a very useful indicator of the model performance in relation to the measured values.

Table 2 Parameters calibrated by the Bayesian calibration procedure

Parameter	Unit	Prior			Post			Ratio	Dist	*n*
		Min	Max	Mean	Mean	St.D.	Median			
Photosynthesis—fixed N response										
(1) (all canopies)	–	0.20	0.60	0.40	0.23	0.03	0.21	0.57	LN	0
Allocation										
(2) f_{leaf} (tree1)	–	0.20	0.60	0.40	0.38	0.10	0.38	0.95	N	3
(3) f_{leaf} (tree2)	–	0.20	0.60	0.40	0.45	0.10	0.46	1.11	N	5
(4) f_{leaf} (field)	–	0.01	0.60	0.31	0.31	0.15	0.32	1.00	U	3
(5) f_{root} (tree1)	–	0.10	0.30	0.20	0.23	0.06	0.25	1.17	LN	5
(6) f_{root} (tree2)	–	0.10	0.40	0.25	0.25	0.09	0.25	0.98	U	4
(7) f_{root} (field)	–	0.10	0.40	0.25	0.21	0.07	0.20	0.84	N	1
Maintenance respiration										
(8) $k_{mrespleaf}$ (tree1)	10^{-3} day^{-1}	1.00	5.00	2.99	1.95	0.87	1.58	0.65	LN	0
(9) $k_{mresproot}$ (tree1)	10^{-3} day^{-1}	1.00	10.00	5.50	5.65	2.42	5.77	1.02	U	5
Leaf litter rate										
(10) l_{Lc1} (tree1)	10^{-3} day^{-1}	0.10	0.30	0.20	0.21	0.06	0.20	1.02	U	4
(11) l_{Lc1} (field)	10^{-3} day^{-1}	0.1	30.0	15.0	14.9	8.7	14.9	0.99	U	3
Decomposition rate coefficients										
(12) k_h	10^{-4} day^{-1}	0.60	6.00	3.30	2.72	1.53	0.00	0.82	N	3
(13) k_L	10^{-2} day^{-1}	0.50	5.0	2.74	1.83	1.24	0.01	0.66	LN	3
Soil moisture response function										
(14) p_{qLow}	vol %	10	30	20	20.3	6.2	19.4	1.01	U	1
(15) p_{qUpp}	vol %	10	30	20	19.3	5.5	19.7	0.97	U	4
Leaf area index										
(16) $p_{l,sp}$ (tree1)	g C m^{-2}	50	150	100	83	32	66	0.83	LN	7
Potential transpiration										
(17) g_{max} (tree1)	10^{-2} m s^{-1}	0.50	2.00	1.25	1.10	0.46	1.02	0.89	LN	3
Water uptake										
(18) ψ_c	cm water	100	3000	1550	1424	820	1292	0.92	N	2
(19) p_1	day^{-1}	0.00	0.60	0.30	0.30	0.17	0.27	0.99	U	1
Soil evaporation										
(20) r_{alai}	s m^{-1}	25	175	73	30	9.5	27	0.30	LN	0
Groundwater level										
(21) z_p	m	−0.50	−0.10	−0.30	−0.20	0.07	−0.19	0.65	LN	4
Soil thermal										
(22) Δz_{humus}	m	0.60	1.20	0.90	0.70	0.11	0.65	0.77	LN	2
(23) x_{hf} (0–50 cm)	–	−0.10	0.50	0.20	0.17	0.13	0.16	0.83	N	3

'Prior' values are assumed to be uniform. 'Post' values are the result of the 10^4 runs. The Ratio is defined as the relationship between 'Post' and 'Prior' mean values. The post distribution function (Dist) is described as LN for log normal, N for Normal and U for Uniform. The number of co-correlations (*n*) with other parameters indicated by having correlation coefficients that were higher than an absolute value of 0.3 is given

The prior distributions were chosen as uniform and non-correlated, with generously set maximum and minimum values. The first step of MCMC was to run an initial simulation with parameter values from a fixed starting point, and to calculate the data likelihood of that point with Eq. 1. Second, a new point in the parameter space was generated and the corresponding data likelihood evaluated, i.e. by running

the model once again with the new, candidate parameter values. The candidate parameters(were generated by adding a vector of random numbers ε to the previous parameter vector θ_j:

$$\theta_{j+1} = \theta_j + \varepsilon. \quad (2)$$

The random numbers in ε have zero mean values and variances equal to a pre-defined fraction (typically 5%) of the range of the prior distributions. In other words, the parameter space is sampled with a step length equal to maximum 5% of the prior uniform distribution. Candidate points were accepted as part of the posterior distributions if the ratio of the corresponding data likelihood value and the data likelihood of the previous accepted point was larger than an acceptance criterion α. Candidate values with lower data likelihood than the previous may be accepted, since α is re-generated for each iteration as a random number between 0 and 1. However, since calculations were made using logarithms, the acceptance criterion was taken as the logarithm of the random number, log α, which has to be smaller than the difference between the logarithms of the data likelihood values of the candidate and the previous point. As an abbreviation of the method proposed by Van Oijen et al. (2005), log α was further multiplied by a scaling parameter β to ensure that a reasonable number of simulations was accepted. The β factor was chosen to be proportional to the lowest absolute value of the sum of log likelihoods obtained. The Bayesian calibration scheme generated a chain of accepted parameter values and corresponding simulation results. If a candidate point was not accepted, the previous accepted point was repeated in the chain. Statistics on parameters and model results, such as mean values, standard deviations, co-variances and correlations, were calculated on the total chain including repeated points (Van Oijen et al. 2005). In the original MCMC proposed by Van Oijen et al. (2005), the chain length and the number of accepted candidate points are the only factors currently available in order to evaluate whether the parameter space has been investigated properly and whether the MCMC has converged towards the posterior distribution. Van Oijen et al. (2005) recommend chain lengths in the order of 10^4–10^5. In this trial case, we used a chain length of 10^4, resulting in 860 accepted points.

Model sensitivity to calibrated parameters

The relative sensitivity of model outputs to the different calibrated parameters, given the variation within the identified posterior distribution, was evaluated using Standardised Rank Regression Coefficients (SRRCs). The parameter SRRCs for a selected model output are multiple linear regression coefficients, estimated using the least squares method, modelling the linear relationship between a selected model output and the parameters in the posterior distribution. Thus, in this context each SRRC is an index expressing the relative sensitivity of the model output for the variation in each parameter individually, taking the variation in other parameters into account. Before calculation, data are standardised and ranked, in order to reduce the non-linearity in the data.

Modelling approach and parameterisation

Plant and soil dynamics in a 73-year old managed coniferous forest ecosystem growing on peat soil were simulated with an hourly resolution in the period 2001–2005. Hourly input data on air temperature, relative humidity, global radiation and wind speed were obtained from measurements at the site, while precipitation was measured at another climate station 1 km from the site (see below).

The calibration procedure was designed to find the best possible model representation of the entire managed forest ecosystem and its development during a 5-year-period. A total of 9,000 simulations were run and sampling was carried out according to the MCMC chain as described above using a step length of 0.05. The prior ranges of the parameters used in the calibration were set sufficiently wide to embrace the most likely posterior values and were based on simulations presented in Karlberg et al. (2006) and Svensson et al. (in this volume).

When the errors in the different calibration data were also defined, a subjective consideration of the importance of the respective variables for the total probability of the model was obtained (see Table 3). Some of the site-specific observations used in the calibration were high resolution time series data (TSD), such as soil temperature and fluxes measured using the eddy covariance technique. All observations

were considered uncertain, but to a degree specified to meet our overall objective of understanding the major carbon flux for our site. Many of the basic parameter values were chosen as fixed values based on previous use of the model (e.g. Svensson et al. in this volume), or following the default values according to the model (see Jansson and Karlberg 2004). For the calibration procedure, the most important model parameters were selected among parameters that were not measured or allocated fixed values (Table 1). In addition, the model structure was changed to allow the model to describe previous findings for this specific site as reported by Berggren Kleja et al. (in this volume).

Biomass estimation

Standing biomass and growth were estimated by Lindroth et al. (in this volume) within a 100 m radius of the flux measuring tower (cf. Fig. 1). Estimations were based on 16 circular plots with a radius of 7 m evenly distributed around the tower, in autumn 2005. Diameter and height were measured on all trees, height growth in the last 5 years and annual ring width in the last 6 years on bore cores in sample trees. By applying secondary functions of height growth and annual ring width, height and diameter were assessed on all tallied trees for the last six years. Dry weight biomass for different fractions of the trees was estimated using biomass functions formulated by Marklund (1988) and the carbon content was assumed to be 50% of the biomass in all fractions. Mean carbon sequestration per year was estimated as the difference in the estimated spatial mean of the total carbon content in living biomass between two consecutive years within the period 1999–2005.

Net ecosystem exchange of CO_2 (NEE)

The NEE was measured using the eddy covariance technique with a system from In Situ Flux Systems AB (Ockelbo, Sweden), which is described in Grelle and Lindroth (1996) and Lindroth et al. (in this volume). It is based on a sonic anemometer (Gill R3) used for wind speed measurement and an infrared gas analyser (LI-6262, LiCor Inc., Lincoln, USA) for CO_2 and H_2O concentration measurements. Data collection and analyses were performed in real time by Ecoflux software. The flux system data analysis was carried out according to the Euroflux methodology (Grelle and Lindroth 1996; Aubinet et al. 2000). The flux data from 2002 and calculations are presented in detail in Lindroth et al. (in this volume).

Manually measured soil CO_2 flux

Gas exchange at the soil surface was measured in the period 2000–2002 by von Arnold et al. (2005a), using dark, static, manually sampled, stainless steel chambers placed on permanently installed collars, each covering an area of 0.2 m^2, as described by Klemedtsson et al. (1997). Ten collars were installed in August 1999. The collars were positioned to cover as much as possible of the differences in peat depth, groundwater level and ground vegetation within the site (see Fig. 1). Fluxes of CO_2 were measured weekly from August–November 1999, July–November 2001, June–September 2002 and biweekly during the rest of the sampling period (except for the period November 1999–April 2000, when no sampling was carried out). At sampling, a lid (height 4–10 cm) equipped with butyl rubber septa was placed on the collars and gas samples were collected at 0, 15 and 30 min intervals after lidding. The gas was analysed by gas chromatography using a Varian 3800 Genesis instrument.

Automatically measured soil CO_2 flux

An experiment was conducted during 2005 at the Asa site to separate in situ the (autotrophic) root respiration (all fluxes linked to C from plants) from heterotrophic respiration caused by decomposition of soil organic matter. The autotrophic CO_2 flux was isolated by cutting the roots (a technique known as trenching) 1 year prior (2004) to the flux studies, in order to allow decomposition of the severed roots within the plots. To avoid in-growth of roots, a landscaping fabric that has been proven to allow drainage from trenched plots was inserted as a root barrier (Lavinge et al. 2004). For further details on the technique and problems concerning separation of heterotrophic and autotrophic soil respiration, see Hanson et al. (2000), Lavinge et al. (2004) and Kuzyakov (2006). The automatic chamber system

Table 3 Variables used to calibrate the CoupModel at the Asa site for scenario modelling of altered groundwater levels

Variable	Measuring period	Number of samples over time	Replicate	Assumed uncertainty Rel/Abs error	Source of information (if other than here)
Soil temperature (°C)					
0.05 m	2001–2004	30543[a]	10	0.15/1	
0.05 m	2005	1294	2	0.15/1	
0.10 m	2005	1294	2	0.15/1	
0.15 m		32100[a]	2	0.15/1	
0.30 m		31860[a]	4	0.15/1	
0.30 m	2005	1294	2	0.15/1	
0.60 m		32090[a]	3	0.15/1	
Groundwater level (m)					
WT L1	2001–2004	23164	1	0.2/0.05	
WT L2	2001–2004	22895	1	0.2/0.15	
ManMean10	2000–2002	25	M[b]	0.2/0.05	von Arnold et al. 2005a, b
Auto05-1	2005	1290	1	0.2/0.05	
Auto05-2	2005	950	1	0.3/0.05	
Latent heat flux	2001–2002	12266	1	$0.3/1e^6$	
Sensible heat flux	2001–2002	12265	1	$0.2/5e^5$	
NEE (CO_2)	2001	6783	1	0.4/2	
NEE (CO_2)	2002	5418	1	0.15/0.1	Lindroth et al. in this volume
Soil respiration (g C m^{-2} day^{-1})	2000–2002	25	M[c]	0.4/4	von Arnold et al. 2005a, b
Soil respiration (g C m^{-2} day^{-1})					
Controls	2005	1572	M[d]	0.15/0.1	
Trenched (heterotrophic only)	2005	1606	M[d]	0.15/0.1	
Biomass change (g C m^{-2})	2001–2005	5	16	0.02/0.1	Lindroth et al. in this volume

[a] Mean number of replicates if different numbers between replicates

[b] Mean values generated from measured groundwater tubes at 10 manual gas chambers

[c] Mean values generated from measurements from 10 manual gas chambers

[d] Mean values generated from three automatic gas chambers

used the same stainless steel collar as was used for the manual measurements (see above). These collars were installed in six plots, three inside and three outside trenched areas, close to the flux tower (Fig. 1). The frames were placed just under the litter layer to avoid disturbance of the fine roots in the humus. The chamber construction was based on a system designed by Chanton et al. (1993). The chamber skeleton was a cubic aluminium framework ($0.9 \times 0.5 \times 0.5$ m^3) walled with 2 mm thick transparent polycarbonate plates and gas-proofed with silicon glue. The lid was opened and closed by a motor-driven cap piston (Linak LA12, Denmark). To minimise a pressure bias, which could affect the CO_2 estimations, a rigid (5 mm Ø) spiral-shaped PVC pipe was inserted through the top cap plate of each chamber. During closure, the chamber air was circulated by two small fans (50 mm Ø) to maintain a uniform CO_2 concentration inside the chamber. Air from the centre of the chamber (0.4 m above ground level) was drawn by a pump (via 5 mm Ø tubing) through CO_2 the infrared gas analyser (PP Systems SBA-4 OEM CO_2 Analyser). The interior and exterior air temperatures were screened 0.4 m above ground level using ventilated thermocouples (Campbell Scientific Ltd, model 107) within a shielding cylinder. Subsequent to each measurement phase, the lid was opened and a larger ventilating fan (80 mm

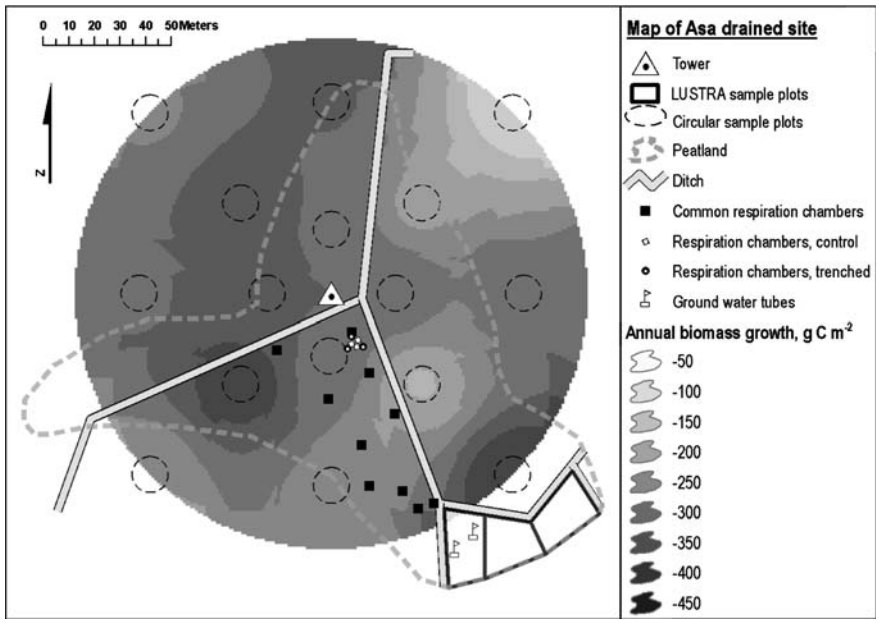

Fig. 1 Map of study site, including location of measurements and biomass sampling plots within 100 m radius from flux tower (mostly within tower footprint area). The variation within the area of mean annual C growth during the study period are shown

Ø) was activated to expel the chamber air. The operation commands were derived from a programmed datalogger (Campbell Scientific Ltd, model CR10, Leicestershire) with support for the software PC 208W (version 2.3). The gas analyser system was automatically calibrated prior to each CO_2 concentration measurement and the values obtained were subsequently averaged, collected and stored (every 30 s) in a memory device. The soil CO_2 flux was calculated from the build-up during the first 5 min after closure of the chamber.

Abiotic measurements

Hourly climatic data on air temperature, global radiation, relative humidity and wind speed were recorded on-site in the flux tower. Global radiation (Eppley PSP), incoming PAR (LiCor Li 190SB), reflected PAR (LiCor Li 190SB) and net radiation (Kipp & Zonen, NR-Lite) were measured at 38 m height, while wind speed (Gill SOLENT RESEARCH R3), air temperature (Rotronic MP101A), air humidity (Rotronic MP101A) and air pressure (Vaisala PTP 100) were measured at 24 m height. During periods when site measurements were unavailable, data from a nearby climatic station ($\sim$1 km) were used. This station also provided precipitation data, measured using a tipping bucket sensor (Campbell Sci., ARG100). Soil temperature was measured (Pentronics P/ALPTW-20) at a large number of vertical and horizontal positions (Table 3). The groundwater level was measured both automatically (Druck PDCR 1830) during 2001–2004 at two locations in LUSTRA wet plots (WT L1 and WTL2) and during 2005 near the flux tower (Auto05-1 and Auto05-2), as well as manually (ManMean10) during the time the manual gas samplings were being performed (see above, von Arnold et al. 2005a, b) (Table 3). The manual groundwater data in Table 3 are mean values of the level at the 10 different manual chambers. The soil heat flux (Hukseflux HFP01SC) was also measured close to the tower. All instruments were connected to dataloggers CR10 or 21X (Campbell Sci. Inc., Utah, USA).

Results and discussion

Calibrated parameter values

The first set of calibrated parameter estimates for C-cycling in a forest on drained organic soil are presented in Table 2. The Bayesian calibration procedure reduced the uncertainties in the model, as 15 of the 23 calibrated parameters were changed to new mean values, different from the assumed prior distributions (see ratios in table). The assumed

uniform prior distribution was also changed to new probability density function for many parameters. This was indicated by the coefficients of variation for the post distributions and the change from uniform to normal or log-normal shape of the distribution functions. The degree of change in estimated parameter mean values was indicated by how much the ratio between the prior and post mean values differed from unity (Table 2). The uncertainty ranges are unique to the specific dataset and calibration, but the distributions including the covariance obtained between different parameters may be used when applying the model to new similar sites and/or new experimental periods. Different degrees of co-correlation were found for parameters, with a maximum for the specific leaf area index [parameter 16, p_{isp}(tree1)], which was correlated (coefficients above 0.3) to seven other parameters (Table 2). Only three parameters, photosynthesis fixed N response [par. 1], maintenance leaf respiration [par. $8k_{mrespleaf}$(tree1)] and soil evaporation [par. 20 r_{alai}], were independent of all other parameters. This demonstrates the importance of considering parameter values from a holistic perspective in relation to other parameters, rather than using them independently. Thus a model should be calibrated for a high number of parameters instead of specific parameter values. The present selection of parameters for calibration might therefore have been sub-optimal if the objective had been to find the best model, i.e. the best agreement with data. However such efforts normally result in non-robust simulations when attempts are made to apply the model to other sites and they cannot be used to understand the model sensitivity and covariance between different parameters in the model. We believe that these simulations showed an accepted degree of similarity with measurements (see below).

The high number of validation data (Table 3) of different pools and fluxes resulted in a robust calibration, which was a reasonably good representation of our system based on our current knowledge. The Bayesian calibration technique offered a solution to the calibration process for process-based models, as previously stated by Van Oijen et al. (2005). However, use of the technique without subjective assessments can be questioned. Both the very different numbers of measurements and the different representation of various variables had an impact on the results, to an extent that was outside our subjective expectations based on the recommendations by Van Oijen et al. (2005). The technique of only specifying uncertainties with respect to absolute and relative errors in each single observation is attractive but may not be optimal if the intention is to place more emphasis on some components of the model compared with others. For instance, the mean value of some flux and state variables may be more important than the total likelihood as estimated by the Bayesian calibration procedure.

Performance of the calibrated model using mean parameter values

The Bayesian-calibrated model had in general a reasonable precision in its soil temperature simulations (Fig. 2), with both high coefficients of determination for linear regression between simulated and measured data as well as a small mean error (Table 4). However, for temperature the simulated values had higher amplitude than the measured data. It is not likely that the differences were due to measuring errors, as the patterns were similar for most positions of the temperature sensors (Table 3), which were spatially distributed in the forest stand and over the whole range of peat depths. The higher amplitude in the simulated soil temperature could have been due to the model having difficulty in accounting for the energy balance of the forest canopy including the field layer. The heat balance of the soil represents a complex system that has many components, especially in the boundary layer

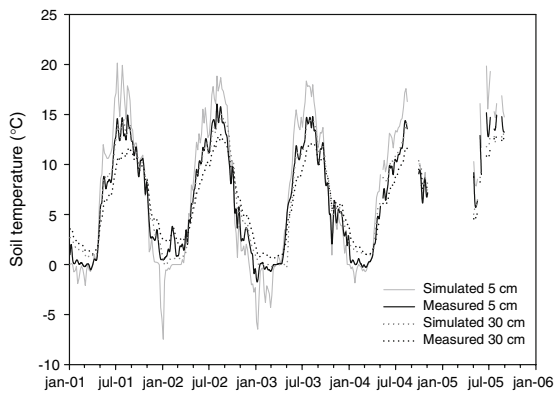

Fig. 2 Mean simulated soil temperature values versus mean measured values for the coniferous-forested drained organic soil at a site in Asa during 2001–2005

between air and soil. The canopy heat balance is very important and therefore errors caused by an imprecise simulation of sensible and latent heat fluxes may also have introduced errors for the soil temperature. As a result, the thermal conductivity parameters (parameters 22 and 23 in Table 2) would not have been adjusted to fit the measured soil temperature pattern quite so well. Previous studies, for example by Gustafsson et al. (2004), have shown that the model is sensitive to radiation balance and to aerodynamic properties within stands, factors that are difficult to describe precisely. Weiss et al. (2006) found a good agreement between modelled and measured peat temperature, for a pine forested bog and for a fen with sparse pine tree stand density. However, they also had a higher amplitude in the simulated temperatures than the measured ones, as we found.

The simulation of the groundwater level with the calibrated mean model and the measured groundwater level at different locations at the site followed the same general temporal pattern (Fig. 3). However, there was lower amplitude in the simulated groundwater levels than in the measured, except for measurements near the tower location during 2005 (Auto05-1 and 2). In general, the model precision was lower for groundwater level than for soil temperature, with less good coefficients of determination and with overestimations of mean groundwater levels for the different measurement locations (Fig. 1, Table 4). The different measuring locations obviously describe different conditions and the model attempted to make a compromise between the different data. Data with a high number of observations, which in this case meant more frequent readings, had a larger impact than data with a lower number of observations, although they had the same assumed accuracy. This made the model fit well to the observed data in 2005 but less well in 2001 and 2002 (automatic generated data vs. manual data, cf. Tables 3 and 4, Fig. 3). The lower correlation between the simulated groundwater levels and the measured levels at the LUSTRA common plots (WT L1 and L2) was expected. The automatic groundwater sensors used in the common field plots for LUSTRA during 2001–2004 were located near the edge of the drained site, close to the ditch, on higher topography and with a less thick peat layer than at the location of the flux tower (Fig. 1). It could therefore be assumed that these sensors would produce lower groundwater levels than those from the main areas of the peat site. Thus, in the prior probability distribution we assumed the values from the LUSTRA common field plots to be less accurate in terms of absolute values (Table 3). The model calibration of groundwater level was not only affected by the number of validation data, but also by the number of additional data used by the model to set the water balance. The calibrated groundwater levels were also driven by evapotranspiration and directly connected to the sensible and latent heat flux simulations; thus using high frequency data from the footprint area around the flux tower. The reasonably good agreement with these energy fluxes (Fig. 4) also forced the simulated groundwater level to be close to the range obtained for 2005, which corresponded to an area close to the tower and the footprint for the flux measurements.

Latent heat flux (Fig. 4) was underestimated, especially during the summer of 2002, when at the same time the sensible heat flux was reasonably well simulated. Again the Bayesian calibration compromised but relied more on the sensible heat flux, which was considered to be more accurate (Table 3). A similar tendency to more accurately simulate the sensible heat flux than the latent has previously been reported by Gustafsson et al. (2004) for a forest in Norunda in central Sweden, where similar data were used.

The NEE of CO_2 as described by the model after the Bayesian calibration was able to mimic the measured data for 2002 (Lindroth et al. in this volume) rather well (Fig. 5, Table 4). The precision in NEE simulations ought to be improved, as the coefficient of determination for the linear regression between simulated and measured data was found to be rather low and the mean error was rather high (Table 4). However, in general the model calibration resulted in an overall improved parameterisation for NEE compared with the prior conditions. In order to further improve the model, predictions of long-term NEE data are needed.

The simulated biomass increase was calibrated using the biomass estimates for the site. The total biomass increase above ground is most likely well estimated from the scaling formula by Marklund (1988). However, the ratios between below- and above-ground biomass and growth over time are uncertain. Thus, in the prior conditions for the calibrations, the accuracy for the estimates of biomass

Table 4 Performance of accepted runs from the Bayesian calibration ($n = 1658$) in relation to different measured variables

Variable name	Unit	ME						r^2					
		Min	Max	Mean	SD	Median	Single run	Min	Max	Mean	SD	Median	Single run
SoilTemp(1) 0.05 m	°C	0.18	2.28	0.71	0.22	0.64	0.68	0.91	0.96	0.95	0.01	0.96	0.95
SoilTemp(2) 0.05 m	°C	0.47	2.71	1.08	0.22	1.01	1.05	0.91	0.97	0.95	0.01	0.96	0.96
SoilTemp(3) 0.05 m	°C	0.05	2.15	0.59	0.22	0.51	0.55	0.90	0.96	0.95	0.01	0.95	0.95
SoilTemp(4) 0.05 m	°C	−0.01	2.09	0.53	0.22	0.45	0.49	0.93	0.97	0.96	0.01	0.96	0.96
SoilTemp(5) 0.05 m	°C	0.34	5.04	2.22	0.44	2.19	2.31	0.67	0.95	0.89	0.04	0.90	0.89
SoillTemp(6) 0.15 m	°C	0.04	2.24	0.62	0.21	0.57	0.60	0.92	0.96	0.95	0.00	0.95	0.95
SoilTemp(7) 0.15 m	°C	−0.30	1.91	0.29	0.21	0.24	0.27	0.91	0.95	0.94	0.01	0.95	0.94
SoilTemp(8) 0.15 m	°C	−0.75	4.29	1.55	0.47	1.62	1.71	0.85	0.97	0.94	0.01	0.94	0.94
SoilTemp(9) 0.3 m	°C	−0.27	1.95	0.34	0.21	0.30	0.30	0.91	0.97	0.95	0.01	0.95	0.95
SoilTemp(10) 0.3 m	°C	−0.09	2.19	0.52	0.21	0.48	0.48	0.92	0.97	0.96	0.01	0.96	0.96
SoilTemp(11) 0.3 m	°C	−0.26	2.02	0.35	0.21	0.31	0.31	0.91	0.96	0.95	0.01	0.95	0.94
SoillTemp(12) 0.3 m	°C	−0.19	2.09	0.42	0.21	0.38	0.38	0.94	0.98	0.97	0.00	0.97	0.97
SoilTemp(13) 0.3 m	°C	−1.82	3.38	0.70	0.54	0.72	0.81	0.91	0.99	0.98	0.01	0.98	0.98
SoilTemp(14) 0.6 m	°C	−0.16	2.10	0.41	0.21	0.35	0.36	0.94	0.99	0.97	0.01	0.97	0.97
SoilTemp (15) 0.6 m	°C	−0.04	2.23	0.54	0.21	0.48	0.48	0.91	0.98	0.96	0.01	0.96	0.96
SoilTemp(16) 0.6 m	°C	−0.12	2.14	0.45	0.21	0.40	0.40	0.95	0.99	0.98	0.01	0.98	0.98
WT L1	m	0.07	0.24	0.18	0.05	0.19	0.16	0.01	0.61	0.26	0.10	0.27	0.43
WT L2	m	0.01	0.18	0.13	0.05	0.14	0.10	0.00	0.58	0.25	0.11	0.26	0.39
ManMean10	m	0.02	0.21	0.14	0.04	0.15	0.10	0.20	0.72	0.46	0.10	0.48	0.62
Auto05-1	m	−0.12	0.20	0.00	0.06	−0.02	−0.03	0.00	0.89	0.68	0.14	0.71	0.70
Auto05-2	m	−0.24	0.19	−0.08	0.09	−0.11	−0.12	0.04	0.68	0.46	0.11	0.49	0.48
Latent heat flux	MJ m^{-2} day^{-1}	0.60	2.40	1.34	0.42	1.41	1.98	0.19	0.68	0.45	0.16	0.46	0.61
Sensible heat flux	MJ m^{-2} day^{-1}	−0. 531	1.57	0.76	0.55	0.73	0.21	0.46	0.69	0.63	0.04	0.64	0.57
NEE CO_2-2001	g C m^{-2} day^{-1}	−0.61	1.62	0.58	0.35	0.59	0.62	0.08	0.53	0.31	0.13	0.35	0.45
NEE CO_2-2002	g C m^{-2} day^{-1}	−0.75	1.32	0.54	0.28	0.63	0.35	0.12	0.63	0.38	0.17	0.30	0.52
Soil respiration (manual)	g C m^{-2} day^{-1}	−0.46	2.20	0.32	0.44	0.20	0.97	0.01	0.63	0.27	0.18	0.29	0.47
Respiration/control	g C m^{-2} day^{-1}	−5.53	1.05	−2.64	0.99	−2.63	−2.29	0.21	0.78	0.68	0.06	0.69	0.65
Respiration/trenched	g C m^{-2} day^{-1}	−1.85	3.24	0.20	0.87	0.19	0.43	0.09	0.75	0.66	0.09	0.68	0.70
Biomass change	g C m^{-2}	−1667	3233	177	584	211	840	0.00	1.00	0.82	0.20	0.89	0.94

Mean error (ME) between simulated and measured values and mean of coefficient of determination (r^2) for linear regression between simulated and measured values. The single run is made using mean of calibrated parameters

was set to have a 10% absolute error (Table 3). The coefficients of determination for the linear regression between the simulated and estimated biomass change agreed well (Table 4). However, on average the model overestimated the biomass change by around 180 g C m^{-2} during the period 2001–2005 compared with estimates based on above-ground tree measurements and calculations of whole-tree biomass by Marklund (1988) equations.

Two different datasets, that reported by von Arnold et al. (2005a) and the automatic measured flux from 2005, were used to calibrate the model to soil respiration. The datasets had different qualities of flux accuracy (Table 3, see also the 'Methods'), which affected the weight the model placed on the different validation variables. The soil respiration as measured by von Arnold et al. (2005a) represented the whole community respiration consisting of both

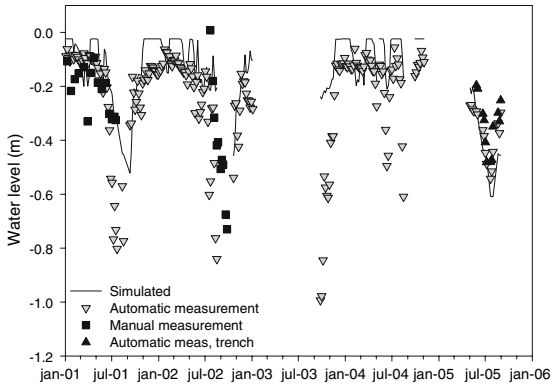

Fig. 3 Simulated and measured groundwater level at different locations within the coniferous forest on a drained organic soil at a site in Asa during 2001–2005

root respiration and its associated CO_2 fluxes, as well as the heterotrophic CO_2 soil flux from degradation of soil organic matter. The calibrated mean model mimicked the data from von Arnold et al. (2005a), but overestimated the soil flux compared with the measured values (Table 4). This result was expected, as there is good reason to assume that the fluxes reported by von Arnold et al. (2005a) partly underestimated the true community flux, since the flux was determined by static chambers over a rather long measuring time (15–30 min). According to Bekku et al. (1995), sampling intervals longer than 20–25 min underestimate the CO_2 flux. Similar results have been reported by Pumpanen et al. (2004), who found that chamber measurements during 30 min underestimated the soil CO_2 flux by about 15%, compared with 10 min of measuring time. These likely underestimates of true flux in von Arnold et al. (2005a) were taken into account in the Bayesian calibration procedure by assigning a higher absolute error in the prior distribution of the long incubations (factor of 4, Table 3); thus low weight was placed on these data compared with those generated by the automatic chambers (a factor of 0.1, Table 3). Despite the low weight placed on the manual measurements and their few numbers of data points, the model output was close to these (Table 4). The underestimation due to a long incubation time is a dynamic factor, increasing with increasing flux rate of CO_2 and was therefore hard to correct for. The model showed this pattern clearly, with good agreement at low fluxes but as the rates increased the measured soil respiration increasingly underestimated

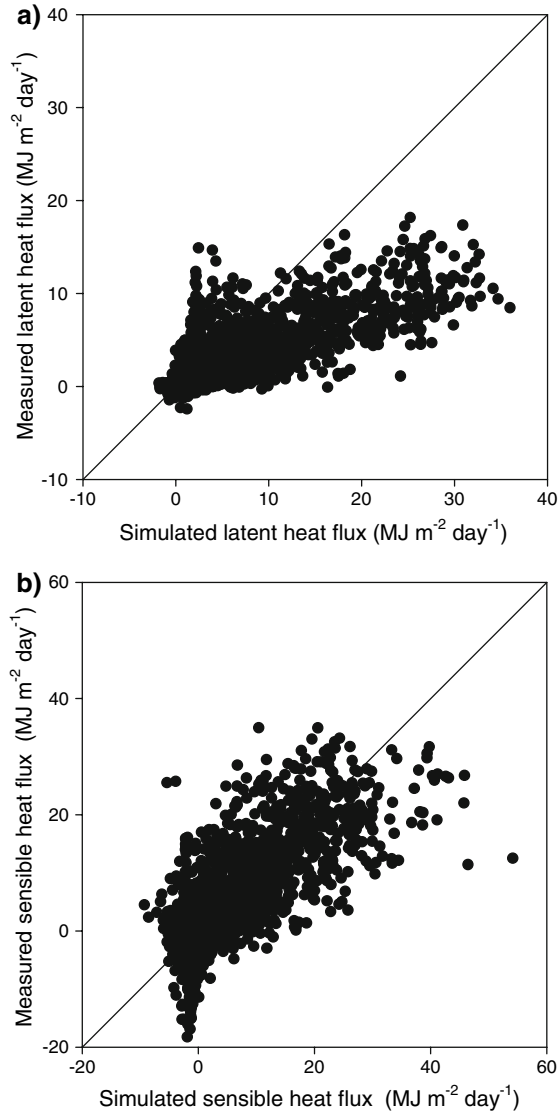

Fig. 4 (**a**) Simulated versus measured latent heat flux and (**b**) simulated versus measured sensible flux, for the coniferous forest on drained organic soils at Asa during 2002. Measured data are from Lindroth et al. (in this volume)

the assumed true flux (Fig. 6). The Bayesian-calibrated model described the dynamics of the soil flux reasonably well over time, but as expected the coefficients of determination for linear regression between simulated and measured data were found to be rather low and the mean error was rather high (Table 4).

The simulated soil respiration and measurements performed in 2005 using the automatic chambers are presented in Fig. 7. The measurements were conducted

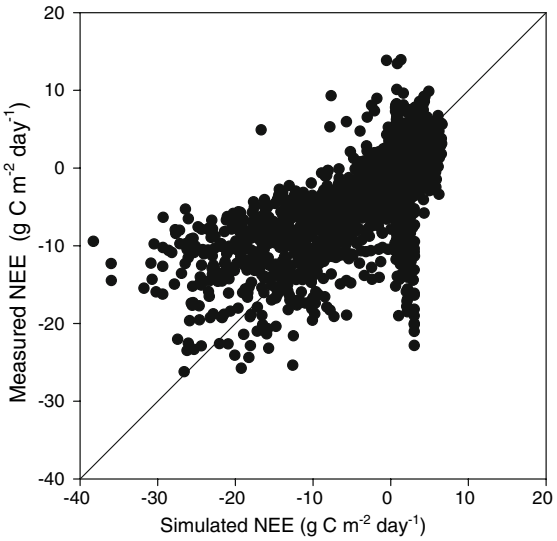

Fig. 5 Simulated versus measured net ecosystem exchange of CO_2 (NEE) at the coniferous forest on a drained organic soil at a site in Asa (measured data from Lindroth et al. in this volume)

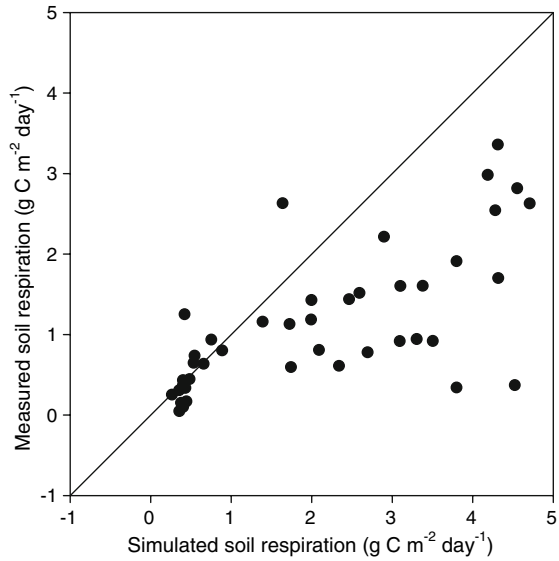

Fig. 6 Simulated versus manually measured (von Arnold et al. 2005a, b) soil respiration at the coniferous forest on a drained organic soil at a site in Asa during 2001 and 2002. Both simulated and measured data as daily mean values

within the footprint of the flux tower, where the model best predicted the soil conditions and used short time measurements (less than 5 min), and therefore ought to be the most accurate of the soil flux measurements. The experiment consisted of two types of measurements, only heterotrophic soil respiration from the trenched plots and the whole community flux (consisting of both heterotrophic and autotrophic respiration) from the control plots. The data from the control plots during 2005 are comparable with those determined by von Arnold et al. (2005a).

Similarly to data measured with manual chambers, the calibrated model described the heterotrophic soil flux measured with automatic chambers well (Fig. 7a, Table 3). The comparison gave both high coefficients of determination for linear regression between simulated and measured data and a rather small mean error (Table 4). In contrast, the heterotrophic respiration from the trenched plots was highly underestimated by the model (Fig. 7b, Table 3).

The soil respiration measurements presented in Figs. 6 and 7b are community flux, consisting of both heterotrophic soil respiration and autotrophic respiration. These fluxes consisted of respiration from soil organic matter, root respiration, heterotrophic respiration due to rhizodeposition, priming effects due to rhizodeposition and mycorrhizal respiration, all with

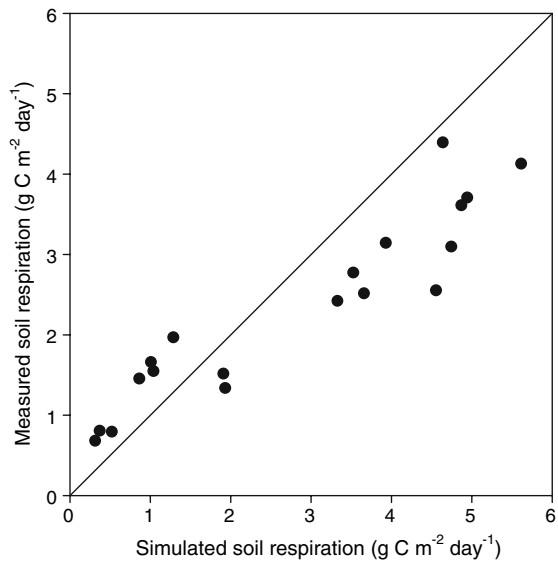

Fig. 7 Simulated versus automatically measured soil respiration at the coniferous forest on a drained organic soil at a site in Asa during 2005. Both simulated and measured data are presented as mean values per day for a 5-day period

different response functions, i.e. for organic matter respiration and mycorrhizal respiration (Heinemeyer et al. 2007). For a more comprehensive description of processes generating the soil respiration flux, as well

as possible problems with assessing these, see Hansen et al. (2000), Kuzyakov (2006) and Heinemeyer et al. (2007). Thus, simulating and measuring specific components of soil flux is far more demanding, since it requires a consistency both in the measurements and in the model representation. Regulating variables from field data interact in time and space, and all of the techniques used to separate the fluxes in the community flux introduce disturbances that affect the flux (Kuzyakov 2006). It is clear that the calibrated CoupModel to a large degree underestimated the total soil respiration measured with automatic chambers (Fig. 7b, Table 4).

Data from the Asa site represented a number of different components of the ecosystem fluxes, which made it possible to also test the overall performance of the model and possible parameters for different processes. However, we were unable to find acceptable agreement with all measurements, which was partly a problem with the model and partly a possible inconsistency in the measurements. Measurement uncertainties were due to differences in space, time, extension and techniques used. The Bayesian calibration procedure accounted for this according to our subjective judgements, presented in the initial settings (Table 3).

Validation data in relation to parameter value

Drainage level and soil temperature are variables known to influence the net C flux in forested, drained peat soils (Silvola et al. 1996). Thus, it was important to mimic the groundwater level fluctuations over time at the site correctly, in order to conduct an accurate simulation of the C flux. There was a clear difference in the parameters that were of high importance for calibrated validation data, linked to their location in space (see Fig. 1), most likely driven by the number of data points and the assumed accuracy of the data. The automatic groundwater level measurements at LUSTRA plots (WT L1 and 2) and the manual measurements (ManMean10) conducted by von Arnold et al. (2005a) were mainly correlated to the initial drainage plane level (parameter 21 Z_p: Table 5). This was also the case for the manually measured soil respiration fluxes at the same locations as the manual groundwater measurements (Table 5, Fig. 1). However, when the model was calibrated to the groundwater levels measured close to the tower (Auto05-1 and 2), parameters more directly linked to the tree activity were of more importance {[(10) l_{lc}, (2) f_{leal}], Table 5} than the groundwater levels measured further away. Measurements conducted in 2005 were located in the dominating part of the footprint of the flux tower; the model calibration is then to a larger degree driven 'into' the footprint area due to the large amounts of data for which we assumed a high accuracy and in this case the model precision was the best in relation to field data (Table 4).

To enable the net CO_2 emissions from drained forested soils to be predicted, it is critical to be able to simulate the groundwater level accurately, since the groundwater level and temperature are the main driving parameters for the soil flux (Silvola et al. 1996). The model performed well for measurements within the footprint area. However, our field data stressed the need for soil and flux measurements well integrated in space, as the tower measurements only represented parts of the site. However for correct model calibration, it is highly important to be able to set the drainage plane accurately, since it also affected the latent heat flux and NEE (Table 5) and therefore the fundamental functions of tree growth. Obviously the ground water level varies both between years and within the area of the different footprints. The additional variables used for calibration during 2005 (Table 3) reflected an area with different aerial representation compared to the data from the other years which makes the interpretation complicated.

Simulation of the mean carbon budget over a 10-year period

The simulated C-budget (Table 6) may differ from the direct comparisons conducted for specific periods. For example, there was reasonably good agreement in the forest biomass change between the measured data (1999 and 2005), with an average difference of about 180 g C m^{-2} (Table 4). For 2002, Lindroth et al. (in this volume) present a measured value of 325 g C m^{-2}, which should be compared with the mean growth rate of 186 g C m^{-2} $year^{-1}$ simulated during the 10-year period. The error may be large for this individual year but on average the biomass after the 10-year period is reasonably precise in relation to a total biomass of 3,700 g C m^{-2}.

Table 5 Selected variables and their correlations with parameter values

Measured variable and time	Parameters with high correlations			Correlation coefficients		
	1	2	3	1	2	3
WT L1	(21) z_p	(17) g_{max} (tree1)	(2) fl_{eaf} (tree1)	0.91	−0.30	−0.24
WT L2	(21) z_p	(17) g_{max} (tree1)	(2) f_{leaf} (tree1)	0.91	−0.29	−0.22
ManMean10	(21) z_p	(17) g_{max} (tree1)	(2) f_{leaf} (tree1)	0.83	−0.43	−0.34
Manual m. CO_2 flux (C) 2002	(21) z_p	(8) $k_{mrespleaf}$(tree1)	(16) p_{lsp} (tree1)	−0.64	0.34	0.32
Latent heat flux	(21) z_p	(8) $k_{mrespleaf}$(tree1)	(16) plsp (tree1)	−0.42	0.19	0.16
Sensible heat flux	(8) $k_{mrespleaf}$(tree1)	(21) zp	(16) plsp (tree1)	−0.46	0.44	−0.36
CO_2 NEE 2005	(5) f_{root} (tree1)	(21) zp	(1) (all)	0.55	0.51	−0.39
Auto05-1	(10) l_{lc} (tree1)	(2) f_{leal} (tree1)	(17) g_{max} (tree1)	0.78	−0.74	−0.72
Auto05-2	(10) l_{lc} (tree1)	(2) f_{leaf} (tree1)	(17) g_{max} (tree1)	0.80	−0.77	−0.75
Automatic CO_2 flux (C)	(4) f_{leaf} (field)	(4) f_{root} (field)	(5) f_{root} (tree1)	0.29	−0.19	−0.19
Automatic CO_2 flux (T)	(2) f_{leaf} (tree1)	(8) $k_{mrespleaf}$(tree1)	(16) p_{lsp} (tree1)	0.37	−0.36	−0.34

For explanation of parameter names, see Table 2

An advantage of using Bayesian calibration techniques was that all outputs were generated as statistical distributions around a mean value, instead of single values with subjective error estimates in the conventional budget estimations as produced for the Asa site based on measured data in Lindroth et al. (in this volume).

The estimated average loss from the soil organic matter (40 g C m^{-2} $year^{-1}$, Table 6) was similar to the estimated loss (32 g C m^{-2} $year^{-1}$) determined by budget calculations from the biomass and NEE in Lindroth et al. (in this volume). The measured NEE data from 2002 (Lindroth et al. in this volume) and our 10-year mean simulations show a net ecosystem uptake of 293 and 146 g C m^{-2} $year^{-1}$, respectively. The estimated uncertainty around the simulated mean value was high, SD = 112 g C m^{-2} $year^{-1}$ compared with 15 g C m^{-2} $year^{-1}$ for the measured mean value based on the information gathered during 2002. This fairly large difference between measured and simulated data stresses the need for further refinement of the model, as well as long-term data for calibration/validation. The calibration here was conducted using data for 2001 and 2002, where the data from 2001 had to be set with a lower accuracy due to technical problems. Thus, the model was more or less calibrated for 1 year of NEE data. This could partly explain the low precision in the model output. NEE has been found to vary widely between years, e.g. the NEE from a pine-dominated forest on drained soil at Norunda varied between −10 and +120 g C m^{-2} $year^{-1}$ during 1995 and 2002 (A. Lindroth unpublished data). It is thus necessary to further test the capacity of the model to estimate NEE. However, this does not necessarily have to be done for forests on drained soils, as it is the general mechanisms that have to be tested and improved.

The heterotrophic soil respiration was strongly correlated to the rate coefficient for humus [(12) Kh], but also to drainage level [(21) z_p] which was very important. However, for total soil respiration including autotrophic root respiration, the drainage level parameter and the photosynthesis fixed N-response parameter [(1) 1] were the most important factors in explaining the variation. Groundwater level is obviously highly important for both, and it in turn is affected by the drainage level, climatic conditions and the system evapotranspiration. The change in soil C storage was correlated to litter and humus decomposition rate coefficients [(13,12) K_l, K_h] rather than the average drainage level. The groundwater level was strongly correlated to most of the carbon fluxes but not to the net change in either the biomass or the soil C storage.

The Bayesian calibration provides a logical method to calibrate mechanistic models in a holistic way, therefore avoiding sub-optimisation (Van Oijen et al. 2005). It also allows for evaluation of uncertainty in

Table 6 Mean C-budget (g m^{-2} $year^{-1}$) over a 10-year period and the most important governing tree parameters with corresponding correlations coefficients

Variable name	Min	Max	Mean	SD	Median	Parameters with high correlations			Correlation coefficients		
						1	2	3	1	2	3
Total carbon balance	−200	567	146	112	142	(1) (a))	(2) f_{root}(tree1)	(12) k_h	0.81	−0.66	−0.64
Total photosynthesis	218	1782	875	152	853	(1) (all)	(21) z_p	(2) fleaf (tree1)	0.77	−0.64	0.49
Total soil heterotrophic respiration	75	505	223	78	199	(12) K_h	(21) Z_p	(13) K_l	0.66	−0.65	0.59
Total soil respiration	209	963	463	120	434	(21) Z_p	(1) (all)	(12) K_h	0.64	0.60	0.46
Total respiration	392	1329	728	130	701	(1) (all)	(21) Z_p	(2) fl_{eaf} (tree1)	0.66	−0.65	0.50
Annual change humus	−228	29	−47	48	−41	(12) K_h	(21) Z_p	(3) f_{leaf} (tree2)	0.90	0.48	0.18
Annual change plant	−75	560	186	77	185	(1)(all)	(5) f_{root} (tree1)	(8) $k_{mrespleaf}$(tree1)	0.79	−0.75	−0.66
Annual change soil	−278	208	−40	74	−31	(13) K_l	(12) K_h	(9) $k_{mresproot}$(tree1)	−0.75	−0.67	−0.50
Evapotranspiration	275	489	380	37	379	(21) Z_p	(17) g_{max} (tree1)	(2) f_{leaf} (tree1)	−0.42	0.31	0.27
Runoff	278	475	369	37	370	(21) z_p	(16) p_{lsp} (tree1)	(17) g_{max} (tree1)	0.40	−0.23	−0.23

key parameters or variables used in the model and how these operate in relation to known links in the C cycle, which is normally complicated due to the high complexity of a large numbers of parameters and variables interacting over time.

Concluding remarks and management implications

Our model application with Bayesian calibration showed that we could successfully reduce the uncertainties after combining model simulations with observations. We have also established a dataset that can be applied either to other sites or to other conditions by using the parameter uncertainties including covariance between parameters. However, it is of course important to further question the validity of the established parameters by making new independent tests. It is obvious that consistent datasets with high resolution will be important in such a context. On the other hand, the Bayesian calibration method allows incorporation of many different kinds of data, which means that many independent sources of information may be used in future investigations.

The calibration showed that it is of highest importance to correctly set the drainage level in the model, which directly affects the groundwater level, in order to simulate the major separate components of the carbon cycle for drained wetlands. This could be used to predict the importance of drainage operations and climate-related conditions that are expected to change the groundwater level.

The effect of drainage on CO_2 emissions will vary with time, as a consequence of the drainage status of the soil. Drained peatlands subside after drainage due to consolidation, shrinkage, compaction and oxidation of the organic matter (Berglund 1996) and thus become wetter. In Sweden, there are at present around 1.5 Mha of drained productive forest land on organic soils (Ernfors et al. in this volume). Of these, 0.2 Mha have drainage systems that are not efficiently draining the soil (Hånell 2004), which could be due to mechanical failure in the drainage system, but (more probably) to peat subsidence after drainage. Increased groundwater levels decrease forest growth, and consequently there is widespread interest among forest owners and state authorities in increasing forest production by repairing and clearing of drainage systems. This in turn affects the net CO_2 fluxes from these forests. Thus, from the model calibration one can assume that the net losses will decrease over time if no remedial drainage operations are conducted, and increase if drainage is improved. However, if no action is taken, forest production will decrease during the restabilising period after clear cutting. For sites with a dense forest canopy the tree transpiration can keep the groundwater level at a sufficient depth without working ditch systems. It is even so that the evapotranspirational losses by the

trees may be restricted if the groundwater levels are below 30 cm for dense tree stands and thus to be able to model the tree evapotranspiration is highly important (Weiss et al. 2006).

In addition to management, the drainage status is also affected by climate. Sweclim (Rummukainen et al. 2004) have modelled the regional climate change for Sweden and they predict that south-west Sweden will become warmer and wetter, while the south-east will become warmer and dryer in the future. Jansson et al. (in this volume) used these data to simulate forest hydrological conditions for dry and mesic soils in Sweden and found increased water stress in the south as a result of higher evaporative demand caused by changes in both meteorological conditions and changed tree growth. Therefore, we can expect that the currently well-drained peat forest soils in the south-west of Sweden will become wetter, while the opposite will occur in the south-east of Sweden. Thus, it is clear from the above that coupled process-based forest models are potentially powerful tools to predict the effect of groundwater levels on net flux from forested organic soils.

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