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Carbon and decomposition model Yasso for forest soils

Jari Liski [a,*], Taru Palosuo [b], Mikko Peltoniemi [c], Risto Sievänen [c]

[a] *Finnish Environment Institute, P.O. Box 140, 00251 Helsinki, Finland*
[b] *European Forest Institute, Torikatu 34, 80100 Joensuu, Finland*
[c] *Finnish Forest Research Institute, P.O. Box 18, 01301 Vantaa, Finland*

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Abstract

Models are needed to estimate dynamics of carbon in forest soils, because changes in soil carbon are laborious to measure, and future levels of soil carbon can only be predicted using models.

Current process-oriented soil carbon models are not suitable to all forestry-related applications. This is because they require specific input information that is not available for all forests, and their time step is shorter than a year which is typically used in forestry.

We developed a dynamic soil carbon model Yasso to be used in forestry applications. Yasso simulates the stock of soil carbon, changes in this stock and the release of carbon from soil on an annual basis. It needs estimates of litter production, information on litter quality and basic data on climate to run.

Yasso consists of five decomposition compartments and two woody litter compartments. Its parameter values were determined based on measurements of litter decomposition and soil carbon.

The reliability of the output of Yasso was assessed by conducting an uncertainty analysis and comparing model-calculated estimates of soil carbon to measurements taken at different forest sites in southern Finland. According to the uncertainty analysis, the estimates for the amount of soil carbon are uncertain by nature, because they depend mostly on uncertain humus parameters. Still, when linked to a forest simulator to calculate litter production, Yasso gave similar estimates for the amount of soil carbon as were measured. The estimates for changes in soil carbon, on the other hand, are more reliable by nature because they depend on more accurately known parameters.

These and other tests conducted so far suggest that Yasso is applicable to forests in a wide range of environments. Further tests will increase confidence in using it for different soils.

Keywords: Carbon; Decomposition; Forest; Model; Organic matter; Soil

1. Introduction

Models are needed to estimate the dynamics of carbon in forest soils. Measuring changes in the amount of

* Corresponding author. Tel.: +358 9 4030 0303;
fax: +358 9 4030 0390.
E-mail address: jari.liski@ymparisto.fi (J. Liski).

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soil carbon is difficult because the carbon density varies a lot more spatially (e.g., Liski, 1995; Morisada et al., 2004). Therefore, model-calculated estimates help to assess the importance of soil to the whole carbon balance of forests. Such estimates are also useful in approximating the number of samples needed when one decides to make the effort and measure the changes in soil carbon. Moreover, models can be used to predict future changes in soil carbon and to explore consequences of different environmental and forest management scenarios.

Dynamic soil carbon models vary in complexity and input information they require (Powlson et al., 1996). CENTURY (Parton et al., 1987) and RothC (Coleman and Jenkinson, 1996) are probably the two most widely used and validated process-oriented soil carbon models worldwide. CENTURY was originally developed for grasslands and RothC for arable soils, but both have also been applied to forest soils (e.g., Peng et al., 1998; Falloon and Smith, 2002; Falloon et al., 2002; Peng et al., 2002). These models operate on a monthly time step and need soil texture and weather variables as their major input data. DocMod (Currie and Aber, 1997) and ROMUL (Chertov et al., 2001; Komarov et al., 2003) are examples of soil models originally developed for forest soils. DocMod was developed to describe leaching from forest floor and, therefore, it does not account for all soil carbon, but that in the forest floor only. ROMUL operates on a daily time step and needs quite detailed weather, litter and soil data to run. FullCAM is a larger model for full carbon accounting in forests (Paul et al., 2003; Paul and Polglase, 2004), and it uses GENDEC model (Moorhead and Reynolds, 1991) to simulate litter decomposition and RothC model (Coleman and Jenkinson, 1996) to simulate soil carbon turnover. Simpler, less process-oriented dynamic soil carbon models with smaller input data requirements are used in some other modeling systems where the soil results form only a part of the relevant output. Examples of such systems are the dynamic global vegetation model LPJ (Sitch et al., 2003), Canadian forest sector carbon budget model (Kurz and Apps, 1999) and a stand-level forest and wood products model GORCAM (Schlamadinger and Marland, 1996). Still another group of soil carbon models is formed by models that describe the decreasing quality of organic matter and its consequently decreasing decomposition rate as the process of decomposition proceeds (e.g., Middelburg, 1989; Liski et al., 1998; Yang and Janssen, 2000; Bosatta and Ågren, 2003). These models contain a smaller number of parameters than the other models but, on the other hand, information on all factors affecting the dynamics of carbon in soil is built in these few parameters.

It is not straightforward to use any of these models for general forestry applications. The detailed models would require input data that are usually unavailable for forests inventoried only for forestry purposes – e.g., soil texture is often not known. Texture may also differ substantially between horizons in forest soils (e.g., Liski and Westman, 1995), and the single-layer models developed for more homogenous soils cannot account for this variability. Moreover, the time step of the detailed models is shorter than a year, which is the typical time step in forestry. It is not easy to divide annual litter estimates between the monthly or the daily time step of these models. The simple models, on the other hand, have been developed for the larger systems they are parts of, and their reliability has not been as thoroughly tested as that of actual soil carbon models. A problem with the models that describe the decreasing quality of the material decomposing and the decreasing rate of decomposition is that it is difficult to know how to modify the values of their few parameters when applying these models to new conditions.

The objective of this study was to develop a dynamic soil carbon model that would be suitable for general forestry applications. This model would require less input information than the detailed soil carbon models and thus it could be used when there is not enough information to apply the detailed models. Still, this model would need to account for the most important processes controlling the dynamics of carbon in forest soils to give reliable results under various conditions.

In this paper, we describe the model called Yasso we developed for such general forestry purposes and how its parameter values were determined, conduct an uncertainty analysis on the model and test the validity of model-calculated estimates for the amount of soil carbon. The validity of Yasso's estimates for the mass loss of different litter types decomposing under different climatic conditions is tested in an other paper (Palosuo et al., 2005). The validity of climatic effects on decomposition in the model and the validity of estimates for the accumulation rate of soil carbon in aging forest stands have been tested earlier (Liski et al., 2003; Peltoniemi et al., 2004). Yasso is technically suitable for use with forestry models, and it has already been linked to forest stand simulators CO2FIX (Masera et al., 2003) and MOTTI (Hynynen et al., 2005) and a region-scale forestry model EFISCEN (Karjalainen et al., 2002), and, in addition, it has been used together with a Swiss forestry model MASSIMO (Thürig et al., 2005).

2. The Yasso model

2.1. Assumptions

Yasso is based on a number of assumptions about decomposition – the assumptions are described below. We are aware that there are other processes and factors that affect the dynamics of carbon in soil, such as various stabilization mechanisms of soil organic matter (e.g., Six et al., 2002; Krull et al., 2003) and interactions in decomposition between different compounds (Berg and McClaugherty, 2003). We omitted them from this model to keep the input data requirements small and to be able to parameterize the model using the data available to us. We discuss the adequacy of this model in this paper based on test results presented in this and other papers (Liski et al., 2003; Peltoniemi et al., 2004; Palosuo et al., 2005).

Assumption 1. Litter and soil organic matter consist of different compound groups, which decompose at their own typical rates (Berg et al., 1982) independent of their origin. The decomposition rate of these groups decreases with an increasing complexity of the compounds.

Assumption 2. Decomposition of woody litter, unlike decomposition of non-woody litter, does not only depend on its chemical composition. This is because its physical characteristics mean that all woody litter is not exposed to microbial decomposition immediately (Swift, 1977).

Assumption 3. Decomposing compounds lose a certain proportion of their mass per unit of time (Olson, 1963).

Assumption 4. A part of the decomposed mass is removed from the soil as heterotrophic respiration or leaching while the rest forms more recalcitrant compounds (Berg et al., 1982; Stevenson, 1982; Oades, 1988). This means that we assumed no formation of more easily decomposable compounds in the process of decomposition unlike in some other soil carbon models, for example CENTURY (Parton et al., 1987) and RothC (Coleman and Jenkinson, 1996). The reason for our deviating assumption was that the formation of these most labile compounds is less important in our model that operates on a longer annual time step than in models using a monthly or daily time step. Including the formation of these compounds would have had little impact on the output of our model.

Assumption 5. Microbial activity and thus the decomposition rates as well as the rate of the exposure of woody litter to microbial decomposition depend on favorable temperature and moisture conditions (Olson, 1963; Meentemeyer, 1978; Berg et al., 1993; Liski et al., 2003). In addition, we assumed that the decomposition of humus is less sensitive to temperature than the decomposition of the more labile compounds following the results of Liski et al. (1999, 2000) and Giardina and Ryan (2000). However, we are aware that this phenomenon is still a subject to debate (e.g., Ågren, 2000; Davidson et al., 2000; Ågren and Bosatta, 2002).

2.2. Model structure

The model consists of five decomposition compartments and two woody litter compartments (Fig. 1). Non-woody litter (foliage and fine roots) entering soil is divided into the decomposition compartments of extractives, celluloses and lignin-like compounds according to its chemical composition (Assumption 1). Woody litter is put into the compartment of fine (branches, coarse roots) or coarse woody litter (stem) depending on its size (Assumption 2). Each of these woody litter compartments has a fractionation rate that determines the proportion of its contents to be released to the decomposition compartments in a time step. Each decomposition compartment has a decomposition rate that determines the proportion of its contents to be removed in a time step (Assumption 3). Fractions of these removed quantities are transferred into the subsequent decomposition compartments having lower decomposition rates while the rest are removed from the system (Assumption 4). The rates of exposure of woody litter to microbial decomposition and the decomposition rates are controlled by temperature and drought (Assumption 5).

2.3. Mathematical formulas

The following variables are used in the mathematical formulas of the model (Fig. 1).

- $u_i(t)$ is the input of litter type i to the system (i = non-woody litter (nwl), fine woody litter (fwl) or coarse woody litter (cwl)),
- $x_i(t)$ is the weight of organic carbon in woody litter compartment i at time t (i = fine or coarse woody litter),
- a_i is the rate of exposure of woody litter i to microbial decomposition,
- $x_j(t)$ is the weight of organic carbon in decomposition compartment j at time t (j = extractives (ext), celluloses (cel), lignin-like compounds (lig), humus (hum1) or more recalcitrant humus (hum2)),
- c_{ij} is the concentration of compounds j in litter type i,
- k_j is the decomposition rate of compartment j, and
- p_j is the proportion of mass decomposed in compartment j transferred to a subsequent compartment ($1 - p_j$ is the proportion removed from the system).

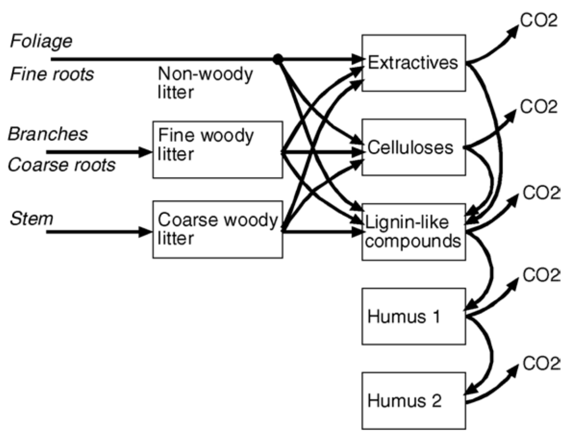

Fig. 1. Flow chart of the model. The boxes represent carbon compartments, the arrows carbon fluxes.

The dynamics of carbon in the litter compartments are described in Eqs. (1) and (2).

$$\frac{dx_{fwl}}{dt} = u_{fwl} - a_{fwl}x_{fwl}, \tag{1}$$

$$\frac{dx_{cwl}}{dt} = u_{cwl} - a_{cwl}x_{cwl}, \tag{2}$$

The decomposition compartments are described in Eqs. (3)–(7).

$$\frac{dx_{ext}}{dt} = u_{nwl}c_{nwl\_ext} + c_{fwl\_ext}a_{fwl}x_{fwl} + c_{cwl\_ext}a_{cwl}x_{cwl} - k_{ext}x_{ext}, \tag{3}$$

$$\frac{dx_{cel}}{dt} = u_{nwl}c_{nwl\_cel} + c_{fwl\_cel}a_{fwl}x_{fwl} + c_{cwl\_cel}a_{cwl}x_{cwl} - k_{cel}x_{cel}, \tag{4}$$

$$\frac{dx_{lig}}{dt} = u_{nwl}c_{nwl\_lig} + c_{fwl\_lig}a_{fwl}x_{fwl} + c_{cwl\_lig}a_{cwl}x_{cwl} + p_{ext}k_{ext}x_{ext} + p_{cel}k_{cel}x_{cel} - k_{lig}x_{lig}, \tag{5}$$

$$\frac{dx_{hum1}}{dt} = p_{lig}k_{lig}x_{lig} - k_{hum1}x_{hum1}, \tag{6}$$

and

$$\frac{dx_{hum2}}{dt} = p_{hum1}k_{hum1}x_{hum1} - k_{hum2}x_{hum2}. \tag{7}$$

The rates of exposure of woody litter to microbial decomposition (a_i) and the decomposition rates (k_j) depend on temperature and summer drought (Eqs. (8) and (9)).

$$k_j(T, D) = k_{j0}(1 + s_j\beta(T - T_0) + \gamma(D - D_0)) \tag{8}$$

$$a_i(T, D) = a_{i0}(1 + \beta(T - T_0) + \gamma(D - D_0)), \tag{9}$$

where T is a temperature variable (mean annual temperature, temperature sum or a logarithm of temperature sum), D is a summer drought variable (precipitation minus potential evapotranspiration from May to September), T_0 and D_0 denote temperature and summer drought in chosen standard conditions, a_{i0} and k_{j0} denote exposure and decomposition rates in these standard conditions, and β and γ are parameters quantifying the temperature and the summer drought

Table 1
Parameter values of the model and their estimated uncertainties under chosen standard conditions[a]

Parameter	Value	Uncertainty		Notes
		Absolute	Relative	
Exposure rates of woody litter to microbial decomposition ($year^{-1}$)				
Fine woody litter (a_{fwl})	0.54	0.077–1.0	±86%	
Coarse woody litter (a_{cwl})	0.030 or 0.077	0.028–0.032 or 0.072–0.083	±5% or ±7%	Alternative values for the same compartment, the smaller value for larger logs (Ø 20–60 cm) and the larger value for smaller logs (Ø 5–20 cm)
Decomposition rates ($year^{-1}$)				
Extractives (k_{ext})	0.48 or 0.82	0.45–0.51 or 0.71–0.93	±6% or ±14%	Alternative values for the same compartment, the smaller value for conifers and the larger value for deciduous plants
Celluloses (k_{cel})	0.30	0.28–0.31	±5%	
Lignin-like compounds (k_{lig})	0.22	0.17–0.29	−23–+32%	
Faster humus (k_{hum1})	0.012	0.002–0.02	−83–+67%	
Slower humus (k_{hum2})	0.0012	0.0017–0.0008	−33–+42%	
Formation of more complex compounds in decomposition (proportion of decomposed mass)				
Extractives to lignin-like compounds (p_{ext})	0.2	0.1–0.3	±50%	
Celluloses to lignin-like compounds (p_{cel})	0.2	0.1–0.3	±50%	
Lignin-like compounds to faster humus (p_{lig})	0.2	0.1–0.3	±50%	
Faster humus to slower humus (p_{hum1})	0.2	0.1–0.3	±50%	

[a] Mean annual temperature 3.3 °C, effective temperature sum (0 °C threshold) 1903 °C days and precipitation minus potential evapotranspiration from May to September −32 mm.

effects. Humus decomposition is less sensitive to temperature than the decomposition of the other compartments; therefore, in Eq. (8), $s_j = 1$, if j = ext, cel or lig, or $s_j < 1$, if j = hum1 or hum2.

2.4. Parameterization

2.4.1. Approach

The parameter values of the model were first determined for climate conditions typical for southern Finland and middle Sweden (mean annual temperature 3.3 °C, effective temperature sum (0 °C threshold) 1903 days and precipitation minus potential evapotranspiration between May and September −32 mm) (Table 1). Then, to obtain the values for other conditions, climatic dependencies were established for the decomposition rates and the rates of the exposure of woody litter to microbial decomposition (Table 2).

It follows from the assumptions our model is based on that the parameter values of the model should be generally applicable to different litter types and conditions. Tests we have conducted so far support

Table 2
Parameter values for the effects of temperature and summer drought in the model when using three alternative temperature variables (Eqs. (7) and (8))

Temperature variable	Effect of temperature (β)	Effect of drought (γ)
Mean annual temperature (MAT, °C)	0.105	0.00274
Effective temperature sum (DD_0, °C days)	0.000387	0.00325
Logarithm of effective temperature sum ($\log DD_0$)	2.48	0.00272

this idea. We have tested the validity of modeling the effects of climate on decomposition rates of various litter types under a wide range of environments from tropical rain forest to arctic tundra (Liski et al., 2003), the validity of modeling the effects of climate and litter quality plus the overall decomposition rate across Canada (Palosuo et al., 2005) and the validity of the estimates for the amount of soil carbon in Finland, Germany and Switzerland (see Fig. 6, Kaipainen et al., 2004; Peltoniemi et al., 2004; Thürig et al., 2005). However, although this basic idea of our model has appeared generally valid, the accuracy of the model can be improved by determining the decomposition rates again using local data (Palosuo et al., 2005).

2.4.2. Parameter values under standard climate

The decomposition rates of the extractives (k_{ext}), the celluloses (k_{cel}) and the lignin-like compounds (k_{lig}), and the transfer proportions of the decomposed extractives and celluloses to the compartment of the lignin-like compounds (p_{ext}, p_{cel}) were determined based on 18 litterbag experiments carried out using Scots pine (*Pinus sylvestris* L.) needle litter in Jädraås, central Sweden (Berg et al., 1991a, 1991b). Two other experiments on birch (*Betula pendula* Roth) leaves were used to determine a specific decomposition rate for the extractives (k_{ext}) of deciduous litter, the only parameter value of the model that varied with tree species (see Assumption 1). The specific value was needed because the extractives of coniferous and deciduous litter consist of different chemical compounds and therefore decompose at different rates. Among all the measurements of the litterbag experiments, those taken at one-year intervals were used to determine the parameter values for the current discrete model version operating on an annual time step. The values of these parameters determined based on litterbag measurements are constrained by the ability of litterbags to represent the actual rates of litter decomposition.

The decomposition rates of the extractives (k_{ext}) and the celluloses (k_{cel}) were determined by minimizing the sum of the squared errors between the measured and the model-calculated mass remaining values (Fig. 2a and b). The decomposition rate of the lignin-like compounds (k_{lig}) was determined in the same way after approximating a common value equal to 0.2 (relative unit) for the transfer proportion of the decomposed extractives (p_{ext}) and celluloses (p_{cel}) to the compartment of the lignin-like compounds (Fig. 1c). Had this proportion been much larger, the resulting k_{lig} value would have been higher than k_{cel}, and thus Assumption 1 of the model would have been refuted. Had it been much smaller, the model would not have reproduced the consistently observed increase and the subsequent decrease in the amount of lignin-like compounds during the first two years of decomposition (Berg et al., 1982) (Fig. 2c).

The decomposition rates of the humus compounds (k_{hum1}, k_{hum2}) were determined based on soil carbon measurements at 26 Scots pine sites along a 5300 year soil chronosequence in southern Finland (Liski et al., 1998) (Fig. 3). According to measurements of biomass production and soil carbon in the conditions of southern Finland, an average litter input equal to 0.413 kg C m^{-2} year^{-1} (0.251, 0.0758 and 0.0866 kg C m^{-2} year^{-1} of non-woody, fine-woody and coarse-woody litter, respectively) results in a soil carbon stock of 10 kg m^{-2} (Mälkönen, 1974; Persson, 1983; Liski and Westman, 1995). We applied this constant litter input to the model, used literature values for its chemical composition (Berg et al., 1982; Hakkila, 1989) and used 0.2 for the transfer proportion of decomposed carbon to the humus compartments (p_{lig}, p_{hum1}). Then, we determined the decomposition rates of the humus compartments by minimizing the sum of the squared errors between the model-calculated and the measured values of soil carbon along the chronosequence. Because litter was not measured, we excluded the woody litter compartments of the model from this comparison.

The rate of the exposure of coarse woody litter to microbial decomposition (a_{cwl}) was determined based on 2840 mass loss measurements of Norway spruce (*Picea abies* Karst.) logs in the Leningrad Region, Russia (Tarasov and Birdsey, 2001). We applied literature values for the chemical composition of the logs (Hakkila, 1989) and determined this rate by minimizing the sum of the squared errors between the model-calculated and the measured mass remaining values (Fig. 4). Different rates of exposure were determined for smaller and larger coarse woody litter because the former decomposed at a significantly higher rate (Tarasov and Birdsey, 2001). A mid-point value between the value for the smaller size class of coarse woody litter and a value equal to one was applied to the compartment of fine woody litter (a_{fwl}) because no data were available.

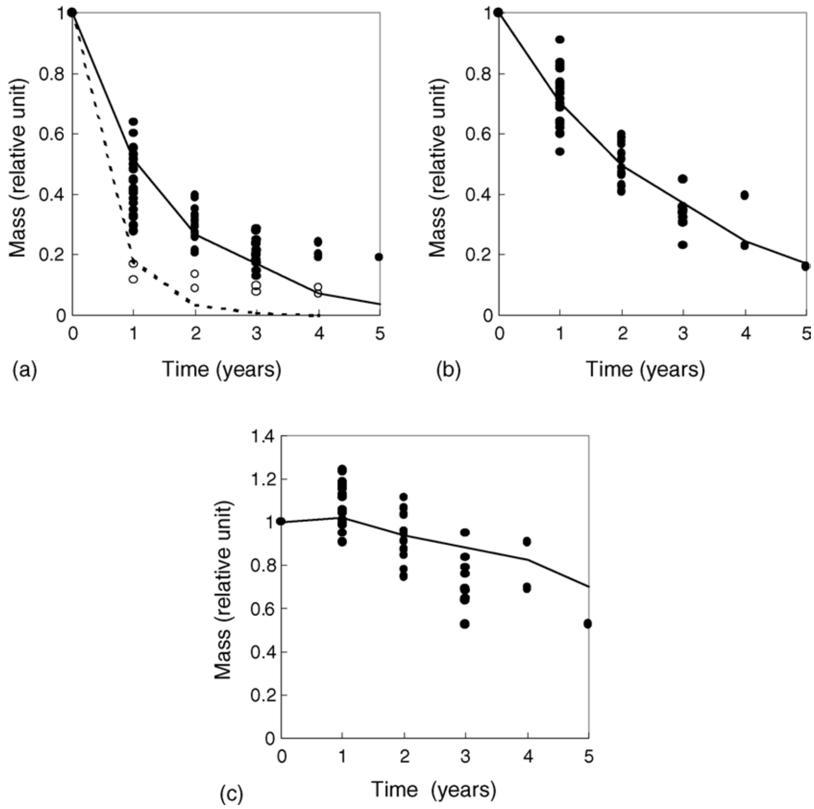

Fig. 2. Determining the decomposition rates of the extractives, the celluloses and the lignin-like compounds (k_{ext}, k_{cel}, k_{lig}), and the transfer fractions of the decomposed extractives and celluloses to the compartment of the lignin-like compounds ($p_{ext,}$ p_{cel}) by fitting the model-calculated estimates of mass remaining to data from litterbag experiments: (a) extractives; (b) celluloses; and (c) lignin-like compounds. The experimental litter was Scots pine (*Pinus sylvestris*) needles except for the open dots in a) which represent measurements of birch (*Betula pendula*) leaves (Berg et al., 1991b).

2.4.3. Climate dependence of the parameter values

The effects of temperature (β) and summer drought (γ) on the decomposition rates and the rates of exposure of woody litter to microbial decomposition were determined based on measurements of the first-year mass loss of Scots pine (*Pinus sylvestris*) needle litter at 34 sites across Europe (Liski et al., 2003) (Table 2). These effects were taken to be linear because they fitted to the data better than any simple curvilinear functions.

To decrease the temperature sensitivity of humus decomposition, following the results of Liski et al. (1999) and Giardina and Ryan (2000), the value of parameter s_j (Eq. (8)) was determined by fitting model-calculated amounts of soil carbon to measurements along a temperature gradient in Finland (Liski and Westman, 1997). Litter input to the model was changed

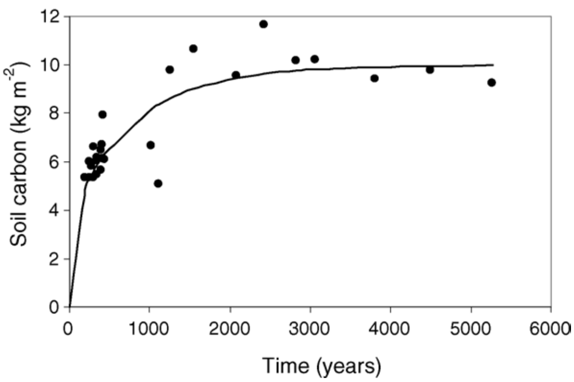

Fig. 3. Determining the decomposition rates of humus (k_{hum1}, k_{hum2}) by fitting the model-calculated estimates for the accumulation of soil carbon to measurements along a soil chronosequence; carbon in litter excluded (Liski et al., 1998).

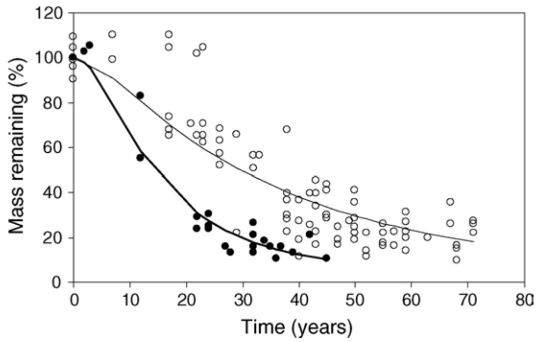

Fig. 4. Determining the rate of exposure of coarse woody litter to microbial decomposition (a_{cwl}) by fitting the model-calculated estimates of mass remaining to measurements of Norway spruce (*Picea abies*) logs; the closed dots and thick line represent logs 5–20 cm in diameter, the open dots and thin line represent logs 20–60 cm in diameter (Tarasov and Birdsey, 2001).

along the gradient in the same way as the production of stemwood changes (Koivisto, 1970; for the details of this approach, see Liski et al., 1999). The value of this parameter for the second humus compartment (s_{hum2}) was assumed to be the square of the value for the first humus compartment (s_{hum1}); an assumption was necessary because the relationship between s_{hum1} and s_{hum2} could not be known, and it was natural to assume that the tolerance of humus increased with an advancing status of decomposition. Values equal to 0.6 and 0.36 were obtained for the first and the second compartments, respectively. Value equal to 1 would have meant that the decomposition of humus was as sensitive to temperature as the decomposition of the more labile compounds.

3. Uncertainty analyses

3.1. Approach

The uncertainty analyses we conducted consisted of three parts. First, we studied the sensitivity of a model-calculated estimate for the amount of soil carbon to each parameter and input value of the model. Second, we assessed uncertainty about each parameter value. Third, we investigated variability in model-calculated soil carbon estimates, subject to the sensitivity of the model to the parameter values and the uncertainty about them.

3.2. Methods

3.2.1. Sensitivity of soil carbon estimates to parameter and input values

A steady-state stock of soil carbon was calculated for a low productivity Scots pine (*Pinus sylvestris*) site in southern Finland using the model, and the effects of a 1% increase in each parameter and input value were studied (Table 3). The steady-state stock was obtained by running the model and using a constant rate of litter input and an annual time step until the stock did not change anymore; this stock was only slightly different from the stock that would have been obtained by solving the equations of the model analytically because of the discrete annual time step used. At the site simulated, the average annual litter production totaled 0.161 kg C m^{-2} of which 0.069, 0.084 and 0.008 kg C m^{-2} was non-woody, fine woody and coarse woody litter, respectively. These values were obtained by multiplying an average tree biomass at such sites by biomass-component-specific turnover rates (Liski et al., 2002). Non-woody litter contained 27% extractives, 51% celluloses and 22% lignin-like compounds (Berg et al., 1982); fine woody litter contained 3% extractives, 65% celluloses and 32% lignin-like compounds; and coarse woody litter contained 3% extractives, 69% celluloses and 28% lignin-like compounds (Hakkila, 1989).

3.2.2. Uncertainty about parameter values

Uncertainty about the decomposition rates of the extractives and the celluloses (k_{ext}, k_{cel}), and also that about the rate of exposure of coarse woody litter to microbial decomposition (a_{cwl}) were quantified as 95% confidence intervals based on the data that were used to determine the values (Table 1, Figs. 2a, b and 4). Uncertainty about the rate of exposure of fine woody litter (a_{fwl}) was assumed to range from the value of the smaller size class of coarse woody litter to a value equal to one, because no data were available to determine this parameter value.

Uncertainty about the fractions of the decomposed extractives and celluloses transferred to the compartment of the lignin-like compounds (p_{ext}, p_{cel}) was approximated by changing their common value and comparing the model-calculated mass of the lignin-like compounds to the measurements (Table 1, Fig. 2c).

Table 3
Effect of a 1% increase (0.1 °C increase in mean annual temperature) in each parameter and input value of the model on a calculated steady-state amount of soil carbon under the chosen standard conditions (see Table 1)

Parameter value	Change in soil carbon (%)
Exposure rates of woody litter to microbial decomposition (year^{-1})	
a_{fwl}	−0.04
a_{cwl}	−0.04
Decomposition rates (year^{-1})	
k_{ext}	−0.01
k_{cel}	−0.07
k_{lig}	−0.07
k_{hum1}	−0.26
k_{hum2}	−0.51
Formation of more complex compounds in decomposition (proportion of decomposed mass)	
p_{ext}	0.05
p_{cel}	0.24
p_{lig}	0.77
p_{hum1}	0.51
Input value	
Litter input (kg year^{-1})	
Input_{nwl}	0.36
Input_{fwl}	0.55
Input_{cwl}	0.09
Chemical composition of litter (mass of compound group of total)	
c_{nwlext}	−0.01
c_{nwlcel}	−0.16
c_{nwllig}	0.14
c_{fwlext}	<0.00
c_{fwlcel}	−0.24
c_{fwllig}	0.25
c_{cwextl}	<0.00
c_{cwlcel}	−0.03
c_{cwllig}	0.02
Climate variables	
MAT (°C)	−0.70
DD_0 (°C days)	−0.49
log DD_0	−0.71
D (mm)	0.08–0.10[a]

[a] Dependent on temperature variable, lowest when MAT was used and highest when DD_0 was used.

The same uncertainty was assumed for the humification fractions (p_{lig}, p_{hum1}).

Uncertainty about the decomposition rate of the lignin-like compounds (k_{lig}) was assumed to range equally much above and below the standard value (0.22 year^{-1}) and to extend from 0.30 year^{-1} (the decomposition rate of cellulose) to 0.14 year^{-1}. A similar uncertainty range was obtained for this parameter by allowing the values of the other parameters that affected the amount of lignin-like compounds in the model (k_{ext}, k_{cel}, p_{ext}, p_{cel}) to vary inside their uncertainty ranges and fitting the model-calculated mass of the lignin-like compounds to the measurements (Fig. 2c).

To determine the uncertainty about the decomposition rates of humus (k_{hum1}, k_{hum2}), the same litter input to the model was used as when determining their standard values (see Parameterization). The decomposition rates of the other three decomposition compartments and the transfer fractions (k_{ext}, k_{cel}, k_{lig}, p_{ext}, p_{cel}) were allowed to vary inside their uncertainty ranges, and the variability of the carbon flux into the first humus compartment was recorded. Assuming that humus represented 83% of soil carbon excluding woody litter, like it did when the standard parameter values were used, the output of the model was fitted to the soil carbon data from the soil chronosequence by adjusting the decomposition rates of the humus compartments (Fig. 3). The variability of k_{hum1} was limited to 0.0001–0.02 year^{-1} and that of k_{hum2} to 0.00001–0.002 year^{-1} to avoid solutions with k_{hum2} larger than k_{hum1}. This would have contradicted Assumption 1 of the model (see Section 2.1).

3.2.3. Variability in soil carbon estimates

Overall uncertainty in the results of the model, subject to the sensitivity of the model to each parameter value and uncertainty about these values, was studied by conducting a Monte Carlo simulation of a forest rotation. A 90-year rotation with two thinnings was simulated for the same Scots pine (*P. sylvestris*) site that was used in the sensitivity analysis, and we started the simulation from the same steady state.

We ran 250 simulations using parameter values randomly selected from even distributions inside their uncertainty ranges (see Table 1). The decomposition rates of the lignin-like compounds and humus (k_{lig}, k_{hum1}, k_{hum2}) were calculated taking into account the values of the other parameters (see Section 2.4).

Annual values of litter production were derived from a time series of biomass development by multiplying the biomass values by component-specific turnover rates (Liski et al., 2002). Additional litter was added to the soil from the harvest residues of a clear-cut in the beginning of the simulation and thinnings during year 43 and year 65. We used the same chemical composition of the litter as we did when analyzing the sensitivity of the model.

3.3. Results

3.3.1. Sensitivity of soil carbon estimates to parameter and input values

The model-calculated estimate for the amount of soil carbon was most sensitive to the humification fractions ($p_{\mathrm{lig}}, p_{\mathrm{hum1}}$) and the decomposition rates of humus (k_{hum1}, k_{hum2}). A change of 1% in these parameter values changed the soil carbon estimate by 0.26–0.77%, depending on the parameter (Table 3). These parameters were the most critical ones because they determined the amount of humus in the model, and humus represented the majority (83%) of the simulated stock of soil carbon.

The input of the different litter types affected the model-calculated estimate of soil carbon according to their shares of the total input (Table 3). This was because, in the model, the amount of soil carbon is proportional to the litter input. For this same reason, the chemical compositions of fine woody litter and non-woody litter were more important than the composition of coarse woody litter, which represented only a minority of the total litter fall in the simulated forest. The concentration of the extractives was less important than the concentrations of the celluloses or lignin-like compounds, because the extractives had the highest decomposition rate and the lowest concentration in the litter.

The model-calculated estimate for the amount of soil carbon was about as sensitive to temperature as to the values of the most critical humus parameters. A 1% change in the effective temperature sum or a 0.1 °C change in mean annual temperature changed the soil carbon estimate by 0.49 or 0.71%. In contrast, the same change in the value of the summer drought index changed the soil carbon estimate by only 0.1%.

3.3.2. Uncertainty about parameter values

The decomposition rates of humus (k_{hum1} and k_{hum2}) and the humification fractions (p_i) appeared as the most uncertain parameter values of the model with their relative uncertainties ranging from 33 to 83%, depending on the parameter (Table 1). Uncertainty about the rate

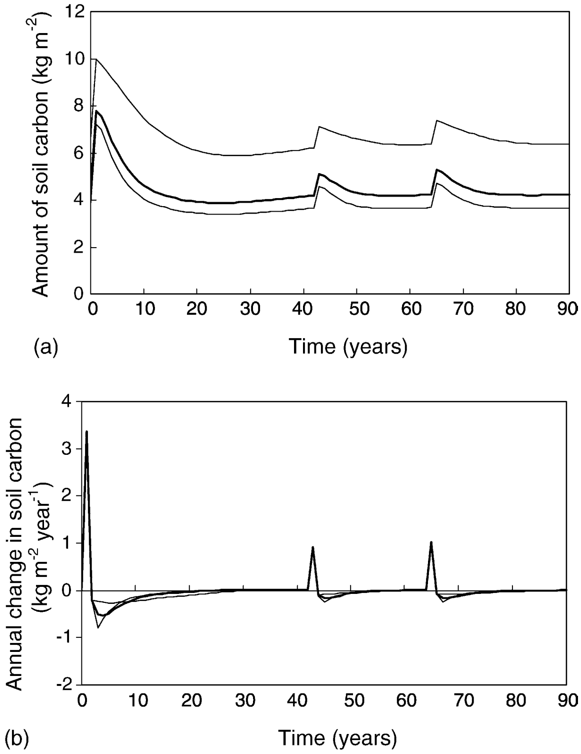

Fig. 5. Effect of uncertainty about the parameter values of the model on the simulated amount of soil carbon (a) and annual change in soil carbon (b) during a 90-year forest rotation at a Scots pine (*Pinus sylvestris*) site in southern Finland. The thin lines show the extremes of 250 simulations that applied random parameter values from their uncertainty ranges; the thick lines show the results when the standard parameter values were used.

of exposure of fine woody litter to microbial decomposition (a_{fwl}) was also high (86%) because there were no actual data to estimate it. The decomposition rates of the extractives and the celluloses (k_{ext}, k_{cel}) were the least uncertain parameter values with their uncertainties equal to only a few percent.

3.3.3. Variability in soil carbon estimates

The sensitivity of the model to the parameter values and the uncertainty about them caused, at most, 2.5–3.5 kg m^{-2} difference in the model-calculated estimates for the amount of soil carbon in the simulated forest (Fig. 5a). The coefficient of variation for the estimates from all the Monte Carlo simulation runs varied from 12 to 15%, depending on the year. These differences in the estimates were mainly caused by uncertainty about the humification fractions (p_{lig}, p_{hum1}) and the decomposition rates of humus (k_{hum1}, k_{hum2}). This was because these were the most uncertain parameter values of the model (Table 1), and they determined the amount of humus that represented the majority of the soil carbon in the model.

Variability in the estimates of the annual changes in the amount of soil carbon differed between the years of the simulation (Fig. 5b). These estimates were largely dependent on the value for the rate of exposure of fine woody litter to microbial decomposition (a_{flw}), which was a highly uncertain parameter value because of the lack of data. When it had a high value, the simulated amount of soil carbon decreased quickly after the harvests, 0.8 kg m^{-2} year^{-1} at most, but the period of decreasing soil carbon was short (20 years after the clear cut and 5 years after the thinnings). When this parameter had a low value, the amount of soil carbon did not decrease as quickly, but the period of the decrease was longer.

The estimates of the annual changes in the amount of soil carbon would have been substantially less variable without the uncertainty about the rate of exposure of fine woody litter to microbial decomposition (a_{flw}). This is because it was mostly carbon in compartments other than the humus that changed from year to year in the simulation, and the parameter values of these other compartments could be determined fairly accurately (Table 1).

4. Validity of soil carbon estimates

4.1. Methods

For testing the validity of Yasso's estimates for the amount of soil carbon, we linked it to an empirical forest stand simulator MOTTI (Matala et al., 2003; Hynynen et al., 2005) that calculates carbon input to soil. Using this combination of models, we estimated the amount of soil carbon at sites of different productivity classes (forest types) and tree species around Hyytiälä forestry field station in southern Finland, and compared these estimates to measurements (Liski and Westman, 1995). We obtained the necessary input variables of MOTTI, i.e. tree species, stand characteristics, location and productivity class, from the paper by Liski and Westman (1995), except for the stand characteristics which we only assumed to be typical for this region.

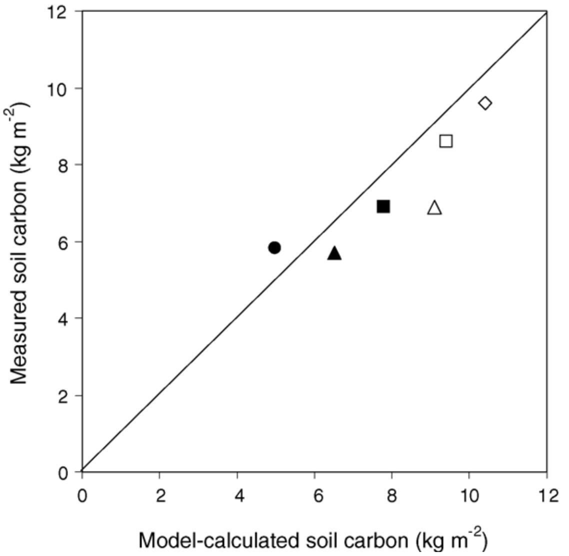

Fig. 6. Model-calculated and measured estimates for the amount of soil carbon at forest sites of different productivity and tree species in southern Finland. Black symbols show Scots pine stands, and white symbols Norway spruce stands. The circle indicates Calluna type sites ($n = 5$ for measurements), the triangles Vaccinium type sites ($n = 7$ for pine, $n = 2$ for spruce), the squares Myrtillus type sites ($n = 4$ for pine, $n = 7$ for spruce), and the diamond Oxalis-Myrtillus type sites ($n = 5$). The forest types are listed above in the order of increasing productivity. The soil carbon estimates represent the organic F/H layer plus the topmost 1 m of the mineral soil layer.

4.2. Results

The model-calculated estimates for the amount of soil carbon were only a little higher, 15% higher on average, than the means of the measurements for the different forest types and tree species (Fig. 6). The least productive Scots pine forests were an exception; for these forests the model-calculated estimate was 14% lower than the mean of the measurements. Excluding this forest type, the amount of soil carbon increased in a similar fashion with increasing site productivity according to the measurements and the model-calculations. It is noteworthy that there was no difference in the increasing trend between the measurements and the model-calculated estimates, although the amount of fine particles in the soils increased also with increasing site productivity and the model did not account for their stabilizing effect on soil carbon; for example, in the topmost 1 m deep mineral soil layer the amount of silt (particle size fraction 2–60 μm) grew from 51 kg m^{-2} in Calluna forest type to 146 kg m^{-2} in Vaccinium forest type, 396 kg m^{-2} in Oxalis-Myrtillus forest type and 483 kg m^{-2} in Myrtillus forest type (Liski and Westman, 1995).

5. Discussion

We started to develop the Yasso model because we could not find a suitable model for our forestry research purposes. Some of the models required more input data than we had or used shorter time steps than we could handle whereas others were specific to the modeling frameworks they were developed for.

Yasso requires only basic data on climate and litter input, it uses annual time steps like forestry calculation systems usually do, and it is an independent model that can be used with any estimates of litter production. The output of Yasso consists of estimates for the amount of soil carbon, changes in this amount, and quantities of carbon released from soil (i.e. mostly heterotrophic respiration).

How reliable is the output of Yasso? Where can the model be applied? What kind of studies is it suitable for? What are the major limitations for its use? The uncertainty analyses and the validity tests reported in this and our earlier papers (Liski et al., 2003; Peltoniemi et al., 2004; Palosuo et al., 2005), as well as other literature, provide us with means to answer these questions.

Yasso's estimates for the amount of soil carbon are uncertain by nature, because the rates of formation and decomposition of humus are poorly known (Table 1, Fig. 5). However, when linked to the forest stand simulators MOTTI (Hynynen et al., 2005) or CO2FIX (Masera et al., 2003) to estimate litter production, the soil carbon estimates were similar to the means of measurements for forest types with different tree species, site productivity and soil properties in southern Finland (Fig. 6, Kaipainen et al., 2004). We conclude that Yasso is suitable for estimating the average amount of soil carbon in these types of forests, but not necessarily at particular sites where the conditions for decomposition and humus formation deviate from the average.

Yasso's estimates for annual changes in soil carbon, which are induced by changes in litter production, are more reliable than the estimates for the amount of soil carbon (Fig. 5). This is because these estimates depend on other soil carbon compounds than humus, and the dynamics of these compounds can be more accurately determined (Table 1). The majority of the remaining uncertainty was caused by the lack of data to determine the rate of exposure of fine woody litter to microbial decomposition. However, the value of this parameter we chose from the wide uncertainty range may not be that far from the actual value. When linked to the MOTTI stand simulator, Yasso estimated a similar accumulation rate of carbon in the soil of aging forests in southern Finland (5.8 ± 1.0 (S.D.) g m^{-2} year^{-1}) as measured (4.7 ± 1.4 (S.D.) g m^{-2} year^{-1}) (Peltoniemi et al., 2004). When linked to the CO2FIX stand simulator, it overestimated the rate a little (6 g m^{-2} year^{-1} in Scots pine stands and 17 g m^{-2} year^{-1} in Norway spruce stands) (Kaipainen et al., 2004). These results suggest that Yasso can be used to estimate changes in soil carbon resulting from changes in litter production in these kinds of forests.

According to the above tests in Finland, the approach of linking Yasso to estimates of litter production is appropriate to estimate the amount of soil carbon and changes in this amount in different types of forests. The geographical extent where Yasso can be used depends on our ability to estimate the rates of decomposition (release of carbon from soil) and litter production (input of carbon to soil).

Among these needs of information, estimating litter production is out of the scope of Yasso development but the validity of the method to model the effects of climate on decomposition has been tested with litterbag data from North and Central America (Liski et al., 2003). The effective temperature sum appeared to be a more general variable than mean annual temperature to explain the effects of temperature on decomposition. Together with summer drought, they explained the majority of differences in mass loss rates between 44 sites ranging from arctic tundra to tropical rainforest across North and Central America (r^2 0.71–0.80 depending on litter type). The effect of temperature sum on mass loss was statistically different between Europe and North plus Central America for only one litter type, and the effect of summer drought for one other litter type. However, the method applied in Yasso tended to overestimate the effects of climate on decomposition in North and Central America, but not as much as a method based on actual evapotranspiration, which is often used to explain the effects of climate on decomposition.

According to this test and assuming that litterbags represent the actual effects of climate on decomposition, Yasso can be applied to estimate the amount of soil carbon and changes in soil carbon under the wide range of environments where the model was calibrated or tested. Litterbags are an established method to study the effects of climate on decomposition, and therefore they have been used for this purpose in extensive research programs (Berg et al., 1993; LIDET, 1995; Trofymow and the CIDET Working Group, 1998). Nevertheless, using litterbag data to calibrate or test a model like Yasso is not free of problems. The litterbags we used were placed on top of forest floor or just below it. They may not represent the effects of climate on decomposition of all soil carbon because a lot of the carbon is found deeper in mineral soil (Liski and Westman, 1995; Batjes, 1996). Furthermore, climate affects conditions differently in mineral soil than in forest floor. Also, clay and silt particles in mineral soil may protect soil organic matter from decomposing and alter the relationship between climate and the rate of decomposition. More tests of Yasso are needed to determine the importance of these factors in quantitative terms.

It was surprising that Yasso estimated the average amount of soil carbon in the different forest types without a bias (Fig. 6) although the soils contained fine particles in very different quantities and these particles are known to stabilize soil organic matter by slowing down its decomposition (Six et al., 2002). In the forests where we tested Yasso, the amount of fine particles also affects site productivity. They increase the water holding capacity of soil and weathering surface and therefore enhance the availability of nutrients in the soil. For these reasons, the soils rich in fine particles are more fertile and vegetation growing on them produces more litter. This effect appeared to be far more important in these soils than the limiting effect of fine particles on decomposition. Consequently, the differences in the amount of soil carbon between the forest types could be explained almost entirely by the differences in litter production. Tests on forest soils where fine particles reduce the rate of decomposition significantly are needed to take this effect into account in Yasso; technically it could be implemented by modifying the decomposition rates of humus according to the content of fine particles in soil.

Other important omissions from Yasso were interactions between decomposition rates of different compounds, for example cellulose and lignin (Berg and McClaugherty, 2003), and the effects of nutrients, especially nitrogen (Berg, 2000). We have studied the significance of these omissions and the adequacy of the current Yasso by testing the model with Canadian litterbag data (Trofymow and the CIDET Working Group, 1998). Results of these tests are reported and discussed in another paper by Palosuo et al. (2005).

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References

Ågren, G.I., 2000. Temperature dependence of soil organic matter, comments on the paper by Liski, J., Ilvesniemi, H., Mäkelä, A., Westman, C.J. Ambio 29 (1) 55.

Ågren, G.I., Bosatta, E., 2002. Temperature response of soil organic matter. Soil Biol. Biochem. 34, 129–132.

Batjes, N.H., 1996. Total carbon and nitrogen in the soils of the world. Eur. J. Soil Sci. 47, 151–163.

Berg, B., Hannus, K., Popoff, T., Theander, O., 1982. Changes in organic components of litter during decomposition. Long-term decomposition in a Scots pine forest. I. Can. J. Bot. 60, 1310–1319.

Berg, B., Booltink, H., Breymeyer, A., Ewertsson, A., Gallardo, A., Holm, B., Johansson, M.-B., Koivuoja, S., Meentemeyer, V., Nyman, P., Olofsson, J., Pettersson, A.-S., Reurslag, A., Staaf, H., Staaf, I. and Uba, L., 1991a. Data on needle litter decomposition and soil climate as well as site characteristics for some coniferous forest sites. Part I. Site characteristics. Report 41, Swedish University of Agricultural Sciences, Department of Ecology and Environmental Research, Uppsala.

Berg, B., Booltink, H., Breymeyer, A., Ewertsson, A., Gallardo, A., Holm, B., Johansson, M.-B., Koivuoja, S., Meentemeyer, V., Nyman, P., Olofsson, J., Pettersson, A.-S., Reurslag, A., Staaf, H., Staaf, I. and Uba, L., 1991b. Data on needle litter decomposition and soil climate as well as site characteristics for some coniferous forest sites. Part II. Decomposition data. Report 42, Swedish University of Agricultural Sciences, Department of Ecology and Environmental Research, Uppsala.

Berg, B., Berg, M.P., Bottner, P., Box, E., Breymeyer, A., De Anta, R.C., Couteaux, M., Mälkönen, E., McClaugherty, C., Meentemeyer, V., Muñoz, F., Piussi, P., Remacle, J., De Santo, A.V., 1993. Litter mass loss in pine forests of Europe and Eastern United States: some relationships with climate and litter quality. Biogeochemistry 20, 127–159.

Berg, B., 2000. Litter decomposition and organic matter turnover in northern forest soils. For. Ecol. Manage. 133, 13–22.

Berg, B., McClaugherty, C., 2003. Plant Litter. Decomposition, Humus Formation, Carbon Sequestration. Springer-Verlag, Berlin, Heidelberg, New York, pp. 286.

Bosatta, E., Ågren, G.I., 2003. Exact solutions to the continuous-quality equation for soil organic matter turnover. J. Theor. Biol. 224, 97–105.

Chertov, O.G., Komarov, A.S., Nadporozhskaya, M., Bykhovets, S.S., Zudin, S.L., 2001. ROMUL – a model of forest soil organic matter dynamics as a substantial tool for forest ecosystem modeling. Ecol. Model 138, 289–308.

Coleman, K., Jenkinson, D.S., 1996. RothC-26.3 – A Model for the turnover of carbon in soil. In: Powlson, D.S., Smith, P., Smith, J.U. (Eds.), Evaluation of Soil organic matter models, Using Existing Long-Term Datasets. Springer-Verlag, Heidelberg, pp. 237–246.

Currie, W.S., Aber, J.D., 1997. Modeling leaching as a decomposition process in humid, montane forests. Ecology 78, 1844–1860.

Davidson, E.A., Trumbore, S.E., Amundson, R., 2000. Soil warming and organic carbon content. Nature 408, 788–789.

Falloon, P., Smith, P., 2002. Simulating SOC changes in long-term experiments with RothC and CENTURY: model evaluation for a regional scale application. Soil Use Manage. 18, 101–111.

Falloon, P., Smith, P., Szabo, J., Pasztor, L., 2002. Comparison of approaches for estimating carbon sequestration at the regional scale. Soil Use Manage. 18, 164–174.

Giardina, C.P., Ryan, M.G., 2000. Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. Nature 404, 858–861.

Hakkila, P., 1989. Utilization of Residual Forest Biomass. Springer-Verlag, Berlin, pp. 568.

Hynynen, J., Ahtikoski, A., Siitonen, J., Sievänen, R., Liski, J., 2005. Applying the MOTTI simulator to analyze the effects of alternative management schedules on timber and non-timber production. For. Ecol. Manage. 207, 5–18.

Kaipainen, T., Liski, J., Pussinen, A., Karjalainen, T., 2004. Managing carbon sinks by changing rotation length in European forests. Environ. Sci. Pol. 7, 205–219.

Karjalainen, T., Pussinen, A., Liski, J., Nabuurs, G.-J., Erhard, M., Eggers, T., Sonntag, M., Mohren, G.M.J., 2002. An approach towards an estimate of the impact of forest management and climate change on the European forest sector carbon budget: Germany as a case study. For. Ecol. Manage. 162, 87–103.

Koivisto, P., 1970. Regionality of forest growth in Finland. Comm. Inst. For. Fenn. 71.2, 1–76.

Komarov, A., Chertov, O., Zudin, S., Nadporozhskaya, M., Mikhailov, A., Bykhovets, S., Zudina, E., Zoubkova, E., 2003. EFIMOD 2 – a model of growth and cycling of elements in boreal forest ecosystems. Ecol. Model 170, 373–392.

Krull, E.S., Baldock, J.A., Skjemstad, J.O., 2003. Importance of mechanisms and processes of the stabilisation of soil organic matter for modelling carbon turnover. Funct. Plant Biol. 30, 207–222.

Kurz, W.A., Apps, J.M., 1999. A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. Ecol. Appl. 9, 526–547.

LIDET, 1995. Meeting the Challenges of Long-Term, Broad-Scale Ecological Experiments, Report 19, US LTER Network Office, Seattle.

Liski, J., 1995. Variation in soil organic carbon and thickness of soil horizons within a boreal forest stand – effect of trees and implications for sampling. Silva Fenn. 29, 255–266.

Liski, J., Westman, C.J., 1995. Density of organic carbon in soil at coniferous forest sites in Southern Finland. Biogeochemistry 29, 183–197.

Liski, J., Westman, C.J., 1997. Carbon storage in forest soil of Finland. 1. Effect of thermoclimate. Biogeochemistry 36, 239–260.

Liski, J., Ilvesniemi, H., Mäkelä, A., Starr, M., 1998. Model analysis of the effects of soil age, fires and harvesting on the carbon storage of boreal forest soils. Eur. J. Soil Sci. 49, 407–416.

Liski, J., Ilvesniemi, H., Mäkelä, A., Westman, C.J., 1999. CO_2 emissions from soil in response to climatic warming are overestimated – the decomposition of old soil organic matter is tolerant of temperature. Ambio 28, 171–174.

Liski, J., Ilvesniemi, H., Mäkelä, A., Westman, C.J., 2000. Reply to the comments by Göran Ågren, Temperature dependence of old soil organic matter: Comments on a paper by Liski et al. Ambio 29 (1), 56–57.

Liski, J., Perruchoud, D., Karjalainen, T., 2002. Increasing carbon stocks in the forest soils of western Europe. For. Ecol. Manage. 169, 159–175.

Liski, J., Nissinen, A., Erhard, M., Taskinen, O., 2003. Climatic effects on litter decomposition from arctic tundra to tropical rainforest. Global Change Biol. 9, 1–10.

Masera, O.R., Garza-Caligaris, J.F., Kanninen, M., Karjalainen, T., Liski, J., Nabuurs, G.J., Pussinen, A., de Jong, B.H.J., Mohren, G.M.J., 2003. Modeling carbon sequestration in afforestation, agroforestry and forest management projects: the CO2FIX V.2 approach. Ecol. Model 164, 177–199.

Matala, J., Hynynen, J., Miina, J., Ojansuu, R., Peltola, H., Sievanen, R., Vaisanen, H., Kellomaki, S., 2003. Comparison of a physiological model and a statistical model for prediction of growth and yield in boreal forests. Ecol. Model 161, 95–116.

Meentemeyer, V., 1978. Macroclimate and lignin control of litter decomposition rates. Ecology 59, 465–472.

Middelburg, J.J., 1989. A simple rate model for organic matter decomposition in marine sediments. Geochim. Cosmochim. Acta 53, 1577–1581.

Moorhead, D.L., Reynolds, J.F., 1991. A general model of litter decomposition in the northern Chihuahuan Desert. Ecol. Model. 56, 197–219.

Morisada, K., Ono, K., Kanomata, H., 2004. Organic carbon stock in forest soils in Japan. Geoderma 119, 21–32.

Mälkönen, E., 1974. Annual primary production and nutrient cycle in some Scots pine stands. Comm. Inst. For. Fenn. 84 (5), 1–87.

Oades, J.M., 1988. The retention of organic matter in soils. Biogeochemistry 5, 35–70.

Olson, J.S., 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44, 322–331.

Palosuo, T., Liski, J., Trofymow, J.A. and Titus, B., 2005. Litter decomposition affected by climate and litter quality – testing the Yasso model with litterbag data from the Canadian Intersite Decomposition Experiment, Manuscript submitted to Ecol. Model., August 2004.

Parton, W.J., Schimel, D.S., Cole, C.V., Ojima, D.S., 1987. Analysis of factors controlling soil organic matter levels in great plains grasslands. Soil Sci. Soc. Am. J. 51, 1173–1179.

Paul, K.I., Polglase, P.J., 2004. Prediction of decomposition of litter under eucalypts and pines using the FullCAM model. For. Ecol. Manage. 191, 73–92.

Paul, K.I., Polglase, P.J., Richards, G.P., 2003. Sensitivity analysis of predicted change in soil carbon following afforestation. Ecol. Model 164, 137–152.

Peltoniemi, M., Mäkipää, R., Liski, J., Tamminen, P., 2004. Changes in soil carbon with stand age – an evaluation of a modeling method with empirical data. Global Change Biol. 10, 2078–2091.

Peng, C., Apps, J.M., Price, D.T., Nalder, I.A., Halliwell, D.H., 1998. Simulating carbon dynamics along the Boreal Forest Transect Case Study (BFTCS) in central Canada, 1, Model testing. Global Biogeochem. Cycles 12, 381–392.

Peng, C., Jiang, H., Apps, M.J., Zhang, Y., 2002. Effects of harvesting regimes on carbon and nitrogen dynamics of boreal forests in central Canada: a process model simulation. Ecol. Model 155, 177–189.

Persson, H.Å., 1983. The distribution and productivity of fine roots in boreal forests. Plant Soil 17, 87–101.

Powlson, D.S., Smith, P., Smith, J.U., 1996. Evaluation of Soil Organic Matter Models. Springer, Berlin, 429 p.

Schlamadinger, B., Marland, G., 1996. The role of forest and bioenergy strategies in the global carbon cycle. Biomass Bioenerg. 10, 275–300.

Sitch, S., Smith, B., Prentice, I.C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J.O., Levis, S., Lucht, W., Sykes, M.T., Thonicke, K., Venevsky, S., 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. Global Change Biol. 9, 161–185.

Six, J., Conant, R.T., Paul, E.A., Paustian, K., 2002. Stabilization mechanisms of soil organic matter: implications for C-saturation of soils. Plant Soil 241, 155–176.

Stevenson, F.J., 1982. Humus Chemistry: Genesis, Composition, Reactions. John Wiley & Sons, New York, 496 p.

Swift, M.J., 1977. The ecology of wood decomposition. Sci. Prog., Oxf. 64, 175–199.

Tarasov, M.E., Birdsey, R.A., 2001. Decay rate and potential storage of coarse woody debris in the Leningrad Region. Ecol. Bull. 49, 137–147.

Thürig, E., Palosuo, T., Bucher, J., Kaufmann, E., 2005. The impact of windthrow on carbon sequestration in Switzerland: a model-based assessment. For. Ecol. Manage. 210, 337–350.

Trofymow, J.A. and the CIDET Working Group, 1998. The Canadian Intersite Decomposition Experiment (CIDET): Project and Site Establishment Report. Report Information Report BC-X-378, Pacific Forestry Centre, Victoria, Canada.

Yang, H.S., Janssen, B.H., 2000. A mono-component model of carbon mineralization with a dynamic rate constant. Eur. J. Soil Sci. 51, 517–529.