

Wood decomposition model for boreal forests

M. Tuomi^{a,b,*}, R. Laiho^c, A. Repo^a, J. Liski^a

^a Finnish Environment Institute, Research Programme for Global Change, Mechelininkatu 34a, P.O. Box 140, 00251 Helsinki, Finland

^b University of Helsinki, Department of Mathematics and Statistics, Gustaf Hällströmin katu 2b, P.O. Box 68, Helsinki, Finland

^c University of Helsinki, Department of Forest Ecology, Helsinki, Finland

ARTICLE INFO

Article history:

Received 14 April 2010

Received in revised form 15 October 2010

Accepted 28 October 2010

Available online 22 November 2010

Keywords:

Bayesian model comparison

Decomposition

Statistical modelling

Woody litter

ABSTRACT

The decomposition of woody litter is a biochemical process, controlled by physical, chemical and biological environmental conditions. To develop a practicable model of this complex process, it is necessary to identify the major controlling factors and quantify their effects. We used four data sets (total $N = 2102$) on mass loss of decomposing woody litter in Northern Europe to extend an earlier decomposition model of non-woody litter and make it suitable for describing also decomposition of woody litter. We compared alternative ways to model the effects of size and chemical composition of woody litter on decomposition using the Bayesian model selection theory. The best model fitted to the diverse data sets (woody litter of four tree species, diameter 0.5–60 cm, time series up to 70 years) with little systematic error. Based on this result, we concluded that the extended model is suitable for describing decomposition of woody litter of the common tree species in the boreal forests studied. According to the model developed, frequently observed sigmoidal patterns in mass loss of woody litter are related to high concentrations of slowly decomposing lignin compounds and these patterns become stronger with an increasing size of decomposing woody litter.

© 2010 Elsevier B.V. All rights reserved.

1. Introduction

Decomposition of woody litter is an important process of carbon cycle in forests (e.g. Laiho and Prescott, 1999). This process is also relevant for biodiversity because it shapes the quality of woody litter, the habitat of many organisms (Siitonen, 2001). Knowledge on decomposition of woody litter is thus needed to understand some of the basic functions of forests and to be able to account for these functions when making forest management decisions.

The decomposition of woody litter is commonly described using two kinds of approaches. On the one hand, there are purely empirical models independent of any process-oriented decomposition model (e.g. Mäkinen et al., 2006; Rock et al., 2008). On the other hand, there are models based on more general descriptions of the microbial decomposition process. For example, Yin (1999) expanded the decomposition model of Ågren and Bosatta (1987) to describe the decomposition of woody litter. In the soil organic matter module of the widely-used CENTURY¹ model (Parton et al., 1987), the decomposition of woody litter follows the same pathways as the decomposition of other lit-

ter but different types of dead wood have specific decomposition rates.

In boreal forests, woody litter decomposes mainly as a result of microbial, essentially fungal, activity but logs and snags lose mass also because of leaching, physical weathering and faunal activity (Harmon et al., 1986; Cornwell et al., 2009). As a biochemical process, the decomposition of woody litter is basically similar to the decomposition of non-woody leaf or fineroot litter. Therefore, it seems logical to try and develop a description of woody litter decomposition on top of a general description of litter decomposition (Yin, 1999). This approach would widen the applicability of any decomposition model lacking the special features of woody litter decomposition (Shevliakova et al., 2009). Further, such a description of woody litter decomposition would benefit from features common to all decomposition already included in the more general model.

There are several reasons for the lower decomposition rate of woody litter compared to non-woody litter (Harmon et al., 1986) that should be considered when modelling woody litter decomposition. First, the chemical quality of woody litter is often poorer from the point of view of decomposers (e.g. Laiho and Prescott, 1999; Cornwell et al., 2009). Second, due to a greater physical size, it takes a longer time for microbes to colonize a piece of woody litter completely than to colonize a smaller piece of non-woody litter.

The objective of this study was to quantify the effects of size and chemical quality of woody litter on the decomposition of this litter

* Corresponding author at: Finnish Environment Institute, Research Programme for Global Change, Mechelininkatu 34a, P.O. Box 140, 00251 Helsinki, Finland. Tel.: +358 400148605; fax: +358 204902350.

¹ www.nrel.colostate.edu/projects/century.

in boreal forests. This analysis is based on the Yasso07² soil carbon and decomposition model (Tuomi et al., 2009). A result of this study is an extension of this model to the decomposition of woody litter. Because the process of woody litter decomposition or the regulating factors are not known in detail, we adopted an empirical approach and compared alternative model structures using a Bayesian model selection technique. The litter and soil organic matter (SOM) decomposition model Yasso07 was chosen as a starting point of this development process because it has appeared to describe decomposition of a wide range of non-woody litter types in an unbiased way across the global climatic conditions (Tuomi et al., 2009).

2. Material and methods

2.1. The Yasso07 model

The Yasso07 model describes the mass loss of decomposing non-woody litter and the related carbon transformations between forms of carbon in soil (Tuomi et al., 2009). The model is mainly based on a large set of foliage and fine root litter decomposition measurements ($N=9605$) from across Europe and North and Central America. Yasso07 has been shown to give unbiased estimates of non-woody litter decomposition for a wide variety of plant species and ecosystem types across the global climate conditions.

In the Yasso07 model, litter is divided according to its chemical composition into four compartments, namely the acid hydrolyzable (A), water soluble (W), ethanol soluble (E), and neither hydrolyzable nor soluble (N) compartments. In addition to these compartments, there is a more recalcitrant humus compartment (H). The mass loss of these compartments is modelled as

$$\dot{x}_Y = \mathbf{A}(C)x_Y + b(t), \quad (2.1)$$

where t denotes time, C the climatic conditions, matrix \mathbf{A} the mass loss and mass flow matrix and vector b the input of carbon to the modelled carbon transformation system. Vector x_Y represents the masses of the AWEN compounds and humus compartments.

The climate dependence of the mass loss is modelled for each compartment $i = \{E, W, A, N, H\}$ as (Tuomi et al., 2008, 2009)

$$k_i(C) = \alpha_i \exp(\beta_1 T + \beta_2 T^2) [1 - \exp(\gamma P_a)], \quad (2.2)$$

where parameters β_1 , β_2 and γ are the temperature and precipitation dependence parameters (Tuomi et al., 2009), and α_i is the mass loss rate parameter of the i th compartment. Climate is described using monthly or annual mean temperature T and annual precipitation P_a .

2.2. Selected models of woody litter decomposition

We developed a series of models to complement the Yasso07 model and describe the mass loss of woody litter. Then, we evaluated the performance of these models against the datasets (see Section 2) using Bayesian methods. The models were constructed according to the following criteria:

- (1) Compatibility with the Yasso07 model of Tuomi et al. (2009).
- (2) Simplicity – the models had to be simple enough to be able to use them in current applications of the Yasso07 model, such as Earth system models (ESMs) or national greenhouse gas inventories.
- (3) Applicability to woody litter of any physical size and chemical composition.

The first criterion is satisfied if the mass loss of coarse woody litter can be described as a generalization of the earlier Yasso07 model version describing the decomposition of non-woody litter Tuomi et al. (2009). The second criterion is satisfied if the model is simple. For instance, the mass loss rate cannot depend on time because this would mean that in an ESM, or in any other global or extensive local application, the starting time of decomposition would have to be saved in a computer memory for all the individual pieces of woody litter, which would not be feasible. The third criterion is satisfied if measurements from several sources can be used in the analysis at the same time and if all these measurements can be described with an adequate precision and accuracy (small random variability and bias). In addition, we required the model to be a parsimonious description of coarse woody litter mass-loss to avoid over-parametrization and to decrease the uncertainty in the model structure without decreasing its accuracy, as was done when developing the non-woody litter version of Yasso07 model (Tuomi et al., 2009).

We tested three different collections of models, each describing the lower decomposition rate of woody litter compared to non-woody litter in a different manner. In models of collection I, woody litter enters a common ‘slowing’ compartment and only from this compartment it is transferred further to the AWEN compartments according to its chemical quality. This approach was used in an earlier version of the Yasso model (e.g. Liski et al., 2005). In models of collection II, there is a specific ‘slowing’ compartment for each AWEN compartment. There is only one model in collection III. This model does not have a ‘slowing’ compartment but the decomposition rates of the AWEN compartments are decreased according to the size of woody litter. The diagrams of the three model collections are shown in Fig. 1.

2.2.1. Model collection I

One of the simplest possible models describing the lower mass loss rate of decomposing body of woody litter compared to that of non-woody litter can be written in a matrix form as

$$\dot{x} = \begin{pmatrix} \dot{x}_S \\ \dot{x}_Y \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ p & \mathbf{A}(C) \end{pmatrix} \begin{pmatrix} k_S(C) d^r x_S \\ x_Y \end{pmatrix} \quad (2.3)$$

where x_S is the mass in a hypothesised ‘slowing’ compartment (S) that is used to make the mass loss of leaf litter and woody litter compatible, $k_S < 0$ is its mass loss rate coefficient, d is the diameter of the decomposing piece of woody litter, C represents the climatic conditions, $p = (p_E, p_W, p_A, p_N, 0)^T$, $p_i \in [0, 1]$, is a column vector describing the transfer of mass from S to each of the AWEN compartment, and $(\cdot)^T$ is used to denote transpose. We assumed that this vector was equal to the initial chemical composition of the woody litter. Parameter $r < 0$ determines how the diameter of woody litter slows down the decomposition rate (Table 1, column “r”). It is assumed to be negative because the larger the trunk, branch or twig, the lower the mass loss rate should be. We also assumed that climate dependence of mass-loss from S was similar to the dependence in the non-woody litter compartments (see Eq. (2.2)) because there was no indication in favour of the opposite in the data.

It is possible to simplify this model even further by assuming that the mass loss depends on the area-to-volume ratio as $A/V \propto d^2/d^3 = 1/d$. This results in having $r = -1$ in Eq. (2.3). Conversely, fitting r as a free parameter should lead to values around -1 if the decomposition was dependent primarily on the area-to-volume ratio. This could be a consequence of the decomposers accessing the whole decomposing body via its surface, causing the larger area-to-volume ratio to increase the total mass-loss rate of the body of woody litter.

The models in collection I consisted of different modifications to the general structure (Eq (2.3), Table 1).

² www.environment.fi/syke/yasso.

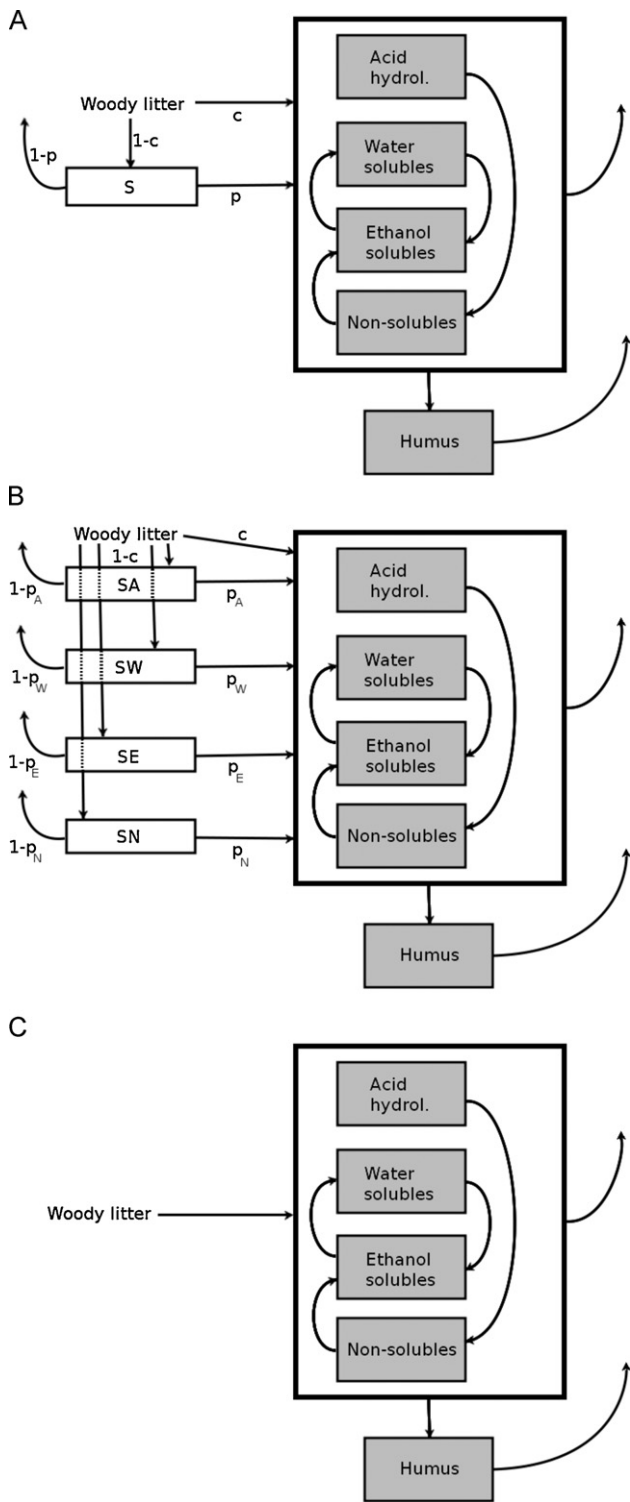


Fig. 1. The diagrams of the model collections I (a), II (b), and III (c).

- (1) The lower mass loss rate of woody litter compared to that of non-woody litter was modelled by allocating fraction c of woody litter directly to the AWEN compartments according to its chemical composition and putting the rest $(1 - c)$ to the S compartment (Table 1, column “ c ”).
- (2) Parameter c does not need to be a constant but can depend on the chemical composition of woody litter. Because the majority of woody litter consists of hemicelluloses, cellulose, and lignin found mostly in the two compartments consisting of the acid

Table 1

Parameters of the models in collection I and their numbers of free parameters K . Free parameters are denoted by X and fixed values by the corresponding numbers. Parameter α represents the mass loss rate from the ‘slowing’ compartment, α_S means it is the same for all chemical compound groups, whereas α_{S1} and α_{S2} denote that it is different between compound groups A and N (see text); parameter c represents the fraction of woody litter bypassing the slowing compartment, whereas c_1 and c_2 mean this fraction was different between acid hydrolysable and neither soluble nor hydrolysable compound groups A and N, respectively; parameter r represents the effect of woody litter size on the mass loss rate of the slowing compartment; parameter ρ represents the fraction of woody litter bypassing the ‘slowing’ compartment but not escaping from the system before entering the AWEN compartments.

Model	K	α_S	α_{S1}	α_{S2}	c	c_1	c_2	r	ρ
Ia	3	X			X			X	1
Ib	2	X			0			X	1
Ic	4		X	X	X			X	1
Id	3		X	X	0			X	1
Ie	5		X	X	X			X	X
If	5		X	X		X	X	X	1
Ig	6		X	X		X	X	X	X

Table 2

Parameters of the models in collection II and their numbers of free parameters K . See text and Table 1 for details.

Model	K	α_{SA}	α_{SW}	α_{SE}	α_{SN}	c	c_1	c_2	r	ρ
IIa	5	X	X	X	X	0			X	1
IIb	6	X	X	X	X	X			X	1
IIc	7	X	X	X	X	X			X	X
IId	6	X	∞	∞	X		X	X	X	X
IIe	5	X	∞	∞	X		X	X	X	1

hydrolysable compounds and the compounds neither soluble nor hydrolysable, we accounted only for these compartments and studied models in which $c = c_1 x_A(0) + c_2 x_N(0)$, where $x_A(0)$ and $x_N(0)$ are the relative initial amounts of these two compound sets in the woody litter, respectively (Table 1, columns “ c_1 ” and “ c_2 ”). For some models, parameter c was fixed to zero representing situations in which all the woody litter was put initially to the S compartment.

- (3) The compartment S was assumed to either have a constant mass loss rate α_S , or alternatively $\alpha_S = \alpha_{S1} x_A(0) + \alpha_{S2} x_N(0)$, which makes the mass loss dependent on the chemical composition as well (Table 1, columns “ α_S ”, “ α_{S1} ”, and “ α_{S2} ”).
- (4) We assumed that a fraction ρ was transferred directly to the fast compounds from S but the rest, $1 - \rho$, was removed from the system either as CO_2 or by some other mass removal processes (Table 1, column “ ρ ”). In some models, parameter ρ was equal to unity, which means that all the mass was transferred from S to the AWEN compartments.

2.2.2. Model collection II

In the model collection II, each of the AWEN compartments was assumed to have a slowing compartment with a specific mass loss rate. These compartments are denoted as α_{SA} , α_{SW} , α_{SE} , and α_{SN} , respectively (Table 2). Parameter c was treated as in collection I, either as a constant or a function of the chemical composition. Some of these models were constructed by fixing α_{SW} and α_{SE} to some large numbers, denoted by infinity signs in Table 2. These models were tested because compartments consisting of the water soluble and ethanol soluble compound groups lose mass relatively rapidly, and also because their initial amounts in woody debris are close to negligible (less than 5%). The equation of these model can be written similarly as Eq. (2.3) but with the above modifications.

2.2.3. Model collection III

In the model collection III, we assumed that the mass loss rate of the AWEN compartments decreased with an increasing diameter d of woody litter. Accordingly, we chose to model the system by

assuming that the matrix \mathbf{A} in Eq. 2.1 was simply multiplied by some size-dependent coefficient $h_S(d)$ – otherwise the system was similar for all litter. Hence, if non-woody litter such as leaves and fineroots have their effective size in this sense close to zero, this size dependence of mass loss can be defined as

$$h_S(d) = \min\{(1 + \phi_1 d + \phi_2 d^2)^r, 1\}, \quad (2.4)$$

which is equal to unity if the size d is negligibly small. There is only one three-parameter model in this collection because the size dependence coefficient contains all the free parameters, namely, ϕ_1 , ϕ_2 , and r . We tested a model with ϕ_2 fixed to zero, but it was immediately found to be an inadequate description and was not considered any further because its posterior probability was several orders of magnitude lower than that of Eq. (2.4). Similarly, the inclusion of third order term in Eq. (2.4) did not improve the fit but introduced an additional unnecessary parameter in the model.

We assumed that an increasing physical size decreased the decomposition rate of woody litter and consequently restricted $h_S < 1$.

2.3. Woody litter decomposition measurements

Four sets of measurements taken in boreal forest were used in this study ($N=2102$). Two of these sets were entirely from Finland (Mäkinen et al., 2006; Palviainen et al., 2004) whereas one extended also to Estonia in the south (Vávřová et al., 2008) and one was from neighbouring Leningrad region in Russia (Tarasov and Birdsey, 2001). Two of the data sets represented mass loss of coarse woody litter, i.e. stems or stumps, while the other two represented mass loss of branches. Time period covered by the measurements ranged from one to 75 years after the start of decomposition. We scaled each dataset to unit mass at the start of decomposition.

The data set of Mäkinen et al. (2006) comprised of mass loss measurements of dead tree stems ($N=1281$) in 58 thinning experiments in southern and central Finland. Some of the trees were downed but some were still standing when the measurements were started. The sites were measured two to twelve times over the last five decades since the 1960s. The mass loss was estimated based on measurements of wood density and volume. Scots pine (*Pinus sylvestris* L.) represented 732 of the trees studied, Norway spruce (*Picea abies* (L.) Karst.) 341 and silver or downy birches (*Betula pendula* Roth. or *Betula pubescens* Ehr.) 208. Time since death ranged up to 61, 38 and 34 years for the pines, spruces and birches, respectively. The diameter at breast height varied from 5 to 32 cm for the pines, 5 to 40 cm for the spruces and 5 to 25 cm for the birches. Mean annual temperature of the sites varied between 2.0 and 6.0 °C and annual precipitation between 500 and 700 mm.

The mass loss measurements of branches (diameter <1 cm) of three species, i.e. Scots pine, Norway spruce and silver birch ($N=360$) were introduced in Palviainen et al. (2004). These measurements were taken in southern Finland at a clear-cut site and an adjacent uncut forest site. There were no differences in the rate of mass loss between the sites and consequently the data were combined for the present study. The mass loss measurements were taken using litter bags, and the data covered the first three years of decomposition. Mean annual temperature varied from 0.7 to 2.1 °C and annual precipitation from 285 to 541 mm at the sites between the measurement years.

The data set of Tarasov and Birdsey (2001) represented mass loss measurements of Norway spruce stems and stumps varying from 5 to 60 cm in diameter ($N=107$). Mass loss was measured by taking samples of dead trees and measuring the volume and mass of the samples in laboratory. Various kinds of information, such as forest inventory data and harvesting records, were used to date the time of death of the sample trees. Mean annual temperature of the

study sites varied from 3 to 5 °C and annual precipitation from 500 to 800 mm.

The data set of Vávřová et al. (2008) comprised of mass loss measurements of Scots pine branch litter (diameter 0.5 or 3.0 mm) at three peatland sites drained for forestry, two in Finland and one in Estonia ($N=354$). The measurements were taken using litter bags, and mass loss was followed annually for 2–4 years depending on site. Mean annual temperature varied from 0.8 to 4.8 °C and annual precipitation from 600 to 730 mm between the sites.

Because uncertainty estimates were not available for any of the datasets, we assessed them ourselves based on the data. We calculated the average deviation of the measurements from the average mass remaining at each point of time since the start of decomposition. The uncertainty estimates, rounded to the nearest 10%, obtained were 20, 10 and 10% in the datasets of Tarasov and Birdsey (2001), Palviainen et al. (2004), and Vávřová et al. (2008), respectively. This method of estimating the uncertainty could not be applied to the data set of Mäkinen et al. (2006) because the measurements were not divided into discrete size classes and measurement times. For this reason, we applied the uncertainty of the other coarse woody litter dataset (20%) also to this set.

2.4. Bayesian model selection

The performance of the different models was compared using the Bayesian model comparison theory (e.g. Jeffreys, 1961; Kass and Raftery, 1995), based on their posterior probabilities given the measurements. Accordingly, we calculated the probability $P(f_k | m)$ for the k th model f_k using all the measurements m_i (we denote $m = (m_1, \dots, m_N)$). The posterior probability of the model given the measurements is defined as

$$P(f_k | m) = \frac{P(m | f_k) P(f_k)}{\sum_{j=0}^q P(m | f_j) P(f_j)}, \quad (2.5)$$

where

$$P(m | f_k) = \int_{\omega_k \in \Omega_k} p(m | \theta_k, f_k) p(\theta_k | f_k) d\theta_k \quad (2.6)$$

and $P(f_k)$ is the *a priori* probability of the k th model, ω_k are its parameters in the parameter space Ω_k , $p(m | \theta_k, f_k)$ is the likelihood function, $p(\theta_k | f_k)$ is the prior density of the parameters, and q is the number of models in the comparison. This Bayesian comparison of different models is more efficient than the more traditional approaches where a null hypothesis is compared to an alternative hypothesis. In the Bayesian framework, any number of hypotheses, or models (q), can be compared simultaneously. An another advantage of the Bayesian model comparison method is that it has a built-in Occam's razor, which guarantees that the models are penalized, resulting in decreased probabilities, if the measurements cannot be used to e.g. quantify all of the parameter values or if there are processes or phenomena described in the models the existence of which is not supported by the data.

We used the Markov chain Monte Carlo (MCMC) method with the Metropolis-Hastings algorithm (Metropolis et al., 1953; Hastings, 1970) to draw samples from the posterior probability densities of the parameters of the different models (see e.g. Tuomi et al., 2008, 2009 for details). These samples can be used to estimate probability densities of the model parameters given the measurements. Hence, with the full posterior densities available, the results are shown as maximum *a posteriori* (MAP) values and 95% confidence sets intervals (the Bayesian credibility sets, see e.g. Kaipio and Somersalo, 2005).

We set the prior probabilities of some model structures to zero because the parameter values obtained made these structures log-

Table 3

Model comparison results. Bayesian model probabilities ($P(f_k | m)$) of the compared models, the corresponding $\chi^2(f_k)$ values and the numbers of free parameters K in the models.

Model (f_k)	K	$\chi^2(f_k)$	$P(f_k m)$
Ia	3	2.10	0
Ib	2	2.51	$<10^{-56}$
Ic	4	2.10	0
Id	3	2.48	$<10^{-55}$
Ie	5	1.91	$<10^{-9}$
If	5	2.09	0
Ig	6	1.90	$<10^{-8}$
Ila	5	2.36	$<10^{-47}$
Ilb	6	2.10	$<10^{-27}$
Ilc	7	1.81	0.21
Ild	6	1.80	0
Ile	5	2.00	$<10^{-17}$
III	3	1.83	0.79

ically impossible. For model Ia, the parameter α_5 was found to decrease without limit (i.e. $\alpha_5 \rightarrow -\infty$). This meant that all the mass initially in the compartment S is transported immediately to the fast compartments, making this model identical to the Yasso07 model for non-woody litter, not its generalization. In models Ic, If, and Ild, the posterior value of parameter r decreased without limit. This made the decomposition rate of the S compartment negligible, i.e. that all the mass initially in the S compartment stayed there *ad infinitum*. This situation is not possible because, eventually, all woody litter should decompose.

3. Results

3.1. Results of the model comparison

The model of collection III had the greatest posterior probability given all the measurements (Table 3). It was therefore considered as the best model out of those tested. It is worth noting that there were two models (Ilc, Ild) that had slightly lower χ^2 values than model III indicating a better fit to the measurements. Nevertheless, the probability values of these models were lower than the probability value of model III, because these models had greater numbers of free parameters (six or seven compared to three) that increased uncertainty about the structures of these models.

According to the model comparison results, the best modelling approach was to extend the Yasso07 model by multiplying the decomposition rate and mass flow matrix $\mathbf{A}(C)$ by a coefficient that depends on the physical size of the litter, as defined in Eq. (2.4). This formulation means that the greater the diameter of woody litter the slower its decomposition in each AWEN compartment. The resulting matrix $\mathbf{A}_d(C, d) = h_5(d)\mathbf{A}(C)$ is equivalent to the original matrix \mathbf{A} for litter diameter $d = 0$, which can be thought to represent non-woody litter.

There are three parameters in the model III: ϕ_1 , ϕ_2 , and r (Table 4). These parameters define the effect of size (diameter) of woody litter on the value of coefficient h_5 . The coefficient h_5 was defined to have the maximum value equal to unity. When

Table 4

Maximum *a posteriori* parameter values of Y07 woody litter submodel, and their 95% confidence limits.

Parameter	Value	Unit	Interpretation
ϕ_1	-1.71 ± 0.16	cm^{-1}	First order size dependence
ϕ_2	0.86 ± 0.10	cm^{-2}	Second order size dependence
r	-0.306 ± 0.013	–	Size dependence power

the parameter values shown in Table 4 were used, this coefficient was smaller than unity approximately when $d > 2$ cm. This means, first, that the earlier version of Yasso07 model developed using non-woody litter can only describe decomposition of woody litter smaller than 2 cm in diameter. Second, this implies that the differences in mass loss between woody litter pieces of such small size arise from chemical composition, not from physical size.

3.2. Fit to the measurements

To evaluate the fit of the best model, model III, to the measurements, we studied the distributions of the model residuals, i.e. the differences between measurements and predictions using the maximum *a posteriori* (MAP) parameter estimates. We summarised these distributions using two numbers, mean (μ) and the standard deviation (σ). The mean measures the difference of the model estimates from the measurements, while the standard deviation represents both measurement uncertainty and an additional uncertainty caused by features affecting woody litter decomposition not accounted for by the model. If $\mu - \sigma \leq 0 \leq \mu + \sigma$, the residuals cannot be said to deviate from zero.

Estimates of mass remaining calculated using model III did not deviate statistically significantly from the measurements in any of the data sets (Table 5). The mean values of the residuals varied from -0.011 to 0.13 between the data sets and the standard deviation values from 0.04 to 0.22 (Table 5).

Although the mean of the residuals was close to zero in each data set (Table 5), there were some systematic characteristics in the residuals. Compared to the data set of Tarasov and Birdsey (2001), the model-calculated estimates of mass remaining were somewhat greater for the smallest diameter class (5–20 cm) after 20 years of decomposition and for the diameter classes (21–40 and 41–60 cm) after 40 years of decomposition (Fig. 2). One reason for these differences may be the center diameters of the classes (12.5, 30.0, and 50.0 cm) used in the model-calculations, that do not account for the variability inside each class. Another reason may be the difficulty in estimating the original diameter of these already well-decayed pieces of woody litter at the time of making the measurements.

Investigating the fit to the measurements by Mäkinen et al. (2006) revealed that the variability of the residuals for the pine and spruce stems increased with an increasing time since the start of decomposition (Fig. 3 top left and middle left panels). This pattern was caused by trees that did not lose any mass despite death. On the other hand, the largest deviations were also associated with the smallest diameters (Fig. 3, top right and middle right panels). It is not possible to say how much each of these factors contributed to

Table 5

Residuals of model III and the datasets studied (mean (μ) and standard deviation (σ)).

Woody litter type	d	μ	σ	Reference
Norway spruce stems and stumps	5–60 cm	-0.10	0.17	Tarasov and Birdsey (2001)
Scots pine stems	5–32 cm	0.05	0.20	Mäkinen et al. (2006)
Norway spruce stems	5–40 cm	0.12	0.20	Mäkinen et al. (2006)
Silver or downy birch	5–25 cm	0.13	0.22	Mäkinen et al. (2006)
Scots pine branches	<1 cm	0.00	0.04	Palviainen et al. (2004)
Norway spruce branches	<1 cm	0.04	0.11	Palviainen et al. (2004)
Silver birch branches	<1 cm	0.06	0.06	Palviainen et al. (2004)
Scots pine branches	0.5–3 cm	-0.011	0.075	Vávřová et al. (2008)

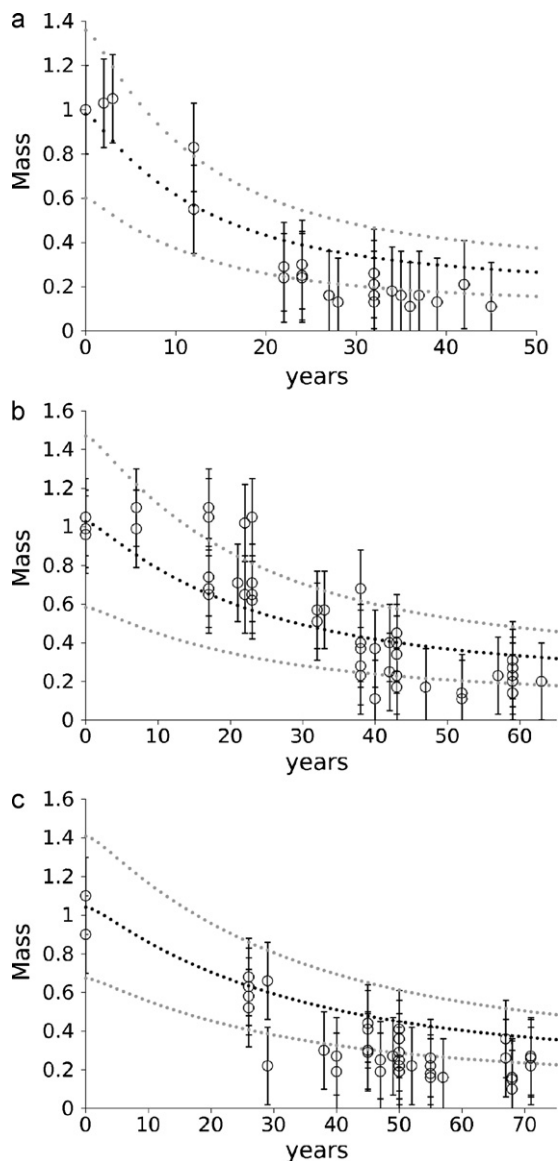


Fig. 2. Mass remaining estimates of decomposing Norway spruce coarse woody litter by diameter class: 5–20 cm (a), 21–40 cm (b), and 41–60 cm (c). The symbols represent measurements (Tarasov and Birdsey, 2001) and the dotted lines estimates calculated using model III using the center values of the diameter classes therein (12.5, 30.0 and 50.0 cm, mean and 95 % limits shown).

the observed patterns. We plotted the residuals instead of mass remaining estimates as a function of time because the data of Mäkinen et al. (2006) was measured as a continuous function of both, time and diameter, not divided into a few discrete size classes or measurement times, as was the case for the other datasets.

The residuals of the two branch litter data sets (Palosuo et al., 2001; Vávřová et al., 2008) did not show any systematic offsets (Figs. 4 and 5).

Considering the wide range of diameters (0.5–60 cm) and difficulties in measuring the long-term mass loss of woody litter, we conclude that model III is a useful extension to the Yasso07 model that gives similar estimates for the mass-loss of woody litter as the measurements used in this study.

3.3. Behaviour of the Yasso07 model extended by model III

To (1) demonstrate the behaviour of Yasso07 model extended using model III and (2) to study the effects of size and chemi-

cal composition on litter decomposition according to this model, we simulated decomposition of each AWEN fraction originating from non-woody litter (diameter 0 cm), branch-sized woody litter (5 cm) and stem-sized woody litter (30 cm) under climate conditions prevailing in boreal forests in southern Finland (annual mean temperature 3.5 °C, annual precipitation 535 mm).

Mass loss of the water soluble compounds was fastest immediately after the start of decomposition, independent of litter size (Fig. 6c and d). This pattern was quite similar for the A fraction, except that an increasing size of woody litter delayed the timing of the highest mass loss rate by a few years (Fig. 6a and b). On the other hand, the mass loss of the ethanol solubles and those neither soluble nor hydrolysable showed a clearly different shape (Fig. 6e–h). The greatest mass loss rate of these fractions originating from non-woody litter occurred 10–20 years after the start of decomposition and this peak was delayed by an increasing size of woody litter. This phenomenon resulted in sigmoidal mass remaining curves of the ethanol soluble compounds and those neither soluble nor hydrolysable.

According to the Yasso07 model extended with model III, the remaining mass of decomposing woody litter shows a sigmoidal pattern over time because this litter is poor in the quickly decomposing water soluble fraction but has high concentrations of the acid hydrolysable and especially neither soluble nor hydrolysable fractions. The sigmoidal pattern becomes stronger with an increasing size of woody litter.

4. Discussion

The data sets analysed in this study covered the most abundant forest tree species in northern Europe, Scots pine, Norway spruce, and silver and downy birches, which show differing decomposition dynamics (Harmon et al., 2000; Mäkinen et al., 2006), as well as a wide range of sizes of woody litter (diameters from 0.5 to 60.0 cm). We evaluated several alternative model structures using Bayesian model comparison method.

To describe the low decomposition rate of woody litter, we tried several model structures that had additional ‘slowing’ compartments, because this approach was used in an earlier version of Yasso model Liski et al. (2005). However, in the Bayesian comparison, each of these models had a lower probability than the model without any ‘slowing’ compartments. This means that the alternative approach was a more reliable way to describe the mass loss of decomposing woody litter.

Regarding the decomposition process, this difference between the modelling approaches suggests that decomposers do not enter the interior of decomposing woody litter gradually, as assumed when using the “slowing compartments”, but are initially present in or at least able to invade the decomposing piece of woody litter relatively rapidly. Indeed, endophytic fungi found in living trees may act as primary colonizers (e.g. Griffith and Boddy, 1990). Despite the effective colonization by decomposers, the decomposition rate of woody litter proceeds slowly because of unfavourable environmental conditions inside woody litter compared to the conditions on the surface (the lack of moisture and/or nutrients). As a result, the physical size limits the decomposition as described by the model III because the greater the woody litter diameter, the greater volume in its interior has these limiting environmental conditions. Unfortunately, the data analysed in this article is not specific enough to test this hypothesis thoroughly. We also note that there were no significant differences between the decomposition rates of standing trees and those in contact with the ground. Hence, these two hypothetical populations were modelled in a similar manner.

The best model structure, model III, fitted to the data with little systematic error. The model underestimated mass loss of

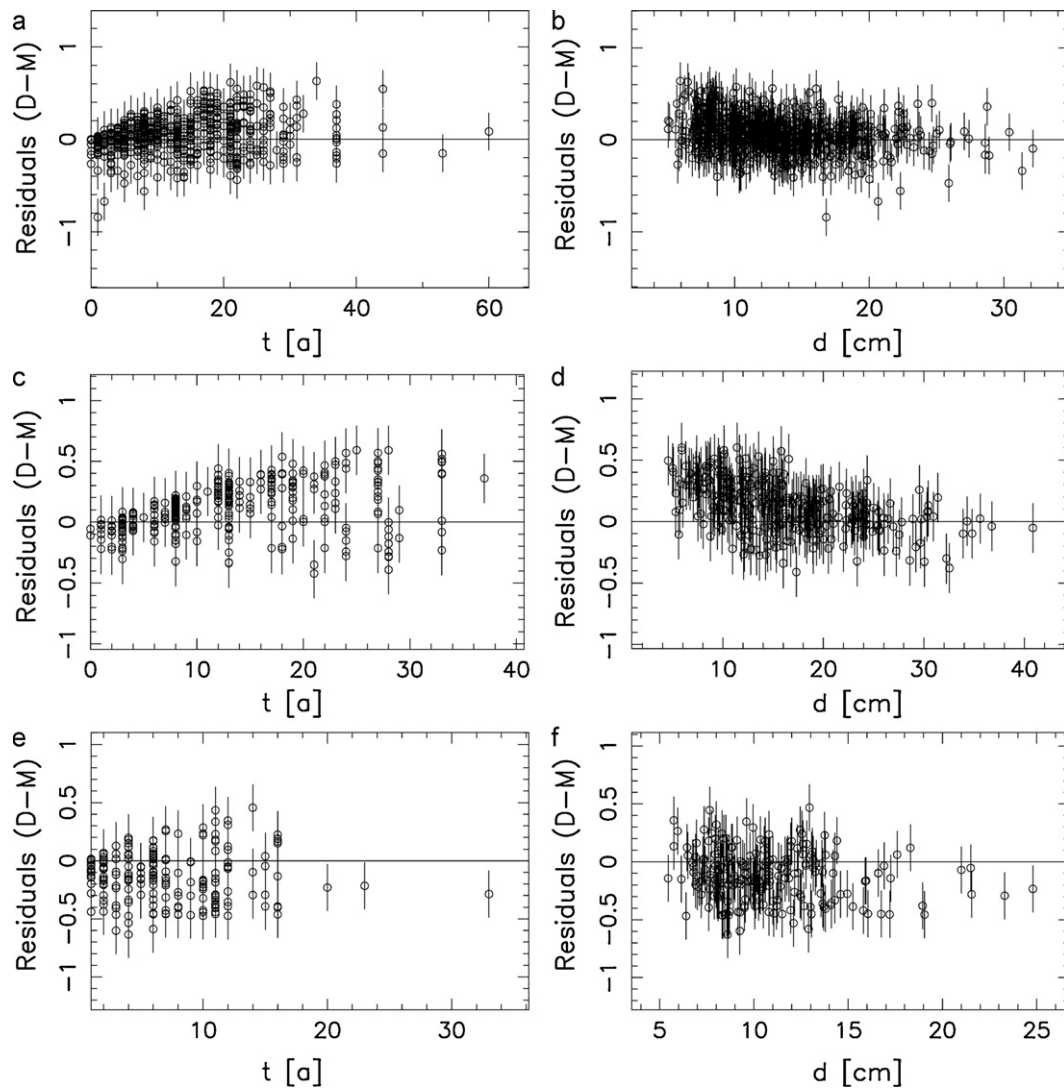


Fig. 3. Residuals of model III and the measurements (Mäkinen et al., 2006) as a function of time (a, c and e) since the start of decomposition and diameter (b, d and f): Scots pine stems (a and b), Norway spruce stems (c, d), and silver or downy birch (e and f).

decomposing Norway spruce stems 20 or 40 years after the start of decomposition in one data set (Fig. 2) and it probably overestimated mass loss of decomposing small-sized (diameter <10 cm) Norway spruce stems in another data set (Fig. 3). Despite these deviations, we think the model fitted to the data adequately and the model is an appropriate tool for estimating decomposition of woody litter of these tree species and diameter classes under these conditions. This extension to describe woody litter exploits the core of the earlier Yasso07 model, which has been shown to be suitable to estimate decomposition of leaf litter at the global scale (Tuomi et al., 2009). It remains to be investigated how the structure of model III could also be used outside the boreal conditions of this study.

Since the Yasso07 model with its current parameter values has been developed to be applicable across the world, it would be quite straightforward to start these investigations. Information on the chemical composition and the diameter of woody litter plus climate data would be used as input information to the model and model-calculated estimates for the mass loss of this woody litter would be compared to measurements available.

Though the active fungal species may affect the decomposition rates of woody litters (Clinton et al., 2009), it was somewhat surprising that the same model could be used to estimate wood decomposition of both coniferous (pine and spruce) and decidu-

ous trees (birch). Birch is usually subject to white-rot whereas pine and spruce are subject to brown-rot. A similar fit of the model to the measurements of both tree types suggests that under natural conditions in forest both cellulose and lignin are decomposed despite of the rot-type. This is probably explained by a diversity of decomposing organisms present in forest and consequently a less strict division of decomposition between these rot-types (Swift, 1977). Another reason is probably the ability of white-rot fungi to decompose both cellulose and lignin (Swift, 1977; Renvall, 1995).

The parameter values of the extension describing woody litter decomposition (model III) and those of the basic Yasso07 model are characterized by probability densities (see Table 3 in Tuomi et al., 2009). These densities make it possible to calculate any uncertainty estimates for the output of the model caused by uncertainty about the parameter values, which in turn are inferred directly from the measurement uncertainty. Today, model-calculated estimates for mass loss of woody litter contribute to national and other greenhouse gas inventories (e.g. Liski et al., 2006), and they are also an important component in assessments of the total greenhouse gas effect of using harvest residues or other wood for energy production (e.g. Palosuo et al., 2001). These are examples of possible practice-oriented applications of our model in which the uncertainty estimates are particularly essential.

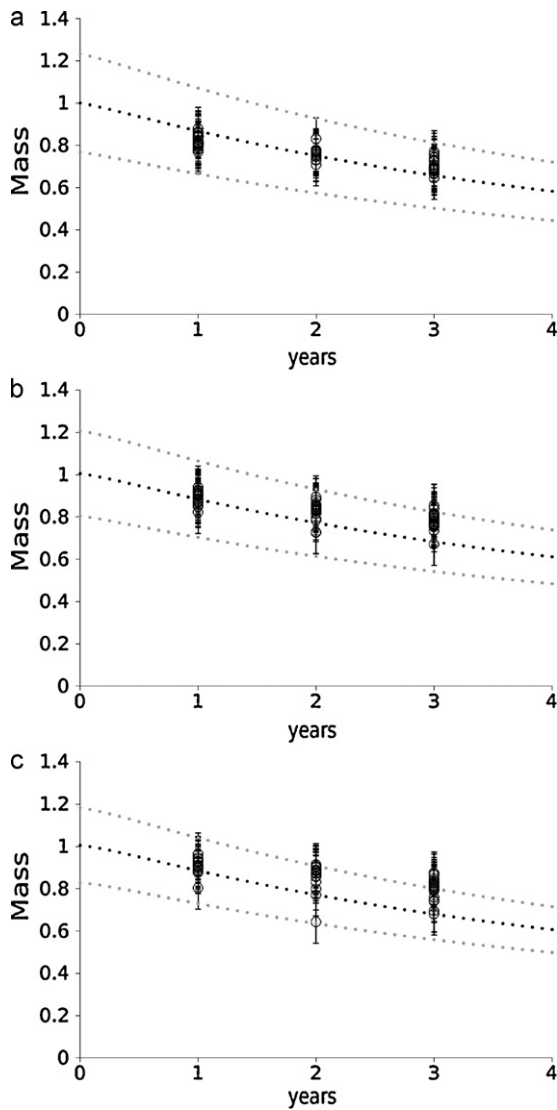


Fig. 4. Mass remaining estimates of decomposing branch litter: Scots pine (a), Norway spruce (b) and silver birch (c). The symbols represent measurements (Palviainen et al., 2004) and the dotted lines estimates calculated using model III (mean and 95 % limits shown).

In many earlier papers, wood decomposition has been described using a negative exponential model, commonly applied for non-woody litters (e.g. Olson, 1963). According to the results of the present study, the mass loss pattern of woody litter follows rather a sigmoidal model (Fig. 6). For some species, a sigmoidal mass loss pattern has also been observed earlier (e.g. Laiho and Prescott, 1999, 2004; Harmon et al., 2000). Means et al. (1992) suggested that the decomposition dynamics of woody litter can be divided into three phases: a slow initial phase, a relatively fast phase as labile carbon compounds and cellulose are decomposed, and a slow final phase of lignin decomposition. Our results imply that the sigmoidal pattern is related to the proportions of slowly decomposing ethanol-soluble and non-soluble fractions. The concentrations of these fractions are relatively high in woody litters, and their proportions increase with increasing diameter when the proportion of heartwood increases (e.g. Venäläinen et al., 2003). Thus, the sigmoidal mass loss pattern may be strengthened with increasing substrate diameter; while differences in initial chemical quality, especially that of heartwood, may introduce differences among tree species (see e.g. Harmon et al., 2000).

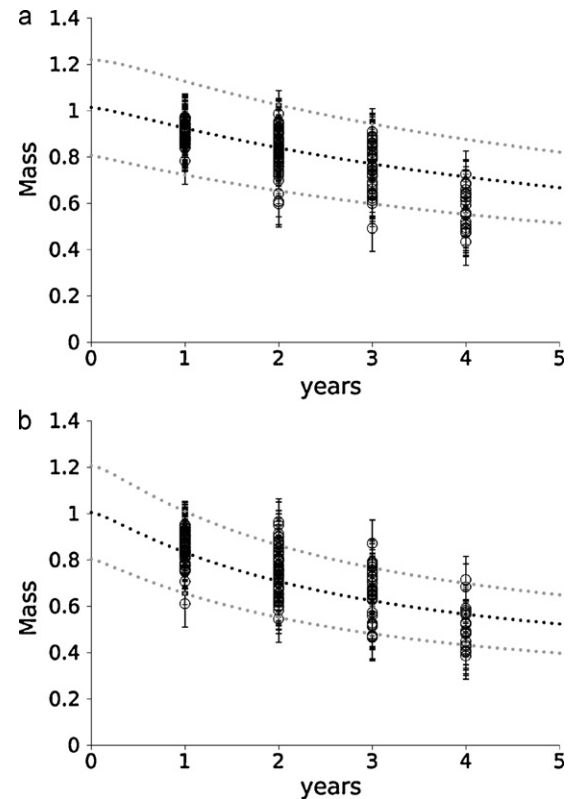


Fig. 5. Mass remaining estimates of decomposing Scots pine branch litter: diameter 0.5 cm (a) and diameter 3.0 cm (b). The symbols represent measurements (Vávřová et al., 2008) and the dotted lines estimates calculated using model III (mean and 95 % limits shown).

An increasing diameter has been suggested to slow down decomposition rates of woody litter also via physical resistance to fungal colonization, and moisture retention capacity (e.g. Harmon et al., 1986). The physical resistance is related to the structure of the woody tissues, and may vary among functional groups and species. Generally, hyphae can move through most vascular conduits, and it is the connections between them that may restrict fungal colonization (Cornwell et al., 2009). The type of wood that may structurally hinder colonization is generally also chemically more resistant to decay (see Cornwell et al., 2009), so it may be difficult to separate these effects. Yet, it seems that the effect may be adequately described using a rather simple suite of chemical parameters only – the AWEN chemical fractions, each described using a different compartment in the Yasso07 model and in this study.

Small-diameter litter dries faster than large-diameter litter, and lack of moisture may slow down decomposition of small-diameter litter (Erickson et al., 1985; Griffith and Boddy, 1990). In large-diameter trunks, moisture may, on the other hand, slow down oxygen diffusion and thus impede decomposition (Harmon et al., 1986). This could further contribute to a more sigmoidal mass loss pattern over time with increasing diameter. According to our results, the diameter-related mechanisms start to affect decomposition rates when the diameter exceeds 2 cm, while smaller-diameter woody litter decomposition is governed by the same driving forces as that of non-woody litter.

Woody litter is generally a good source of energy but a poor source of nutrients relative to other litters. Cord forming decomposer fungi may transfer nutrients to new high-energy resources such as woody litter from outside (soil or previously utilized other resources) (Boddy, 1999; Harris and Boddy, 2005; Fricker et al., 2008). However, low nutrient availability in the substrate partially diverts the investment of energy towards nutrient acquisition,

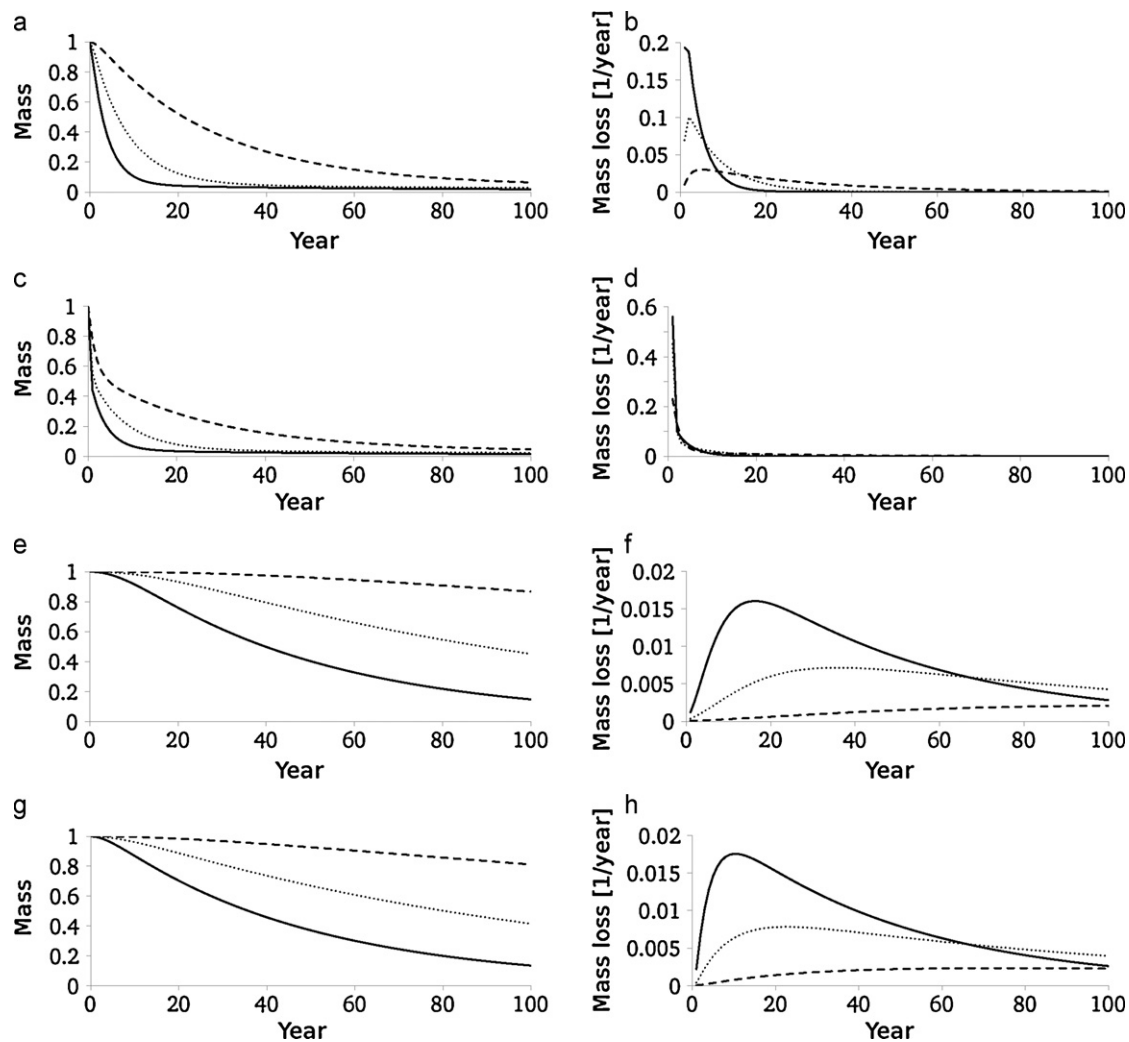


Fig. 6. Mass remaining (a, c, e and g) in and mass loss rate (b, d, f and h) of each AWEN fraction originating from non-woody litter (diameter 0 cm, continuous lines), branch-sized woody litter (5 cm, dotted lines) and stem-sized woody litter (30 cm, dashed lines) under climate conditions prevailing in boreal forests in southern Finland (mean annual temperature 3.5 °C, annual precipitation 535 mm) simulated using Yasso07 and model III for 100 years. (a and b) acid solubles; (c and d) water solubles; (e and f) ethanol solubles, and (g and h) the compounds that are neither soluble nor hydrolysable.

which may slow down decomposition (Sinsabaugh et al., 1993; Weedon et al., 2009). Our model implicitly involves an energy-based approach. Since the rate of wood decomposition often correlates positively with its N and P concentrations (Weedon et al., 2009), introduction of a nutrient-based rate regulator might still improve the model. However, the available measurements did not contain the necessary nutrient data for this purpose.

Acknowledgements

We are indebted to H. Mäkinen, M. Palviainen, and T. Penttilä for providing the measurements. We also thank P. Punttila for assistance. M. Tuomi and J. Liski were funded by the Maj and Tor Nessling Foundation (project “Soil carbon in Earth System Models”) and the Academy of Finland (project 107253).

References

Ågren, G.I., Bosatta, E., 1987. Theoretical analysis of the long-term dynamics of carbon and nitrogen in soil. *Ecology* 68, 1181–1189.
 Boddy, L., 1999. Saprotrophic cord-forming fungi: meeting the challenge of heterogeneous environments. *Mycologia* 91, 13–32.
 Clinton, P.W., Buchanan, P.K., Wilkie, J.P., Smail, S.J., Kimberley, M.O., 2009. Decomposition of *Nothofagus* wood in vitro and nutrient mobilization by fungi. *Canadian Journal of Forest Research* 39, 2193–2202.

Cornwell, W.K., Cornelissen, J.H.C., Allison, S.D., Bauhus, J., Eggleton, P., Preston, C.M., Scarff, F., Weedon, J.T., Wirth, C., Zanne, A.E., 2009. Plant traits and wood fates across the globe: rotted, burned, or consumed? *Global Change Biology* 15, 2431–2449.
 Erickson, H.E., Edmonds, R.L., Peterson, C.E., 1985. Decomposition of logging residues in Douglas-fir, western hemlock, Pacific silver fir, and ponderosa pine ecosystems. *Canadian Journal of Forest Research* 15, 914–921.
 Fricker, M.D., Lee, J.A., Bebb, D.P., Tlalka, M., Hynes, J., Darrah, P.R., Watkinson, S.C., Boddy, L., 2008. Imaging complex nutrient dynamics in mycelial networks. *Journal of Microscopy – Oxford* 231, 317–331.
 Griffith, G.S., Boddy, L., 1990. Fungal decomposition of attached angiosperm twigs: I. Decay community development in ash, beech and oak. *New Phytologist* 116, 407–415.
 Harmon, M., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15, 133–302.
 Harmon, M.E., Krankina, O.N., Sexton, J., 2000. Decomposition vectors: a new approach to estimating woody detritus decomposition dynamics. *Canadian Journal of Forest Research* 30, 76–84.
 Harris, M.J., Boddy, L., 2005. Nutrient movement and mycelial reorganization in established systems of *Phanerochaete velutina*, following arrival of colonized wood resources. *Microbial Ecology* 50, 141–151.
 Hastings, W., 1970. Monte Carlo sampling method using Markov chains and their applications. *Biometrika* 57, 97–109.
 Jeffreys, H., 1961. *The Theory of Probability*. The Oxford University Press.
 Kaipio, J., Somersalo, E., 2005. *Statistical and computational inverse problems*. Applied Mathematical Sciences, 160.
 Kass, R.E., Raftery, A.E., 1995. Bayes factors. *Journal of the American Statistical Association* 430, 773–795.

- Laiho, R., Prescott, C.E., 1999. The contribution of coarse woody debris to carbon, nitrogen, and phosphorus cycles in three Rocky Mountain coniferous forests. *Canadian Journal of Forest Research*, 29, 1592–1603.
- Laiho, R., Prescott, C.E., 2004. Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. *Canadian Journal of Forest Research* 34, 763–777.
- Liski, J., Palosuo, T., Peltoniemi, M., Sievänen, R., 2005. Carbon and decomposition model Yasso for forest soils. *Ecological Modelling* 189, 168–182.
- Liski, J., Lehtonen, A., Palosuo, T., Peltoniemi, M., Eggers, T., Muukkonen, P., Mäkipää, R., 2006. Carbon accumulation in Finland's forests 1922–2004 – an estimate obtained by combination of forest inventory data with modelling of biomass, litter and soil. *Annals of Forest Science* 63, 687–697.
- Mäkinen, H., Hynynen, J., Siitonen, J., Sievänen, R., 2006. Predicting the decomposition of scots pine, norway spruce and birch stems in Finland. *Ecological Applications* 16, 1865–1879.
- Means, J.E., MacMillan, P.C., Cromack Jr, K., 1992. Biomass and nutrient content of Douglas-fir logs and other detrital pools in an old-growth forest. *Canadian Journal of Forest Research* 22, 1536–1546.
- Metropolis, N., Rosenbluth, A.W., Rosenbluth, M.N., Teller, A.H., Teller, E., 1953. Equations of state calculations by fast computing machines. *Journal of Chemical Physics* 21, 1087–1092.
- Olson, J.S., 1963. Energy-storage and balance of producers and decomposers in ecological systems. *Ecology* 44, 322–331.
- Palosuo, T., Wihersaari, M., Liski, J., 2001. Net greenhouse gas emissions due to energy use of forest residues – impact on soil carbon balance. In: Pelkonen, P., Hakkila, P., Karjalainen, T., Schlamadinger, B. (Eds.), *Woody Biomass as an Energy Source – Challenges in Europe*. European Forest Institute Proceedings, 39, pp. 115–122.
- Palviainen, M., Finér, L., Kurka, A.-M., Mannerkoski, S., Piirainen, S., Starr, M., 2004. Decomposition and nutrient release from logging residues after clear-cutting of mixed boreal forest. *Plant and Soil* 263, 53–67.
- Parton, W.J., Schimel, D.S., Cole, C.V., Ojima, D.S., 1987. Analysis of factors controlling soil organic levels of grasslands in the Great Plains. *Soil Science Society of America Journal* 51, 1173–1179.
- Renvall, P., 1995. Community structure and dynamics of wood-rotting Basidiomycetes on decomposing conifer trunks in northern Finland. *Karstenia* 35, 1–51.
- Rock, J., Badeck, F.W., Harmon, M.E., 2008. Estimating decomposition rate constants for European tree species from literature sources. *European Journal of Forest Research* 127, 301–313.
- Siitonen, J., 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins* 49, 11–41.
- Shevliakova, E., Pacala, S.W., Malyshev, S., Hurtt, G.C., Milly, P.C.D., Caspersen, J.P., Sentman, L.T., Fisk, J.P., Wirth, C., Crevoisier, C., 2009. Carbon cycling under 300 years of land use change: Importance of the secondary vegetation sink. *Global Biogeochemical Cycles* 23, GB2022. doi:10.1029/2007GB003176.
- Sinsabaugh, R.L., Antibus, R.K., Linkins, A.E., McClaugherty, C.A., Rayburn, L., Weiland, T., 1993. Wood decomposition – nitrogen and phosphorus dynamics in relation to extracellular enzyme activity. *Ecology* 74, 1586–1593.
- Swift, M.J., 1977. The ecology of wood decomposition. *Science Progress (Oxford)* 64, 175–199.
- Tarasov, M.E., Birdsey, R.A., 2001. Decay rate and potential storage of coarse woody debris in the Leningrad Region. *Ecological Bulletin* 49, 137–147.
- Tuomi, M., Vanhala, P., Karhu, K., Fritze, H., Liski, J., 2008. Heterotrophic soil respiration – comparison of different models describing its temperature dependence. *Ecological Modelling* 211, 182–190.
- Tuomi, M., Thum, T., Järvinen, H., Fronzek, S., Berg, B., Harmon, M., Trofy-mow, J.A., Sevanto, S., Liski, J., 2009. Leaf litter decomposition – estimates of global variability based on Yasso07 model. *Ecological Modelling* 220, 3362–3371.
- Vávřová, P., Penttilä, T., Laiho, R., 2008. Decomposition of Scots pine fine woody debris in boreal conditions: implications for estimating carbon pools and fluxes. *Forest Ecology and Management* 257, 401–412.
- Venäläinen, M., Harju, A.M., Kainulainen, P., Viitanen, H., Nikulainen, H., 2003. Variation in the decay resistance and its relationship with other wood characteristics in old Scots pines. *Annals of Forest Science* 60, 409–417.
- Weedon, J.T., Cornwell, W.K., Cornelissen, J.H.C., Zanne, A.E., Wirth, C., Coomes, D.A., 2009. Global meta-analysis of wood decomposition rates: a role for trait variation among tree species? *Ecology Letters* 12, 45–56.
- Yin, X.W., 1999. The decay of forest woody debris: numerical modeling and implications based on some 300 data cases from North America. *Oecologia* 121, 81–98.