Leaf litter decomposition—Estimates of global variability based on Yasso07 model

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ABSTRACT

Litter decomposition is an important process in the global carbon cycle. It accounts for most of the heterotrophic soil respiration and results in formation of more stable soil organic carbon (SOC) which is the largest terrestrial carbon stock. Litter decomposition may induce remarkable feedbacks to climate change because it is a climate-dependent process. To investigate the global patterns of litter decomposition, we developed a description of this process and tested the validity of this description using a large set of foliar litter mass loss measurements (nearly 10,000 data points derived from approximately 70,000 litter bags). We applied the Markov chain Monte Carlo method to estimate uncertainty in the parameter values and results of our model called Yasso07. The model appeared globally applicable. It estimated the effects of litter type (plant species) and climate on mass loss with little systematic error over the first 10 decomposition years, using only initial litter chemistry, air temperature and precipitation as input variables. Illustrative of the global variability in litter mass loss rates, our example calculations showed that a typical conifer litter had 68% of its initial mass still remaining after 2 decomposition years in tundra while a deciduous litter had only 15% remaining in the tropics. Uncertainty in these estimates, a direct result of the uncertainty of the parameter values of the model, varied according to the distribution of the litter bag data among climate conditions and ranged from 2% in tundra to 4% in the tropics. This reliability was adequate to use the model and distinguish the effects of even small differences in litter quality or climate conditions on litter decomposition as statistically significant.

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1. Introduction

Litter decomposition plays a crucial role in the global carbon cycle. Carbon dioxide emissions from the decomposition of soil organic carbon (SOC) are equal to about 60 Pg of carbon per year, which is about seven times as much as the annual emissions of fossil carbon (IPCC, 2007). Most of these emissions originate from the decomposition of the relatively labile litter. Litter decomposition results also in formation of more stable organic compounds. These compounds represent the majority of all SOC (Davidson and Janssens, 2006), which is the largest terrestrial carbon stock, equal to about 2300 Pg (Jobbágy and Jackson, 2000), or three times the atmospheric carbon stock today (IPCC, 2007).

Litter decomposition will respond to changes in climate and, because of its great importance to the global carbon cycle, there may be remarkable feedbacks to the future climate change. Litter decomposition is also considered a complex process controlled by numerous other factors. To understand this process and to improve the estimates of the role of litter decomposition in the global carbon cycle, a global model of litter decomposition is needed.

A variety of approaches has been applied to estimate litter decomposition at large geographical scales. These approaches can be divided into three groups, (1) regression models based on litter bag studies (e.g. Meentemeyer, 1978; Berg et al., 1993; Trofymow et al., 2002; Zhang et al., 2007) or on soil respiration measurements (e.g. Lloyd and Taylor, 1994), (2) specific dynamic soil carbon

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models comprising of compartments (e.g. Parton et al., 1987; Jenkinson, 1990) or models based on a theory of continuous SOC quality (Bosatta and Ågren, 2003) and (3) less specific dynamic soil carbon models used for investigating the dynamics of nitrogen mineralization (Manzoni et al., 2007; Parton et al., 2007) or applied to national carbon accounting (e.g. Kurz and Apps, 2006; Liski et al., 2005) or to dynamic global vegetation models (e.g. Sitch et al., 2003) or earth system models (ESMs) (e.g. Jones et al., 2005).

A particular challenge in developing SOC decomposition models is that the internal SOC pools of the models and especially carbon fluxes between the pools cannot easily be determined from measurement data (Christensen, 1996; Elliott et al., 1996). Therefore, it is a common practice to make a decision of the fluxes first and then quantify the parameters determining the magnitudes of these fluxes based on measurement data (e.g. Moorhead et al., 1999).

To investigate the global patterns of litter decomposition, we wanted to avoid this uncertainty stemming from the prefixed model fluxes and assumed that any fluxes between the SOC pools of our model were possible. Then, we determined these fluxes and the values of all other model parameters directly from a global data set of litter mass loss measurements (Gholz et al., 2000; Trofymow et al., 1998; Berg et al., 1991a, b, 1993) using the Markov chain Monte Carlo (MCMC) method with Metropolis–Hastings algorithm (Metropolis et al., 1953; Hastings, 1970). We also required that the same parameter values should fit to the entire global data set so that our litter decomposition model would be applicable across climate conditions worldwide and to a wide variety of litter types.

Our aim was to calculate the full posterior probability density of model parameters, i.e. the joint probability density of all the free parameters in the model given the measurements. Possibilities to calculate such statistical uncertainty estimates have been lacking from previous SOC models although they are necessary if we want to evaluate the reliability of model results in a statistical sense. The uncertainty estimates can only be calculated in a meaningful way if the model is not over-parameterized. When building the model we required that there were no modelling errors introduced by over-parameterization. We also required that the model we developed fulfilled the Occamian principle of parsimony, which means that we chose the simplest model structure from a set of almost equally good alternatives. These requirements were made to find a reliable model whose prediction uncertainties are known reliably.

The objectives of this study were, first, to develop a global model of foliage litter decomposition that met the above requirements, and second, to estimate the global patterns of foliage litter decomposition and their uncertainty using this model.

2. Materials and methods

2.1. Measurements

To develop the global model of foliage litter decomposition, we used litter bag data from 97 sites across Europe, and North and Central America (Table 1). The data from the USA and Central America were collected within the LIDET network (Gholz et al., 2000) and the data from Canada within the CIDET network (Trofymow et al., 1998), whereas the data from Europe originated from several research projects (Berg et al., 1991a, b, 1993). The study sites covered a wide range of climate conditions in terms of temperature and precipitation (Fig. 1 a), which are the most important climate factors affecting litter decomposition (Meentemeyer, 1978; Berg et al., 1993; Aerts, 1997; Liski et al., 2003; Parton et al., 2007).

The litter bag datasets consisted of measurements for foliage litter of 34 plant species including several coniferous and deciduous trees (Table 2). The initial chemical composition was measured
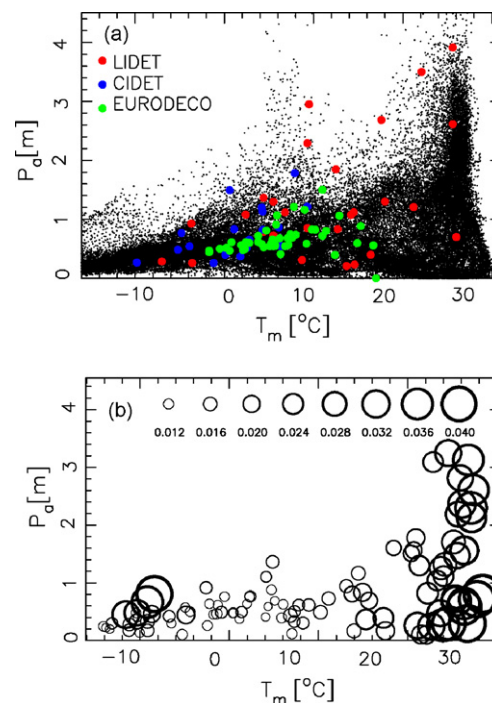

Fig. 1. (a) Distribution of the global climate conditions on land (black dots) from the CRU 2.1 database (New et al., 2002) and the 97 litterbag measurement sites (LIDET sites red, CIDET sites blue and EURODECO sites green). Variables T_m and P_a are the mean annual temperature and annual precipitation, respectively. LIDET, CIDET and EURODECO measurement sites are in the USA and Central America, Canada, and Europe, respectively. (b) 95% confidence intervals as a function of climate for estimates of mass remaining after 2 years of decomposition (a unitary initial mass) calculated using the Yasso07 model. The error is shown for 100 randomly selected climatic conditions. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

for each litter type and the loss of mass was followed for 3.1–10.2 years (Gholz et al., 2000; Trofymow et al., 1998; Berg et al., 1991a, b, 1993). In addition to the total mass loss, the mass loss of chemical compound groups was measured at seven Swedish study sites (Berg et al., 1991a, b). Together the datasets comprised 9605 data points. The LIDET data consisted of values for individual litter bags, whereas the Canadian data points were averages of 4 litter bags collected at the same time (Trofymow et al., 2002). Most of the European data points were averages of 25 litter bags (Berg et al., 1991a, b). Thus, the data was received using approximately 70,000 litter bags.

In addition to the litter bag data, we used a dataset on accumulation of SOC at 26 sites along a 5500 year long soil chronosequence in southern Finland (Liski et al., 1998, 2005). This data provided us with both information on formation of humus from decomposing litter and humus decomposition.

2.2. The model

The Yasso07 model developed in this study is a generalization of an earlier Yasso soil carbon model (Liski et al., 2005). Yasso07 is based on three assumptions of litter decomposition:

(1) Non-woody litter consists of four compound groups, i.e. compounds soluble in a non-polar solvent, ethanol or dichloromethane (denoted using E), or in water (W), and compounds hydrolysable in acid (A) and neither soluble nor hydrolyzable at all (N). Each group has its own mass loss rate independent of the origin of the litter. These compound groups are called the labile groups.

Table 1
The litter bag study sites.

Dataseries	Latitude [°]	Longitude [°]	Elevation [m]	Ecosystem	Dataseries	Latitude [°]	Longitude [°]	Elevation [m]	Ecosystem
LIDET	44.23	−122.18	500	Temperate Coniferous	EURODECO	60.63	13.62	400	Boreal
LIDET	68.63	−149.57	760	Alpine Grassland	EURODECO	66.37	20.03	405	Boreal
LIDET	9.17	−79.85	30	Wet Tropical	EURODECO	48.28	2.68	83	Temperate
LIDET	64.75	−148.00	300	Boreal Coniferous	EURODECO	59.63	14.97	178	Boreal
LIDET	38.87	−105.65	1300	Temperate Coniferous	EURODECO	43.67	7.97	447	Mediterranean
LIDET	45.40	−93.20	230	Humid Grassland	EURODECO	52.68	23.78	165	Temperate
LIDET	40.82	−104.77	1650	Dry Grassland	EURODECO	59.12	15.73	70	Boreal
LIDET	35.00	−83.50	700	Temperate Deciduous	EURODECO	38.12	−6.20	2	Mediterranean
LIDET	17.95	−65.87	80	Dry Tropical	EURODECO	64.30	16.33	330	Boreal
LIDET	43.93	−71.75	300	Temperate Deciduous	EURODECO	52.03	5.70	45	Temperate
LIDET	42.53	−72.17	335	Temperate Deciduous	EURODECO	53.00	9.95	81	Temperate
LIDET	32.50	−106.75	1410	Shrubland	EURODECO	41.78	−5.43	760	Mediterranean
LIDET	58.00	−134.00	100	Boreal Coniferous	EURODECO	56.43	14.58	140	Boreal
LIDET	42.40	−85.40	288	Agriculture	EURODECO	39.42	9.25	80	Mediterranean
LIDET	39.08	−96.58	366	Humid Grassland	EURODECO	39.33	16.45	1210	Mediterranean
LIDET	10.00	−83.00		Wet Tropical	EURODECO	58.55	15.85	58	Boreal
LIDET	18.32	−65.82	350	Wet Tropical	EURODECO	52.47	13.23	35	Temperate
LIDET	40.28	−105.65	3160	Alpine Forest	EURODECO	59.73	14.55	220	Boreal
LIDET	10.30	−84.80	1550	Wet Tropical	EURODECO	66.13	20.88	58	Boreal
LIDET	33.50	−79.22	2	Saltmarsh Wetland	EURODECO	60.27	16.08	185	Boreal
LIDET	46.00	−89.67	500	Temperate Coniferous	EURODECO	60.82	16.50	185	Boreal
LIDET	40.05	−105.60	3650	Alpine Grassland	EURODECO	60.55	13.73	375	Boreal
LIDET	47.83	−123.88	150	Temperate Coniferous	EURODECO	69.75	27.02	90	Boreal
LIDET	34.33	−106.67	1572	Shrubland	EURODECO	59.52	17.27	30	Boreal
LIDET	33.50	−117.75	500	Shrubland	EURODECO	50.57	5.98	370	Temperate
LIDET	29.75	−82.50	35	Temperate Coniferous	EURODECO	65.78	20.62	135	Boreal
LIDET	37.50	−75.67	0	Saltmarsh Wetland	EURODECO	57.42	15.67	105	Boreal
CIDET	52.72	−106.12	472	Cool Temperate Steppe	EURODECO	60.23	17.47	580	Boreal
CIDET	49.53	−57.83	50	Cool Temperate Subalpine Moist/Wet Forest	EURODECO	56.60	13.25	135	Boreal
CIDET	47.63	−83.23	460	Cool Temperate Subalpine Moist/Wet Forest	EURODECO	52.33	22.98	142	Temperate
CIDET	48.92	−54.57	115	Cool Temperate Subalpine Moist/Wet Forest	EURODECO	41.10	14.60	1100	Mediterranean
CIDET	56.32	−94.85	140	Boreal Moist/Wet Forest	EURODECO	57.20	12.58	155	Boreal
CIDET	56.32	−94.85	125	Boreal Moist/Wet Forest	EURODECO	64.35	19.77	260	Boreal
CIDET	50.55	−118.83	650	Cool Temperate Moist Forest	EURODECO	60.58	13.57	435	Boreal
CIDET	68.32	−133.53	73	Boreal Moist Forest	EURODECO	50.52	20.63	191	Temperate
CIDET	51.00	−115.00	1530	Warm Temperate Subalpine Wet Forest	EURODECO	58.40	13.65	128	Boreal
CIDET	45.42	−73.95	48	Cool Temperate Moist Forest	EURODECO	52.57	5.78	−5	Temperate
CIDET	47.32	−71.13	670	Cool Temperate Subalpine Rainforest	EURODECO	58.07	14.13	245	Boreal
CIDET	55.92	−98.62	288	Cool Temperate Subalpine Moist/Wet Forest	EURODECO	32.82	21.85	600	Tropical Dry
CIDET	55.92	−98.62	260	Cool Temperate Subalpine Moist/Wet Forest	EURODECO	32.82	21.85	300	Tropical Dry
CIDET	53.22	−105.97	476	Cool Temperate Moist Forest	EURODECO	66.53	20.18	280	Boreal
CIDET	45.92	−77.58	173	Cool Temperate Moist Forest	EURODECO	60.92	14.02	350	Boreal
CIDET	50.60	−127.33	100	Cool Temperate Wet Forest	EURODECO	40.82	14.48	250	Mediterranean
CIDET	54.87	−66.65	500	Cool Temperate Subalpine Rain Tundra/Wet Forest	EURODECO	59.82	16.55	63	Boreal
CIDET	48.63	−123.70	355	Cool Temperate Wet Forest	EURODECO	56.40	13.08	80	Boreal
CIDET	51.83	−104.92	536.5	Cool Temperate Steppe	EURODECO	58.10	13.28	135	Boreal
CIDET	54.60	−126.30	1100	Cool Temperate Subalpine Moist Forest	EURODECO	63.22	14.47	325	Boreal
CIDET	60.85	−135.20	667	Cool Temperate Subalpine Moist Forest	EURODECO	55.65	13.32	46	Boreal
EURODECO	42.73	−8.75	530	Mediterranean					

Table 2

The properties of litter bag datasets used to calculate the Yasso07 model solution: litter species, numbers of measurements (N_m) measurement timelines (Δt), ranges of mean annual temperature ($T_{m,min}$, $T_{m,max}$), amplitude of annual temperature variations ($T_{a,min}$, $T_{a,max}$) and precipitation ($P_{a,min}$, $P_{a,max}$), and initial nitrogen contents (N-cont.). Data sets with chemical composition measured as a function of time are denoted by ⋆.

Name	Species	N_m	Δt [a]	$T_{m,min}$ [°C]	$T_{m,max}$ [°C]	$T_{a,min}$ [°C]	$T_{a,max}$ [°C]	$P_{a,min}$ [m]	$P_{a,max}$ [m]	N-cont. [%]	Reference
spine*	*Pinus sylvestris*	1196	5.42	3.8	3.8	11.4	11.4	0.722	0.722	0.40	Berg et al. (1991a,b)
lpine*	*Pinus contorta*	128	3.97	3.8	3.8	11.4	11.4	0.722	0.722	0.40	Berg et al. (1991a,b)
birch*	*Betula pubescens*	148	4.00	3.8	3.8	11.4	11.4	0.722	0.722	0.70	Berg et al. (1991a,b)
harad*	*Pinus sylvestris*	256	4.00	1.3	1.3	12.2	12.2	0.650	0.650	0.40	Berg et al. (1991a,b)
manja*	*Pinus sylvestris*	240	3.00	1.0	1.0	13.1	13.3	0.700	0.700	0.40	Berg et al. (1991a,b)
norrl*	*Pinus sylvestris*	176	3.33	1.2	1.2	11.8	11.8	0.595	0.595	0.40	Berg et al. (1991a,b)
nenne*	*Pinus sylvestris*	236	3.06	6.2	6.2	9.8	9.8	0.930	0.930	0.40	Berg et al. (1991a,b)
acsal	*Acer saccharum*	695	10.05	−7.0	26.0	0.8	20.7	0.209	3.914	0.81	Gholz et al. (2000)
ambrl	*Ammophila breviligulata*	21	10.22	−3.6	22.1	2.0	20.7	0.260	3.500	0.67	Gholz et al. (2000)
angel	*Andropogon gerardii*	35	9.75	−7.0	26.0	2.1	15.8	0.284	1.847	0.62	Gholz et al. (2000)
aspnl	*Populus tremuloides*	126	6.09	−9.8	9.3	5.3	20.5	0.261	1.783	0.61	Trofymow et al. (1998)
beecl	*Fagus grandifolia*	125	6.09	−9.8	9.3	5.3	20.5	0.261	1.783	0.66	Trofymow et al. (1998)
belul	*Betula lutea*	24	8.98	−3.7	26.0	2.0	17.4	0.700	3.500	1.60	Gholz et al. (2000)
boerl	*Bouteloua eriopoda*	35	8.04	−7.0	25.6	0.9	20.7	0.233	3.914	0.86	Gholz et al. (2000)
bogrl	*Bouteloua gracilis*	35	8.01	−7.0	25.6	0.8	17.4	0.209	2.952	0.96	Gholz et al. (2000)
bsprl	*Picea mariana*	126	6.09	−9.8	9.3	5.3	20.5	0.261	1.783	0.70	Trofymow et al. (1998)
cedal	*Thuja plicata*	126	6.09	−9.8	9.3	5.3	20.5	0.261	1.783	0.59	Trofymow et al. (1998)
cegrl	*Ceanothus greggii*	32	9.00	6.8	26.0	0.8	13.8	0.700	2.952	1.33	Gholz et al. (2000)
conul	*Cornus nuttalii*	20	9.75	5.5	25.6	0.9	13.8	0.310	3.914	0.81	Gholz et al. (2000)
dfirl	*Pseudotsuga menziesii*	126	6.09	−9.8	9.3	5.3	20.5	0.261	1.783	0.65	Trofymow et al. (1998)
drgll	*Drypetes glauca*	623	10.05	−7.0	26.0	0.8	20.7	0.209	3.914	1.97	Gholz et al. (2000)
fagrl	*Fagus grandifolia*	43	7.99	−7.0	25.6	0.8	17.4	0.284	2.952	0.85	Gholz et al. (2000)
fernl	*Pteridium aquilinum*	126	6.09	−9.8	9.3	5.3	20.5	0.261	1.783	0.82	Trofymow et al. (1998)
fescl	*Festuca hallii*	126	6.09	−9.8	9.3	5.3	20.5	0.261	1.783	0.64	Trofymow et al. (1998)
jpinl	*Pinus banksiana*	126	6.09	−9.8	9.3	5.3	20.5	0.261	1.783	1.25	Trofymow et al. (1998)
komyl	*Kobresia myosuroides*	20	10.04	−3.6	25.6	0.9	20.7	0.233	3.914	1.07	Gholz et al. (2000)
latrl	*Larrea tridentata*	42	7.07	−7.0	26.0	0.8	15.5	0.233	3.500	2.14	Gholz et al. (2000)
litul	*Liriodendron tulipifera*	25	8.03	−3.6	22.1	2.0	20.7	0.260	3.500	0.72	Gholz et al. (2000)
lpilb	*Pinus contorta*	623	4.00	0.6	9.8	7.7	15.1	0.469	0.911	0.40	Berg et al. (1993)
piell	*Pinus elliottii*	187	10.00	−7.0	26.0	0.8	20.7	0.260	3.914	0.36	Gholz et al. (2000)
pirel	*Pinus resinosa*	536	10.22	−7.0	25.6	0.9	20.7	0.209	3.914	0.59	Gholz et al. (2000)
pistl	*Pinus strobus*	25	10.05	−7.0	12.7	9.0	15.5	0.284	2.291	0.62	Gholz et al. (2000)
psmel	*Pseudotsuga menziesii*	32	7.99	−7.0	18.0	9.0	15.5	0.284	2.291	0.82	Gholz et al. (2000)
quprl	*Quercus prinus*	685	10.22	−7.0	26.0	0.8	20.7	0.209	3.914	1.03	Gholz et al. (2000)
rhmal	*Rhododendron macrophyllum*	114	9.03	−7.0	25.6	0.8	15.8	0.233	3.914	0.42	Gholz et al. (2000)
spall	*Spartina alterniflora*	61	9.04	−7.0	26.0	0.8	20.7	0.260	3.914	0.71	Gholz et al. (2000)
spilb	*Pinus sylvestris*	672	5.39	−1.7	16.7	4.8	15.1	0.443	1.500	0.40	Berg et al. (1993)
tamml	*Larix laricina*	126	6.09	−9.8	9.3	5.3	20.5	0.261	1.783	0.56	Trofymow et al. (1998)
thpll	*Thuja plicata*	675	10.22	−7.0	26.0	0.8	20.7	0.209	3.914	0.62	Gholz et al. (2000)
trael	*Triticum aestivum*	706	10.22	−7.0	26.0	0.8	20.7	0.209	3.914	0.38	Gholz et al. (2000)
wbirl	*Betula papyrifera*	126	6.09	−9.8	9.3	5.3	20.5	0.261	1.783	0.70	Trofymow et al. (1998)

(2) The mass loss rates of the compound groups depend on the climatic conditions that can be described simply by using temperature and precipitation.

(3) Decomposition of the compound groups results in mass loss from the system and in mass flows between the compound groups. In addition, the mass loss of the four compound groups results in formation of more recalcitrant humus (H).

The first assumption is justified by earlier studies showing that the above chemical groups decompose at different rates (Berg et al., 1982), and that this grouping differentiates litter types according to decomposition rate (Palosuo et al., 2005). The second assumption was based on results of several earlier studies (e.g. Meentemeyer, 1978; Berg et al., 1993; Aerts, 1997; Liski et al., 2003; Parton et al., 2007). The third assumption follows from a general view on carbon cycling in soil that involves transformations of organic compounds. This includes the break-down of complex compounds and the formation of simpler ones in chemical decomposition reactions, which are catalyzed by enzymes excreted by soil microbes; the uptake of the simplest compounds by soil microbes; and the formation of carbon dioxide and synthesis of biomass in the metabolism of soil microbes.

Yasso07 was formulated according to these hypotheses. All parameter values were treated as free parameters when the model was fitted to the data. Hence, Yasso07 is a set of first order differ-

ential equations and defined as:

$$\dot{\mathbf{x}}(t) = \mathbf{A}(\mathbf{C})\mathbf{x}(t) + \mathbf{b}(t), \quad \mathbf{x}(0) = \mathbf{x}_0 \qquad (1)$$

where $\mathbf{x} = (x_A, x_W, x_E, x_N, x_H)^T$ is a vector describing the masses of the five compartments as a function of time (t); $\mathbf{A}(\mathbf{C})$ is a matrix describing the decomposition rates and the mass flows between the compartments as a function of climatic conditions ($\mathbf{C}$); vector $\mathbf{b}(t)$ is the litter input to the soil. Vector $\mathbf{x}_0 = (x_{A,0}, x_{W,0}, x_{E,0}, x_{N,0}, x_{H,0})$ is the initial state of the system and $x_{i,0}$ the initial chemical composition, with i referring to A, W, E, N and H. Matrix $\mathbf{A}$ is defined as a product of the mass flow matrix $\mathbf{A}_p$ and the diagonal decomposition coefficient matrix $\mathbf{k}(\mathbf{C}) = \mathrm{diag}(k_A, k_W, k_E, k_N, k_H)(\mathbf{C})$, where k_i are the decomposition rate coefficients of the compartments. The mass flow matrix is defined as:

$$\mathbf{A}_p = \begin{pmatrix} -1 & p_1 & p_2 & p_3 & 0 \\ p_4 & -1 & p_5 & p_6 & 0 \\ p_7 & p_8 & -1 & p_9 & 0 \\ p_{10} & p_{11} & p_{12} & -1 & 0 \\ p_H & p_H & p_H & p_H & -1 \end{pmatrix}, \qquad (2)$$

where $p_i \in [0, 1]$ are the relative mass flow parameters between the compartments. It is further assumed that $k_i = k_i(\mathbf{C})$, for all i, and that the sum of parameters p_i, describing the mass flows out of any of the compartments, does not exceed unity. This mass flow matrix

was selected because all the possible flows between A, W, E and N are present. This is the most general model structure that can still be presented as a linear differential equation (Eq. 1).

The climate dependence of the decomposition rate factors k_i is formulated as:

$$k_i(\mathbf{C}) = \alpha_i \exp(\beta_1 T + \beta_2 T^2)(1 - \exp[\gamma P_a]), \tag{3}$$

where T is temperature (Celcius scale) and P_a is the annual precipitation and α_i, β_1, β_2 and γ are free parameters. This form of the temperature dependence was justified earlier by Tuomi et al. (2008).

We also tried to determine the separate values of these free parameters for each compound group, but it resulted in an over-parameterized model and a lower posterior probability. This happened because mass loss was measured by compound group only at the Swedish study sites (see Table 2). Consequeuntly, we had to apply the same parameter values for each compound group.

The intra-annual variations in temperature resulting from seasonal changes were approximated by using a sinusoid:

$$T(t) = T_m + T_a \sin\left(\frac{2\pi t}{t_P}\right), \tag{4}$$

where $T_a = (1/2)(T_{m,\max} - T_{m,\min})$ and $T_{m,\max}$ and $T_{m,\min}$ are the maximum and minimum mean monthly temperatures, respectively, and t_P is the period of 1 year.

The full inverse solution, i.e. the probability density of the parameter vector θ, was found by sampling the parameter space with the MCMC method. After a burn-in period, the proposal density was constructed to allow for the convergence of the chain to the posterior density with an acceptance rate of approximately 0.3. With the full probability density available, we then calculated the maximum *a posteriori* (MAP) point estimate and Bayesian 95% confidence set for the model parameter vector.

When calculating the posterior density, we used a Gaussian likelihood function for the measurements, such that:

$$f(\theta|m) \propto \exp\left(-\frac{1}{2}\sum_i \omega_i S_i\right)\pi(\theta), \tag{5}$$

where $f(\theta|m)$ is the conditional posterior density of the model parameters with the condition that measurements $m = (m_1, \ldots, m_i, \ldots)$ have been made and $\pi(\theta)$ is the prior density of the parameters. Variable S_i is the common sum of squared residuals of measurement set m_i and ω_i is some relative weight of measurements m_i. These weights were set to balance between data sets with large number of measurements containing little information and data sets with few measurements but high information content.

Finding the MAP estimate is equal to finding $\hat{\theta}$ that approximately satisfies the conditions:

$$\hat{\theta} = \underset{\theta}{\arg\min} \sum_i \omega_i S_i \tag{6}$$

and

$$\hat{\theta} = \underset{\theta}{\arg\min} S_i \tag{7}$$

for all the data sets m_i simultaneously. The weights ω_i were selected so that the latter condition is satisfied as well. This is basically made to extract all the information on model parameters from the measurements and to make sure that there is as little systematic error between the model and any of the measurement sets as possible.

We chose not to calculate the standard goodness-of-fit measures, the r^2-values for the different datasets, because they provide no extra information in addition to the residuals between model with MAP parameter values and measurements. Also, to use the r^2-values, they should be compared with corresponding values calculated using different models. As there are no other models that predict the climate dependent time-evolution of the A, W, E, N and H compounds, this comparison could not be made.

We tested several alternative structures within the model framework set by our three assumptions, such as different precipitation dependence functions or different temperature or precipitation dependences for the different compound sets. These structures were compared using the model probabilities according to the Bayesian model selection theory, which automatically contains the Occam's razor and therefore penalises unnecessarily complicated model structures. These probabilities were defined as:

$$P(g_j|m) = \frac{P(m|g_j)P(g_j)}{\sum_k P(m|g_k)P(g_k)},$$

$$P(m|g_j) = \int_{\theta_j \in \Omega_j} f(m|\theta_j, g_j)\pi(\theta_j|g_j)d\theta_j \tag{8}$$

where g_j is the jth model structure, $\theta_j \in \Omega_j$ are its parameters, $P(g_j|m)$ is its likelihood and $P(g_j)$ its prior probability. These prior probabilities were all set equal. We simply selected the structure that has the highest probability according to Eq. (8) with respect to all the measurements available. Despite that Bayesian methods have proven usefull in several statistical problems (e.g. Ellison, 2004; Lichter et al., 2005; Tuomi et al., 2008), according to our knowledge, this is the first time Bayesian methods are applied to the decomposition process of foliage litter.

When fitting the parameters of Yasso07 model to the data, we noticed that the level of mass loss rate was higher in the European litter bag measurements compared to the North or Central American ones. The same difference has been observed already earlier (Palosuo et al., 2005). It is probably caused by a larger mesh size and smaller litter mass used in the European litter bags. This may have caused more leaching and thus overestimates of mass loss in Europe. To account for this difference, we introduced a scaling factor to the model and determined its value together with the other parameter values. This scaling factor had a narrow normal distribution with a mean equal to 0.58 and 95% of the probability distribution between 0.56 and 0.60. The need to include the scaling factor in the analysis adds uncertainty to the results of this study. However, this uncertainty is related mostly to the estimated level of decomposition, whereas the estimated effects of climate and litter quality on decomposition are less dependent on the litter bag type. This happens because there were no systematic differences in the climate or litter quality effects between Europe and North and Central America despite the differences in the litter bags.

3. Results

We were able to establish a global description of foliage litter decomposition process using the large data set of litter bag measurements and advanced mathematical methods of complex inverse problems.

The model fitted the data with little systematic error with respect to any variable investigated. The residuals, i.e. the differences between model-calculated estimates and measurements, did not deviate significantly from zero for 31 litter types out of 34 when looking at the 68% confidence intervals (Fig. 2 a). With a 95% confidence level, none of the litter types deviated from zero (not shown) For one of the deviating types (*Kobresia myosuroides*), there were only 20 data points, which makes it more probable that these measurements deviated by pure chance. The residuals were not correlated with either the time elapsed since the start of decom-
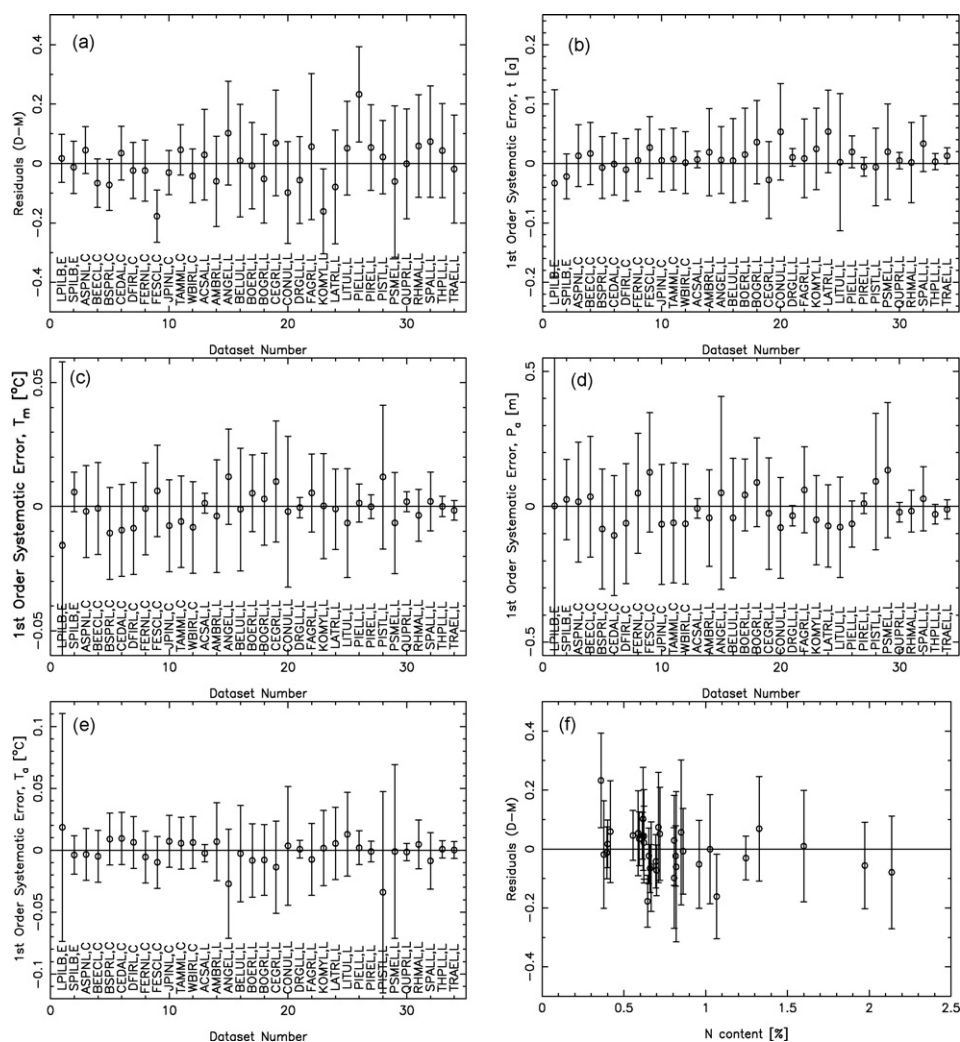
Fig. 2. Model residuals (data−model) by litter type (a), linear 1st order systematic trends in the residuals by litter type as a function of time since the start of decomposition (b), annual mean temperature (c), annual precipitation (d), difference between the coldest and warmest months of the year (e), and the residuals as a function of the initial nitrogen concentration of the litter types (f). The error bars are 1σ values, and thus they cover 68% of the probability density. Letters E, C and L after dataset names refer to EURODECO, CIDET and LIDET, respectively.

Table 3
Maximum *a posteriori* parameter values of Yasso07 and the 95% confidence limits.

| Parameter	Value	Unit	Interpretation
α_A	0.66 ± 0.11	a^{-1}	Decomposition rate parameter of A
α_W	$4.3 + 1.6, 4.3 - 1.0$	a^{-1}	Decomposition rate parameter of W
α_E	0.35 ± 0.08	a^{-1}	Decomposition rate parameter of E
α_N	0.22 ± 0.06	a^{-1}	Decomposition rate parameter of N
p_1	0.32 ± 0.08	–	Relative mass flow magnitude, W → A
p_2	$0.01 + 0.14, 0.01 - 0.01$	–	Relative mass flow magnitude, E → A
p_3	$0.93 + 0.03, 0.93 - 0.11$	–	Relative mass flow magnitude, N → A
p_4	$0.34 + 0.18, 0.34 - 0.15$	–	Relative mass flow magnitude, A → W
p_5	$0.00 + 0.07, 0.00 - 0.00$	–	Relative mass flow magnitude, E → W
p_6	$0.00 + 0.07, 0.00 - 0.00$	–	Relative mass flow magnitude, N → W
p_7	$0.00 + 0.01, 0.00 - 0.00$	–	Relative mass flow magnitude, A → E
p_8	$0.00 + 0.01, 0.00 - 0.00$	–	Relative mass flow magnitude, W → E
p_9	$0.01 + 0.07, 0.01 - 0.01$	–	Relative mass flow magnitude, N → E
p_{10}	$0.00 + 0.01, 0.00 - 0.00$	–	Relative mass flow magnitude, A → N
p_{11}	$0.00 + 0.06, 0.00 - 0.00$	–	Relative mass flow magnitude, W → N
p_{12}	$0.92 + 0.04, 0.92 - 0.15$	–	Relative mass flow magnitude, E → N
β_1	7.6 ± 2.0	$10^{-2}\,^{\circ}C^{-1}$	Temperature dependence parameter
β_2	-8.9 ± 6.5	$10^{-4}\,^{\circ}C^{-2}$	Temperature dependence parameter
γ	-1.27 ± 0.20	m^{-1}	Precipitation dependence parameter
p_H	0.040 ± 0.009	–	Mass flow to humus
α_H	$3.3 + 0.6, 3.3 - 0.7$	$10^{-3}\,a^{-1}$	Humus decomposition coefficient
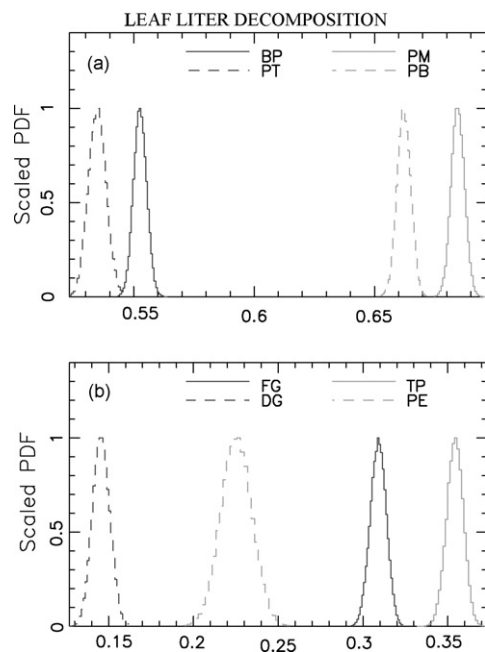
Fig. 3. Probability densities of Yasso07 estimates for litter mass-remaining after 2 years of decomposition (a unitary initial mass) in different climate zones. A characteristic coniferous and deciduous species selected for each climate zone, tundra *Picea mariana* (PM) and *Betula papyrifera* (BP), the boreal zone *P inus banksiana* (PB) and *Populus tremuloides* (PT), the temperate zone *Thuja plicata* (TP) and *Fagus grandifolia* (FG), and the tropics *Pinus elliottii* (PE) and *Drypetes glauca* (DG). The latitude, longitude, T_m, T_a and P_a of these sites are: tundra 56.32°, −94.85°, −4.0 °C, 10.1 °C, 0.50 m; the boreal zone 53.22°, −105.97°, −2.4 °C, 9.7 °C, 0.59 m; the temperate zone 35.00°, −83.50° 13.9° C 5.1 °C, 1.72 m; the tropics 9.17°, −79.85°, 26.0 °C, 0.6 °C, 2.86 m.

position or any climate variable (Fig. 2 b-e). The residuals were also uncorrelated with the initial nitrogen concentration of the litter species despite the fact that we did not include the effect of nitrogen in the model (Fig. 2f). The nitrogen concentration ranged from 0.3 to 2.2%. The lack of systematic error means that the description of foliage litter decomposition in the model is, on average, valid for the global climate conditions and the range of litter characteristics covered by the litter bag data. The error in the results of the model is thus of random nature which can be characterized by probability densities with zero mean.

Fitting the model to the data revealed that there were four major carbon fluxes between the labile compartments (Table 3). Two of them were towards the compartments with higher decomposition rates representing breakdown of complex compounds and formation of simpler and labile ones during the decomposition process. The other two were towards the other direction indicating a re-synthesis of more complex compounds in the process. The other fluxes between the labile compartments were negligible. Four percent of the combined mass loss of the labile compartments resulted in humus formation.

The decomposition rates were significantly different between the five compound groups included in the model (Table 3). The decomposition rate of the water soluble compounds was an order of magnitude higher than the corresponding rates of the other three labile compound groups. Among these groups, the decomposition rates decreased from the acid hydrolyzable compounds to the non-polar extractable and the acid unhydrolyzable compounds. The decomposition rate of the humus compartment was two orders of magnitude lower.

The calculated estimates for the mass-loss rates of foliage litter were statistically significantly different among sites selected to represent tundra, the boreal zone, the temperate zone and the tropics and, within each site, among a typical coniferous and deciduous litter types (Fig. 3). The probability densities of these estimates represent uncertainty caused by uncertainty about the parameter values of the model. The uncertainties of model predictions in Fig. 1 b show the magnitude of 95% confidence intervals as a function of climatic conditions for a decomposing body with an unitary initial mass. This uncertainty followed the distribution of the litter bag data across the global climate conditions (Fig. 1). It was smallest for the boreal and temperate zones where most of the study sites were located, and largest for the coldest tundra and the tropics which had only a few study sites.

Illustrative of the global variability in the mass-loss rate of foliage litter, the coniferous litter of tundra (*Picea mariana* needles) had about 68% of its mass still remaining after two years of decomposition, while the deciduous litter of the tropics (*D rypetes glauca* leaves) had only about 15% remaining (Fig. 3). The values of the decomposition rate parameters of the model were up to 13 times higher in the tropics compared to the northern boreal zone (Fig. 4). The decomposition rates are not directly comparable to the mass loss rates because decomposition results also in transfer of carbon between the compartments inside the model.
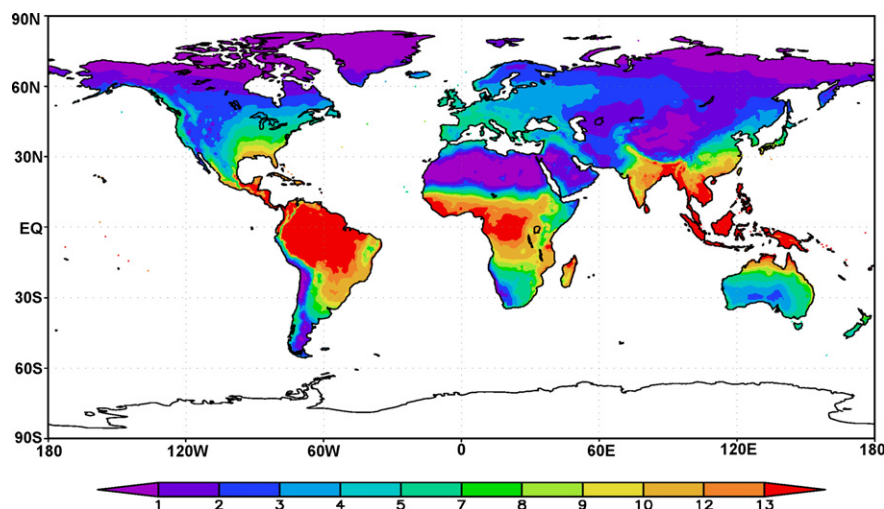

Fig. 4. Estimated geographic variations in the leaf litter decomposition rate. A unitary rate corresponds to climatic conditions where $T_m = 0$ °C, $T_a = 0$° C and P_a is sufficiently large to not limit the decomposition.

4. Discussion and conclusions

The aim of this study was to estimate the global patterns of foliage litter decomposition after developing an appropriate model for this purpose. We required that the model was globally applicable and the results were accompanied by uncertainty estimates.

We found that the results of the Yasso07 model did not deviate systematically from the mass loss measurements of different litter types across the global climate conditions (Fig. 2) for 31 litter types out of 34 when looking at the 68% confidence intervals (1σ) and for none of the litter types when looking at the 95% intervals (2σ). The lack of the systematic deviation means that the probability densities of the results of the model represent the random uncertainty caused by uncertainty about the parameter values of the model (Fig. 1 b, 3). Based on these results, we conclude that Yasso07 met the requirements we set for the global model.

We formulated the Yasso07 model according to three assumptions of foliage litter decomposition (see Section 2.2). Comparison of the model results to the measurements provides us with means to evaluate the validity of these assumptions.

Regarding the first assumption, the decomposition rates of the four labile compound groups differed statistically significantly from each other (Table 3). When applying the same group-specific rates independent of litter type, the Yasso07 model estimated the mass loss rate of 31 litter types out of 34 without a statistically significant systematic error (Fig. 2a). These results support the validity of the first assumption. In addition, they suggest that the mass loss of different litter types can be estimated based on the initial division of the mass to the four compound groups over, at least, the first 10 years of decomposition, which was the time period covered by our data.

Regarding the second assumption, temperature and precipitation appeared indeed as the major climate factors affecting foliage litter decomposition at the global scale. After their effects were accounted for, the results of the Yasso07 model did not deviate from the mass loss measurements in any climate-related way (Fig. 2 b–e). Temperature and precipitation, combined in various ways, have been used to explain the effects of climate on litter decomposition already earlier (Meentemeyer, 1978; Berg et al., 1993; Aerts, 1997; Liski et al., 2003; Parton et al., 2007). We tested also different combinations of these two variables to find the final and best model. The Gaussian formulation of the temperature effects was based on our earlier comparison of alternative formulations (Tuomi et al., 2008). Unfortunately, the data did not allow us to test whether the effects of temperature or precipitation differed between the compartments. Trying to fit separate values of these parameters resulted in an over-parameterized model and a lower posterior probability.

Regarding the third assumption, the information in the measurement, based on the parameter probability densities, was sufficient for distinguishing four major carbon fluxes between the labile compartments and a flux to the humus compartment in addition to the fluxes out of the system. These fluxes were identified without direct measurements of the fluxes themselves. Yet, our model fits to a general view of microbial litter decomposition and humus formation (Stevenson, 1982). Two of the internal fluxes were towards more labile compartments representing probably a break-down of complex compounds by exoenzymes exudated by soil microbes. The flux from the water soluble materials to acid hydrolysable ones may represent synthesis of more complex compounds in the metabolism of the soil microbes. The flux from the ethanol soluble compartment to the non-soluble one is more difficult to explain. It may be a result of the fitting procedure of the model to the data that led to rather similar decomposition rates of these compartments. Recalcitrant humus is formed from decomposition products in chemical reactions (Stevenson, 1982) explaining probably the flux to the humus compartment.

Process-modellers may consider it as a weakness that we applied the strongly empirical method without *a priori* information to determine the fluxes of the model. However, it was the only method that we could use because direct measurements of the fluxes are lacking, especially at this extensive geographical scale. Adair et al. (2008) ignored fluxes between carbon pools in their model when studying litter decomposition across North and Central America. However, the common view of the decomposition process (Stevenson, 1982) and more detailed decomposition models indicate that such internal fluxes exist (Parton et al., 1987).

Determining fluxes between compartments is a common problem in developing dynamic compartmental soil carbon models because these fluxes cannot usually be measured (e.g. Christensen, 1996; Elliott et al., 1996). For this reason, it is common to decide about the fluxes before determining the parameter values of the model (e.g. Moorhead et al., 1999). This practise adds uncertainty to the structure of the model that is difficult to control. To avoid this problem, we determined each flux of the Yasso07 model from the measurements (Table 2). The ability to indentify the fluxes from the rather unspecific litter bag measurements is an indication of the power of the mathematical methods we used.

It was surprising that the Yasso07 model fitted to the data as well as it did even though the nitrogen concentration of the litter types or other characteristics of nitrogen availability at the sites, such as site fertility, were not accounted for in the model at all. Moreover, the residuals were not correlated with the initial nitrogen concentration of the litter species (Fig. 2f). Nitrogen is considered as an important regulator of decomposition and in many other models it is used as a controlling input variable (e.g. Parton et al., 1987; Jenkinson, 1990). According to the results of this study, climate and chemical litter quality are still stronger controls of decomposition at the global scale. Once their effects were modelled carefully, the effects of nitrogen could not be distinguished from the remaining variability in the data. Nitrogen effects may still be important at smaller scales or in more detailed experiments.

It is difficult to compare the reliability of litter decomposition estimates calculated using Yasso07 and other models. The reason is that error in the results of the other models has not been assessed in a similar probabilistic sense. The regression models of litter decomposition have been evaluated mainly on the basis of Pearson correlation values or r^2 values (e.g. Berg et al., 1993; Aerts, 1997), and little attention has been paid to the reliability of the results (e.g. Tuomi et al., 2008). Even if some r^2 values were available for other globally applicable models fitted to similar measurements, they could not be used for comparison easily. This is because the r^2 values depend on error estimates of individual measurements and if these errors have not been measured they need to be approximated or estimated by the modeller. More importantly, however, the r^2 values tell us nothing about the possible over-parameterization of the model. Increasing the number of free parameters in a model always improves the fit to the data and thus increases the r^2 value. However, errors introduced in the model structure at the same time may actually make the results of the model less reliable. For this reason, to assess the reliability of a model, it is necessary to ensure that the model is not over-parameterized. For this purpose, the Bayesian model probabilities provide a superior tool. To our knowledge, the only model that has been proven parsimonious in this sense, and is capable of describing litter decomposition process globally and presenting the results as statistical probability densities, is the one presented here.

Yasso07 is based on a biological process-oriented view of litter decomposition process although we used advanced mathematical methods to develop the model. A fundamental prerequisite we set to the model, was that its structure was not over-parametrized. This was necessary in order to determine unequivocal values for the parameters of the model. Such values were needed to obtain an

unequivocal description of the biological process, test this description in the light of the litter bag data and calculate reliability estimates (probability densities) for the results of the model. This modelling approach we used is different from most of the earlier approaches taken to model litter decomposition at extensive geographical scales (e.g. Berg et al., 1993; Moorhead et al., 1999; Trofymow et al., 2002; Liski et al., 2003; Adair et al., 2008). However, it was the approach that made it possible for us to meet the objectives of this study. Alternatively, had we chosen the so-called mechanistic modelling approach, it would have been impossible to calculate uncertainty estimates for model predictions. The reason is that only some of the relevant processes can be measured directly and these measurements are only rarely available in global scale.

The global patterns of foliage litter decomposition calculated with this model, agreed broadly with earlier estimates (Matthews, 1997). A detailed comparison was impossible, because the parameters represented in the studies were somewhat different, soil respiration (Matthews, 1997) vs. relative effect of climate on litter decomposition rate (Fig. 4). The global patterns were also quite similar to those of net primary productivity (Schuur, 2003; Cramer et al., 1999). This was expected because both processes depend strongly on temperature and precipitation.

The results of Yasso07 were reliable enough to distinguish the differences in litter mass loss rates between the sites representing four climate zones (tundra, boreal zone, temperate zone and tropics) and two litter types (coniferous, deciduous) inside each site. As a matter of fact, already a 3% difference in remainig mass values (relative to the initial mass) appeared as statistically significant between the tundra and the boreal site. This difference was caused by only a $1.6°$ C higher annual mean temperature at the boreal site. Similar climate warming is expected to take place as soon as over the next few decades at the high latitudes, and some regions have warmed by this much or more already (IPCC, 2007). Based on these differences in the decomposition rates between the current litter types and the currently prevailing climate conditions, Yasso07 model is reliable enough for distinguishing small changes in the litter decomposition rates over relatively short periods of time in response to climate change.

Using a large dataset of litter bag measurements and advanced mathematical methods of complex inverse problems we were able to develop a globally applicable description of foliage litter decomposition process and present this description in an exact mathematical form. This model, Yasso07, can be used for estimating the effects of changing climate and litter type on soil carbon decomposition in statistical sense. Our study supported the results of previous studies in that temperature and precipitation are the main factors affecting litter decomposition. Our results suggest, however, that nitrogen content of litter or site fertility parameters have a negligible effect on litter decomposition rates at the global scale. Because of the uncertainty estimates we produced for the parameter values of the model, Yasso 07 is currently the only model that can be used for evaluating how large the changes in the climate and/or litter type have to be before significant statistical differences can be detected by modelling.

We conclude that Yasso07 is suitable for estimating foliage litter decomposition of a wide variety of plant species across the global climate conditions. As a result of its general yet parsimonious structure, it can be used as a litter decomposition module in larger ecosystem models or earth system models.

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