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Modeling forest leaf-litter decomposition and N mineralization in litterbags, placed across Canada: A 5-model comparison

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ABSTRACT

The performances of five carbon (C) and nitrogen (N) cycling models (FLDM, CENTURY, SOMM, DOCDOM and CANDY) were compared for their ability to quantify mass and N remaining in 10 g leaf-litterbags across the wide range of litter types and sites of the Canadian Intersite Decomposition Experiment (CIDET), over a 6-year period. These models differ in their structure and assumptions, number of compartments, predictor variables and coefficients. Calibrated model outputs displayed similar but not identical trends for mass and N remaining, but differed substantially in mass and N contents per model-defined compartments. The quality of fit between model calculations and data varied as follows: FLDM > CENTURY > DOCMOD > CANDY > SOMM for mass remaining ($0.73 < r^2 < 0.92$), and FLDM > DOCMOD > CENTURY > SOMM > CANDY for the changing N concentrations inside the bags ($0.40 < r^2 < 0.80$). FLDM calculations were the most consistent by CIDET site (21), litter type (10), and years of litterbag retrieval (1993–1998). Best-fitted models were used to project mass remaining and N concentrations inside the bags over the next 50 years, using mean July and January air temperatures, and annual precipitation and initial litter composition as independent predictor variables. Projected model outputs converged for mass remaining, but diverged for the N concentrations, i.e., (1 ± 0.5) g and (2 ± 1)% at year 50, respectively.

1. Introduction

Predicting the rate at which forest litter decomposes is an important aspect of assessing past, current and future carbon (C) and nitrogen (N) responses of forests under changing climate conditions. For this, there is a need to test the reliability and accuracy of existing models, and also to continue with the development of new models (Knorr et al., 2005; Powlson, 2005; Zhang et al., 2007). Recent studies have therefore focused on producing data on actual rates of forest litter decay for a wide range of litter, site and climate conditions. Among these studies are: the Long-Term Intersite Decomposition Experiment (LIDET) in the United States (LIDET, 1995), the Decomposition Study in Europe (DECO: Jansson and Reurslag, 1992), and the Canadian Intersite Decomposition Experiment (Trofymow and CIDET Working Group, 1998). Factors that influence the rate of organic matter degradation are well known, namely litter quality (Heal et al., 1997), litter temperature and moisture,

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associated drying and wetting cycles (Fierer and Schimel, 2002; Borken et al., 2003), nutrient availabilities (Walse et al., 1998), forest activities (Prescott et al., 2004), and microbial composition (Jenkinson et al., 1991; Berg and Matzner, 1997; Gillon et al., 1999). To some extent, these factors are already incorporated in organic matter (or C) and N cycling models such as SOMM and ROMUL (Chertov et al., 2001; Chertov and Komarov, 1997), CENTURY (Parton et al., 1987; CENTURY, 2000), CANDY (Franko et al., 1995), CBM-CFS2 (Kurz and Apps, 1999), DOCMOD (Currie and Aber, 1997), GENDEC (Moorhead and Reynolds, 1991), MBL-GEN (Rastetter et al., 1991), FLDM (Zhang et al., 2007) and Yasso (Liski et al., 2005). The number, types and functions of pools and processes considered in these models vary. In many cases, distinctions among pools and processes are made according to their dynamics: as in CENTURY, with metabolic, active, slow, passive pools; as in SOMM, with litter (L), fermentation (F), and humus (H) pools; as in CBM-CFS2 with very fast and slow soil C pools, as in FLDM with fast, slow, and very slow litter fractions, and as in CANDY, with biologically active and soil organic matter pools. In other models, pool distinctions are made according to litter composition, as in MBL-GEM with cellulose, "lignin" and humus pools. Various combinations of structural and functional pools exist, i.e., woody, lignocellulose, cellulose, extractive, and microbial pools in DOCDOM, and labile, holocellulose, resistant, dead and live microbial pools in GENDEC.

The models also vary in terms of mechanisms proposed to simulate the transformation of each organic matter or C and N pool into CO_2 and mineralized N. Some formulations such as GENDEC explicitly include microbial components to allow for microbial biomass, growth and mortality simulations. Other models assume microbial involvement through provision of microbial biomass pools with a prescribed C/N ratio of 8 or so (DOCMOD, CANDY and CENTURY). SOMM quantifies soil microbial and mesofaunal processes but without explicit soil microbial and mesofaunal biomass pools. In addition, DOCMOD estimates the production of dissolved organic matter.

Recent model reviews have focused on the utility of 1-, 2-, or 3-compartment models for quantifying CO_2 release from soil organic matter degradation with respect to changing climate conditions (Knorr et al., 2005; Powlson, 2005). This paper presents a 5-model comparison study involving FLDM and the published and readily formulated CENTURY, SOMM, DOCDOM, CANDY models, using the 1992–1998 CIDET leaf-litterbag data to calibrate and verify the model results for mass remaining and N concentrations, by site and litter type. Three of these models (CENTURY, CANDY and SOMM) were included in a previous review of nine ecosystem-type C models concerning their performance in predicting changing levels of soil organic matter at well-known study locations (Smith et al., 1997). The objective of the research presented in this paper addressed these questions:

- Which of these 5 models is most efficient in terms of quantifying organic matter decomposition and N mineralization within the CIDET litterbags, by litter type and climate for the range of sites across Canada?
- How does model formulation affect calibration efficiencies?
- How do C and N pool predictions based on a priori parameter values (deduced independently from controlled laboratory and field studies) compare with best-fitted model calculations?

2. Materials and methods

2.1. The CIDET data

CIDET is a cooperative study with the objective to study the influence of litter quality, climate and microclimate on the rate of litter decomposition and N mineralization in forests covering a range of ecoclimatic provinces in Canada (Trofymow and CIDET Working Group 1998). For this study, litter was collected in the fall of 1991 from 10 vegetation species, i.e., Trembling aspen (*Populus tremuloides*), American beech (*Fagus grandifolia*), Douglas fir (*Pseudotsuga menziesii*), White birch (*Betula papyrifera*), Jack pine (*Pinus banksiana*), Black spruce (*Picea mariana*), Tamarack (*Larix laricina*), Western redcedar (*Thuja plicata*), Bracken fern (*Pteridium aquilinum*), Plains rough fescue (*Festuca hallii*). Ten grams of each litter type were put into 0.5 mm mesh litterbags, and placed on quadruplicate plots on each of 21 sites across Canada during the fall of 1992 (18 uplands, 3 wetlands, Table 1). The fresh litter was subjected to total elemental analysis (C, N and P) and proximate analyses (non-polar extractable, water-soluble extractable, acid-hydrolyzable, acid-unhydrolyzable, and ash fractions) (Trofymow et al., 1995). Litterbags were retrieved annually each fall from 1993 to 1998, to yield an overall sample size of 1470 (21 sites × 10 litter types × 7 years, including the year of litterbag placement), all within-site replicates averaged. Retrieved litterbag results for mass remaining and total mass and N content from 1992 to 1998 were, inter alia, already reported and analyzed by Trofymow et al. (2002) and Moore et al. (2006). Site weather data for this time period (Environment Canada, 2006) were obtained from nearby Meteorological Services Canada weather stations (Trofymow and CIDET Working Group 1998).

2.2. Model structures and formulations

The 5 models differ in the number and type of C and N litter compartments, conversion processes between compartments, mathematical formulations, and number of coefficients needed for model initialization and calibration (Fig. 1, Appendix A). Model outputs were obtained in three ways: (1) using published model specifications and parameter values; (2) calibrating the model coefficients with the CIDET data; (3) re-calibrating the models when the initial calibrations failed to yield sufficiently precise parameter estimates. The rules used to decide which mass (or C) and N pools and flows to include in each model, and how to connect these pools and flows with one another, were based on simple suppositions about microbial litter-to-humus conversions. These rules refer to:

- assuming first-order kinetics such that the rate of decay and transfers from one pool to another are assumed to be proportional to the size of the decaying pool;

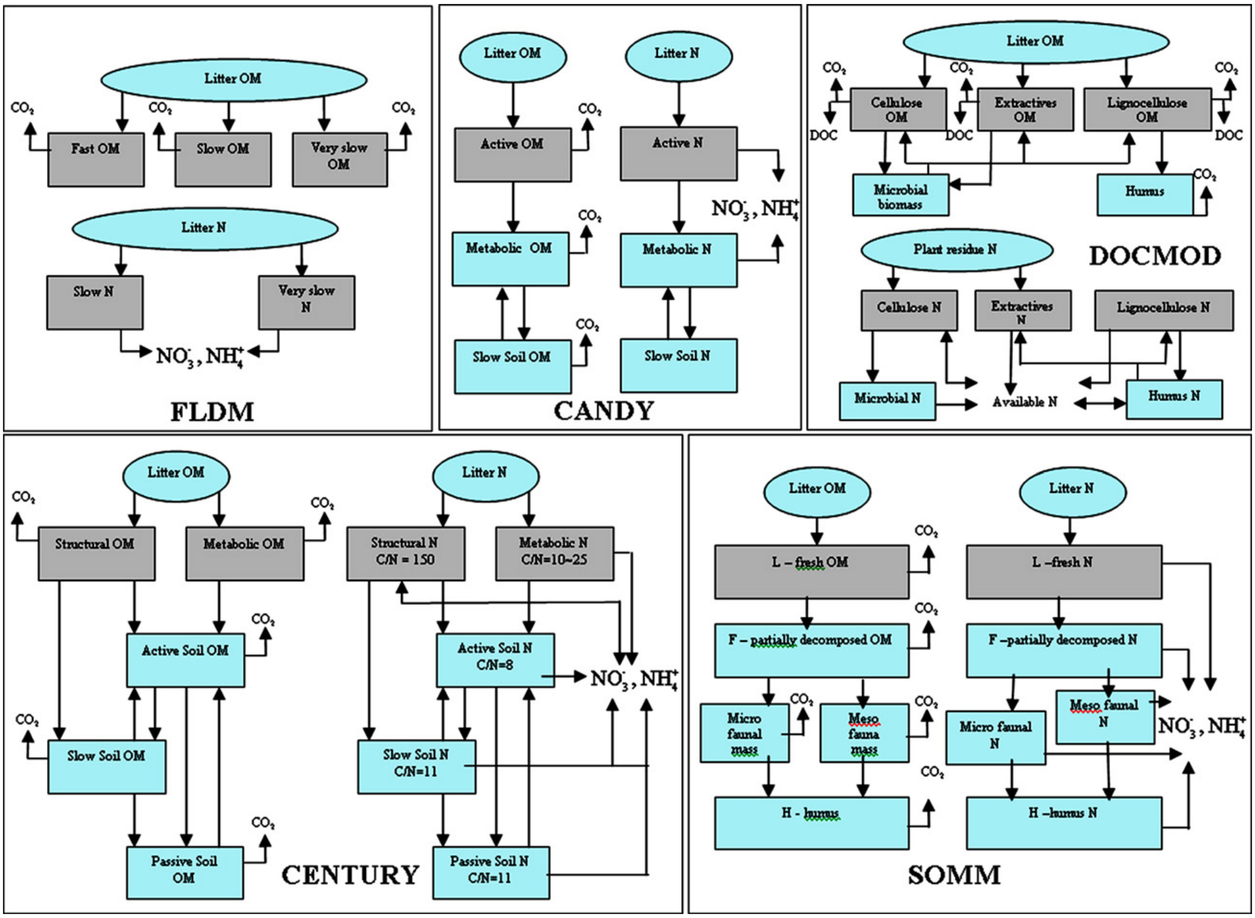

Fig. 1 – Flow charts for the FLDM, CANDY, DOCMOD, CENTURY and SOMM models. Pools shaded grey are initialized with non-zero mass and N amounts, as per initial CIDET litter chemistries. The initial proportion of the litter mass or N assigned to each pool is either preset (CANDY, CENTURY, DOCMOD and SOMM) or calibrated (FLDM).

Table 1 – CIDET site locations and corresponding weather stations (Trofymow and CIDET Working Group 1998)

Site name	Code	Province/Territory	Latitude	Longitude	Elevation (m)	Climate region
Batoche	BAT	Saskatchewan	52.73	106.13	472	Transitional grassland
CB Rocky Harbour	CBR	Labrador	49.55	57.84	50	Maritime low boreal
Chapleau	CHA	Ontario	47.64	83.24	460	Humid low boreal
Gander	GAN	Newfoundland				Maritime mid-boreal
Gillam1	GI1	Manitoba	56.33	94.51	140	Low subarctic
Gillam2	GI2	Manitoba	56.32	94.86	125	Low subarctic
Hidden Lake	HID	British Columbia	50.55	118.83	650	Moist montane, Southern cordilleran
Inuvik	INU	Yukon	68.32	133.54	73	High subarctic
Kananaskis	KAN	Alberta	51.01	115.00	1530	Montane, Southern cordilleran
Morgan Arboretum	MAR	Quebec	45.43	73.95	48	Humid mid-cool temperate
Montmorency	MON	Quebec	47.32	71.14	670	Perhumid low boreal
Nelson House1	NH1	Manitoba	55.93	98.62	288	Subhumid high boreal
Nelson House2	NH2	Manitoba	55.92	98.43	260	Subhumid high boreal
Prince Albert	PAL	Saskatchewan	55.92	98.43	476	Subhumid high boreal
Petawawa	PET	Ontario	53.23	?	173	Humid high-cool temperate
Port McNeill	PMC	British Columbia	50.61	127.34	100	Maritime south pacific cordilleran
Schefferville	SCH	Labrador	54.88	66.65	500	Low subarctic
Shawnigan Lake	SHL	British Columbia	48.64	123.71	355	Coastal south pacific cordilleran
Termundee	TER	Saskatchewan	51.84	104.92	537	Transitional grassland
Topley	TOP	British Columbia	54.61	126.31	1100	Boreal southern cordilleran
Whitehorse	WHI	Yukon	60.85	135.21	667	Boreal northern cordilleran

- specifying initial pool sizes "a priori" through direct measurement, or through calibration; not easily measured or quantified components refer to "fast", "structural", "metabolic", "slow", "very slow", "fermented", "humified", "passive" and "active" pools of the decaying litter;
- allowing simple pool-based C loss proportioning between CO_2 loss and pool-to-pool C transfer;
- assuming C-based N transfers, with prescribed C/N ratios for specific pools; note that strict adherence to constant pool- or process-based C/N ratios leads to implicit N gains or losses that invoke just-in-time or inadvertent N mineralization or adsorption of exogenous N, as in GENDEC, CANDY, and DOCMOD; with FLDM, this uptake is explicit;
- relating the rates of decay and N mineralization to litter temperature and moisture as these vary over time;
- converting original model C or organic matter pools into mass pools.

The total Mass to C conversion ratio was generated from the initial CIDET litter quality data (Trofymow et al., 1995), and is given by

$$\{M/C\} = (1.443 \pm 0.07) + (0.007 \pm 0.001)\text{initial\_acid\_hydrolyzable\_fraction}(\%) + (0.011 \pm 0.002)\text{initial\_water\_extractable\_fraction}\ (\%) + (0.013 \pm 0.005)\text{initial\_ash}(\%), \qquad r^2 = 0.93$$

Throughout this paper we use the term acid-unhydrolyzable residue (AUR) to refer to the final residual fraction remaining after proximate analysis. Depending upon the litter type, the AUR fraction has been shown to contain a mixture of C compounds in varying proportions, including condensed tannins, phenolics, waxy alkyl compounds as well as true lignins (Preston et al., 1997), and has been erroneously referred to as "lignin" in many model formulations.

2.3. *Model realizations, initialization, calibrations and performance checks*

Each of the 5 models was realized within the ModelMaker software (1999) to take advantage of its built-in Simplex and Marquardt least-squares fitting routines for the purpose of model optimization and parameter calibrations. Model calculations for mass remaining and N concentrations started with the original parameter values quoted in the literature (when available), and proceeded by calibrating some or all of the coefficients based on all of the available CIDET data. Re-calibrations of the adjustable CENTURY, DOCMOD, and CANDY coefficients were done by constraining those coefficients with large least-squares error estimates. The values of these particular coefficients would either be fixed to their original values, or set to zero in cases where doing so would decrease the inter-parametric co-dependencies, and would therefore also accelerate the model iterations towards optimal convergence. Model calibrations and re-calibrations were not done for SOMM: all of its parameter values were kept as published. FLDM was calibrated with a_0, a_1, and a_2 or l_1 and l_2 as part of its adjustable parameter set. Model calculations proceeded as follows:

- Initialize each model for each CIDET site and litter type, starting with an initial litter mass of 10 g, and with corresponding initial N concentration and other variables used to account for the initial litter composition, i.e., initial pool sizes for mass and N.
- Calculate mass remaining and N concentrations through simultaneous numerical integration of the model-specific differential equations using several integration methods (Euler, Mid-point, Runge-Kutta, Burlisch-Stoer) at sufficiently small time steps to ensure numerical consistency of model outputs.
- Use the end-of-year CIDET data for the automated least-squares fitting procedure to calibrate models using all of adjustable coefficients simultaneously, with published pre-set values serving as initial values.
- Compare actual versus modeled values by way of plotting their differences (residuals), the parameter of determination r^2, the root-mean–square error (RMSE), the mean error (ME), and several model performance criteria, namely Akeiko's information criterion (AIC), Schwarz's criterion (SC) and the log-likelihood criterion (LL), by model.
- For each model, evaluate r^2 and ME, for all cases, by litter type, by CIDET site, and by year, to determine how the best available results of each model represent the CIDET data variations across the 10 litter types, and across the large variations in site and climate conditions.

Additional model performance checks involved (1) evaluating the precision of the various parametric estimates and associated correlations following model calibration and re-calibration and (2) inspecting and analyzing time series and scatter plots of actual mass remaining and N concentrations versus estimated values.

Values for the varying *f*(climate) expressions were generated for the entire 1992–1998 period from the monthly weather data at each CIDET site, using:

- mean January and July air temperatures, and annual precipitation for FLDM;
- mean monthly soil temperature, and monthly precipitation and potential evapo-transpiration for CENTURY;
- mean monthly soil moisture and temperature for CANDY and SOMM;
- monthly actual evapo-transpiration, estimated from mean monthly temperature, and monthly precipitation for DOCMOD.

Mean annual, January and July air temperatures and annual precipitation rates at each CIDET site for the 1992–1998 period can be found in Zhang et al. (2007). The Forest Hydrology Model ForHyM (Balland, 2003) was used to produce daily estimates for potential and actual evapotranspiration, and soil moisture and temperature, by soil depth. These were then summarized by month to enable the CANDY and SOMM calculations.

3. Results and discussion

Original, calibrated and/or re-calibrated parameter values for the CENTURY, DOCMOD, CANDY and FLDM models are

Table 2 – Original, calibrated and re-calibrated parameter values for the CENTURY, DOCMOD, CANDY, FLDM models to estimate leaf-litter mass and N concentrations in CIDET litterbags

	Default value	Calibrated value	+/− Error estimate	Re-calibrated value	+/− Error estimate	Re-calibration/ default factor	Unit
CENTURY parameter							
k_1	0.076	0.21	0.02	0.21	0.02	2.81	$year^{-1}$
k_2	0.28	3.3	0.8	3.3	0.8	11.69	$year^{-1}$
k_3	0.11	0.27	0.05	0.27	0.05	2.47	$year^{-1}$
k_4	0.0038	0.0	0.1	0.030	0.006	8.00	$year^{-1}$
k_5	0.0013	0.0	7.2	0.0013	–	1	$year^{-1}$
p_{fm0}	0.85	0.46	0.03	0.46	0.03	1	
p_{fm1}	0.018	0.009	0.00	0.009	0.00	0.49	
Active CN	8	7.6	1.0	7.7	0.9	0.96	–
Slow CN	11	12	3	12	3	1.12	–
Passive CN	11	11	8	11	–	1	–
Structural CN	150	72	12	72	12	0.48	–
DOCMOD parameter							
p_{AET}	0.00189	0.0069	0.0002	0.0083	0.0002	4.4	mm^{-1}
AET	595	444	55	349	22	0.59	mm
k_m	0.63	1.0	1.1	0.63	–	1	$year^{-1}$
k_{E0}	0.115	0.044	0.020	0.019	0.005	0.16	$year^{-1}$
k_{E1}	0.5	0	–	0	–	0	$year^{-1}$
k_{C0}	0.0476	0.78	0.40	0.772	0.005	16.2	$year^{-1}$
k_{LC0}	0.0011	0.030	0.012	0.026	0.006	23.4	$year^{-1}$
k_{LC1}	0.053	0.0001	0.0049	0	–	0.0	$year^{-1}$
k_{Hh0}	0.0016	0.9	4.0	0.0029	0.0008	1.8	
k_{Hs0}	0.0059	0.022	0.009	0	–	0	
k_{NLC0}	0.0142	0.0003	0.0052	0.011	0.009	0.80	
k_{NLC1}	−0.951	−0.76	0.23	−0.19	0.42	0.20	
CN_B	16.7	13.2	2.8	13.2	2.8	0.8	–
CANDY parameter							
p		0.71	0.03	0.721	0.033		mm^{-1}
E_a		132,941	4052	132,270	4033		$J\,mole^{-1}$
k_a		0.56	11.5	0	–		$year^{-1}$
k_1		0.17	0.028	0.164	0.024		$year^{-1}$
k_{bom}		0.026	0.6	0.016	0.003		$year^{-1}$
k_s		0.28	25	0	–		$year^{-1}$
η		0.47	0.15	0.46	0.021		
CN	8.5	28.1	1.1	28.0	0.881	3.3	–
	Default value	Calibrated value[a]	+/− Error estimate	Re-calibrated value[b]	+/− Error estimate	Calibration/ default factor	Unit
FLDM parameter							
k_1/k_2		19.8	2	15.7	1.8		
k_2		0.377	0.014	0.503	0.028		$year^{-1}$
k_3/k_2		0.292	0.023	0.348	0.016		–
p_1		87.8	2.2	83.2	2.1		°C
p_2		831	11.4	808	11.7		mm
E_a		61,690	2312	59,944	2342		$J\,mole^{-1}$
CN_{MB}		8					
CN_{final}		25.8	2.5	25.1	1.7		–
$N_{uptake1}$		0.000642	0.000174				
$N_{uptake2}$		0.5					
a_0 (l_1)		−6.6	0.2	0.5	0.01		–
a_1 (l_2)		0.116	0.003	0.0149	0.0002		1/%
a_2		0.104	0.003	–	–		1/%
a_3		0.155	0.015	0.231	0.018		1/%
a_4		55.5	1.5	57.9	2.7		1/%

[a] Calibrated FLDM model refers to estimating the fast fraction from; $M1/M = \exp[a_0 + a_1$ initial_acid_extractable_fraction (%) $+ a_2$ initial_water_extractable_fraction (%)].

[b] Re-calibrated FLDM model refers to estimating the fast freaction from $M1/M = l_1 - l_2$ initial_lignin_fraction (%).

shown in Table 2. With CENTURY, parametric calibration changes were generally minor, except with major upward shifts (2.5–11.7 times) for the structural, metabolic, active, and slow decomposition coefficients k_i ($i = 1–4$). The best-fitted CENTURY calculations suggested faster mass losses from the non-passive leaf-litter pools toward the slow and passive pools than what would occur without these adjustments. The value for k_5, used for simulating the rate of passive litter decomposition, was kept at 0.0013, to allow for a gradual build-up of the passive pool. The CIDET data from 1992 to 1998 did not allow for a precise calibration of this particular coefficient. The downward calibration of the p_{fm0} (from 0.85 to 0.55) and p_{fm1} (from 0.018 to 0.010) coefficients reduced the originally set size of the metabolically active pool in favour of the structural pool. The original C/N ratios for the active, slow and passive pools remained essentially unchanged during the calibration and/or re-calibration process, while the structural C/N ratio dropped from 150 to 72, which – in turn – implied that the structural pools of leaf-litter would contain more N than originally set. These differences may be due to CENTURY calibrations involving leaf, root, bark and wood litter rather than leaf-litter only.

With DOCMOD, calibration adjustments were needed for the coefficients that determine the dynamics of the extractable, cellulose, lignocellulose and humus pools. Some of these coefficients became either independent of their anticipated LCI dependence ($k_{E1} = 0$; $k_{LC1} = 0$), or dropped out altogether ($k_{Hs0} = 0$). At the same time, mass losses from the cellulose and lignocellulose pools were calibrated to occur considerably faster than originally formulated: $k_{C0} = 0.772$ instead of 0.0476; $k_{LC0} = 0.026$ instead of 0.0011. The opposite occurred with the extractable pool: $k_{E0} = 0.019$ instead of 0.115. Hence, the best-fitted calibrated DOCMOD coefficients suggested faster than anticipated mass losses from structural components (cellulose and lignocellulose) and associated transfers to the humus pool. For the N concentrations calculation, downward adjustments were needed for the k_{NLC0}, k_{NLC1}, and CN_B coefficients, thereby suggesting a higher retention of N within the lignocellulose pool, and a somewhat lower than originally anticipated C/N ratio for the microbial pool.

With CANDY, original default parameter values were not available. Calibrating this model led to fairly consistent and unambiguous parameter estimates except for those that determine the rate of soil organic matter build-up (k_s) and loss (k_a). Setting these coefficients equal to 0 even improved the best-fitted results, especially for N following the concurrent upward adjustment of the original C/N ratio from 8.5 to 28. Hence, retaining the present formulation for the forward and backward organic matter and N transfers between the slow pool (SOM) and the biologically active pool (BOM) would have led to a sub-optimal solution. With that, the CANDY calibrations reverted to that of a simple two-component model, with SOM = 0. The C/N = 28 adjustment, furthermore, changed the interpretation of BOM from being a microbial pool to a less well defined "slow" organic matter pool. Similarly, the interpretation of the η parameter changed from being a microbial retention parameter to a simple mass loss parameter while some of the litter would gradually transform from its original state into the humified state.

The lack of intra-annual CIDET data, and the relatively short time (1992–1998) of the currently available data limited the precision by which non-linear regression procedures can estimate the coefficients of the very fast and very slow decay processes. For example, longer-term data would be needed to get better estimates for k_5 in CENTURY, k_s and k_a in CANDY, and k_{Hs0} in DOCMOD. Intra-annual data would be needed to get a good estimate for the microbial turn-over parameter k_m in DOCMOD. Optimizing this model with the year-end CIDET data produced a rather imprecise k_m estimate (1.0 ± 1.1).

Best-fitted FLDM parameter values (Table 2, bottom) were all fairly precise, with error estimates about 10% or less, as already reported and discussed by Zhang et al. (2007). Briefly:

- the values for the fast-decomposing fraction, as determined by the a_0, a_1, and a_2 (or the l_1 and l_2) calibrations, increased with increasing water-extractable and acid-hydrolyzable levels, or with decreasing AUR levels;
- the positive number for a_3 implied that an increasing ash content would decrease the slow fraction, and increase the very slow fraction; this increase would be similar to the clay- and silt-stabilizing effect on humic matter within the CENTURY and SOMM formulations;
- the values of the 3 decay coefficients k_1, k_2, k_3 were not affected by variations in litter composition nor climate;
- initially higher N concentrations translated into higher N-mineralization rates, i.e., higher n_2/k_2 values; these values, however, were all calculated to be <1, thereby implying that the decaying litter would, at least initially, be more conservative with respect N losses than with mass losses; also, the best-fitted n_2/k_2 values were determined to be smaller by a factor of 0.53 ± 0.14 on the three wetland sites (BAT, GI2 and NH2) than the 18 upland sites. This means that N mineralization rates in the surface-placed litterbags would be slower on wetland (peatland) soils than on upland soils. In contrast, there were no consistent differences in upland versus wetland mass losses.

As already mentioned, parameter adjustments were not done for SOMM. This model contains 61 coefficients, all empirically derived by way of independent process studies, with most of these coefficients expressing the moisture and temperature sensitivity of the specific mass and N turn-over processes as captured by this model. This is in contrast to the simplified climate-dependency formulation for each of the other four models, allowing only few adjustable climate coefficients, namely p_1, p_2 and E_a (FLDM), p_{AET} and AET' (DOCMOD), p_{AET} and E_a (modified climate algorithm for CANDY), or two pre-determined functions that depend on precipitation and air temperature (CENTURY). The p coefficients in this listing are simple scale adjusters for precipitation (p_1, FLDM), air temperature in winter (p_2, FLDM), or annual evapotranspiration rates (p_{AET}, CANDY; DOCMOD). The E_a parameter (FLDM, CANDY) reflects the overall sensitivity of the decay process to air temperature, particularly during summer, with mean monthly July air temperature as soil temperature indicator, also assumed to take the role of "activation energy" as part of the kinetic process formulations. In this regard, the FLDM estimate of $61{,}700 \pm 2300\,\mathrm{J\,mole^{-1}}$ is within the experimentally determined range from 43,000 to 76,000 $\mathrm{J\,mole^{-1}}$ for fast

Table 3 – Model performance comparisons: statitistical summary

Statistics	FLDM, calibrated	CENTURY			DOCMOD			CANDY		SOMM, default
		Default	Calibrated	Re-calibrated	Default	Calibrated	Re-calibrated	Calibrated	Re-calibrated	
Mass remaining (g/bag)										
WSS	671	9,192	1,388	1,353	2,737	1,648	1,546	1,826	1,826	3,346
AIC	9,590	13,429	10,651	10,611	11,655	10,909	10,809	11,053	11,049	11,930
SC	9,648	13,466	10,688	10,643	11,708	10,962	10,846	11,090	11,076	11,930
LL	−12,230	−14,153	−12,764	−12,745	−13,263	−12,890	−12,843	−12,966	−12,966	−13,411
r^2	0.92	0.69	0.83	0.83	0.45	0.80	0.81	0.77	0.77	0.73
ME	−0.050	2.05	0.007	0.007	−0.41	0.038	0.038	0.051	0.051	0.792
RMSE(%)	8.0	29.6	11.5	11.3	16.1	12.5	12.1	13.2	13.2	17.8
m (adj. parameters)	11	7	7	6	10	10	7	7	5	0
N concentration (%)										
WSS	60	401	138	136	277.6394	104	123	174	174	171
AIC	6,042	8,832	7,262	7,242	8,297	6,849	7,098	7,604	7,600	7,559
SC	6,105	8,891	7,321	7,290	8,366	6,918	7,151	7,646	7,631	7,559
LL	−10,455	−11,851	−11,066	−11,058	−11,581	−10,857	−10,985	−11,240	−11,240	−11,225
r^2	0.80	0.45	0.51	0.52	0.22	0.64	0.57	0.40	0.40	0.60
ME	−0.043	−0.41	0	0	−0.17	−0.02	0.023	−0.03	−0.034	−0.181
RMSE(%)	25.5	66.0	38.7	38.5	54.9	33.6	36.6	43.5	43.5	43.1
m (adj. parameters)	12 (1)	11 (4)	11 (4)	9 (3)	13 (3)	13 (3)	10 (3)	8 (1)	6 (1)	0

WSS: weighted sum square of residuals; Aikaike's information criterion AIC: $n\ln(\mathrm{WSS})+2m$; Schwarz criterion SC: $n\ln(\mathrm{WSS})+m\ln(n)$; Log Likelihood criterion: $-n/2\ [\ln(2\pi)+\ln(\mathrm{WSS}n)+1]$; mean error ME: sum of residuals/n; root mean square error RSME%: $100\times\mathrm{sqrt}(\mathrm{WSS/N})/\mathrm{average\ (actual)}$; *m* (adj. parameters for N concentration: number in brackets are in addition to number of parameters required for the mass calculations.

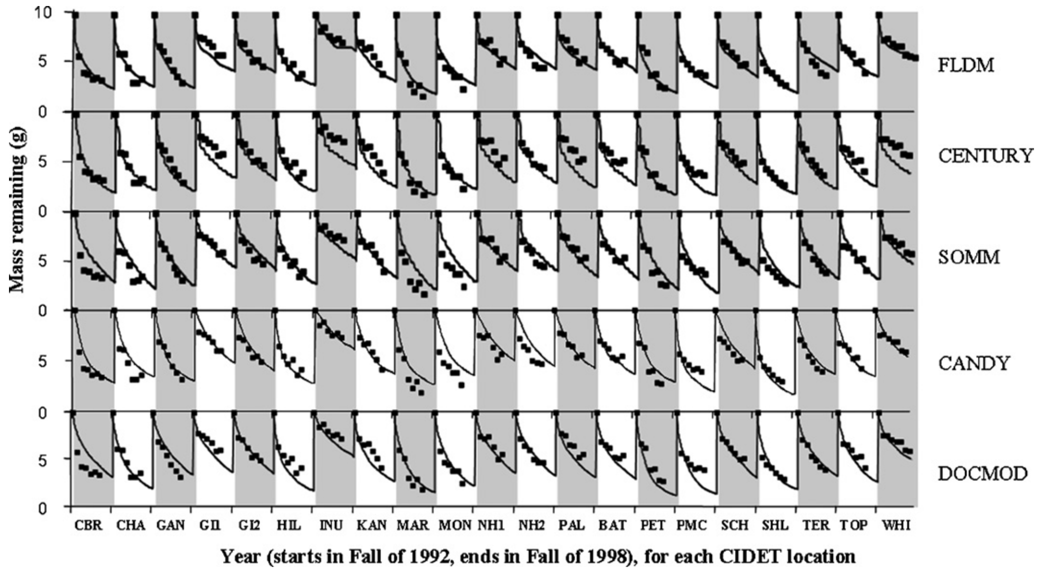

Fig. 2 – Actual (dots) and re-calibrated model best-fitted (lines) mass (g) remaining in decaying aspen litterbags for each consecutive year from 1992 to 1998 at each CIDET site (site codes and names in Table 1), by model (FLDM, CENTURY, SOMM, CANDY and DOCMOD).

to very slowly decaying soil organic matter fractions, respectively (Knorr et al., 2005), and also corresponds to the E_a value of 73,700 J mole^{-1} derived from weekly soil respiration measurements (Borken et al., 2003).

Actual versus best-fitted plots for mass remaining and N concentrations are shown in Figs. 2 and 3 to illustrate the overall performance of each of the 5 models at each CIDET site for each of the six consecutive years for the aspen litter type. These plots show a general pattern of model-data conformance, although the extent of fit varies by model. In particular, the calculations conform to the pattern of initially rapidly decreasing mass and gradually increasing N concentrations, but the extent CENTURY and DOCMOD conformance with the data was much enhanced through calibration and re-calibration.

Scatterplots of best-fitted mass remaining and N concentration residuals are shown in Fig. 4 for all CIDET sites, litter types and years, by model. Also included in this Figure is a table for the intercepts, slopes, and r^2 values for the scatter-plot trend lines, to reveal the extent of bias among the residuals, by model. From this, it is apparent that FLDM had the least scatter and an insignificant bias. The best-fitted residuals for the CENTURY model were more scattered than the FLDM residuals, but also not biased. The SOMM and DOC-

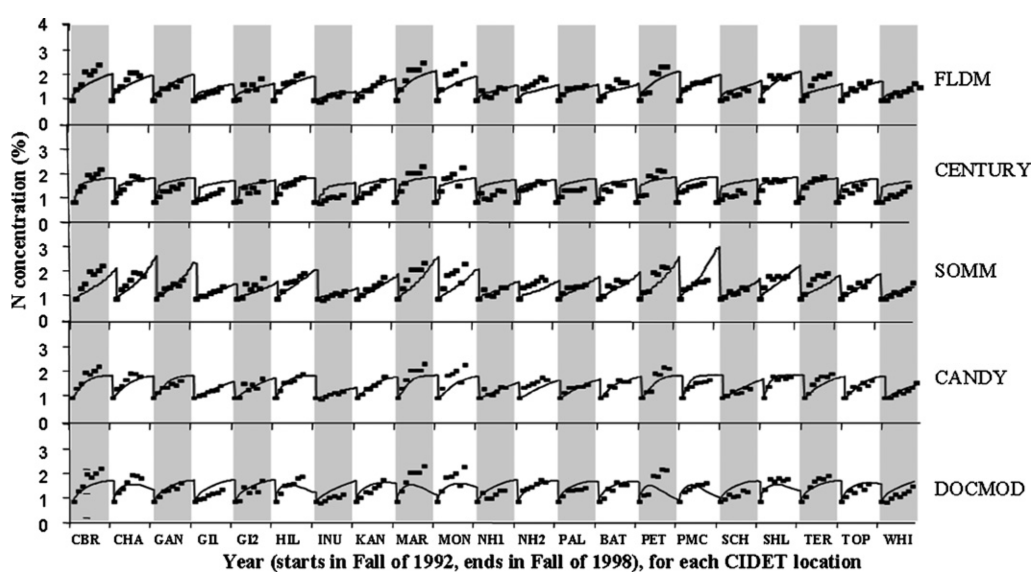

Fig. 3 – Actual (dots) and re-calibrated model best-fitted (lines) N concentrations (%) in decaying aspen litterbags for each consecutive year from 1992 to 1998 at each CIDET site (site codes and names in Table 1), by model (FLDM, CENTURY, SOMM, CANDY and DOCMOD).

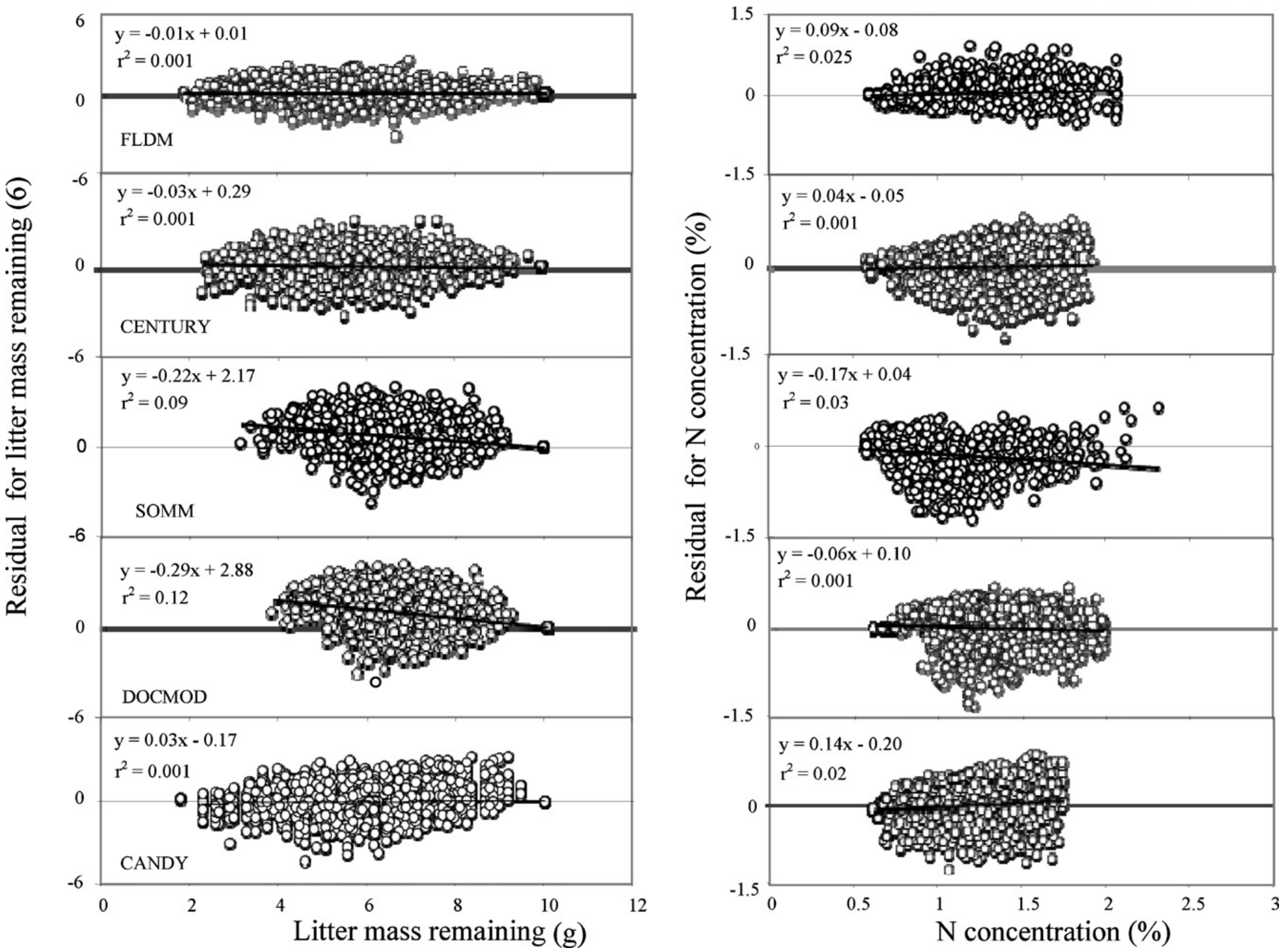

Fig. 4 – Residuals values for actual vs. re-calibrated best-fitted litter mass (g) remaining and N concentration (%) in decaying litterbags at each CIDET site, by model (FLDM, CENTURY, SOMM, DOCMOD and CANDY). Also shown are the trend-line statistics for each plot (linear equations, with intercept, slope, and r^2).

MOD residuals produced bunched scatter plots, and these were generally biased towards slow decomposition and low N concentrations with advancing decay. The CANDY scatter plot was biased in the opposite way, and bunched the most. For all 5 models, there was an increase in relative scatter from the mass to the N concentration plots, with an implicit constraint of not exceeding the simulated N concentrations at about 2%, or smaller, depending on model prescribed or calibrated C/N ratios. Larger relative errors with the N concentrations compared to mass remaining calculations must, in part, be due to error propagation, with the error in determining mass remaining logically embedded in the N concentration calculations. In addition, the bunching of the N concentration residuals within the N scatter plots suggests model-specific limitations in capturing all of the main variations associated with the N concentration data, even after calibration or re-calibration.

The values for the goodness-of-fit or model performance are presented in Table 3 for each of the 5 models. It appears that these indicators are highly correlated with one another, with the weighted sum of squares (WSS) being the main source of these correlations, as expected. Table 3 confirms that the calibrated FLDM consistently performed better than the other models, both in their original (CENTURY, DOCMOD and SOMM) versions, and in their calibrated and re-calibrated (CENTURY, DOCMOD and CANDY) versions. This was further affirmed by the best-fitted mass and N concentration evaluations summarized in Table 4 (top portion), showing best-fitted r^2 values by CIDET site (or local climate conditions), and litter type (or initial litter composition). For mass remaining by site, CANDY had the lowest r^2 value (0.72) with the widest range (0.54), while FLDM had the highest average r^2 value (0.93) and the least range (0.10). Similarly, for mass remaining by litter type, FLDM had the highest r^2 values (0.92) with lowest range (0.08), while SOMM had the lowest r^2 value (0.81), and DOCMOD ($r^2 = 0.83$) had the highest range (from 0.75 to 0.94, i.e., 19). FLDM therefore outranked the other models in capturing the climate-dependent decay variations across the CIDET sites. For the N concentrations by site (Table 4), FLDM produced the highest r^2 values 0.85 with a range of 0.23, while CANDY had the lowest r^2 value of 0.34 with a range of 0.51. For the N concentrations by litter type, FLDM produced r^2 values 0.76 with a range of 0.20, while DOCMOD produced an average r^2 value of 0.43 with a range of 0.49. Hence, FLDM therefore also outranked the other models in capturing the N concentrations variations by climate and litter type variations. By implication,

Table 4 – Model comparison results: r^2 and error values (averages and ranges) for the best fitted (calibrated) mass remaining and N concentration calculations, by species and CIDET sites

	Mass remaining (g)					N concentration (%)				
	FLDM	Century	SOMM	CANDY	DOCMOD	FDLM	Century	SOMM	CANDY	DOCMOD
r^2										
Species										
Average	0.92	0.87	0.81	0.86	0.83	0.76	0.69	0.62	0.69	0.43
Range	0.88\0.96	0.82\0.93	0.71\0.87	0.79\0.92	0.75\0.94	0.64\0.84	0.44\0.82	0.36\0.72	0.54\0.8	0.2\0.69
Sites										
Average	0.93	0.82	0.74	0.72	0.84	0.85	0.48	0.66	0.34	0.69
Range	0.87\0.97	0.62\0.92	0.46\0.87	0.35\0.90	0.70\0.93	0.70\0.93	0.27\0.69	0.52\0.78	0.10\0.61	0.34\0.80
Errors (ME)										
Average										
	−0.03	0.01	0.79	0.05	0.04	−0.04	0.00	−0.18	−0.03	0.02
Species										
Min/max	−0.07\0	−0.69\0.93	−0.41\2.29	−1.07\1.51	−0.73\1.01	−0.18\0.02	−0.4\0.28	−0.5\0.09	−0.55\0.41	−0.28\0.17
Site										
Min/max	−0.65\0.38	−0.87\0.80	−0.49\1.88	−0.96\0.76	−1.7\1.64	−0.19\0.08	−0.19\0.15	−0.5\0.04	−0.24\0.19	−0.34\0.28

SOMM is not calibrated.

FLDM therefore also outranked the other models in terms of the N mineralization calculations.

The best-fitted ME values for each of the calibrated models by litter type and site in Table 4 (bottom part) were all fairly small. This includes the ME values for the un-calibrated SOMM model, with an average positive bias of +0.79 g for mass remaining, a range of 2.36 g by site, and a range of 2.70 g by litter type. For the N concentrations, SOMM ME values were only slightly negatively biased at −0.18%, with ME ranges comparable to those of the CENTURY, DOCMOD and CANDY models. FDLM had the smallest ME range for mass and N remaining, by litter type and by site.

Shown in Fig. 5 are plots for fraction of N remaining versus %mass remaining within the litterbags. These plots reveal the extent to which of the 5 models simulate exogenous N uptake above the initial N content per litterbag, especially during the early phase of mass loss. The CENTURY and DOCMOD models appear to capture exogenous N uptake quite well, but lack a general conformance with the CIDET data by litter type and site, as indicated with Table 4. In contrast, the FLDM and SOMM simulated N concentrations are more conservative with respect to exogenous N uptake. The CANDY calculations for N remaining are neither sensitive to litter type or CIDET site. In general, the FLDM results reflect the average trends of N remaining per litter type quite well. These calculations also affirm the general expectation that – across litter types – net N uptake should increase with increasing initial C/N ratio, being highest for tamarack and lowest for jack pine. As mentioned, exogenous N uptake – as calculated – arises from requiring fixed C/N ratios. In nature, this uptake is entirely possible through the open litter-bag mesh, but the data and the calculations suggest that sustained extra year-end net N absorption is not always occurring, especially for leaf-litter with high initial N concentrations (or low C/N ratios). For further details and theoretical developments about N remaining versus C remaining in decomposing litter, see Moore et al. (2006), Parton et al. (2007) and Manzoni et al. (2008).

A final inter-model comparison test is shown in Table 5, listing r^2 values for mass remaining and N concentrations for each of the 6 years of the CIDET litterbag emplacement. This table ranks the overall goodness–of-fit of these models for mass remaining, by year, as follows:

FLDM > Trofymow et al. (2002) > CENTURY > DOCMOD > CANDY > Yasso > SOMM.

For the N concentrations, the models follow this ranking sequence:

FLDM > SOMM > DOCMOD > CENTURY > CANDY.

Included in this ranking and in Table 5 are the r^2 values for mass remaining in CIDET years 1, 3 and 6, for an empirical multiple-regression model as reported by Trofymow et al. (2002), and by Palosuo et al. (2005) for the Yasso model. This model separates the decaying forest litter into soluble, holocellulose, and "lignin-like" pools, and 2 humus pools. In general, the analysis by Trofymow et al. (2002) generated a good fit between the CIDET data and modeled mass remaining using initial litter composition (AUR, ash, phenolics and carboxylics) and climate conditions (mean annual temperature, summer and winter precipitation) as independent variables. This particular analysis led to a series of multiple regression equations for mass remaining, with the simplest equations containing 7–9 variables, 8–10 regression coefficients, and overall r^2 values varying from 0.75 to 0.80. Note that the Yasso model, calibrated with European data, but uncalibrated for the CIDET data, gave litter mass estimates that were slightly better than those from the uncalibrated SOMM model.

We now illustrate how the modeled mass, C and N pools vary with time, for each model: Fig. 6 displays these projections for aspen litter at the Morgan Arboretum site in Southern Quebec from 1992 to 1998, for the individual summed pools in each model, while Fig. 7 shows the projected aspen litter

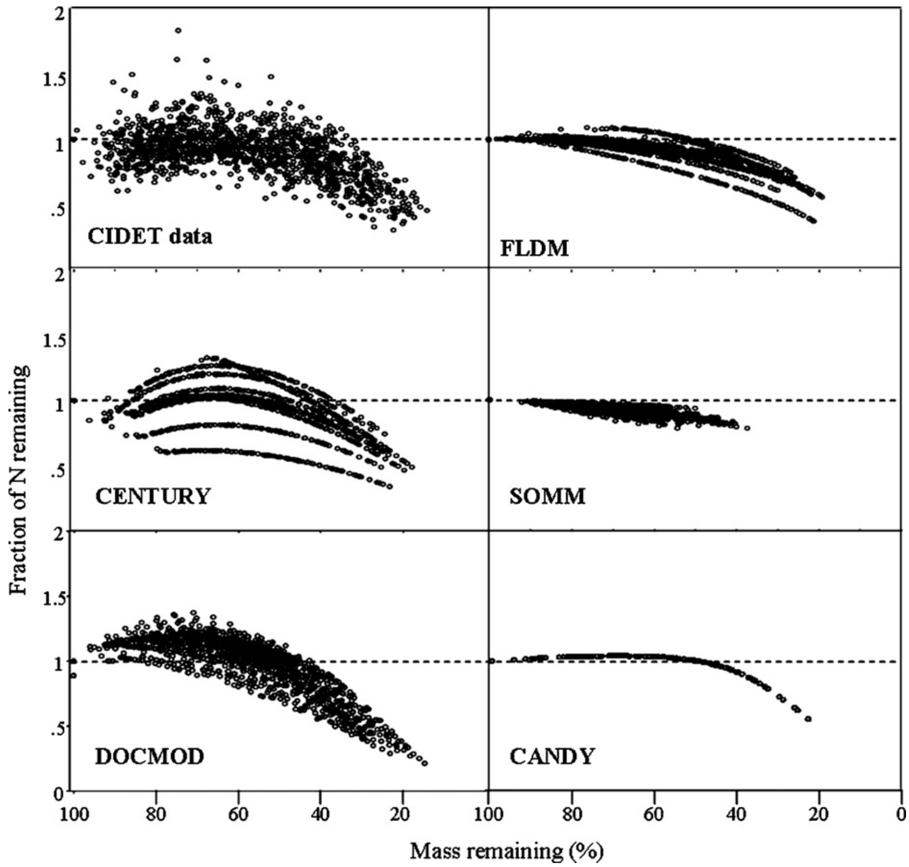

Fig. 5 – Fraction of N remaining vs. %mass remaining in the CIDET litterbags from 1992 to 1998, actual and simulated with CENTURY, DOCMOD, CANDY, SOMM, and FLDM, with a net N uptake provision.

total mass remaining and N concentrations from 1992 to 2042, by model. From this, we note specific model similarities and variations as follows:

- The FLDM and the re-calibrated CENTURY model generated fairly similar trends for mass remaining. The other 3 models projected a slower rate of decay (Figs. 6 and 7).
- There is similarity between the very slow mass fraction of FLDM, and the combined structural and slow mass pools of CENTURY. There is also a similar, complementary trend for the fast (FLDM) and metabolic (CENTURY) mass pools, and the slow (FLDM) and active (CENTURY) mass pools, although the estimates for the CENTURY pools are somewhat larger than the corresponding FLDM pools (Fig. 6).
- Trends for the slow or humus pools for mass and N (CENTURY, SOMM and DOCMOD) are similar, but best-fitted and predicted pool sizes differ considerably (Fig. 6).

Table 5 – Comparison of 1992–1998 CIDET data and best-fitted model results for r^2 associated with mass remaining and N concentration, by year: calibrated or recalibrated for FLDM, CENTURY, CANDY, DOCMOD; uncalibrated for SOMM, and as reported by Trofymow et al. (2002) and Paluoso et al. (2005)

Years	Mass remaining (g)							N concentration (%)				
	FLDM	CENTURY	SOMM	CANDY	DOCMOD	Yasso[a]	Trofymow[b]	FLDM	CENTURY	SOMM	CANDY	DOCMOD
1	0.79	0.60	0.35	0.28	0.51	0.32	0.76	0.72	0.23	0.55	0.06	0.64
2	0.80	0.63	0.36	0.43	0.54	0.63	0.29	0.39	0.11	0.50		
3	0.82	0.64	0.37	0.48	0.52	0.48	0.74	0.78	0.32	0.48	0.12	0.60
4	0.81	0.65	0.40	0.53	0.55	0.73	0.32	0.44	0.17	0.44		
5	0.82	0.67	0.46	0.56	0.62	0.68	0.33	0.38	0.20	0.21		
6	0.82	0.67	0.47	0.58	0.61	0.56	0.71	0.72	0.29	0.46	0.17	0.17
Average	0.81	0.64	0.40	0.48	0.56	0.45	0.74	0.71	0.30	0.45	0.14	0.43
Range	0.02	0.07	0.12	0.30	0.11	0.24	0.05	0.15	0.10	0.16	0.14	0.47

[a] Upland sites only (18).
[b] Multiple regression model, with ln(mass remaining) as dependent variable.

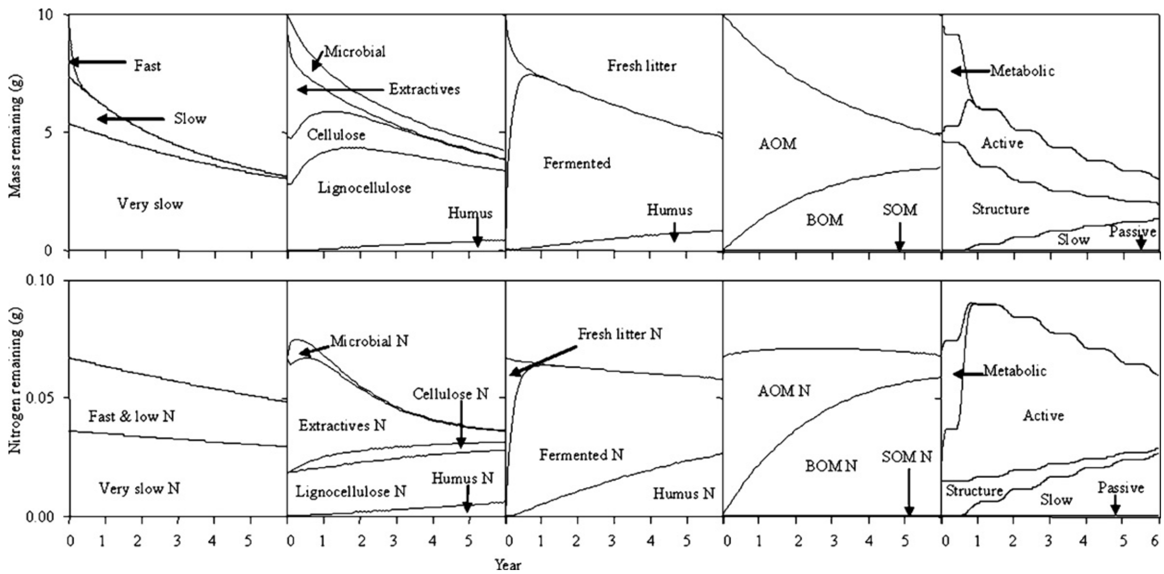

Fig. 6 – Comparison of estimated mass and nitrogen amounts (g) remaining in each FLDM, CENTURY, SOMM, CANDY and DOCMOD litter pool (respectively) from 1992 to 1998, for decaying aspen litterbags at the Morgan Arboretum (MAR) site.

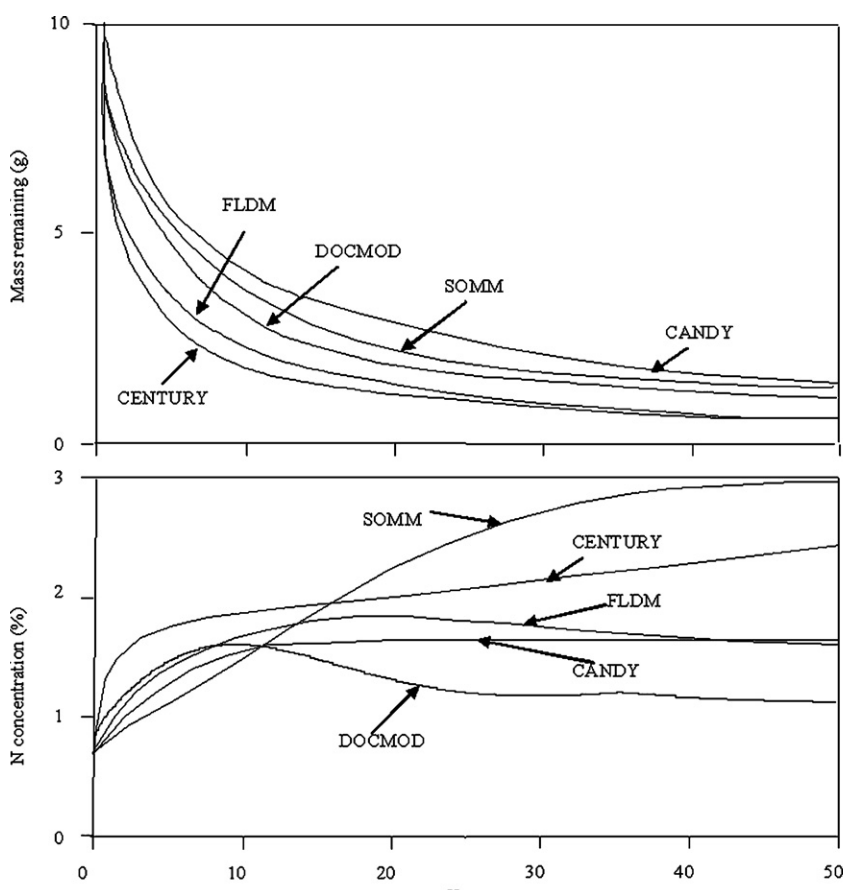

Fig. 7 – Comparison of 50-year FLDM, CENTURY, DOCMOD, SOMM and CANDY model projections for mass remaining (g) and N concentrations (%) in aspen litterbags placed at the Morgan Arboretum (MAR) site.

- In correspondence with Fig. 5, the plots for N remaining show a fairly gradual loss with SOMM, and an initial N gain followed with N losses with CENTURY, CANDY, DOCMOD, CANDY and FLDM, especially during the first years of litterbag placement (Fig. 6).
- Overall N concentrations for the decaying aspen litter are projected to remain fairly consistent from model to model for the first 6 years or so after litterbag placement, but then diverge: after 50 years of litter-bag placement, SOMM predicts N concentrations at about 3%, while FLDM and CANDY predict N concentrations at about 1.5%, and DOCMOD predicts N concentrations at about 1% (Fig. 7). With CENTURY, N concentrations continue to drift upwards. In part, these differences stem from the varying model requirements for fixed (CENTURY, DOCMOD, CANDY and SOMM) or flexible (FLDM) C/N ratios within the humified litter pools, and in part to the rather slow estimates for the decay of some of the non-humified litter pools (e.g., lignocellulose and DOCMOD).

4. Concluding remarks

In examining the conformances of the 5 litter-decomposition models of this study with respect to the two CIDET data variables, namely mass and N remaining in the decaying leaf litter, we determined that:

- The models differ substantially in detail and magnitude in their estimates for mass and N remaining in the litterbags over time, especially without calibration; hence, a priori parameterization falls short in representing the variation in CIDET data over time due to litter type and site.
- Calibrating and re-calibrating reduced but did not fully eliminate the differences between the data and the FLDM, CENTURY, DOCMOD, CANDY and SOMM model estimates; with FLDM, these differences were smallest, consistently leading to unaccounted mass and N concentration variations of <12 and <36%, respectively, by site and by litter type.
- The models also vary in the number of pools and processes considered, and in terms of process formulation. With FLDM, leaf-litter is initially allocated to three pools (fast, slow, and very slow), and these pools are then assumed to decay independently of each other while being influenced by climate in the same way. With CANDY and SOMM, leaf-litter decay is considered to follow a sequential process from its original state through the biologically active state to the humified state. With CENTURY and DOCMOD, initially separate pools (e.g., extractive, cellulose, and lignocellulose pools with DOCMOD, and structural and metabolic pools with CENTURY) are transferred to intermediate microbial, active and/or slow pools to passive humus pools. In contrast, SOMM differs from CANDY, CENTURY and DOCMOD models by disallowing a build-up of metabolic or microbial biomass while still quantifying humus through macro-faunal and microbial mediated processes.
- Data and model calculations confirm the possibility of net exogenous N uptake; the extent of this uptake, however, is small, is mainly noticeable in the early phase of litterbag placement, and appears to decrease with decreasing C/N ratios within and across the leaf-litterbags.
- With FLDM, between pool transfers from the fast to slow, and from the slow to very slow pools were originally considered but the corresponding transfer coefficients quickly converged to 0 within the least-squares fitting process (details not shown here). In qualitative and general terms, this suggests that leaf-litter decay primarily proceeds through pool diminutions and associated modifications rather than pool-to-pool transfers from fast to slow to very slow. How well this formulation predicts litter decay over longer time periods or for other sites and litter types remains to be seen.
- While the CENTURY, DOCMOD, CANDY and SOMM models use single pre-determined first-order turn-over rates for the slowest pools, FLDM generates OM (or C) and N turn-over rates for the very slow pool that gradually decrease with increasing mass loss (Zhang et al., 2007).
- Models with many pools and processes (CENTURY, DOCMOD and SOMM) are not necessarily better than models with few pools and processes (FLDM and CANDY) when it comes to achieving good conformances between actual data and model estimates. In general, more complex models require greater model formulation, initialization and parameter estimation efforts. In particular, satisfactory convergence towards precise and unambiguous parameter values cannot be achieved when the models are "over-parameterized". This tends to occur when pools, processes and coefficients are (1) too closely linked or complementary to one another, either directly or indirectly through feedback loops and (2) when the available data do not represent the ranges and scales of the particular pools and processes targeted by the model. Hence, only a subset of the CENTURY, DOCMOD and CANDY coefficients could be calibrated with the CIDET data.
- There is a need to calibrate the various model compartments in CENTURY, CANDY, SOMM and DOCMOD when data on the chemical fractions in decaying leaf-litter become available. At this time, cross-linking interpretations among the pools of the 5 models are tentative, e.g., for decaying leaf-litter only, the very slow FLDM pool could be interpreted as combination of the slow and structural CENTURY pools, and the slow CENTURY pool is similar to the humus pools of SOMM and DOCMOD in size and development over time. This may change, however, when decomposition data from litter assemblies other than leaf-litter alone are subject to similar scrutiny.
- Intra-annual and long-term predictions concerning leaf-litter decay and N mineralization remain uncertain. Undoubtedly, greater certainties can be achieved with data on intra-annual mass and N, and by expanding the data period from 1992–1998 to 1992–2002 once the additional CIDET data become available. This presumes that the litterbags receive no additional mass from the adjacent litter accumulations. Even if this were the case, there would still be many uncertainties regarding the short- and long-term projections. For example, is the N content within litterbags affected by adjacent N availabilities, especially by way of forest fertilization and other forest activities (Prescott et al.,

2004)? What would be the final N concentrations or final C/N ratios of well-humified matter within the litterbags? Will mass and N contents in the litterbags actually approach 0 over time, and if so, what would be the convergence rate towards this end point?

The pools and processes represented by each model are not easily separable or measurable because of inter-mingling of particulate with non-particulate matter, leaves with woody litter, humified with non-humified matter, microbe-free with microbe-permeated litter, and dead with living microbial biomass (Wander, 2004). Comprehensive studies on the changing composition of decaying litter over widely ranging conditions are rare, and would be difficult and costly if extended over decades with frequent intra-annual bag sampling and analysis of mass, C, N, ash, cellulose, and AUR fractions (e.g.). Other factors that influence the decomposition dynamics within the litterbags such bag size, mesh openings, litter piece size (diameter, length of leaves, twigs, branches, logs, and roots), and bag placement on or within the soil profile may also have to be determined to address related uncertainties.

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Appendix A. Model formulations

FLDM (Zhang et al., 2007). This forest litter decomposition model estimates mass and N loss from three non-interacting mass and N pools (Trofymow et al., 2002):

- a fast decomposing fraction, representing the easily metabolized and solubilized components of fresh litter, such as sugar, soluble organic acid, proteins, and other metabolically active organic and mineral substances;
- a slowly decomposing fraction, which would mainly be composed of cellulose, hemicellulose and other structure-supporting materials of organic and mineral origin;
- a very slow (metastable) fraction, mainly consisting of humifying organic matter, and fairly insoluble inorganic debris.

In FLDM, the initial fast, slow and very slow leaf-litter partitioning is derived from the initial specifications for water- and acid-hydrolyzable, AUR, and ash contents. The FLDM nitrogen compartments are partitioned in the same way, except that the fast compartment is combined with the slow compartment, assuming that the very easily mineralized N is re-absorbed by the slowly decomposing fraction. Moreover, in FLDM, it is recognized that the rate of N mineralization relative to the rate of mass loss is slower, i.e., the fresh litter is more conservative in terms of N retention than mass loss, to the degree that the rate of mass loss eventually becomes limited by the rate of N release.

The FLDM is an end-of-year, fall-to-fall predictor of mass and N remaining in leaf-litterbags. The rate at which mass loss occurs is set to be dependent of the size of each compartment (as determined by the initial fast, slow, and very slow organic matter partitioning), and by local soil moisture and temperature conditions, as these vary each year from cold and frosty (as captured by the average January temperature) to warm (as captured by the July temperature), and from dry to moist to wet (as represented by annual precipitation amounts).

FLDM calculates N release and retention in proportion to the decomposition rates for the slow and very slow pools. Furthermore, the eventual C/N ratio of the decaying litter is set to be consistent with what is normally found in the humus layer (H layer) of the forest floor when present. Within the formulation of this model, M, C, and N refer, respectively, to the leaf-litter mass, C, N pools, and 1, 2, 3 denote the fast, slow and very slow fractions. In detail:

$$M = M_1 + M_2 + M_3, \tag{A.1}$$

$$C = C_1 + C_2 + C_3 \tag{A.2}$$

and

$$N = N_1 + N_2 + N_3. \tag{A.3}$$

Nitrogen concentrations are symbolized by

$$[N] = \frac{N}{M}; \quad [N_1] = \frac{N_1}{M_1}; \quad [N_2] = \frac{N_2}{M_2}; \quad [N_3] = \frac{N_3}{M_3}. \tag{A.4}$$

The initial fast, slow, and very slow fractions are estimated as follows:

$$\begin{aligned}\frac{M_1}{M} = \frac{N_1}{N} &= \exp[a_0 + a_1\,\text{initial\_acid\_extractable\_fraction}(\%) \\ &\quad + a_2\,\text{initial\_water\_extractable\_fraction}(\%)] \\ &= l_1 - l_2\,\text{initial\_AUR\_fraction}(\%)\end{aligned} \tag{A.5}$$

$$\frac{M_2}{(M_2+M_3)} = \frac{N_2}{(N_2+N_3)} = \exp[-a_3\,\text{initial\_ash}(\%)] \qquad (A.6)$$

with a_0, a_1, a_2 (or l_1, l_2) and a_3 as calibration coefficients. The rate of litter decomposition and N mineralization are represented by

$$\frac{dM_1}{dt} = -K_1M_1; \qquad K_1 = k_1 f(\text{climate}) \qquad (A.7)$$

$$\frac{dM_2}{dt} = -K_2M_2; \qquad K_2 = k_2 f(\text{climate}) \qquad (A.8)$$

$$\frac{dM_3}{dt} = -K_3M_3(t);$$
$$K_3 = k_3 f(\text{climate})\left\{1-\left\{\frac{M}{C}\right\}CN_{\text{final}}[N_3](1-\frac{n_3}{k_3})\right\} \qquad (A.9)$$

$$\frac{dN_1}{dt} = \frac{n_1}{k_1}[N_1]\frac{dM_1}{dt} \qquad (A.10)$$

$$\frac{dN_2}{dt} = \frac{n_2}{k_2}[N_2]\frac{dM_2}{dt} \qquad (A.11)$$

$$\frac{dN_3}{dt} = \frac{n_3/k3\;[N_3]dM_3/dt}{\{1-\{M/C\}CN_{\text{final}}[N_3](1-n_3/k_3)\}} \qquad (A.12)$$

such that $n_1 = n_2$ and $n_3/k_3 = n_2/k_2 = a_4[N]_{\text{initial}}$, with k_1, k_2, k_3 and a_4 as calibration coefficients. The following adjustment was made to accommodate net N absorption above original N contents as observed for some the CIDET and LIDET litterbags and other studies (Moore et al., 2006; Parton et al., 2007; Manzoni et al., 2008):

$$\text{net}_{\text{exogenous\_N}}\,\text{uptake}\;(N_2\;\text{pool}) = k_{\text{exo\_N}}\left(\frac{CN}{CN_{MB}}-1\right)\frac{dM}{dt} \qquad (A.13)$$

with $k_{\text{exo\_N}}$ as an adjustable but time-, composition- and climate-independent N uptake coefficient, and CN and CN_{MB} as the C/N ratios of the decaying litter and of the microbial biomass within this litter, respectively. Keeping all FLDM coefficients fixed (as in Table 2, bottom), setting $CN_{MB} = 8$, and proceeding with least-squares fitting as described in the main text produced an estimate for $k_{\text{exo\_N}}$, namely $0.00064 \pm 0.00017\,\text{year}^{-1}$. This adjustment did not affect any of the FLDM results in Table 2 in a numerically significant way, but doing so enhanced the N concentration estimates during the first few years after litterbag placement.

In FLDM, the rate of litter decay and N mineralization for each litter fraction is related to changes in climate condition in the same way, whether these are directly traced to daily or monthly soil temperature and moisture estimates, or indirectly to annual changes in annual precipitation and mean January and July air temperatures. The latter is obtained by setting

$$f(\text{climate})_{\text{FLDM}} = \left[\min(1, \text{ppt}/p_1) + \frac{T_{\text{Jan}}}{p_2}\right] \times \exp\left[-\left(\frac{E_a}{R}\right)\left(\frac{1}{(T_{\text{July}}+273)}-\frac{1}{288}\right)\right] \qquad (A.14)$$

with p_1 and p_2 as coefficients, R as the universal gas constant, and E_a representing the activation energy of the overall litter decay process, with reference to 15 °C (=288 K) as standard temperature. FLDM has, in total, 11–12 adjustable coefficients, depending on using the initial AUR or initial water-extractable and acid-hydrolyzable fractions for specifying the initial M_i/M and N_i/N fractions, respectively.

CENTURY (Parton et al., 1987). The CENTURY model, when applied to leaf-litter only, has 5 C pools: structural (S_r), metabolic (M_b), microbial (or active, A_c), slow (S_l), and passive (P_a). The un-decomposed litter is divided into the structural and metabolic pools, as determined by the AUR/nitrogen ratio: the higher this ratio, the more of the organic matter in the litter is considered to be structural. Carbon from the structural and metabolic pools is partitioned into CO_2 losses and complementary transfers to the active and slow pools, and from there more CO_2 losses with complementary transfers to the passive pool. Pool-centered decomposition rates are obtained by reducing a maximum decomposition rate by a multiplicative function that depends on mean July temperatures and annual precipitation rates. The changing pool sizes are quantified as follows:

$$\frac{dS_r}{dt} = \text{Litter}\;(1-F_M) - K_1S_r \qquad (A.15)$$

$$\frac{dM_b}{dt} = \text{Litter}\;F_M - K_2M_b \qquad (A.16)$$

$$\frac{dA_c}{dt} = 0.45K_1S_r(1-L_{Sr}) + 0.45K_2M_b + 0.45K_5P_a + 0.42K_4S_l - K_3A_c \qquad (A.17)$$

$$\frac{dS_l}{dt} = 0.7K_1L_{Sr}S_r + K_3A_c(1-F(T_x)-0.004) - K_4S_l \qquad (A.18)$$

$$\frac{dP_a}{dt} = 0.03K_4S_l + 0.004K_3A_c - K_5P_a \qquad (A.19)$$

$$K_1 = -k_1\exp(-3LS_r)f(\text{climate})_{[\text{CENTURY}]} \qquad (A.20)$$

$$K_i = -k_i f(\text{climate})_{\text{CENTURY}} \qquad (A.21)$$

with $i = 1, 2, 3, 4, 5$ referring Sr, M_b, A_c, S_l and P_a, respectively, k_i denoting the maximum decomposition rates for each organic matter pool, and L_{Sr} as the AUR ("lignin") fraction in the structural pool. In addition,

$$f(\text{climate})_{\text{CENTURY}} = M_dT_d \qquad (A.22)$$

with, M_d and T_d denoting soil moisture and temperature effects, presented in the form of 0–1 multiplication factors that depend on local precipitation rates and air temperatures, respectively. Furthermore,

$$F_M = p_{\text{fm0}} + p_{\text{fm1}}L/N \qquad (A.23)$$

with F_M as the metabolic fraction of the organic residue $F_s = (1-F_M)$ a the structural fraction, and L/N a the AUR ("lignin")/nitrogen ratio. Finally,

$$F(T_x) = 0.85 - 0.68\,T_x \tag{A.24}$$

with T_x is a soil texture coefficient, set at 0 when the clay + silt content of leaf-litter is 0, as would be the case for the CIDET litterbags.

The N pools and processes are considered to have same structure as the C pools and processes, with prescribed C/N ratios by pool type: 150 for the structural pool, 8 for the active pool, and 11 for the slow and passive pools. N rates entering or leaving the pools are adjusted such that the C/N ratio of each pool remains fixed, except for the C/N ratio of the metabolic pool which is allowed to vary. External N inputs via atmospheric deposition, fertilizer applications or N_2 fixation were all set to 0. Altogether, this formulation contains 19 coefficients. Eleven of these, i.e., k_i, $p_{fm0} + p_{fm1}$, and the C/N ratios for structural, active pool, slow and passive pools were considered adjustable. The M_b, A_c, S_l and P_a numbers for the pool-to-pool transfer coefficients were kept as quoted originally. The combined C pool was converted into a single leaf-litter mass estimate with the FLDM-defined and species-specific mass-to-C conversion ratio {M/C}.

DOCMOD (Currie and Aber, 1997). This model formulates leaf-litter decay with 5 carbon pools: lignocellulose (LC), unprotected cellulose (C), acid-soluble extractives (E), microbial biomass (B), and humus (H). Ash-free foliage is partioned into the LC, C and E pools. AUR mass and acid-hydrolyzable mass are added to the LC pool in equal amounts. The remainder of the acid-hydrolyzable mass is added to the C pool. Except for LC and H, N transfer rates are calculated from the corresponding organic matter transfer rates, and dividing these C pools by their assigned C/N ratio. For the LC pool, special provisions are made: to absorb N when N concentrations are low, and to mineralize N when N concentrations are high. For the humus pool, N is set to be mineralized at a lower rate than the humus mineralization rate to reach a specific C/N end-ratio. The climate dependencies of the rate processes are related to location-specific annual evapo-transpiration rates, as follows:

$$\frac{dM_{LC}}{dt} = 0.5k_m M_B - r(AET)\,[1 - \exp(-K_{LC})]M_{LC} \tag{A.25}$$

$$\frac{dM_C}{dt} = 0.1k_m M_B - r(AET)[1 - \exp(-K_L)]M_C \tag{A.26.1}$$

$$\frac{dM_E}{dt} = 0.4k_m M_B - r(AET)[1 - \exp(-K_E)]M_E \tag{A.27}$$

$$\frac{dM_B}{dt} = \frac{0.21dM_LC}{dt} + \frac{0.54dM_C}{dt} + \frac{0.23dM_E}{dt} - k_m M_B \tag{A.28}$$

$$\frac{dM_H}{dt} = \frac{1}{3d}\frac{M_{LC}}{dt} - r(AET)[1 - \exp(-K_H)]M_H \tag{A.29}$$

$$\frac{dN_{LC}}{dt} = M_{LC}\left[k_{NLC1} + k_{NLC1}\left(\frac{N_{LC}}{M_{LC}}\right)\right] - r(AET)[1 - \exp(-K_{LC})]N_{LC} \tag{A.30}$$

$$\frac{dN_C}{dt} = 0.1k_m N_B - r(AET)[1 - \exp(-K_L)]N_C \tag{A.31}$$

$$\frac{dN_E}{dt} = 0.4k_m N_B - r(AET)[1 - \exp(-K_E)]N_E \tag{A.32}$$

$$\frac{dN_B}{dt} = \frac{[0.21dM_{LC}/dt + 0.54dM_C/dt + 0.23dM_E/dt]}{CN_B - k_m N_B} \tag{A.33}$$

$$\frac{dN_H}{dt} = \frac{1}{3r(AET)}[1 - \exp(-K_{LC})]N_{LC} - r(AET)\,[1 - \exp(-K_H)]N_H \quad \text{if}\frac{C}{N} < 21, \text{else}$$
$$\frac{dN_H}{dt} = \frac{1}{3r(AET)}[1 - \exp(-K_{LC})]N_{LC} \tag{A.34}$$

with

$$r(AET) = \frac{\exp(p_{AET}\ AET - 244)}{\exp(p_{AET}\,AET' - 244)} \tag{A.35}$$

$$K_{LC} = k_{LC0} + k_{LC1}LCI \tag{A.36}$$

$$K_C = k_{C0}(1 - LCI) \tag{A.37}$$

$$K_E = k_{E0} + k_{E1}LCI \tag{A.38}$$

$$K_H = k_{Hh0} \tag{A.39}$$

for hardwoods;

$$K_H = k_{Hs0} \tag{A.40}$$

for softwoods

$$LCI = \frac{AUR}{AUR + \text{holocellulose}} \tag{A.41}$$

where M_{LC}, M_C and M_E represent the litter mass portions for the LC, C, and E pools; r(AET) is the climate factor; AET is an estimate for the local annual total evapotranspiration in millimeters; N_{LC} is the nitrogen mass in the LC pool; and k_m, k_{LC0}, k_{LC1}, k_{C0}, k_{E0}, k_{E1}, k_{NLC0}, k_{NLC1}, CN_B, p_{AET}, AET′, k_{Hh0}, and k_{Hs0} are 13 adjustable coefficients, selected from a total of 21 coefficients. For simplicity, the combined Carbon pool is converted to the leaf-litter mass pool using the FLDM-defined and species-specific M to C conversion ratio {M/C}.

CANDY (Franko et al., 1995). The organic matter decomposition and nitrogen mineralization components of the CANDY model refer to three organic matter pools: the added organic matter (AOM) pool, the biologically active soil organic matter (BOM) pool, and the stabilized soil organic matter (SOM) pool. All rate processes are collectively quantified with identical sensitivities to changes in soil moisture and temperature. The equations of this model are as follows:

$$\frac{dC_{AOM}}{dt} = -K_{AOM}C_{AOM} \tag{A.42}$$

$$\frac{dC_{BOM}}{dt} = K_A C_{SOM} + K_{AOM}C_{AOM} - (K_{BOM} + K_S)C_{BOM} \tag{A.43}$$

$$\frac{dC_{SOM}}{dt} = K_S C_{BOM} - K_A C_{SOM} \quad (A.44)$$

with C_{AOM} as the pool size of the added organic matter, C_{BOM} as the biological active soil pool, C_{SOM} as the stabilized soil organic matter pool

$$K_{AOM} = k_{AOM}\, f(\text{climate})_{CANDY} \quad (A.45)$$

$$K_{BOM} = k_{BOM} f(\text{climate})_{CANDY} \quad (A.46)$$

$$K_A = k_A f(\text{climate})_{CANDY} \quad (A.47)$$

$$K_S = k_S f(\text{climate})_{CANDY} \quad (A.48)$$

where K_{AOM} is the decay rate parameter for the AOM pool, K_{BOM} is the decay rate of the BOM pool, K_A and K_S are the forward and backward transferring rate coefficients between the metabolic pool and the slow pool, k_{AOM}, k_{AOM}, k_A, k_S and η are coefficients, with η referring to microbial uptake portion of dC_{AOM}/dt.

The original description of the CANDY model included details on soil moisture and temperature estimates, but did not show how the resulting values were incorporated into the decomposition and N mineralization process formulation. Instead, we set:

$$f(\text{climate})_{CANDY} = W_{FF} P_{AET} \exp\left[-\left(\frac{E_a}{R}\right)\left(\frac{1}{(T_{FF}+273)} - \frac{1}{288}\right)\right] \quad (A.49)$$

where, W_{FF} is the moisture content of the litter; T_{FF} is the temperature of the litter; and P_{AET} and E_a are coefficients.

In CANDY, the C/N ratio of the BOM and SOM pools is originally set at $CN_{BOM} = CN_{SOM} = 8.5$. This number was then used to determine the rate of N release from these pools, once dC_{BOM}/dt and dC_{SOM}/dt were determined. The release of N from AOM is computed from dC_{AOM}/dt and the initial C/N ratio of this pool. Altogether, this model has 8 adjustable coefficients: k_{AOM}, k_{AOM}, k_A, k_S, η, P_{AET}, E_a and CN_{BOM}.

SOMM (Chertov and Komarov, 1997). This model presents organic matter decomposition in three stages, using 5 mass and 5N compartments: at the first stage, part of the litter layer (L pool) is set to be lost through biochemical degradation and fermentation thereby contributing to the fermentation layer (F pool). At the second stage, the fermented organic matter is lost through heterotrophic respiration and transformed into humus (H pool). At this stage, fermented matter is digested by microbial organisms, and soil mesofauna (e.g. earthworms), with the former producing humus with C/N ratio of 15 and the latter producing humus with a C/N ratio of 15. At each stage, the rates of the litter mineralization, fermentation and humification are empirically related to ash and N content of the decaying litter, and to local soil temperature and moisture estimates. Estimated dependencies of rates to soil temperature and moisture vary with each process. Formally, SOMM is built on the following expressions:

$$\frac{dL}{dt} = L_0 - (K_1 + K_3)L \quad (A.50)$$

$$\frac{dF}{dt} = K_3 L - (K_2 + K_4 + K_5)F \quad (A.51)$$

$$\frac{dH}{dt} = 1.6\left[K_4\left(\frac{C}{N}\right)_{b1} + K_5\left(\frac{C}{N}\right)_{b2}\right] F\_N - K_6 H \quad (A.52)$$

$$\frac{dB_1}{dt} = 0 \quad (A.53)$$

$$\frac{dB_2}{dt} = 0 \quad (A.54)$$

with K_4F as microbial consumption, $1.6K_4(C/N)_{b1}F\ N$ as humus production, and $K_4F\ 1.6K_4(C/N)_{b1}F\ N$ as microbial respiration, K_5F as mesofaunal consumption, $1.6K_5(C/N)_{b2}F\ N$ as humus production, and $K_5F\ 1.6K_5(C/N)_{b2}F\ N$ as mesofaunal respiration. Also,

$$K_i = k_i\ \text{fi}\ (\text{climate})_{SOMM} \quad (A.55)$$

$$f_i(\text{climate})_{SOMM} = g_i(T) g_i(W) \quad (A.56)$$

where: K_1 (L mineralization), K_2 (F mineralization), K_3 (fermentation of litter), K_4 (humification by microfauna), K_5 (humification by macrofauna), K_6 (humus mineralization) represent the transfer coefficients of organic matter from one pool to another; k_i ($i = 1$–6) are the corresponding coefficients that are – in turn – related to the initial ash and nitrogen content of the litter with additional coefficients; $g_i(T)$ and $g_i(W)$ are empirically derived functions with further coefficients to determine the influence of moisture and temperature on each decomposition process; C/N_{b1} and C/N_{b2} are the C/N ratio of the microbial (B_1) and soil mesofauna (B_2) biomass, respectively.

In SOMM, the mass to C ratio is set to 1.6. In addition, L_N, F_N and H_N refer to the nitrogen content of the L, F, H components, calculated as:

$$\frac{dL\_N}{dt} = L_0\_N - (0.1K_1 + K_3)L\_N \quad (A.57)$$

$$\frac{dF\_N}{dt} = K_3 L\_N - (K_4 + K_5)F\_N \quad (A.58)$$

$$\frac{dH\_N}{dt} = 0.8(K_4 + K_5)F\_N - K_6 H\_N \quad \text{if } C/N < 8, \quad \text{else}$$

$$\frac{dH\_N}{dt} = 0.8(K_4 + K_5)F\_N - 0.8K_6 H\_N \quad (A.59)$$

$$\frac{dB_1\_N}{dt} = 0 \quad (A.60)$$

$$\frac{dB_2\_N}{dt} = 0 \quad (A.61)$$

with $K_4F\ N$ as microbial N consumption, $0.8K_4F\ N$ as microbial humus N production, $0.2K_4F\ N$ as microbial N mineralization, $K_5F\ N$ as mesofaunal consumption, $0.8K_5F\ N$ as humus N production, $0.2K_5F\ N$ as mesofaunal N mineralization, and K_6H_N as humus N mineralization. Altogether, SOMM contains 61 experimentally determined coefficients

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