Modeling mass and nitrogen remaining in litterbags for Canadian forest and climate conditions

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Zhang, C. F., Meng, F-R., Trofymow, J. A. and Arp, P. A. 2007. **Modeling mass and nitrogen remaining in litterbags for Canadian forest and climate conditions**. Can. J. Soil Sci. **87**: 413–432. A new Forest Litter Decomposition Model (**FLDM**) is presented to simulate mass, N and carbon/nitrogen ratios (C/N) according to the 1992–1998 leaf litterbag data of the Canadian Intersite Decomposition Experiment (CIDET). This experiment involved 10 litter types, with litterbags placed on the ground of 18 upland and 3 wetland sites across Canada. The calibrated model, based on first-order reaction kinetics, calculates total mass, N concentration and C/N for each litter type and location using: three compartments (fast, slow, and very slow); four parameters for compartment initialization; three for compartment-based decay; three to assess the climate influence on decay; and one each to determine the rate of N-mineralization and the final C/N ratio. With FLDM, the initial fast fraction is determined from the initial water-extractable and acid-hydrolyzable or acid-unhydrolyzable portions of the litter; the initial ash content determines the ratio between the slow and very slow fractions. Mean July and January air temperatures, and annual precipitation, determine the climate effect on litter decay. Initial N concentration and the upland-wetland difference determine the N-mineralization coefficient. Model performance was fairly consistent by litter type, location, and year: r^2 ranged from 0.83 to 0.97, from 0.64 to 0.92 and from 0.54 to 0.93 for mass remaining, N concentration and C/N, respectively.

Key words: Forest litterbags, organic matter decomposition, N concentrations, climate, litter type, CIDET

Zhang, C. F., Meng, F. R., Trofymow, J. A. et Arp, P. A. 2007. **Modélisation de la masse et de l'azote résiduels des sacs de litière dans les conditions climatiques et forestières du Canada**. Can. J. Soil Sci. **87**: 413–432. Les auteurs présentent un nouveau modèle de décomposition de la litière forestière (MDLF) simulant la masse, la concentration de N et le ratio carbone/azote (C/N) à partir des données recueillies entre 1992 et 1998 dans le cadre de l'Expérience canadienne sur la décomposition interstationnelle (ECDI). L'expérience consistait à placer des sacs contenant dix sortes de litière sur le sol à 18 endroits en milieu sec et à 3 en milieu humide au Canada. Étalonné d'après la cinétique de la réaction de premier ordre, le modèle permet d'établir la masse totale, la concentration de N et le ratio C/N pour chaque type de litière et chaque emplacement à partir des trois compartiments (décomposition rapide, lente et très lente), de quatre paramètres initiaux, de trois paramètres pour la décomposition dans chaque compartiment, de trois autres pour l'incidence du climat sur la décomposition et d'un dernier pour le taux de minéralisation du N ainsi que le ratio C/N final. Le MDLF détermine la fraction initiale qui se décompose rapidement à partir des fractions initiales de litière extractibles à l'eau et hydrolysables ou pas à l'acide. La concentration initiale de cendres sert à établir le ratio entre la fraction à décomposition lente et celle à décomposition très lente. La température moyenne de l'air en juillet et en janvier et les précipitations annuelles déterminent l'incidence du climat sur la décomposition de la litière. La concentration initiale de N et la variation entre le milieu sec et le milieu humide établit le coefficient de minéralisation du N. Le modèle a une performance assez uniforme pour le type de litière, l'emplacement et l'année. La valeur r^2 varie de 0,83 à 0,97, de 0,64 à 0,92 et de 0,54 à 0,93 respectivement pour la masse résiduelle, la concentration de N et le ratio C/N.

Mots clés: Sacs de litière forestière, décomposition de la matière organique, concentration de N, climat, type de litière, ECDI

Several recent studies have focused on empirically clarifying and quantifying the process of C and N release from decomposing plant residues including forest litter, to determine the contributions of terrestrial ecosystems to the global carbon cycle within the context of world-wide and regional climate change. Among these studies are: the Long-Term Intersite Decomposition Experiment in the United States (LIDET 1995), the Decomposition Study in Europe (DECO) (Jansson and Reurslag 1992), and the Canadian Intersite Decomposition Experiment (CIDET) (Trofymow et al. 1995; Trofymow and CIDET Working Group, 1998; Trofymow et al. 2002). In principle, factors that influence the rate of organic matter degradation are well known, namely litter quality (Heal et al. 1997), temperature and moisture, associated drying and wetting cycles (Fierer and Schimel 2002; Borken et al. 2003), nutrient availabilities (Walse et al. 1998), and microbial composition (Jenkinson et al. 1991; Aber et al. 1998; Berg and Matzner 1997; Gillon et al. 1999 a, b). To some extent, these factors are included

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Abbreviations: **CBM-CFS**, Carbon Budget Model – Canadian Forest Sector; **CIDET**, Canadian Intersite Decomposition Experiment; **FLDM**, Forest Litter Decomposition Model

in models designed to simulate rates of organic matter accumulation and decomposition in terrestrial ecosystems, such as Carbon Budget Model – Canadian Forest Sector (CBM-CFS) (Kurz and Apps 1999), CENTURY (Parton et al. 1993; CENTURY 2000), ROMUL (Chertov et al. 2001), Yasso (Palosuo et al. 2005) and others (e.g., McGill 1996; Smith et al. 1997). These models generally vary in number of compartments, conditions, and processes. Specific algorithms are based on a mixture of empirically derived regression results, and assumed and/or theoretically derived relationships. Recent reviews focused on the utility of one-, two-, or three-compartment models for quantifying CO_2 release from soil organic matter degradation with respect to changing climate conditions (Knorr et al. 2005; Powlson 2005). The CIDET experiment was initiated in 1992, and involved the placement of about 11 000 litterbags, comprising 10 foliage types, 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 red cedar (*Thuja plicata*), Bracken fern (*Pteridium aquilinum*), Plains rough fescue (*Festuca hallii*) and wooden blocks of western hemlock (*Tsuga heterophylla),* at 21 sites (18 upland sites, 3 wetland sites), across the major ecoclimate regions of Canada (Trofymow et al. 2002).

The final CIDET litterbag collection occurred in 2004. Thus far, data from 1992 to 1998 have been used to quantify the overall changes in mass or rates of litter decay by way of multiple regression analyses, using climate variables and substrate variables as decay predictors (Moore et al. 1999; Preston et al. 2000; Trofymow et al. 2002). The resulting quality of fit between an empirically developed multiple-regression model with only seven predictor variables and the data for mass remaining was shown to be fairly high, with an overall r^2 value of 0.80 (1993 to 1998 data only; Trofymow et al. 2002). Recent papers have examined other aspects of the 1992–1998 data, by comparing differences in the litterbag mass and nutrient dynamics at paired wetland – upland sites (Moore et al. 2005), and the foliar litterbag C, N, and P dynamics at the 18 upland forest sites (Moore et al. 2006). There has also been an examination of the data by way of the Yasso model (a five-compartment soil carbon model; Palosuo et al. 2005).

This paper presents the formulation, calibration and performance of a three-compartment forest litter decomposition model (FLDM) designed to calculate mass remaining, N concentrations and C/N ratios in the CIDET leaf litterbags, by litter type, climate, and site conditions, based on the law of mass conservation and first-order reaction kinetics, and on the CIDET expectations that:

- litter decay can be quantified by compartmentalizing the litter into three fractions: fast, slow and very slow, and that the mineralization of organic matter, including C, N and other nutrients in each fraction, can be tracked over time;
- this compartmentalization can be derived from the initial elemental (C, N) water-extractable, acid-hydrolyzable and acid-unhydrolyzable fractions and ash content;
- the rate of decay varies according to the initial chemical composition of the litter, and that this rate also depends on local climate and microclimate, according to local site conditions;
- the rate of litter decay may be influenced by the absorption of exogenous nutrients, especially N.

Additional expectations dealt with the following:

- that the model would address the decay process as not only being moisture-, temperature- and substrate-controlled at the beginning but also becoming C-limited towards the final stage;
- that the rate of N mineralization process differs from the rate of organic matter mineralization, i.e., the C/N ratio varies dynamically from beginning to end, and therefore constitutes model output rather than input;
- that the CIDET-calibrated model would, at least in principle, be numerically efficient and practical to allow leaf litter decomposition projections for a wide range of conditions while restricting input requirements to already available and/or easily generated data.

MODEL DESCRIPTION

The FLDM model is based on earlier suggestions that net annual changes in mass and nutrient contents in forest litterbags can be approximated by way of an exponential decay formulation for each of three theoretical compartments (Minderman 1968; Paul and Voroney 1980; Parton et al. 1987; LIDET 1995; Trofymow and CIDET Working Group 1998). These compartments refer, conceptually, to:

- a fast decomposing fraction, representing the easily metabolized components of fresh litter, such as sugar, soluble organic acids, proteins, and other metabolically active organic and mineral substances;
- a slowly decomposing fraction, mainly composed of cellulose, hemicellulose and other structure-supporting materials of organic and mineral origin;
- a very slow fraction, mainly consisting of resistant organic compounds in the acid-un-hydrolyzable fraction, including compounds such as lignin and fairly insoluble inorganic materials.

A state-dependent first-order kinetic expression for a three-compartment model is given by:

$$dM_i(t)/dt = -k_i(S)\,M_i(t) \quad (1)$$

where

$$M(t) = M_1(t) + M_2(t) + M_3(t) \quad (2)$$

is the total mass remaining at any time t, and where: $i = 1$, 2, 3 denotes the fast, slow, and very slow decomposing compartments, respectively; $M_i(t)$ is the mass remaining in the ith compartment at time t; $k_i(S)$ is the time-independent but state – dependent coefficient of the rate of change function for the ith compartment; and S refers to the state of the litterbag, as defined by litter type, nutrient content, moisture content, and temperature.

For the N content of the litterbags, we hypothesize that the rate of change of N_i (the N content of the i^{th} compartment) is – in analogy to M_i – proportional to N_i, i.e.,

$$dN_i(t)/dt = -n_i(S)\,N_i(t) \quad (3)$$

where $n_i(S)$ is the time-independent but state-dependent coefficient of the net N mineralization process. We further specify that

$$[N(t)] = \{[N_1(t)]\,M_1 + [N_2(t)]\,M_2 + [N_3(t)]\,M_3\} / M(t) \quad (4)$$

is the total N concentration in the litterbag at any time t, and

$$[N_i(t)] = N_i(t)/M_i(t)$$

are the N concentrations of each compartment at time t. For the purpose of model initialization, we set:

$$M_1(t=0) = M(t=0)\,g \quad (5)$$

$$M_2(t=0) = e\,M(t=0)\,(1-g) \quad (6)$$

$$M_3(t=0) = (1-e)\,M(t=0)\,(1-g) \quad (7)$$

where e and g are mass partitioning coefficients, i.e., g is the fraction of the fast-decomposing component of the litter, and e proportions the non-fast fraction into the slow and very slow fractions.

As decomposition proceeds, we need to ensure that the C/N ratio of the remaining mass inside in litterbags will approach a C/N ratio that is normal for well-humified forest litter, i.e., CN_{final}. Hence, we set

$$dM_1(t)/dt = -k_1(S)\,M_1(t) \quad (8)$$

$$dM_2(t)/dt = -k_2(S)\,M_2(t) \quad (9)$$

$$dM_3(t)/dt = -k_3(S)\,M_3(t)\,\{1 - MC_{conversion}\,CN_{final}\,[N_3(t)]\,(1 - n_3(S)/k_3(S))\} \quad (10)$$

where $MC_{conversion}$ is a parameter that converts carbon mass into litter mass. It is assumed that $MC_{conversion}$, when set equal to $M(t)/C(t)$, remains fairly constant throughout the litter decomposition process. If so, then $MC_{conversion}$ can be evaluated from the initial mass and C contents, i.e.,

$$MC_{conversion} = M(t=0) / C(t=0).$$

For initializing N in each of the three compartments, we set

$$N_1(t=0) = N(t=0)\,g,$$

$$N_2(t=0) = e\,N(t=0)\,(1-g),$$

$$N_3(t=0) = (1-e)\,N(t=0)\,(1-g),$$

thereby assuming that $N(t)$ is portioned in the same way as $M(t)$, and we set

$$dN_1(t)/dt = -n_1(S)\,N_1(t) = n_1(S)/k_1(S)\,[N_1(t)]\;dM_1(t)/dt \quad (11)$$

$$dN_2(t)/dt = -n_2(S)\,N_2(t) = n_2(S)/k_2(S)\,[N_2(t)]\;dM_2(t)/dt \quad (12)$$

$$dN_3(t)/dt = -n_3(S)\,N_3(t) = n_3(S)/k_3(S)\,[N_3(t)]\;dM_3(t)/dt / \{1 - MC_{conversion}\,CN_{final}\,[N_3](t)\,(1 - n_3(S)/k_3(S))\} \quad (13)$$

where $n_i(S)$ and $k_i(S)$ denote state-dependent rate coefficient functions, with S referring to the state of the litter bag and its surroundings, i.e., moisture content, temperature, and chemical composition of the substrate and of the litterbag surroundings. In this formulation, the rate of N loss is not only directly proportional to the amount of N in the litterbag, but also directly proportional to the rate of mass loss. This implies that when the relative mass and N losses are equal, i.e., when $dM_i/dt/M_i(t) = dNt(t)/N_i(t)$, then $n_i(S) = k_i(S)$. For this condition N concentrations would remain unchanged with increasing state of decay. When $n_i(S) < k_i(S)$, litterbags would be more conservative with respect to N_i loss than to M_i loss, and N_i concentrations would therefore increase over time, as reported by Berg et al. (1999). The opposite would occur when $n_i(S) > k_i(S)$.

The model requires explicit expressions for $k_i(S)$ and $n_i(S)$. To facilitate this, we assume that the rate parameters for litter decomposition and N mineralization are primarily independent of mass and nitrogen remaining in each compartment, but could be affected by substrate and climate conditions. We further assume that differences in local climate conditions dictate the rate of microbial activities regardless of microbial community type. Certainly, there is no to little microbial activity when the litter is frozen. As the temperature increases, microbial activities would become more and more active, depending on the prevailing soil moisture condition, with warm and moist conditions being optimal. We therefore set

$$k_i(S) = k_i\,f(\text{climate}) \text{ and } n_i(S) = n_i\,f(\text{climate}) \quad (14)$$

where f(climate) is the climate dependent part of $k_i(S)$ and $n_i(S)$, and k_i and n_i are simple proportionality coefficients. With this, we are assuming that:

- both $k_i(S)$ and $n_i(S)$ relate to changes in climate in the same way,
- $n_i(S)$ is proportional to $k_i(S)$,
- k_i and n_i are climate-independent but litter-specific parameters,
- the compartmental n_i/k_i ratios (the relative N retention coefficients of the decaying matter per compartment) are therefore also considered to be climate independent.

We now formulate f(climate) such that this function reflects expected regional changes in soil moisture (from dry to wet; from unfrozen to frozen), and soil temperature, as follows:

$$f(\text{climate}) = \{(\min(1, \text{ppt}/p_1) + T_{Jan}/p_2)\exp(-(Ea/R)(1/(T_{July}+273) - 1/288))\} \quad (15)$$

where p_1 and p_2 are parameters, Ea is the activation energy of the overall decay process, and R is the universal gas con-

stant (= 8.31 J mole^{-1} C^{-1}). In this, we use annual precipitation (ppt, in mm) and monthly January air temperature (T_{Jan}, in °C) as surrogate variables to capture the effect of low soil moisture and frost on the annual rate of litter decomposition, at each site. The exponential term in Eq. 15 is intended to capture the effect of summer temperatures on the rate of decomposition, with mean July air temperature (T_{July}, in °C) as surrogate for soil temperature. It is assumed that the rate of decay will not be affected by high rates of precipitation once these rates exceed a certain threshold at which soil moisture contents are already sufficiently high. In Eq. 15, this threshold is denoted by p_1. An exception to this may occur when the rate of decay drops on account of very high precipitation inputs, i.e., in excess of 2000 mm (Schuur 2001). Altogether, f(climate) is set to become 1 when: ppt ≥ p_1, T_{Jan} = 0°C, and T_{July} = 15°C. For a recent discussion about general decomposition trends with climate, see Prescott et al. (2004).

The long-term implications of the above formulation are such that, as t approaches infinity:

- $dM(t)$ / $dN(t)$ becomes equal to $M(t)$ / $N(t)$ which finally becomes $MC_{conversion}\ CN_{final}$, which is equal to 1/$[N]_{final}$, with $[N]_{final}$ being the final N concentration in the decomposing litter;
- both $N(t)$ and $M(t)$ approach 0.

For the fast and slow fractions (i = 1 and 2), the half-lives for mass remaining are given by

$$t_{i,1/2} = -\ln(0.5) / k_i\ (S). \tag{16}$$

For the very slow fraction, the half-life is given by

$$t_{3,1/2} = -\ln(0.5) /\{k_3(S)\ \{1 - MC_{conversion}\ CN_{final}\ [N_3(t)]\ (1 - n_3(S)/k_3(S))\}\}. \tag{17}$$

Hence, $t_{3,1/2}$ is set to change not only with climate condition and litter type, but also with time towards a final value given by

$$t_{3,1/2} = -\ln(0.5) / n_3(S). \tag{18}$$

The above formulation implies that the N mineralization process is gradually becoming the rate-limiting component of the overall litter decomposition process.

A flowchart of FLDM is presented in Fig. 1, as realized in STELLA (1998). Here, boxes refer to the mass and N reservoirs, broad arrows represent annual losses from these reservoirs, and thin arrows show logical connections, such as:

- the influence of each compartment on decomposition rate and rate of N mineralization,
- the combining of the mass and nitrogen reservoirs to compute total mass and nitrogen remaining as the sum of each of these reservoirs, by litter type, and by site.

METHODS

Data

A compilation of the CIDET data, as used for model initialization and calibration, is presented in Table 1 (specifying details about site location, climate, forest and soil type) and Table 2 (specifying details about site, geographic location, climate, stand and soil type). Climate data (annual precipitation, mean annual temperature, and mean monthly July and January temperatures for each year 1992–1998) were derived from Meteorological Service Canada weather stations (Environment Canada 2000) nearest to each site (Trofymow and CIDET Working Group 1998). In Table 3, initial elemental concentrations, and water- and non-polar extractables, acid-hydrolyzable and -unhydrolyzable residues (AUR), and ash contents are compiled (Trofymow et al. 1995; Trofymow and the CIDET Working Group 1998).

Experimental design and methods for the CIDET have been described by Trofymow and the CIDET Working Group (1998). Briefly, litterbags (target weight 10 g, mean actual weight = 9.947 g, 99% range from 9.07 to 10.20 g, each containing one litter type from 10 different sources, Table 1) were installed in 1992 at each of 21 sites (18 upland and 3 wetland sites), in replicates. This replication involved four separate 5 × 11 m plots within a 4 ha area, with each plot at least 30 m apart from another plot, to minimize pseudo-replication. Initial bag placement on the ground and subsequent retrievals occurred in the fall of each consecutive year. Samples were composited by site and litter type prior to determining mass remaining and elemental (C, N, P) concentrations (Trofymow and the CIDET Working Group 1998). The data used in this study refer to the initial (1992) and 1993 to 1998 litterbag results.

Multiple regression analysis of the pertinent Table 3 entries produced a generalized equation for the $MC_{conversion}$ parameter, namely:

$$MC_{conversion} = (1.443 \pm 0.07) + (0.007 \pm 0.001)\ \text{acid\_hydrolyzable\_fraction (\%)} + (0.011 \pm 0.002)\ \text{water\_extractable\_fraction (\%)} + (0.013 \pm 0.005)\ \text{Ash(\%)} \quad r^2 = 0.93 \tag{19}$$

Model Calibrations

In principle, there is no way to determine any of the above model parameters and their associated functions as listed in Table 4 a priori. Furthermore, pool sizes for $M_i(t)$ and $N_i(t)$ are not easily quantified by actual measurement due to the fuzziness of the three-compartment concept, and the chemical and biological uncertainties and ambiguities that are associated with specifying actual fast, slow, and very slow fractions (Wander 2004). Nevertheless, model calibrations and optimization can be done by comparing model output with actual $M(t)$, $[N(t)]$, $C(t)$ and $C(t)/N(t)$ values over time, by litter type, and by site condition by way of non-linear regression analysis . To do this, we developed a Step 1–Step 2 procedure to match model output with the CIDET data for $M(t)$, $[N(t)]$, and $C(t)/N(t)$. This procedure involved the realization of FLDM (Eqs. 1 to 19, plus additional equations below) within the ModelMaker modeling framework (1998), and by using the built-in least-squares nonlinear regression iteration routines (Simplex and Marquardt) for model optimization and parameter calibration, and for sta-

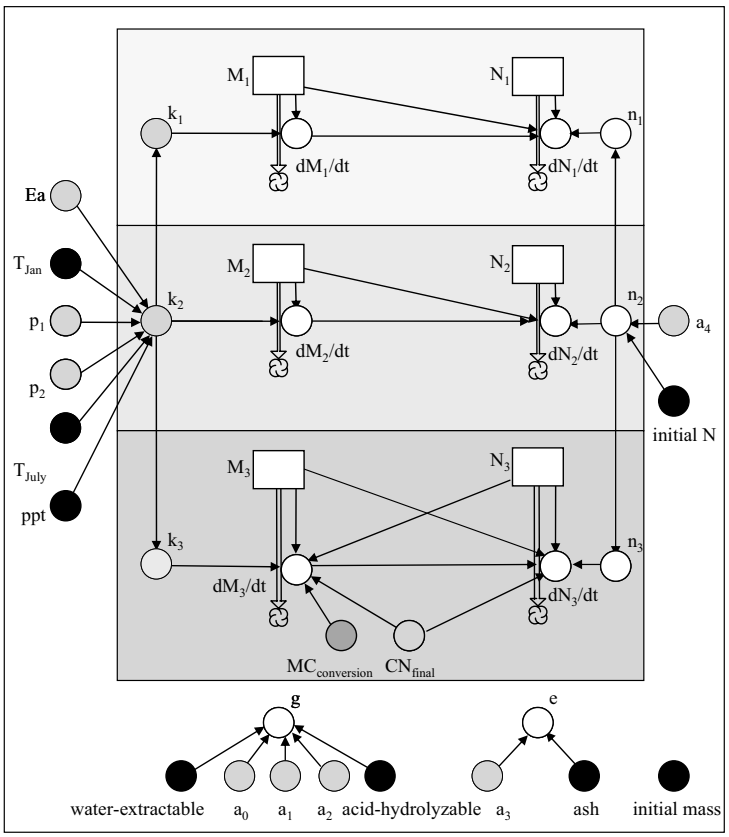

Fig. 1. Overview of the three-compartment model, designed to evaluate annual mass loss and N concentrations in CIDET litterbags. Boxes represent mass and N pools within each compartment. Broad arrows denote mass or N loss from pools. Circles refer to entry points for specific information dealing with model control, such as the rate equations and parameter values. Black circles refer to input variables (e.g., annual precipitation, ppt). Grey circles refer to fixed (dark-grey), or adjustable (light-grey), parameters. White circles and squares refer to output variables. The model tracks mass and nitrogen pool sizes as affected by climate conditions, over time, starting from initial values for mass and N.

tistical reporting. Generally, this routine started with initial "default" values for each of the parameters, and finished when successive Simplex and/or Marquardt iterations converged to a non-changing sum of squares of the residuals between simulated and actual $M(t)$, $[N(t)]$, and $C(t)/N(t)$ values. For this analysis, total sample size for each of $M(t)$, $N(t)$, and $C(t)/N(t)$ was 1470 (= 21 sites × 10 litter types × 7 years); this included all the 1993–1998 data, plus the initial conditions for 1992. Since $M(t)$ values ranged from about 0.1 to 10 g, $N(t)$ values ranged from 0.5 to 2.5%, and $C(t)/N(t)$ values ranged from about 15 to 100, we decided to change the default weighting for $C(t)/N(t)$ residuals from 1 to 0.01. Doing so still prioritized the least-squares fitting of $M(t)$, and gave secondary priority to the least-squares fitting of $[N(t)]$ and $C(t)/N(t)$. This fitting procedure was applied to all data and parameters at the same time. The model was slightly modified by adding the N pool of the fast fraction to the N pool of the slow fraction.

Step 1

Parameters p_1, p_2, Ea, and CN_{final} were assumed to be non-changing across litter type, site, and compartment. The k_i parameters were assumed to be non-changing across litter type and site, but were expected to vary by compartment such that $k_1 > k_2 > k_3$, by definition. Parameters e, g and n_i were also assumed to be non-changing across site, but were considered to depend on litter type. Based on these specifications, there were 57 parameters requiring calibration: 30 (10 litter types × 3 compartments) for n_i, 10 each for "e" and "g", plus k_1, k_2, k_3, p_1, p_2, Ea, and CN_{final}. We then calibrated all of these parameters by way of the least-squares fitting routine, and searched for patterns of similarity among the 30 n_i values and best-fitted N losses from all litterbags. The following was found:

- N losses from the fast and slow fractions were both found to be proportional to N_1 and N_2 in the same way, such that

$$n_1 = n_2 \tag{20}$$

- N losses from N_2 and N_3 were found to be directly proportional to dM_2/dt and to dM_3/dt, respectively, hence the relative N mineralization coefficients were found to be the same for the slow and very slow fractions, i.e.,

$$n_3 / k_3 = n_2 / k_2 \tag{21}$$

Table 1. CIDET litterbag sites: general site descriptors (from Trofymow and CIDET Working Group 1998)

Location	Code[z]	Province	Ecoclimatic region	Dominant forest cover	Soil
Batoche	**BAT**	Saskatchewan	Grassland	None	Limno Mesisol
CB Rocky Harbour	CBR	Newfoundland	Low Boreal	Fir-birch-spruce	Podzol/Gleysol
Chapleau	CHA	Ontario	Low Boreal	Pine-spruce	Orthic Drystic Brunisol
Gander	GAN	Newfoundland	Maritime Mid-Boreal	Spruce-fir-birch	Gleyed Ferro-Humic Podzol
Gillam	G11	Manitoba	Low Subarctic	spruce-larch	Brunisolic Static Cryosol
Gillam	**G12**	Manitoba	Low Subarctic	None	Typic Fibrisol
Hidden Lake	HID	British Columbia	Southern Cordilleran	Hemlock-cedar-birch	Orthic Humo-Ferric Podzol
Inuvik	INU	Northwestern Territories	High Subarctic	Spruce-birch-spruce	Cryic Gleysol
Kananaskis	KAN	Alberta	Southern Cordilleran	Pine-spruce-poplar	Orthic Eutric Brunisol
Morgan Arbortetum	MAR	Quebec	Humid Mid-Cool Temperature	Beech-mapl	Orthic Gerro-Humic Podzol
Montmorency	MON	Quebec	Perhumid Low Boreal	Fir-birch-spruce	Orthic Ferro-Humic Podzol
Nelson House	NH1	Manitoba	Subhumid High Boreal	Pine	Orthic Dystric Brunisol
Nelson House	**NH2**	Manitoba	Subhumid High Boreal	None	Typic Fibrisol
Prince Albert	PAL	Saskatchewan	Subhumid Low Boreal	Pine	Orthic Regosol
Petawawa	PET	Ontario	Humid High Cool Temperature	Pine	Humo-Ferric Podzol
Port McNeill	PMC	BC	Maritime South Pacific Cordilleran	Hemlock-fir	Hymo-Ferric Podzol
Schefferville	SCH	Quebec	Low Subarctic	Spruce-larch	Gleyed Dystric Brunisol
Shawnigan Lake	SHL	BC	Coastal South Pacific Cordilleran	Douglas-fir	Orthic Drystic Brunisol
Termundee	TER	Saskatchewan	Transitional Grassland	Aspen	Chernozem/Gleysol
Topley	TOP	British Columbia	Boreal Southern Cordilleran	Pine-fir-spruce	Hemimor/Orthic Gray Luvisol
Whitehorse	WHI	Yukon	Boreal Northern Cordilleran	Pine-spruce-aspen	Orthic Eutric Brunisol

[z]Site codes in bold font indicate wetland sites.

Table 2. CIDET litterbag sites: geographic locations, climate (annual averages) and surface soil characteristics (from Trofymow and CIDET Working Group 1998)

					Temperature				Forest floor				
Location	Code[z]	Latitude	Longitude	Altitude m	Jan.	July (°C)	Ann.	Ppt. (mm yr^{-1})	Type	Depth (cm)	C (%)	N (%)	C/N
Batoche	**BAT**	52°43′N	106°7′W	472	–21.5	17.4	0.1	398	FH/O	10	24.4	0.81	30.2
CB Rocky Harbour	CBR	49°32′N	57°50′W	50	–5.7	15.7	4.2	1200	LFH	8.2	43.2	1.20	35.9
Chapleau	CHA	47°38′N	83°14′W	460	–16.9	16.8	1.1	834	LFH	8.5	35.7	1.02	34.9
Gander	GAN	48°55′N	54°34′W	115	–6.2	16.5	4.3	1130	LFH	9.5	45.8	0.74	62.1
Gillam 1	G11	56°19′N	94°51′W	140	–28	15	–5.2	485	LFH	15	38.3	1.05	36.4
Gillam 2	**G12**	56°19′N	94°51′W	125	–28	15	–5.2	485	Of	10	42.1	1.04	40.6
Hidden Lake	HID	50°33′N	118°50′W	650	–5.7	18.1	6.3	547	LFH	11	38.8	1.12	34.6
Inuvik	INU	68°19′N	133°32′W	73	–29.6	13.6	–9.8	266	O	6.1	41.7	0.98	42.8
Kananaskis	KAN	51°00′N	115°00′W	1530	–10.2	14.1	2.8	657	LFH	6	38.3	1.16	32.9
Morgan Arbortetum	MAR	45°25′N	73°57′W	48	–10.6	21	6.1	863	LFH	4.6	31.6	1.13	27.9
Montmorency	MON	47°19′N	71°8′W	670	–14.7	12.6	0.6	1494	LF	3.8	43.6	0.93	46.7
Nelson House 1	NH1	55°55′N	98°37′W	280	–26.6	15.6	–3.9	542	LF	1	30.7	0.53	58.2
Nelson House 2	**NH2**	55°55′N	98°37′W	260	–26.6	15.6	–3.9	542	Of	10	43.4	0.85	50.8
Prince Albert	PAL	53°13′N	105°58′W	476	–21.5	17.4	0.1	398	LFH	2.5	28.1	0.60	47.2
Petawawa	PET	45°55′N	77°35′W	173	–12.9	16.6	4.3	822	LFH	5.5	41.9	1.22	34.4
Port McNeill	PMC	50°36′N	127°20′W	100	2.4	13.6	7.9	1783	LF	9.3	47.0	1.12	42.1
Schefferville	SCH	54°52′N	66°39′W	500	–22.8	12.6	–4.8	769	LFH	4.3	36.6	0.76	48.2
Shawnigan Lake	SHL	48°38′N	123°42′W	355	1.8	17.1	9.3	1215	LFH	5.1	41.2	0.85	48.8
Termundee	TER	51°50′N	104°55′W	536.5	–19.1	18.4	1.8	371	LFH	5.8	15.0	0.90	16.6
Topley	TOP	54°36′N	126°18′W	1100	–12.3	14.1	2.5	513	LF	8	39.7	1.05	37.6
Whitehorse	WHI	60°51′N	135°12′W	667	–20.7	14.1	–1.2	261	LF	5	33.0	1.15	28.7

[z]Site codes in bold font indicate wetland sites.

This implied that parameters n_1 and n_3 can be derived from specifying n_2, k_2 and k_3, thereby decreasing the number of Step 1 adjustable parameters to 37 (Table 5, top).

Step 2

We examined the best-fitted Step 1 values for n_2, e and g (30 entries altogether) in relation to initial litter composition (Table 3). This was done by way of regression analysis in order to: (1) further decrease the overall number of adjustable parameters needed to represent the inherent variability of $M(t)$, $N(t)$ and $C(t)/N(t)$; (2) interpret the rate of mass and N loss from the litterbags in an ecologically meaningful way, by litter type and changing climate conditions. Doing this produced:

- two alternative equations for determining the fraction of the fast decomposing litter, namely:

$$g_1 = \exp[a_0 + a_1 \text{ water\_extractable\_fraction (\%)} + a_2 \text{ acid\_hydrolyzable\_fraction (\%)}], \quad (22)$$

Table 3. CIDET litterbag type: initial chemical composition, % (from Preston et al. 2000), including C/N ratio

										Proximate chemical fractions			
Litter type	C	N	C/N	P	S	Ca	Mg	K	Ash	Non-polar extractable	Water-soluble	Acid hydrolyzable	AUR
Trembling aspen	46.8	0.67	69.9	0.13	0.16	2.05	0.16	1.23	8.38	8.75	35.42	33.7	14.4
American beech	47.0	0.71	66.2	0.04	0.2	0.99	0.25	0.08	7.05	7.25	12.90	45.3	28.0
White birch	48.0	0.72	66.7	0.04	0.1	0.875	0.24	0.26	3.38	6.52	35.94	30.3	24.0
Western red cedar	49.7	0.64	77.6	0.05	0.12	1.68	0.09	0.11	7.2	10.72	10.51	36.5	35.6
Bracken fern	46.3	0.88	52.6	0.07	0.12	0.77	0.31	0.43	7.21	2.26	9.04	49.1	32.9
Plains rough fescue	43.8	0.71	61.7	0.06	0.15	0.37	0.13	0.5	9.22	9.06	12.86	58.5	11.2
Douglas fir	49.6	0.7	70.9	0.11	0.27	1.28	0.11	0.16	6.74	10.27	11.48	41.6	30.3
Jack pine	49.7	1.28	38.8	0.13	0.14	0.46	0.12	0.27	2.65	6.97	15.24	42.4	32.8
Black spruce	49.5	0.73	67.8	0.08	0.28	0.66	0.09	0.22	4.16	10.92	19.85	37.0	28.3
Tamarack	48.8	0.59	82.6	0.02	0.32	0.66	0.24	0.31	5.89	9.35	31.10	30.1	24.0

Note: Ca (%) as quoted for the jack pine litter in the CIDET establishment report (45.5 mg g^{-1}) is incompatible with a 2.65% Ash(%) content.
The number entered here is 10 times less than the original number, to provide numerical consistency.
Ash(%) and all the extracted fractions to the right of the Ash(%) column are based on total dry litter weight.
AUR: acid-unhydrolyzable residue (a mixture of organic compounds, including lignin).

Table 4. Symbols

Symbols	Definitions	Units	Equation(s)
Compartments and variables			
$M_i(t)$	Mass remaining in the ith litter-bag compartment (i = 1, 2, 3); fast: $M_1(t)$, slow: $M_2(t)$, very slow: $M_3(t)$; t is time	g	1
$M(t)$	Total mass remaining in the litter bag at time t	g	2
$M_i(t = 0)$	Initial mass in each compartment (i = 1, 2, 3); t = 0	g	5,6,7
$MC_{conversion}$	Organic matter to organic Carbon conversion factor		19
$N_i(t)$	Total nitrogen remaining in each compartment (i = 1, 2, 3)	g	3
$N(t)$	Total nitrogen content remaining in the litter bag at time t	g	4
$N_i(t = 0)$	Initial total nitrogen content in each compartment (i = 1, 2, 3); t = 0	g	5,6,7
$[N(t)]$	Total nitrogen concentration in litter bag at time t	g g^{-1}	4
$[N_i(t)]$	Total nitrogen concentration in each compartment (i = 1, 2, 3) at time t	g g^{-1}	5
$k_i(S)$	State-dependent litter decomposition coefficient for each compartment (i = 1, 2, 3)	$year^{-1}$	1
$n_i(S)$	State-dependent nitrogen mineralization coefficient for each compartment (i = 1, 2, 3)	$year^{-1}$	3
f(climate)	Function expressing effects of climate variations on litter-bag decomposition and nitrogen mineralization		14,15
ppt	Annual precipitation	mm	15
T_{Jan}	Monthly mean air temperature, January	°C	15
T_{July}	Monthly mean air temperature, July	°C	15
R	Universal Gas Constant; = 8.31 J $mole^{-1}$ C^{-1}		15
Optimization parameters			
e	$M_2(t)/[M_2(t) + M_3(t)]$; slow portion of non-fast fraction; Step 1 parameter, by litter type		5,6,7
g	$M_1(t)/M(t)$; fast fraction; Step 1 parameter, by litter type		5,6,7
n_i/k_i	Relative N mineralization ratio, by compartment (i = 1, 2, 3); Step 1 parameters, by litter type	$year^{-1}$	14
k_i	Organic matter mineralization coefficients, by compartment (i = 1, 2, 3)	$year^{-1}$	14
p_1	Parameter associated with precipitation	mm	15
p_2	Parameter associated with T_{Jan} (to reflect extent of soil freezing	°C	15
Ea	"Activation energy" parameter, associated with T_{July}	J $mole^{-1}$	15
a_0, a_1, a_2	Parameters associated with determining "g", Step 2 only		22
l_1, l_2	Alternative parameters associated with determining "g", Step-2 only		23
a_3	Parameter associated with determining "e", Step 2 only		24
a_4	Parameter associated with determining n_2/k_2, Step 2 only		25
CN_{final}	Final CN ratio		10

and

$$g_2 = l_1 - l_2 \text{ AUR\_fraction (\%)} \quad (23)$$

- one equation for determining the proportion between the slow and very slow fraction:

$$e = \exp[-a_3 \text{ ash(\%)}] \quad (24)$$

- one equation for n_2/k_2:

$$n_2 / k_2 = a_4[N(t)]. \quad (25)$$

with a_0, a_1, a_2, a_3, a_4, l_1 and l_2 as regression coefficients. The total number of all the Step 2 parameters is 12 (Table 5, bottom).

RESULTS

Step 1

Best-fitted Step 1 results for k_1, k_2, k_3, n_2 / k_2, p_1, p_2, Ea, e, g, and CN_{final} are listed in Table 5 (top part). These results

Table 5. CIDET litterbag analysis: parametric values, and goodness-of-fit descriptors for Step-1 and Step-2 optimization

Step 1 results	Litter-type specific parameters						Parameters held in common				Goodness of fit			
	g		e		n_2/k_2							$M(t)$	$[N(t)]$	$C(t)/N(t)$
Litter type	estimate	± error	estimate	± error	estimate	± error		Unit	Estimate	± error		(g)	(%)	
Trembling aspen	0.226	0.009	0.395	0.038	0.258	0.040	k_1/k_2		7.46	0.77	Mean error	–0.03	–0.04	2.6
American Beach	0.063	0.008	0.374	0.038	0.217	0.044	k_2	year^{-1}	0.405	0.023	RMSE[z]	0.60	0.18	7.3
Bracken fern	0.110	0.009	0.431	0.042	0.558	0.045	k_3/k_2		0.124	0.012	r^2	0.93	0.84	0.83
Black spruce	0.117	0.010	0.652	0.034	0.552	0.034					Sample size	1470	1470	1470
Douglas fir	0	–	0.567	0.037	0.384	0.041					Parameters	26	11	
Plains rough fescue	0.454	0.009	0.280	0.048	0.516	0.039	p_1	°C	88.4	2.0				
Jack pine	0.102	0.009	0.565	0.043	0.720	0.036	p_2	mm	825	10	Initial			
Tamarack	0.079	0.009	0.375	0.040	0.287	0.051	Ea	J mole^{-1}	62,462	2064	conditions	$M(t=0)$	$N(t=0)$	
White birch	0.223	0.018	0.622	0.033	0.354	0.024					Predictor			
Western red cedar	0	–	0.284	0.040	0.702	0.052	CN_{final}		25.6	3.8	variables	7(6)[y]		
Step 2 results	g_1	g_2	e		n_2/k_2									
Trembling aspen	0.26	0.323	0.376	–	0.372	–	k_1/k_2		19.8	2.0	Mean error	–0.02	–0.04	2.4
American Beach	0.10	0.110	0.439	–	0.394	–	k_2	year^{-1}	0.377	0.014	RMSE[z]	0.67	0.20	7.7
Bracken fern	0.10	0.033	0.431	–	0.489	–	k_3/k_2		0.292	0.023	r^2	0.92	0.80	0.81
Black spruce	0.08	0.106	0.615	–	0.405	–					Sample size	1470	1470	1470
Douglas fir	0.06	0.074	0.455	–	0.389	–					Parameters	10	2	
Plains rough fescue	0.45	0.373	0.341	–	0.394	–	p_1	°C	87.8	2.2				
Jack pine	0.09	0.035	0.734	–	0.711	–	p_2	mm	831	11.4	Initial			
Tamarack	0.11	0.173	0.503	–	0.328	–	Ea	J mole^{-1}	61,690	2312	conditions	$M(t=0)$	$N(t=0)$	
White birch	0.19	0.173	0.674	–	0.400	–					Predictor			
Western red cedar	0.03	0.000	0.432	–	0.355	–	CN_{final}		25.8	2.5	variables	7(6)[y]		

Step 2 regression equations predict litter specific e and g parameters from initial litter chemistry, as follows:
g_1 = exp(–9.1 ± 0.2) + (0.119 ± 0.002) acid_hydrolyzable_fraction(%) + (0.107 ± 0.003) water_hydrolyzable_fraction(%); Eq. 22.
g_2 = (0.547 ± 0.007) – (0.016 ± 0.0002) AUR_fraction (%); Eq. 23.
n_2/k_2 = (0.555 ± 0.015) $[N(t=0)]$, $[N(t=0)]$ in%); Eq. 25.
e = exp[–0.155 ± 0.015) ash(%)]; Eq. 24.

[z]RMSE is root mean square of error.
[y]Predictor variables: water-extractable and acid-hydrolyzable fraction, or AUR fraction; ash fraction; precipitation; average July and January temperatures, initial N concentrations.

indicate that the Step 1 model optimization was quite effective in capturing litter- and climate-related variations of the CIDET data, with $r^2 = 0.93$ for $M(t)$, $r^2 = 0.84$ for $[N(t)]$, and $r^2 = 0.83$ for $C(t)/N(t)$. This was further coupled with a fairly low error of estimate for all the best-fitted parameter values, with average error estimates at

9.6% for e (range 5.3 to 17.2);
6.3% for g (range 0 to 13.4);
12.2% for n_2 (range 6.6 to 24.1);
10.3, 5.8, and 9.5% for k_1, k_2 and k_3, respectively;
14.8% for CN_{final}; and
2.5, 1.4, and 3.7% for the climate-related p_1, p_2, and Ea parameters.

Due to the unavoidable error propagation, r^2 values for $[N(t)]$ and $C(t)/N(t)$ were generally lower than for $M(t)$: restrictions in fitting $M(t)$ therefore compromised the fitting of $[N(t)]$ and $C(t)/N(t)$.

Shown in Table 6 are details about the best-fitted residuals, as calculated by litter type (top), and by site (bottom). These residuals generally clustered about 0 within the standard deviations of the residuals. For $M(t)$, all residuals by litter type were not significantly different from 0. For $[N(t)]$, 3 of the 10 residuals by litter type were not significantly different from 0, while the others showed a small negative bias, meaning that the model would slightly under-predict $[N(t)]$. For $C(t)/N(t)$, 8 of the 10 litter-type residuals had a small positive bias. For $M(t)$ and $[N(t)]$, about 1/3 of the residuals by site were not significantly different from 0. For $C(t)/N(t)$, 18 of the 21 residuals had a small positive bias by site. Note that the presence or absence of a bias in the above calculations depends in part on the standard deviation (SD) per site or per litter type: larger SD values would lead to a lower incidence of bias, as shown by e.g., the western red cedar entries. In general, the Step 1 results suggest that the best-fitted model calculations by litter type were generally consistent with the $M(t)$, $[N(t)]$, and $C(t)/N(t)$ data across all the CIDET sites.

Figure 2 provides a visual comparison of the best-fitted Step 1 results for the initial fast, slow and very slow litter composition assignments (bottom), generated from the e parameter (i.e., the ratio of slow to very slow fraction), the g parameter (i.e., the fast fraction), and the corresponding best-fitted relative N-mineralization coefficient values (n_2/k_2), as listed in Table 5. These results suggest an absence of the fast fraction in the leaf litter from Douglas-fir and western red cedar, with the latter also having the largest very slow fraction, followed by American beech. The slow fraction is calculated to be most prominent in black spruce, jack pine, white birch, and Douglas-fir leaf litter. With regard to n_2/k_2 (i.e., the rate of N mineralization relative to organic matter loss), highest values were computed for black spruce and jack pine leaf litter; the lowest values (to be interpreted as highest rate of N retention relative to organic matter loss) were obtained for the leaf litter from American beech and tamarack.

Step 2

Determining the a_0, a_1, a_2, a_3, a_4, l_1 and l_2 coefficients for Eqs. 22 to 25, and re-determining all the other parameters at the same time by way of the Step 2 re-iterations led to:

- the expressions listed in the bottom part of Table 5,
- the regression plots of the Step 2 parameters in relation to the Step 1 parameters (Fig. 3, top), and
- the resulting comparison plots for the Step 2–Step 1 generated parameters (Fig. 3, bottom).

These results show that:

- The values for g (the fast-decomposing fraction) increase with increasing water-extractable and acid-hydrolyzable levels, or with decreasing AUR levels; therefore, leaf litter from white birch and trembling aspen would have the most mass in the fast fraction, while leaf litter from western red cedar and Douglas-fir would have the least mass $[M_1(t = 0) = 0\ g]$ in this fraction (Fig. 3); conversely, these species would have the lowest and largest mass in the slow and very slow fractions, respectively.
- The positive number for a_3 in Eq. 26 implies that an increasing ash content would decrease the slow fraction, and increase the very slow fraction. Therefore, plains rough fescue and western red cedar have a low, and black spruce have a relatively high amount of mass in the slow fraction and a relatively low amount of mass in the very slow fraction of their leaf litter (Fig. 3, Table 5).
- The estimated n_2/k_2 values were found to depend on the initial litterbag N concentration (or C/N ratio) by way of Eq. 25 ($r^2 = 0.32$, Fig. 2). Hence, initially higher N concentrations (lower C/N ratios) translate into higher N-mineralization rates (i.e., higher n_2/k_2 values). The Step 2 derived n_2/k_2 value for western red cedar, however, weakens this trend, with this value dropping from the Step 1 estimate of 0.702 to 0.355. In contrast, the Step 1 and Step 2 derived n_2/k_2 values of 0.720 and 0.711 for jack pine confirm this trend relative to the other litter types.

In general, the Step 2 model calculated $M(t)$, $[N(t)]$, and $C(t)/N(t)$ with an RMSE precision of 0.67 g, 0.20%, and 7.7, respectively (Table 5). As with the Step 1 model, r^2 values for $[N(t)]$ and $C(t)/N(t)$ were lower than for $M(t)$. Visual presentations of the goodness-of-fit achieved after the Step 2 model optimization for $M(t)$, $[N(t)]$, and $C(t)/N(t)$ are provided in Figs. 4 to 6 for white birch, American beech, black spruce, and plains rough fescue, respectively. The changes in the N concentrations were least well captured at MAR, MON, PMC, SHL and TER (Fig. 5). For the three wetlands (BAT, GI2, NH2), best-fitted N concentrations were generally slightly below actual values (Fig. 5). This indicated that the N mineralization rates of the litterbags were lower on the wetland sites than the upland sites. In contrast, there were no consistent $M(t)$ differences between the upland and wetland litterbags: the mean residual error MRE was < 0 at BAT/PAL, and > 0 at GI1/GI2 and NH1/NH2.

Altogether, the Step 2 model captured the overall $M(t)$, $[N(t)]$ and $C(t)/N(t)$ variations quite well, as indicated by the residual plots of Fig. 7, and by the best-fitted r^2 values and associated error analysis in Table 7. In all cases, absolute MRE values were less than the associated standard deviation values (SD), by litter type, and by site. In comparison with Table 6, Table 7 shows that the Step 2 parameter reduction caused only minor deviations from the Step 1 $M(t)$, $[N(t)]$ and $C(t)/N(t)$ calculations, by litter type and by site. Among this, deviations were highest for western red cedar

Table 6. CIDET litterbag study: Step 1 error analysis, by species (top) and site (bottom)

	Mass remaining (g)				N concentration (%)				C/N			
Species	ME	SD	r^2	p(ME = 0)	ME	SD	r^2	p(ME = 0)	ME	SD	r^2	p(ME = 0)
Trembling aspen	–0.03	0.54	0.94	0.513	–0.05	0.19	0.77	0.002	2.1	7.2	0.76	0.001
American beech	–0.01	0.60	0.91	0.779	–0.03	0.16	0.78	0.029	3.3	8.1	0.69	0.000
White birch	–0.02	0.64	0.91	0.769	0.02	0.14	0.77	0.171	2.1	5.5	0.69	0.000
Western red cedar	–0.03	0.57	0.95	0.557	–0.02	0.14	0.84	0.051	0.2	7.0	0.75	0.766
Bracken fern	–0.01	0.61	0.93	0.868	–0.09	0.14	0.81	0.000	5.5	6.1	0.82	0.000
Plains rough fescue	–0.04	0.48	0.96	0.354	0.00	0.20	0.73	0.774	3.7	4.6	0.88	0.000
Douglas fir	–0.03	0.53	0.94	0.476	–0.04	0.21	0.69	0.018	–0.1	3.4	0.68	0.790
Jack pine	0.00	0.66	0.90	0.947	–0.03	0.12	0.82	0.014	2.7	8.2	0.78	0.000
Black spruce	–0.06	0.67	0.93	0.285	–0.18	0.22	0.78	0.000	4.6	5.5	0.85	0.000
Tamarack	–0.07	0.71	0.88	0.247	–0.01	0.15	0.64	0.378	1.9	12.0	0.56	0.056
	Mass remaining (g)				N concentration (%)				C/N			
Site	ME	SD	r^2	p(ME = 0)	ME	SD	r^2	p(ME = 0)	ME	SD	r^2	p(ME = 0)
BAT	–0.09	0.70	0.87	0.266	–0.06	0.17	0.80	0.006	5.9	8.6	0.81	0.000
CBR	0.21	0.48	0.96	0.000	–0.17	0.15	0.90	0.000	6.1	5.1	0.90	0.000
CHA	0.22	0.55	0.96	0.001	–0.09	0.18	0.86	0.000	4.8	7.2	0.80	0.000
GAN	–0.05	0.40	0.97	0.312	–0.02	0.14	0.88	0.344	2.0	4.2	0.93	0.000
G11	–0.65	0.61	0.88	0.000	0.07	0.11	0.88	0.000	–2.3	7.5	0.82	0.011
G12	0.12	0.47	0.93	0.045	–0.07	0.16	0.82	0.001	3.2	7.3	0.81	0.000
HID	–0.11	0.49	0.96	0.057	–0.02	0.13	0.92	0.219	2.2	4.3	0.93	0.000
INU	0.03	0.40	0.90	0.480	0.05	0.10	0.86	0.000	–3.9	9.5	0.77	0.001
KAN	–0.63	0.53	0.93	0.000	0.01	0.12	0.93	0.442	0.5	5.0	0.91	0.359
MAR	–0.04	0.69	0.94	0.648	–0.08	0.19	0.88	0.000	3.6	4.6	0.93	0.000
MON	0.00	0.38	0.97	0.996	–0.19	0.19	0.84	0.000	7.3	5.2	0.89	0.000
NH1	0.02	0.41	0.94	0.746	–0.01	0.11	0.91	0.566	1.8	6.8	0.83	0.034
NH2	0.28	0.47	0.92	0.000	–0.14	0.15	0.82	0.000	8.9	5.0	0.89	0.000
PAL	–0.23	0.42	0.94	0.000	–0.04	0.14	0.89	0.015	3.0	5.6	0.89	0.000
PET	–0.52	0.66	0.93	0.000	–0.03	0.16	0.92	0.097	1.5	4.4	0.93	0.006
PMC	0.38	0.75	0.90	0.000	–0.02	0.22	0.70	0.393	2.6	6.3	0.84	0.001
SCH	–0.08	0.50	0.93	0.191	0.08	0.14	0.84	0.000	–3.0	7.9	0.77	0.002
SHL	0.14	0.41	0.97	0.005	0.08	0.21	0.77	0.001	0.4	6.1	0.86	0.586
TER	0.38	0.65	0.91	0.000	–0.18	0.24	0.71	0.000	9.2	8.5	0.75	0.000
TOP	0.18	0.64	0.92	0.019	–0.06	0.18	0.85	0.011	1.8	6.2	0.86	0.019
WHI	–0.18	0.37	0.93	0.000	0.01	0.13	0.86	0.664	–0.7	7.2	0.85	0.449

ME, mean error = best-fitted – actual. Sample size for each species: 148; for each site: 70
MSD, mean standard deviation.

litter, with r^2 dropping from 0.84 (Step 1) to 0.64 (Step 2). This corresponds with the above mentioned Step 1 and Step 2 change for n_2/k_2.

Using AUR instead of the water-extractable and acid-hydrolyzable contents as litter-partitioning indicators or predictors only made a little difference to the final Step 2 results: r^2 values for $M(t)$, $N(t)$ concentrations and $C(t)/N(t)$ ratio remained high at 0.90, 0.81, and 0.80. This result confirms that a high AUR content leads to a larger fraction of slow and very slow decomposing litter. We note, however, that using the initial AUR content by itself is not as consistent in determining the fast litter fraction as what is obtained by using the initial water-extractable and acid-hydrolyzable contents instead (Fig. 2).

Step 1–Step 2 Summary

The Step 1 and Step 2 calibration results were reasonably consistent with one another, in spite of the drop in the number of adjustable parameters from 37 to 12, or 11 (Table 5). A detailed comparison of the Step 1 and Step 2 residuals for $M(t)$, $[N(t)]$, and $C(t)/N(t)$ confirmed that the Step 2 residuals were only slightly larger than the Step 1 residuals, thereby implying that the gain in generality that was achieved with Step 2 optimization did not compromise the overall model performance (Table 5, 6, 7). In summary, the above procedures identified:

- mean monthly air temperatures for January and July, and annual precipitation as suitable predictor variables to estimate the effect of climate on net end-of-year litter decomposition;
- initial water-extractable and acid-hydrolyzable fractions or initial AUR content as useful variables for specifying the fast decomposing fraction of leaf litter;
- initial ash concentration as a means to partition the slow from the very slow litter fractions;
- initial litterbag N concentrations and C/N ratios as additional variables for capturing the overall N retention or release dynamics of the decaying litter, over time.

DISCUSSION

Model Results in Reference to the Original CIDET Hypotheses

It has been hypothesized that the annual CIDET sampling would allow for quantification of the slow and very slow decay processes, but the fast-decaying fraction would be lost within the first year (CIDET Hypothesis 1). The model results show that this is generally the case for the southern locations (e.g., Hidden Lake, Morgan Arboretum, Port

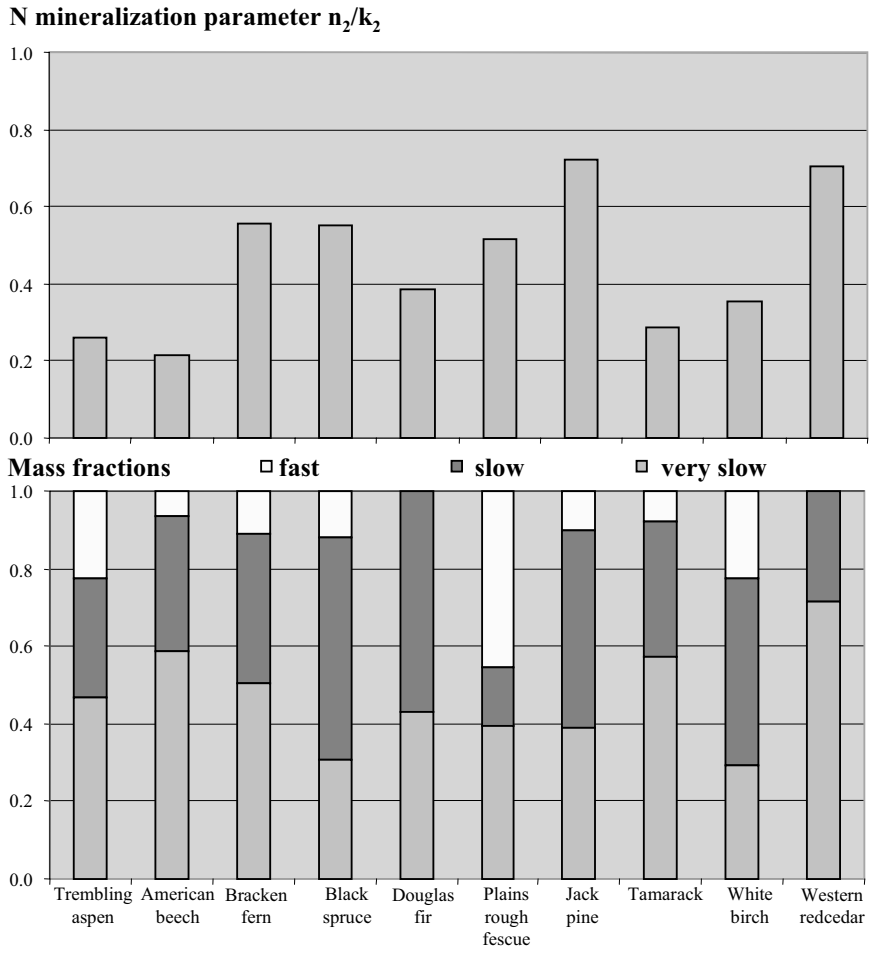

Fig. 2. Distribution of the nitrogen mineralization parameter n_2/k_2 (top) and the fast, slow, and very slow litter mass fractions [Step 1 generated g, $(1 - g)e$ and $(1 - g)(1 - e)$ values, respectively], in CIDET litterbags (bottom), by species.

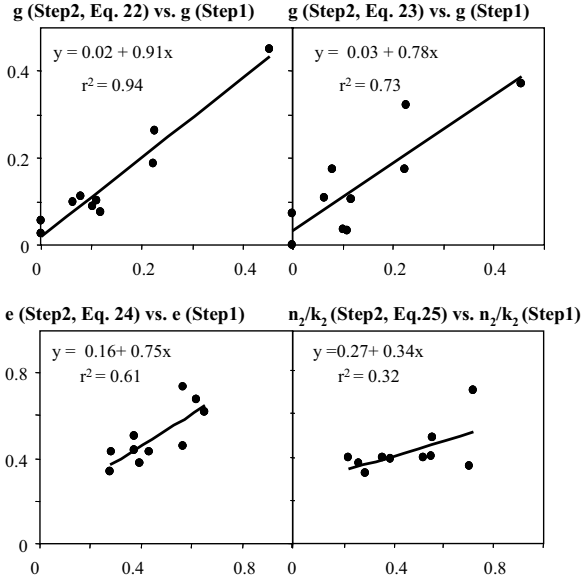

Fig. 3. Step 2 re-parametrization of the Step 1 results. Top: regression plots for best-fitted g_1 (Step 2, Eq. 22) and g_2 (Step 2, Eq. 23) values versus best-fitted g (Step 1) values. Bottom: best-fitted e (Step 2, Eq. 24) and n_2/k_2 (Step 2, Eq. 25) versus best-fitted e and n_2/k_2 Step 1 values.

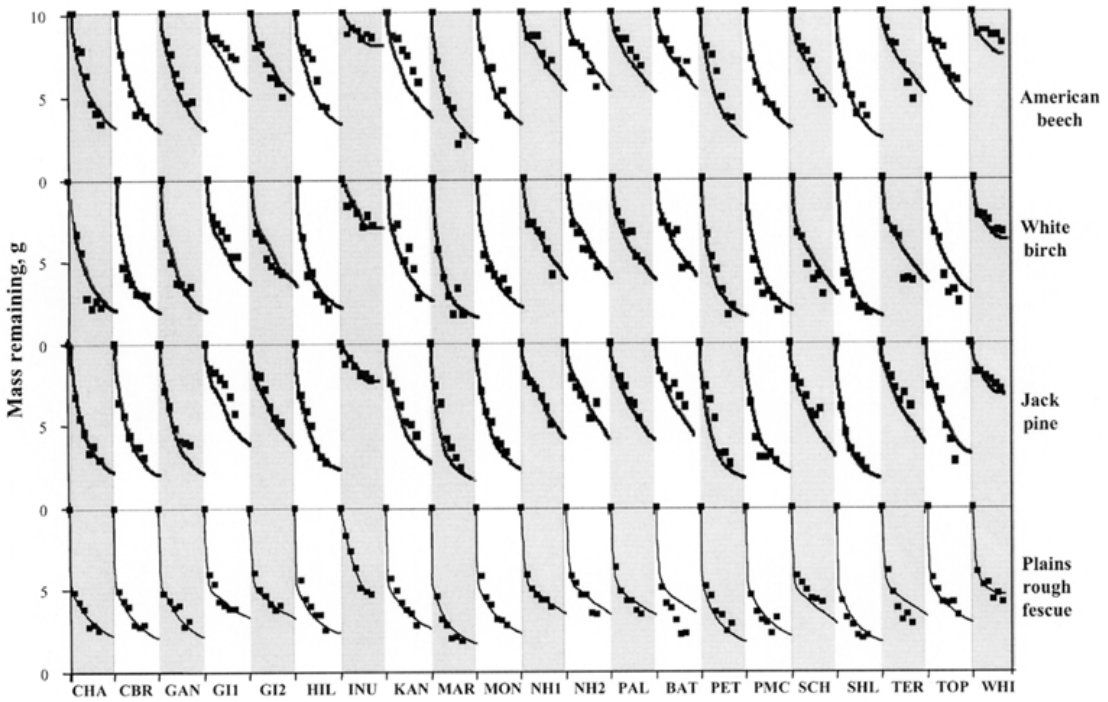

Fig. 4. Comparison of Step 2 best-fit versus actual mass remaining in CIDET litterbags, over time (by year), for American beech, white birch, jack pine, and plains rough fescue, by litter type and site with each plot starting in 1992.

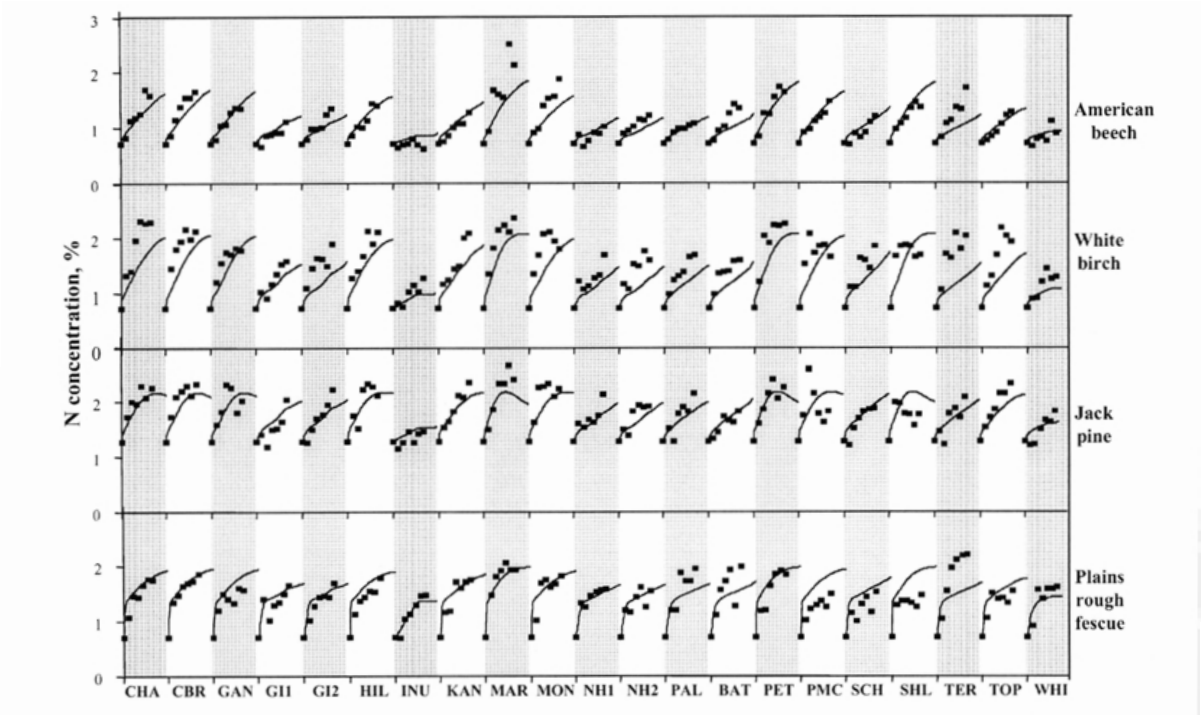

Fig. 5. Comparison of Step 2 best-fit versus actual N concentrations in CIDET litterbags, over time (by year), for American beech, white birch, jack pine, and plains rough fescue by litter type and site, with each plot starting in 1992.

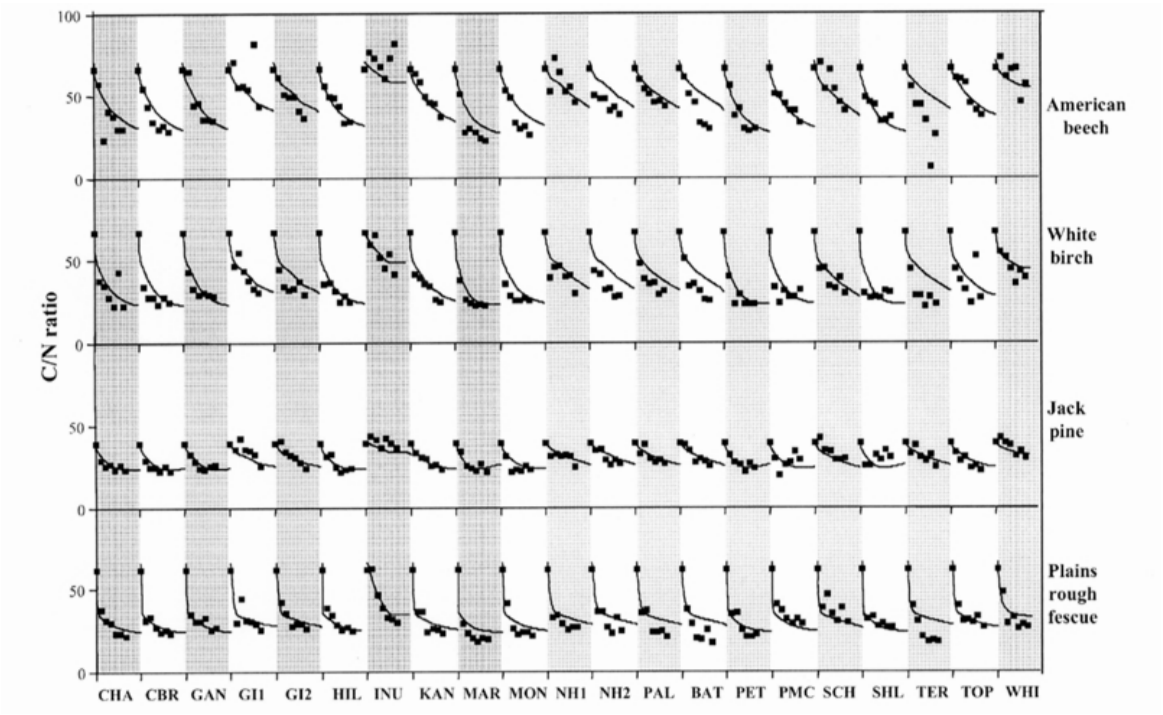

Fig. 6. Comparison of Step 2 best-fit versus actual C/N values in CIDET litterbags, over time (by year), for American beech, white birch, jack pine, and plains rough fescue by litter type and site, with each plot starting in 1992.

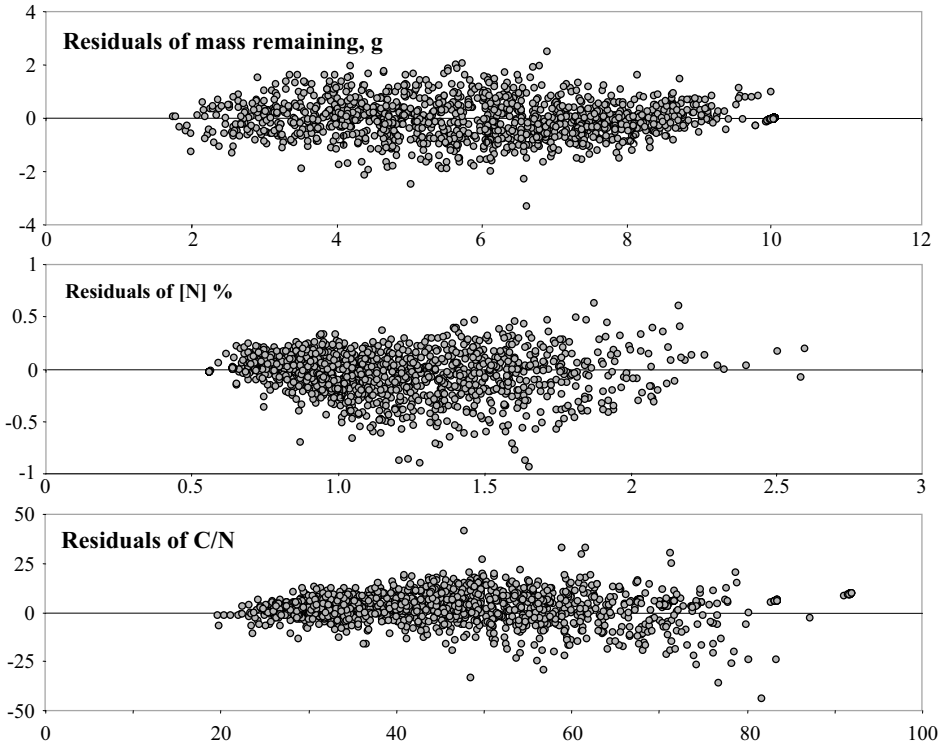

Fig. 7. Comparison of residuals (CIDET actual – FLDM Step 2 best-fitted values) for mass remaining (top), N concentrations (mid) and C/N ratio (bottom) versus FLDM Step 2 best-fitted values.

Table 7. CIDET litterbag study: Step 2 error analysis, by species (top) and site (bottom)

	Mass remaining (g)				N concentration (%)				C/N			
Species	ME	SD	r^2	p(ME = 0)	ME	SD	r^2	p(ME = 0)	ME	SD	r^2	p(ME = 0)
Trembling aspen	–0.14	0.56	0.93	0.004	–0.07	0.20	0.77	<0.001	2.2	7.3	0.75	<0.001
American beech	–0.29	0.61	0.91	<0.001	–0.04	0.16	0.79	0.028	3.2	8.2	0.69	<0.001
White birch	0.12	0.67	0.93	0.001	–0.25	0.24	0.77	0.685	6.7	5.7	0.84	<0.001
Western red cedar	–0.34	0.74	0.87	<0.001	0.09	0.14	0.64	0.001	–4.1	11.9	0.54	0.032
Bracken fern	0.18	0.65	0.91	0.003	0.00	0.15	0.76	<0.001	2.7	5.5	0.69	<0.001
Plains rough fescue	–0.01	0.48	0.96	0.727	0.06	0.21	0.71	0.001	2.7	4.7	0.88	<0.001
Douglas fir	0.16	0.64	0.93	<0.001	–0.12	0.15	0.82	0.021	6.1	6.1	0.83	0.890
Jack pine	–0.29	0.57	0.94	<0.001	–0.04	0.22	0.66	0.093	0.0	3.5	0.66	0.620
Black spruce	0.45	0.60	0.94	0.038	–0.04	0.15	0.82	<0.001	1.2	6.9	0.76	<0.001
Tamarack	–0.07	0.71	0.90	<0.001	–0.01	0.12	0.82	<0.001	2.9	8.3	0.77	<0.001
	Mass remaining (g)				N concentration (%)				C/N			
Site	ME	SD	r^2	p(ME = 0)	ME	SD	r^2	p(ME = 0)	ME	SD	r^2	p(ME = 0)
BAT	–0.09	0.78	0.83	0.337	–0.06	0.18	0.78	0.007	5.7	9.0	0.79	<0.001
CBR	0.22	0.57	0.94	0.002	–0.17	0.19	0.84	<0.001	5.8	5.1	0.89	<0.001
CHA	0.23	0.63	0.94	0.003	–0.09	0.20	0.82	<0.001	4.5	6.5	0.83	<0.001
GAN	–0.04	0.55	0.95	0.498	–0.02	0.17	0.82	0.411	1.6	5.6	0.87	0.017
G11	–0.64	0.67	0.85	<0.001	0.06	0.13	0.85	<0.001	–2.5	8.4	0.77	0.016
G12	0.13	0.50	0.92	0.035	–0.07	0.18	0.77	0.001	3.1	7.8	0.78	0.002
HID	–0.10	0.60	0.93	0.177	–0.02	0.15	0.87	0.265	1.9	4.8	0.91	0.001
INU	0.04	0.43	0.88	0.390	0.05	0.10	0.85	<0.001	–3.9	9.8	0.75	0.001
KAN	–0.63	0.62	0.91	<0.001	0.01	0.15	0.89	0.571	0.3	6.3	0.86	0.700
MAR	–0.04	0.80	0.92	0.688	–0.08	0.22	0.84	0.006	3.2	5.0	0.91	<0.001
MON	0.00	0.45	0.96	0.952	–0.19	0.21	0.81	<0.001	6.9	4.9	0.90	<0.001
NH1	0.02	0.48	0.92	0.739	–0.01	0.12	0.89	0.516	1.6	7.4	0.80	0.072
NH2	0.28	0.52	0.91	<0.001	–0.14	0.16	0.78	0.000	8.7	5.3	0.87	<0.001
PAL	–0.22	0.54	0.91	0.001	–0.04	0.15	0.86	0.018	2.9	6.6	0.85	<0.001
PET	–0.51	0.75	0.92	<0.001	–0.03	0.20	0.86	0.186	1.1	5.7	0.89	0.100
PMC	0.39	0.70	0.91	<0.001	–0.02	0.24	0.64	0.407	2.2	5.9	0.85	0.003
SCH	–0.07	0.64	0.88	0.373	0.07	0.16	0.78	<0.001	–3.2	9.2	0.69	0.005
SHL	0.15	0.49	0.96	0.012	0.08	0.23	0.68	0.004	0.0	6.7	0.82	0.993
TER	0.38	0.74	0.88	<0.001	–0.18	0.25	0.67	<0.001	9.1	8.3	0.75	<0.001
TOP	0.19	0.71	0.90	0.027	–0.06	0.20	0.80	0.018	1.6	6.7	0.84	0.051
WHI	–0.19	0.44	0.90	0.001	0.01	0.14	0.84	0.715	–0.8	7.7	0.83	0.365

ME, mean error = best-fitted – actual. Sample size for each species: 148; for each site: 70
MSD, mean standard deviation.

McNeill, Shawnigan Lake), but this is not the case for the northern locations (i.e., Inuvik, Whitehorse, Gillam, Nelson House, Prince Albert, Schefferville, Termundee, Topley).

It has been hypothesized that the decay of fast and slow compartments would depend on climate and initial chemical composition of the litter, but the very slow stage would be affected by climate only (CIDET Hypotheses 2 and **3**). The Step 1 and Step 2 procedures revealed that the rate of decay was indeed strongly affected by these factors. However, the climate-induced changes for each of the three compartments were essentially found to be unaffected by the initial litter composition.

While the model represents the CIDET data for mass, N concentrations, and C/N ratios quite well, it is possible that even better and perhaps less biased calibrations could be achieved by substituting the above-ground values for air temperature and precipitation by actual moisture and temperature conditions within the litterbags (CIDET Hypothesis 4). In the absence of actual measurements, this substitution would involve estimating forest floor temperatures and moisture contents. Our analysis suggests that this substitution would likely produce only a small but perhaps consistently unbiased improvement for fitting $M(t)$, $[N(t)]$ and $C(t)/N(t)$ by site, and this may also lead to improved estimates for Ea, CN_{final}, and k_1. The detailed regression analysis conducted by Trofymow et al. (2002) suggested that additional climate variables such as summer and winter precipitation could further capture some of the climate-related variations within the CIDET data. Other factors such as local microtopography, drainage, soil pH, soil drainage and differences in forest floor type, microbial communities, and atmospheric deposition could all be additional contributors to litter decay and N mineralization. Our analysis, however, suggests that all of these can only provide minor adjustments to the overall mass and N retention and release projections, but may assist in further exploring underlying cause-and-effect relationships.

It has also been hypothesized that the decomposing litter will eventually enter a metastable phase, once the ligno-cellulose ratio exceeds 0.5, and the very slow decay process would dominate (CIDET Hypothesis 6). The data and the Step 1 and Step 2 optimization procedures did not reveal a clear threshold demarcation from fast to slow, or from slow to very slow, at least not within the period of measurement. Furthermore, the Step 1 and Step 2 model optimization results indicated that chemically-derived variables were not

needed for determining the 3 $k_i(S)$ functions, i.e., the rate-of-decay coefficients for the fast, slow and very slow fractions. Instead, the optimization procedures identified the initial water-extractable and acid-hydrolyzable (so called "cellulose") portions or AUR content (so called "lignin"), and the initial ash concentrations as the most significant determinants to partition the litter into its fast, slow and very slow fractions.

It has been hypothesized that exogenous N and nutrient absorption would accelerate litter decay (CIDET Hypothesis 5, Berg and Matzner 1997). Hobbie (2000), Hobbie et al. (2002), and Prescott et al. (2004) reported N-accelerated decay, but only for the fast fraction when decay is N-limited. Hagedorn et al. (2003) found that N additions decreased the rate of decay for well-humified organic matter, but only when the N availability increased by at least an order of magnitude. Limpens and Berendse (2003) reported that incubating sphagnum litter with and without N treatments (from 0 to 80 kg ha^{-1} yr^{-1}) did not affect mass loss. The above formulation in its present form is set to be consistent with zero retention of exogenous N, and is therefore consistent with the alternative hypothesis that exogenous N absorption does not accelerate litter decay.

Other Matters Concerning N and C/N Ratios

Increased N concentrations due to partial N retention with increasing mass loss have already been reported and discussed elsewhere, notably by Berg et al. (1999), and Limpens and Berendse (2003). For litter type and location-specific details regarding the changing N concentrations and C/N ratios from 1992 to 1998 (actual and modeled), see Fig. 5. These increases are generally consistent with the FLDM calculations even though the model is set to disallow exogenous N absorption. Detailed observations about actual % N remaining in each CIDET litter bag produced a pattern of small to no exogenous N retention, with a few exceptions (Moore et al. 2005, 2006): significant temporary N retention above the original amount was most prevalent with birch leaf litter at all locations, and for various species at some locations, most notably at Montmorency (MON, boreal forest), Termundee (TER, transitional grassland) (Fig. 5), and occasionally at other locations as well (e.g., Morgan Arboretum, or MAR, esp. with beech). Modifying the model calculations by setting

$$dN_i(t) / dt = n_i / k_i [N_i(t)] \, dM_i(t)/dt + n_{i,env} \, h(S), \qquad (26)$$

where $n_{i,env}$ is a parameter, and $h(S)$ is a generalized state function to account for location-specific variations in bag-surrounding N availability (i = 2, 3), was not successful because doing so reduced the overall quality of fit. As a result, absorption of exogenous N above the original N content as suggested by Eq. 26 is not sustained, but appears to be site- and/or species-specific, and fairly exceptional. Moore et al. (2005, 2006) concluded that net absorption and subsequent loss of exogenous N should be considered as a common component of the decay process, and would likely be due to microbially induced N transfers across the bag fabric, with higher N absorption rates at first, and higher N release rates later as initial inside/outside C/N differences would subside.

Shown in Fig. 9 are FLDM-generated plots for black spruce and jack pine litterbag N concentrations, C/N ratios and mass remaining over the course of 25 yr by climate condition or location (cool to warm, dry to wet). For the first 7 yr since litterbag placement, calculated $C(t)/N(t)$ drop quickly from about 70 into the general C/N range of the forest floor substrates on which the litterbags were placed: see Table 2 for C/N ratios of the forest floor substrates at the CIDET sites, and Fig. 6 for actual and modeled C/N values. The best-fitted value for the final C/N ratio was about 26 ± 4 (Table 5), which is generally lower than what is shown in Table 3 for the LFH substrates of the CIDET sites, with C/N = 16 at the transitional grassland site (Termundee) being a notable exception. In well-humified organic matter of mineral soils, C/N ratios are even lower (Berg et al. 1999). For actual forest floor samples, values as low as 16 are unlikely, even for well-humified litter, because of new leave, twig, log and root inputs, and additional inputs derived from physical disturbances such as tree uprooting and faunal biomixing. The CN_{final} value itself remains somewhat uncertain: using values from 20 to 30 did not affect the overall model fit.

Other Matters Concerning Initial Litter Composition

The partitioning of litter or soil organic matter into various fractions has recently been reviewed by Wander (2004) from physical, chemical and biological perspectives. The approach taken above differs from the many reviewed perspectives in this publication by using an empirical approach that leads to the partitioning of the litter as an outcome of the optimization process, rather than an *a priori* input. While this approach cannot provide specific details about the physical, chemical and biological nature of the three fractions so simulated, it provides a numerically efficient means to quantify and visualize the end-of-year three-compartment representation of the decaying material, as affected by litter type and climate. This is illustrated in Fig. 8 by way of climate-sensitivity predictions for the decay of the fast, slow and very slow compartments for three litter types (western red cedar, aspen, and fescue), and two climate locations (Inuvik, Northwest Territories; Morgan Arboretum, southern Quebec).

Another factor that might influence the results of this analysis is that the assumption of constancy regarding the mass-to-carbon ratio (i.e., $MC_{conversion}$) of the forest litter may not be true. If this assumption holds, then C would be lost from the litter bag rates at the same relative rate as the mass, and the remainder of the litter would also be lost at the same relative rate. A detailed analysis of the actual values for $M(t)/C(t)$ revealed that:

- these values remained generally fairly close at their initial values, but there was a weak trend towards higher values with increasing decomposition time, regardless of site location, as revealed by regression analysis involving all $C(t)$ and $M(t)$ data:

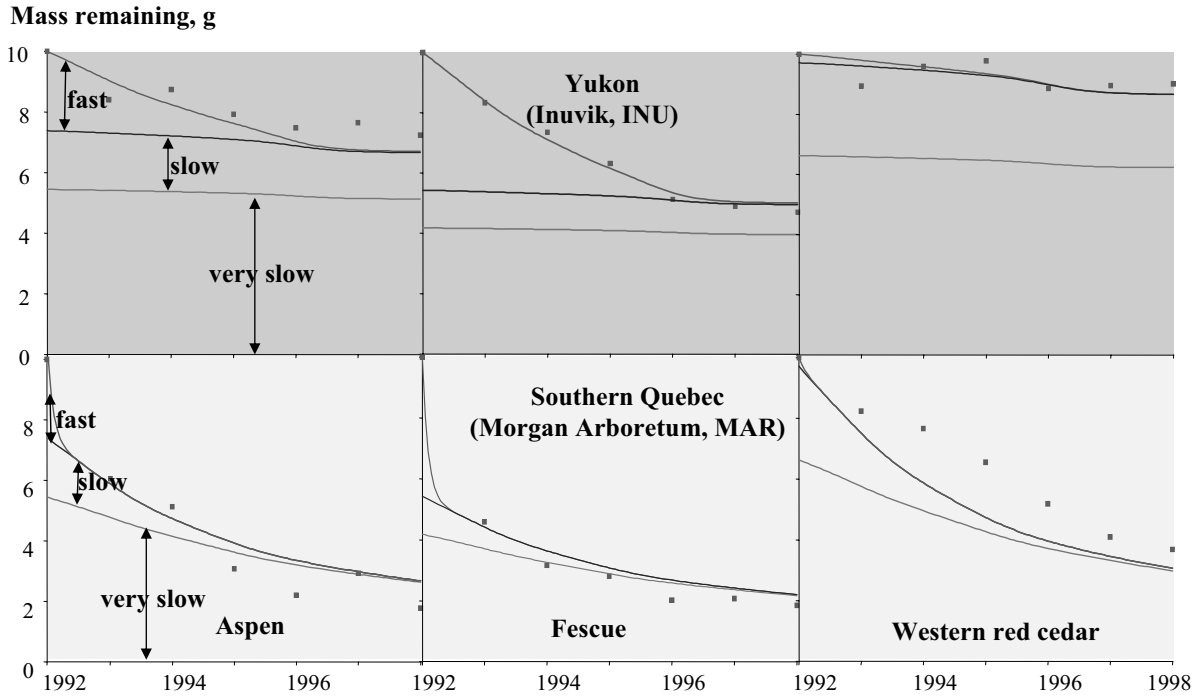

Fig. 8. FLDM generated plots of fast, slow and very slow fractions and original CIDET data of mass remaining in litterbags over time, for aspen, western red cedar, and plains rough fescue, at Inuvik (Northwest Territories), and Morgan Arboretum (southern Quebec).

$$C(t)/M(t),\ \% = (47.7 \pm 0.3) + (1.3 \pm 0.1)\ \{1 - \exp[-(.83 \pm 046)\ t]\};\ r^2 = 0.01$$

- when further analyzed by litter type, slight positive trends were observed for black spruce, aspen, western red cedar, jack pine, a slight negative trend was observed for plains rough fescue, and no trends were observed for the other species (Table 8).

We observe that: (1) the positive trends may arise from a gradual loss of oxygen-rich carbon compounds, as part of the overall humification process (Preston et al., in press); (2) the no-change trend indicates that the C and non-C fractions are decaying at about the same relative rates; (3) the negative trend could be due to a high silica content in plains rough fescue (e.g., Shewmaker et al. 1999; Finell 2003). High silica content in plains rough fescue is suggested by relatively low Ca, Mg, and K levels while ash content still amounts to 9.22% (Table 3). For more information on ash and silica contents in forest litter, see Loomis (1982).

About the Wetland Sites

There were no consistent $M(t)$ differences between the upland and wetland CIDET sites, as also noted and discussed by Moore et al. (2005). Laiho et al. (2004) reported similar results for Scots pine litterbags when placed along a drainage gradient in a peatland forest. These authors suggested that the general moisture and temperature conditions at and within the top portion of forested peatland soils would be similar to those of forested upland soils, and this would therefore explain the general lack of difference by drainage. Generally, the rate of decay in wetlands is known to decrease with increasing soil depth and with the associated change from aerobic to anaerobic conditions (Moore et al. 2005).

While rate of mass loss was not consistently affected by upland versus wetland placement of the litterbags, $[N(t)]$ values were significantly higher on the wetlands than on the uplands. This increase implied a lower N mineralization rate on the wetland sites. Subsequent calculations with the CIDET data led to the following result relevant to N mineralization:

$$n_2(\text{wetlands}) / n_2(\text{uplands}) = 0.53 \pm 0.14.$$

Lower N mineralization rates in wetlands have already been reported by Ohrui et al. (1999) and others (Grigal and Homann 1994). These lower rates would likely not be due to increased moisture contents in the litterbags. Instead, the lowered N mineralization rate may be due to an allelopathic suppression of the N-mineralization process. Such a suppression has been reported to be induced by leaf-litter leachates from shrubby vegetation such as *Kalmia angustifolia* (Yamasaki et al. 2002), and *Ledum palustre* (labrador tea) and *Empetrum hermaphrodium* (crowberry; see Castells et al. 2005). In contrast, leachates from bryophytes such as *Sphagnum* sp. and *Hylocomium splendens* did not affect the N mineralization rate (Castells et al. 2005).

Table 8. Carbon concentration in decomposing CIDET litter bag, versus time (years) since bag placement, linear regression analysis model: Carbon concentration (%) = intercept + slope × time (years)

Litter type	Intercept	Standard error	*P* value	Slope	Standard error	*P* value	r^2
Trembling aspen	47.9	0.4	<0.001	0.22	0.09	<0.001	0.028
American beech	47.6	0.3	<0.001	0.02	0.06	0.794	0.019
Bracken fern	47.0	0.4	<0.001	–0.20	0.09	0.022	0.028
Black spruce	50.1	0.3	<0.001	0.43	0.06	<0.001	0.201
Douglas fir	49.8	0.3	<0.001	–0.01	0.06	0.838	0.015
Plains rough fescue	43.4	0.4	<0.001	–0.43	0.08	<0.001	0.148
Jack pine	50.4	0.3	<0.001	0.34	0.07	<0.001	0.120
Tamarack	49.2	0.3	<0.001	–0.04	0.06	0.505	0.049
White birch	48.9	0.4	<0.001	0.30	0.08	<0.001	0.075
Western red cedar	49.6	0.3	<0.001	0.25	0.07	<0.001	0.063

More About Climate Effects

Potential climate effects have recently been discussed in reference to the rate of decay of mineral soil organic matter, in the context of temperature sensitivity (or supposed lack thereof) and related activation energies by fast, slow, and very slow fractions (Knorr et al. 2005). These authors found *Ea* to increase from 43 000 to 76 000 J mol^{-1} from the fast to the very slow fraction, respectively. Our best-fitted Step 1 and Step 2 model optimization estimates for Ea amounted to 62 000 J mol^{-1} for all three fractions. Optimizing *Ea* separately did not produce significantly different *Ea* numbers for each fraction, thereby justifying the assumption that climate affects the decay parameters of each fraction similarly, at least at the annual scale, and within the general context of Eq. 15. *Ea* values for the fast and slow fractions, however, might decrease to smaller values with determinations done at a finer time scale of days and months rather than years, as suggested by Knorr et al. (2005). However, Borken et al. (2003) reported an *Ea* value of 73 700 J mol^{-1} based on weekly soil respiration measurements over the course of 150 d. For the same situation, these authors also reported a linear increase in the rate of soil respiration with increasing soil moisture content, after accounting for the temperature effect. These determinations involved organic and mineral soil layers, with moisture ranging from < 10 to 250%, and from <10 to 30%, respectively.

At the hourly to daily scale, soil CO_2 would generally be released during short-lived pulses after each wetting event, with peak and duration of each pulse increasing with the amount of water added (Borken et al. 2003). Over the course of a year, the numerical accumulation of these pulses would likely accentuate the linearity between net litter mass loss and annual soil moisture input. For example, replacing the expression "min(1, ppt/p1)" with "1 – exp(– ppt/p1)" in Eq. 15 noticeably reduced the quality of the optimal Step 1 and Step 2 fit for $M(t)$, $[N(t)]$, and $C(t)/N(t)$ (details not shown).

Schuur (2001) suggested that litter decay rates may decrease when annual precipitation increases beyond 2000 to about 5000 mm. In the model, this effect can be implemented by replacing the "min(1, ppt/p1)" expression by "min(1, ppt/p1) [1 – b max(0, ppt/p1 – 1)", with b as a parameter. The range of the CIDET annual precipitation range was, however, too small to evaluate *b*.

The climate-affected half–lives for the slow fraction of the CIDET litterbags were determined to vary between 1 and 15 yr from the southern to northern locations, respectively. For the fast fraction, these numbers ranged from 0.08 to 1.2 yr. For the very slow fraction, the numbers varied from 8 to 105 yr initially. Specific values for each litter type and location can be generated by way of Eqs. 16, 17 and 18 and Table 5.

Comparison with Other Model Results

The CIDET data for $M(t)$ at the 18 upland sites have been analyzed before by Trofymow et al. (2002), who developed a model to forecast likely $ln[M(t)]$ changes in relation to monthly climate conditions and substrate type. These authors were able to explain 81% of the variations from 1993 to 1998 with a seven-variable model, generating year-specific r^2 values of 0.76, 0.74 and 0.71 for 1993, 1995 and 1998, respectively. The initial litterbag mass (≈ 10 g), however, was not part of this analysis: subsequent back calculations to $t = 0$ under-estimated this value. With FLDM, initial mass and N contents are part of the modeling and fitting protocol. In comparison, FLDM simulated the same upland data with an overall r^2 value of 0.85 and with year-specific r^2 values of 0.78, 0.78 and 0.80 for 1993, 1995, and 1998, respectively (details not shown here). The overall r^2 was 0.92 when the initial mass was included, i.e., similar to the Table 5 value for all of the 21 sites.

More recently, Palosuo et al. (2005) evaluated the CIDET data from 18 upland sites with the Yasso model (Liski 2005). This model also partitions litter into three components, namely extractives, cellulose (acid-hydrolyzable), and lignin-like, and deals with climate variations by considering extent of drought and temperature. These authors obtain year-specific r^2 values of 0.32, 0.48, and 0.56 for the 1993, 1995, and 1998 CIDET data, respectively. This fit would have increased to 0.50, 0.58 and 0.66, respectively, by deleting the data for fescue and tamarack.

CONCLUDING REMARKS

Holding all mass, N concentration, and C/N ratio parameters constant across litter type slightly reduced the amount of explained variance from what was obtained by determining these parameters separately for each litter type. However, this small loss in explained variance led to a considerable

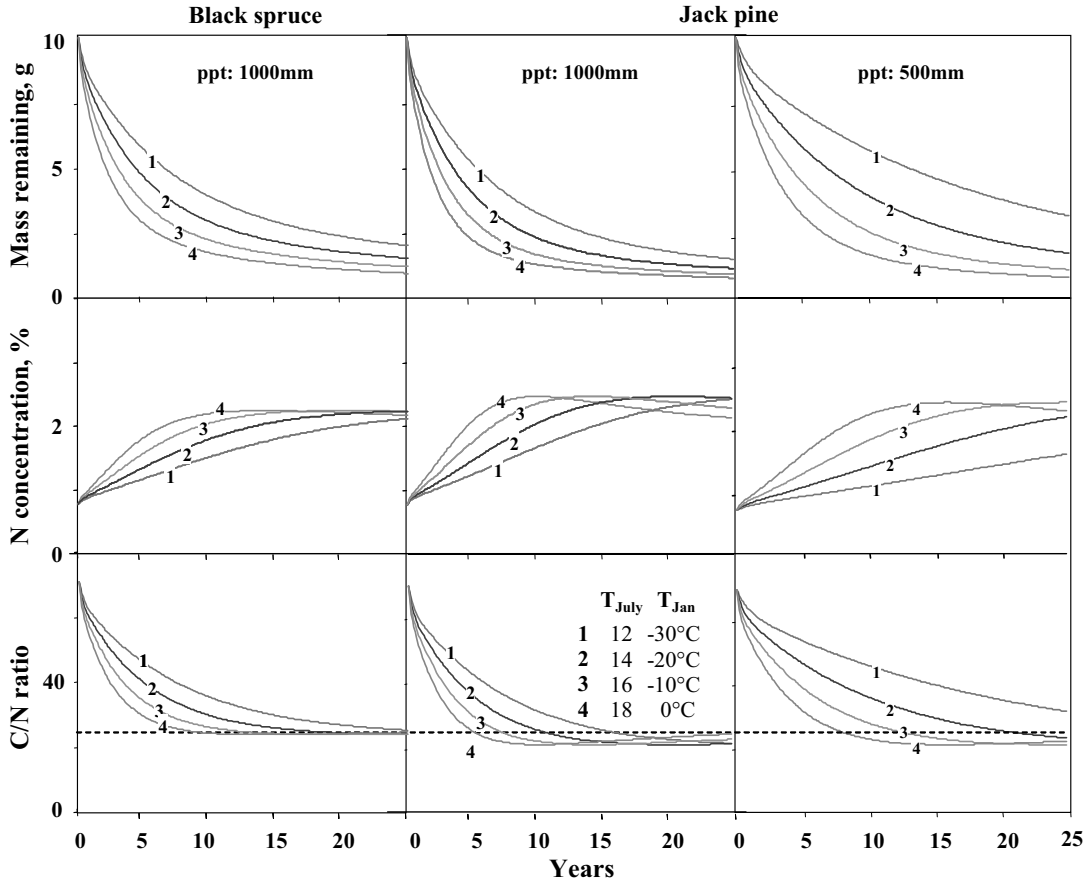

Fig. 9. Comparison of FLDM projections for mass remaining (top), N concentrations (middle) and C/N ratios (bottom) in black spruce and jack pine litterbags, for 25 yr, using the optimized Step 2 parameters, for select climate conditions: annual precipitation 1000 or 500 mm, and four temperature conditions (1 to 4) starting from T_{July} = 12ºC and T_{Jan} = –30ºC, to T_{July} = 18ºC and T_{Jan} = 0ºC.

gain in terms of model generality. Therefore, accepting initial N, ash, AUR (or water-extractable and acid-hydrolyzable) litter fractions, and annual precipitation and mean January and July air temperatures, as predictor variables was found to be sufficient to estimate mass and N remaining in the CIDET litterbags. This model may therefore serve as a means to predict mass loss, N concentrations and C/N ratios for a variety of decaying forest litter types across Canada and other countries with similar climate conditions. Further work with data other than the CIDET, however, is required to determine whether or not this expectation can be confirmed.

In recent literature discussions (Grace and Rayment 2000; Giardina and Ryan 2000), it has been suggested that an accurate quantification of the slow and very slow fractions of soil organic matter is important for assessing the impact of climate warming on the release of additional CO_2 from soils. This is because the pool sizes of these fractions are quite large, and because the very slow fraction may have a greater thermal sensitivity than the other fractions (Knorr et al. 2005). This paper demonstrates that:

- for forest litter, there is no apparent change in the thermal sensitivity from the fast to the very slow fractions, at least not at the annual scale (*Ea* values are similarly high for all three fractions, at 62 000 J mol^{-1}); Borken et al. (2003) suggested that this would also be so for the daily scale;
- under changing climates, the greatest change in CO_2 release from decaying litter can be expected to occur in regions where cool summers change to warm summers, where dry regions become moist, and where cold winters become temperate; the combination of warmer summers and winters coupled with increased precipitation would produce the greatest change;
- in addition to being climate sensitive, the rates of mass and N release from the litter were found to vary with the initial proportions of the fast, slow, and very slow decaying fractions (see Table 5);
- the decaying litter was generally found to be conservative in terms of N retention and release, thus leading to increasing N concentrations, with highest initial increases observed and calculated for those litter types and conditions that favor fast decay; altogether, the interplay between litter decomposition, N mineralization and N release was observed and calculated to produce a wide spectrum of N concentrations and C/N ratios within the decaying litter, as affected by litter type and climatic conditions, over time;

- while the proposed model captures the overall trends associated with leaf litter decay and N mineralization quite well, further attention needs to be given to those cases where specific substrate and site combinations do not comply with the model assumptions, e.g., temporary retention and subsequent release of exogenous N, as observed with the birch leaf litter at two quite different CIDET locations (Montmorency and Ternmundee). To what extent net N absorption and mineralization may depend on e.g., initial N concentrations, bag-external N availabilities, or bag-internal C/N ratios requires further attention.

It should be remembered that all of the above refers to observed and projected trends for leaf-litter only. For other litter types, such as coarse woody debris and decaying roots, trends associated with the mass and N may differ considerably over time, with type and size of debris and changing climate conditions (Creed et al. 2004; Moore et al. 2005).

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