WOOD DECOMPOSITION AND NITROGEN MINERALIZATION MODELLING ACROSS NORTH AND CENTRAL AMERICA

by

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ABSTRACT

This thesis focuses on modelling above- and below-ground mass loss and nitrogen (N) dynamics based on wooden dowels [*Gonystylus bancanus* (Miq.) Kurz] of the decadal Long-term Intersite Decomposition Experiment (LIDET) data. These dowels were placed at 27 locations across North and Central America, involving tropical, temperate and boreal forests, grasslands, wetlands and the tundra. The dowel, inserted vertically into the soil with one half remaining exposed to the air, revealed fast mass and N losses under warm and humid conditions; and slow losses under wet as well as cold and dry conditions. The model formulation, referred to as the Wood Decomposition Model WDM, related these losses to (i) mean annual precipitation, mean monthly January and July air temperatures primarily, and (ii) mean annual actual evapotranspiration (AET) secondarily at each location. The resulting calibrations conformed well to the time-in-field averages for mass remaining by location: R^2 = 0.83 and 0.90 for the lower and upper parts of the dowels, respectively. These values dropped, respectively, to 0.41 and 0.55 for the N concentrations, and to 0.28 and 0.43 for N remaining.

Key words: annual actual evapotranspiration, LIDET, Long-term Intersite Decomposition Experiment, mass loss, modelling, nitrogen mineralization, North America, precipitation, temperature, Wood Decomposition Model.

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Most of the material presented in this thesis has been published in Smith et al. (2011) and is represented here with slight structural and contextual modifications, and with permission from Elsevier (Ecological Modelling, licence number 3197270178256) to reproduce Figs 3 to 9, and Tables 1 to 5.

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INTRODUCTION

Predicting the rate at which wood decays and mineralizes is important for assessing past, current and future ecosystem-level Carbon (C) and Nitrogen (N) responses to varying and changing climate conditions (Laiho & Prescott 2004). Quantifying these processes, however, is a complex task because of their dependence on wood type, piece size, shape, density, lignin content, presence of wood preservatives, configuration of placement, wood-consuming organisms at work, and antecedent conditions (Harmon *et al.* 1995, Stevens 1997; Zhenbang *et al.* 1998). For example, woody debris that remains dry mineralizes slower than when moist (Berg *et al.* 1993). Moisture provides optimal conditions for the entry and growth of decay-causing organisms such as fungi, bacteria, insects and wood dwellers (Pertersen & Luxton 1982; Griffith & Body 1991; Boddy & Watkinson 1995; Temnuhin 1996; Frey *et al.* 2003 Brischke & Rapp 2008a; Brischke & Rapp 2008b). Wood placed into the ground may decay more quickly than wood resting on the ground, depending on differences in moisture content and the physical, chemical and biological conditions of the adjacent soil (Busse 1994; van der Wal *et al.* 2007). With regard to N, decaying wood has low N concentrations prior to decay (Hungate 1940). Hence, transfer of exogenous N from adjacent soil and decaying litter is likely to occur on account of physicochemical processes such as diffusion from N-enriched soil solution into wood and biological processes such as N_2 fixation, and transfer of exogenous N and other nutrients into the wood via invading organisms, especially fungal mycelia (Becker 1971; Ausmus 1977; Frey *et al.* 2003). Decaying wood may therefore provide temporary storage for N and other nutrients for later use (Boddy & Watkinson 1994; Pyle & Brown 1999).

In general, wood represents a large portion of annual forest litter accumulations on top of the forest floor or within it; forest litter also accumulates within the mineral soil in the form of decaying roots (Harmon *et al.* 1986; Scheu & Schauermann 1994). Local forest disturbances due to, e.g., fire, insects, storms and harvesting add to this accumulation of snags, harvest residues, and wholetrees blowdown. Under moist and warm conditions associated with high rates of evapotranspiration, rates of wood decay and N gains and losses in fallen or soil-emplaced wood would be highest, while they would be least under consistently cold and dry conditions (Meentemeyer 1978; Griffith & Boddy 1991; Currie *et al.* 2010). It is, however, not known to what extent wood decomposition and N uptake and losses influence one another, and how these rates vary above and below the ground within and across ecosystems from tropical to arctic biomes. The literature suggests that wood and litter decomposition is influenced by edaphic qualities of sites more than by substrate quality (Sinsabaugh, *et al.* 1993). Wood decomposition is also affected by variations in soil moisture and temperature (Harmon & Sexton 1995; Currie & Aber 1997; Wells & Body 1995; Liski *et al.* 2003).

Recent studies on forest litter decay across widely ranging site and climate conditions have produced data on wood decay. Among these studies are: the Long-term Intersite Decomposition Experiment in the United States (LIDET, 1995; Parton *et al.* 2007; Adair *et al.* 2008), the Decomposition Study in Europe (DECO: Jansson & Reurslag 1992), the wood stability study by Jurgensen *et al.* (2003, 2006), and the

Canadian Intersite Decomposition Experiment (CIDET: Trofymow and CIDET Working Group, 1998; Preston *et al.* 2009 a, b) and the International Research Group on Wood Preservation (IRG, Jurgensen *et al.* 2003).

The ensuing model formulation followed the earlier work on the Forest Litter Decomposition Model FLDM by Zhang *et al.* (2007; 2008). This model uses first- to second-order rate equations for leaf litter decay and N mineralization, and invokes a gradual transitioning from an initially fast and perhaps N-limited decay, to slow and eventually C-limited mass and N losses from the increasingly humified litter residue. A similar transitioning can be expected to occur in decaying wood. Other models used to predict litter decomposition refer to the Yasso model (Liski *et al.* 2005) and the ROMUL model (Chertov *et al.* 2001). The Yasso model, a three-compartment exponential decay model has been calibrated using the European data set (Berg 1993; Liski *et al.* 2003) and the Canadian Intersite Decomposition Experiment (CIDET) data set. The ROMUL model requires more compartments than the Yasso and FDLM models for tracking forest litter decay through time. ROMUL is therefore more demanding in terms of its input requirements, but uses a calibration-free, empirically based parameterization in its compartment-to-compartment process formulations.

THESIS OBJECTIVE

The objective of this thesis is to quantify and model the extent of above- and below-ground mass and N loss and N concentrations in the dowels of the LIDET experiment as it was conducted over the course of a decade across 27 location and several ecosystem types (boreal to tropical). Specifically, the model uses time-in-field and climate variables such as annual rates of actual evapotranspiration, (as opposed to potential evapotranspiration) precipitation, and mean monthly July and January temperatures as primary predictor variables for above- and below-ground mass loss, and related changes in dowel C and N concentrations.

METHODS

DOWEL PLACEMENT AND STUDY LOCATIONS

According to Harmon and Sexton (1996) and Harmon *et al.* (1999), wooden dowels (61cm long, 13mm in diameter, oven-dry wood density of $0.62 g/cm^3$) of a tropical hardwood species (*Gonystylus bancanus* [Miq.] Kurz*;* generally referred to as "ramin"), were placed at 27 locations across North and Central America over the course of several years from 1990 to 1995. This was done in cooperation with local forest research stations and volunteer groups (Fig. 1; LIDET 1995). The locations chosen represent a cross-section of biomes (Table 1), i.e., tundra (2) wetlands (2), boreal forests (2), temperate coniferous forests (5), temperate deciduous forests (5), tropical forests (5), and grasslands (6). Dowel emplacement occurred in two separate years at 24 locations, and only in one year at three locations. At each location, 48 dowels were placed on level ground 1 m apart along a straight line, with four replicates available for retrieval for up to 10 years, depending on personnel and resources available at each location, and on decomposition progress towards irretrievability (Table 2). The lower half of each dowel was inserted into the ground, leaving the other half exposed to the air (Fig. 2). The 1990, 1991 and 1992 dowels were placed into the ground without mesh wrapping, while dowels placed in 1994 and 1995 were mesh-wrapped (1 mm mesh size) to enable complete recovery of the decaying wood.

Upon retrieval, dowels were analyzed for total mass remaining and N, ash and moisture content. The resulting data were organized by dowel part (upper, lower), field emplacement year (2), location (27), time-in-field (up to 10 years), and replication (up to 4 per location and per retrieval year), yielding data for 2273 out of 4320 potential combinations for statistical analysis (Table 2). This difference was due to a number of facts: (i) a complete set of dowels was not installed at all locations, (ii) retrieval did not occur each year at all locations, (iii) retrieval of the buried portions was not always possible, (iv) some of the dowels were lost. Some of the missing dowels were replaced. These replacements were marked with flagging tape and a metal tag, and were wrapped in mesh so as to separate the dowels from other decomposing organic material.

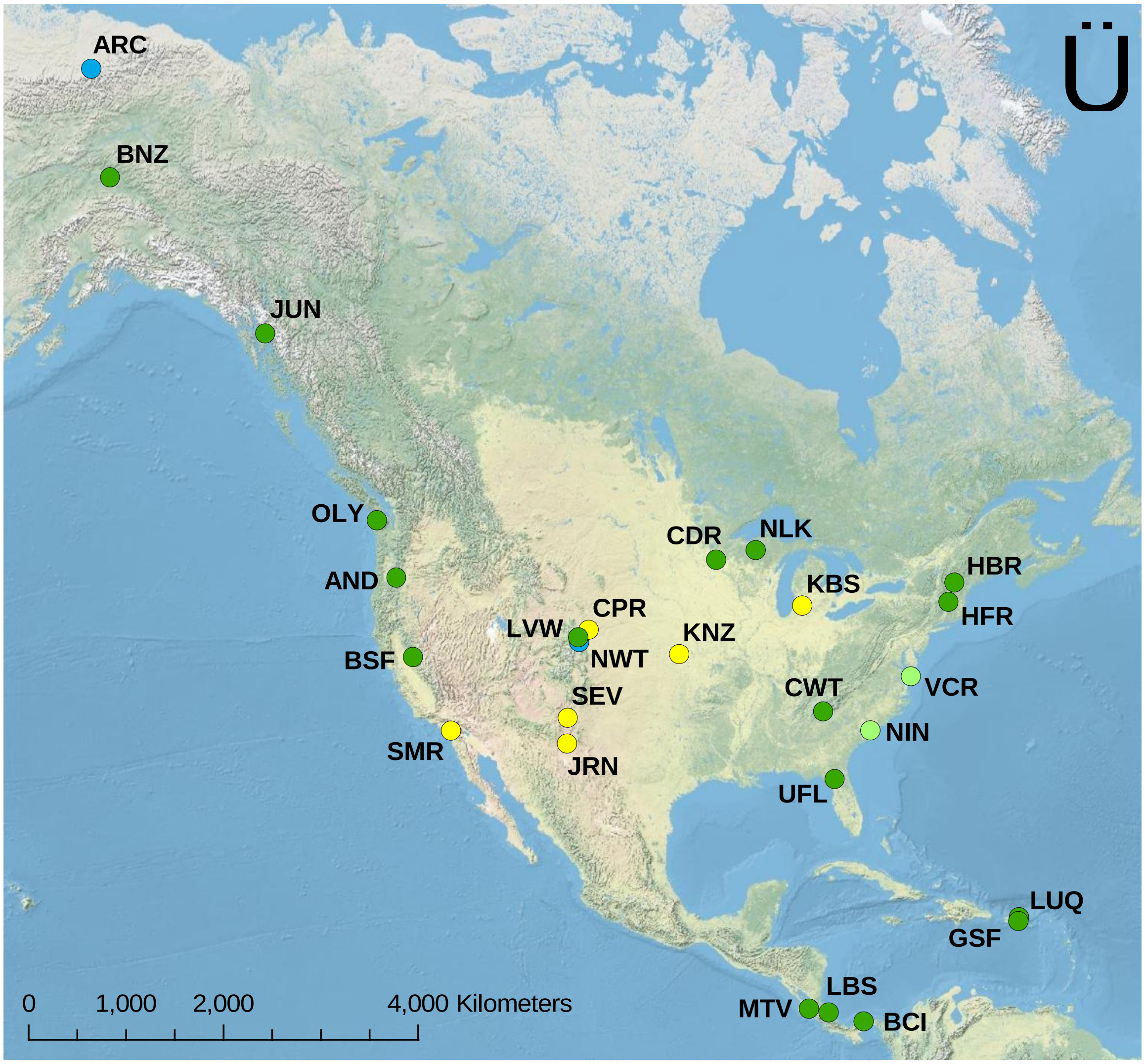

Fig. 1. Locations of Long-term Intersite Decomposition Experiment (LIDET) sites across North America (Basemap copyright © 2013 National Geographic Society).

Table 1. Longterm Intersite Decomposition Experiment (LIDET) locations and ecosystem types, elevation, mean annual values for precipitation, January and July temperatures and actual evapotranpiration for 27 sites across North and Central America.

	Location	State / Country	Ecosystem	Lat.	Long.	Elev. (m)	Ppt (cm)	AET (cm)	Tjan (°C)	Tjul (°C)
BNZ	Bonanza Creek Experimental Forest	Alaska	Boreal Forest	64°45'	148°00'	300	40.3	36.0	-24.9	16.4
LVW	Loch Vale Watershed	Colorado	Boreal Forest	40°17'	105°39'	3160	109.6	85.1	-9.3	14.6
JUN	Juneau	Alaska	Temperate Conifer Forest	58°00'	134°00'	100	287.8	49.5	-5.6	12.9
NLK	North Temp. Lakes (Trout Lake Station)	Wisconsin	Temperate Deciduous Forest	46°00'	89°40'	500	67.7	64.9	-12.5	19.1
OLY	Olympic National Park	Washington	Temperate Conifer Forest	47°50'	123°53'	150	153.1	79.4	5.1	16.2
AND	H.J. Andrews Experimental Forest	Oregon	Temperate Conifer Forest	44°14'	122°11'	500	230.9	76.4	0.3	18.3
BSF	Blodgett State Research Forest	California	Temperate Conifer Forest	38°52'	120°38'	1300	124.4	75.3	9.4	23.4
HBR	Hubbard Brook Experimental Forest	New Hampshire	Temperate Deciduous Forest	43°56'	71°45'	300	139.6	71.2	-8.7	18.8
CDR	Cedar Creek Natural History Area	Minnesota	Temperate Woodland Humid Grassland	45°24'	93°12'	230	82.3	73.3	-13.5	21.2
HFR	Harvard Forest	Massachusetts	Temperate Deciduous Forest	42°40'	72°15'	335	115.2	85.1	-6.9	20
MTV	Monte Verde	Costa Rica	Tropical Elfin Cloud Forest	10°18'	84°48'	1550	268.5	108.4	18.3	16.8
UFL	University of Florida	Florida	Temperate Conifer Forest	29°45'	82°30'	35	123.8	116.6	15.3	26.8
CWT	Coweeta Hydrology Laboratory	North Carolina	Temperate Deciduous Forest	35°00'	83°30'	700	190.6	117.3	3	21.5
GSF	Guanica State Forest	Puerto Rico	Dry Tropical Forest	17°57'	65°52'	80	50.8	50.2	24.9	27.7
BCI	Barro Colorado Island	Panama	Humid Tropical Seasonal Forest	9°10'	79°51'	30	269.2	136.8	25.2	25.6
LUQ	Luquillo Experimental Forest	Puerto Rico	Humid Tropical Forest	18°19'	65°49'	350	336.3	123.4	20.8	24.8
LBS	La Selva Biological Station	Costa Rica	Humid Tropical Forest	10°00'	83°00'	35	409.9	169.9	24.9	25.9
SMR	Santa Margarita Ecological Reserve	California	Annual Grassland	33°29'	117°09'	500	24.0	23.6	12	20
SEV	Sevilleta	New Mexico	Warm Semi-desert	34°29'	106°40'	1572	25.4	25.2	2.9	25
JRN	Jornada Experimental Range	New Mexico	Warm Semi-desert	32°30'	106°45'	1410	29.8	29.2	3.8	26
CPR	Central Plains Experimental Range	Colorado	Temperate Shortgrass	40°49'	104°46'	1650	44.0	43.0	-3.1	21.6
KNZ	Konza Prairie Research	Kansas	Temperate Tallgrass	39°05'	96°35'	366	79.1	74.7	-2.7	26.6
KBS	Kellogg Biological Station	Michigan	Agro Ecosystem	42°24'	85°24'	288	81.1	70.6	-5.1	22.5
VCR	Virginia Coast Reserve	Virginia	Wetland	37°30'	106°40'	0	113.8	99.3	3.1	25
NIN	North Inlet (Hobcaw Barony)	South Carolina	Wetland	33°30'	79°13'	2	149.1	120.6	8.4	26.9
NWT	Niwot Ridge & Green Lakes Valley	Colorado	Tundra	40°03'	105°37'	3650	124.9	64.7	-13.2	8.2
ARC	Arctic Site, Toolik Lake	Alaska	Tundra	44°14'	122°11'	760	32.7	28.4	-20.3	10.8

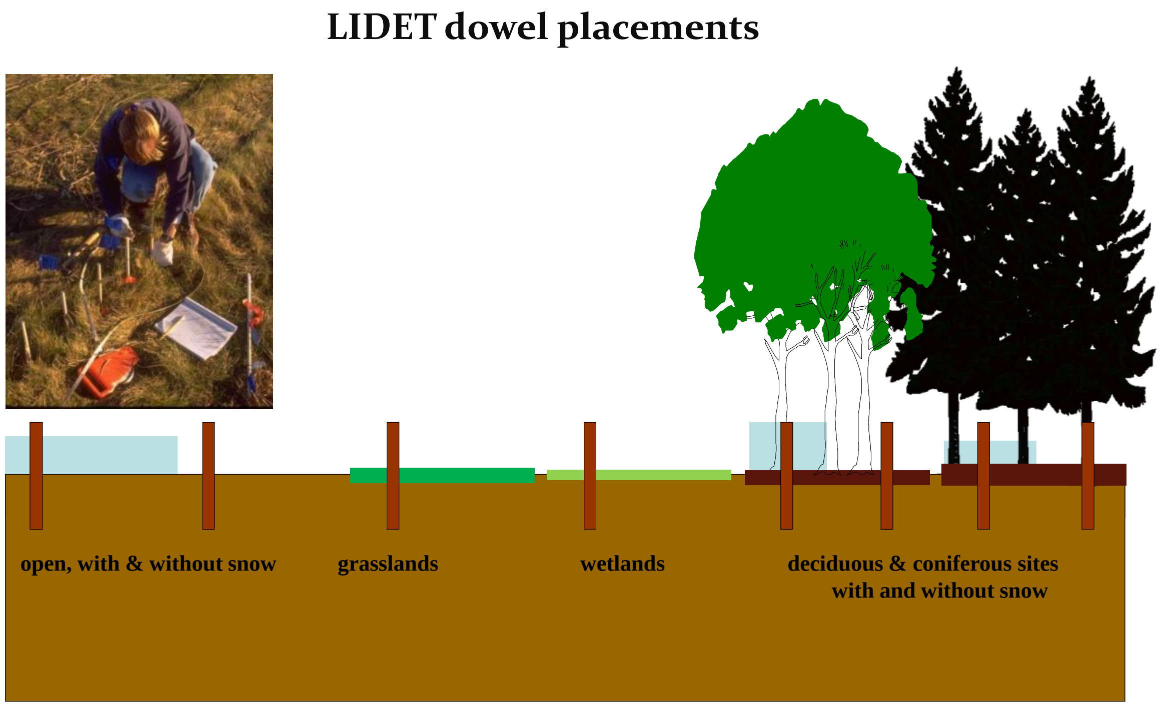

Fig. 2. Dowel placements across ecotypes for the Long-term Intersite Decomposition Experiment (LIDET) showing several ecotypes included within the 27 sites. Image top left: http://andrewsforest.oregonstate.edu/research/intersite/lidet/lidet_meth/img0053.jpg.

After collection, dowels were pooled by year in the field, location, and above- versus below-ground portion. The combined material was laboratory analyzed through oven-dry weighing at 55°C until the mass was stable. Chemical analyses for N, and ash were performed by infrared reflectance spectroscopy (Baron *et al.* 1990-2001); with 25% of the pooled samples used to calibrate the infrared reflectance spectroscopy procedures by way of Kjeldahl N (for total N), and ashing at 500°C (for total ash). Metal ion concentrations were determined using Inductively Coupled Argon Plasma spectrometry, or iCAP. The LIDET data were compiled into one spreadsheet, listed by location (27 sites), year of dowel placement (5 years 1990-1995), upper and lower dowel parts (2), time in field (up to 12 years), and replicates per time-in-year on-site (4), as shown in Table 2.

Table 2. Years when dowel placements occurred, number of years that dowel retrieval occurred, and total number of upper and lower dowel parts retrieved.

Location (See table 1)	Number of years with dowel retrieval following dowel placement[a]					Total number of dowel parts retrieved	
	1990	1991	1992	1994	1995	above-ground	below-ground
BNZ	10	-	-	6	-	63	63
LVW	-	10	-	7	-	66	56
JUN	-	4	-	1	-	20	20
BSF	-	-	10	7	-	68	67
AND	10	-	-	6	-	61	53
OLY	7,6	-	-	6	-	49	41
UFL	8,5	-	-	5	-	45	32
NLK	2	-	-	-	-	8	8
HBR	6	-	-	2	-	31	28
CDR	8,7	-	-	6	-	48	38
HFR	10,9	-	-	6	-	63	54
CWT	10,5	-	-	6,5	-	48	34
GSF	-	10,9	-	2	-	45	43
MTV	-	-	7,6	1	-	28	23
LBS	9,8	-	-	2	-	36	35
BCI	-	-	6	-	-	22	23
LUQ	10	-	-	-	-	40	38
SMR	8,6	-	-	5	-	44	40
SEV	8	-	-	4	-	46	44
JRN	10	-	-	7	-	63	61
CPR	10	-	-	6	-	64	53
KNZ	9	-	-	5	-	55	48
KBS	2	-	-	5	-	28	28
VCR	-	7,6	-	4	-	30	28
NIN	5	-	-	-	-	16	15
ARC	10	-	-	-	5	55	60
NWT	9	-	-	5	-	51	47
					Sum	1193	1080

[a] Single number for whole dowel retrieval; two numbers when whole upper or lower dowel parts are missing for a particular year.

WOOD DECOMPOSTION MODEL (WDM) FORMULATION

It is hypothesized that the wooden dowels lose mass (Eq. 1) and lose or gain N (Eq. 2) according to the following formulation (Forest Litter Decomposition Model FLDM; Zhang *et al.* 2007, 2008):

$$\frac{dM}{dt} = -k_m(S) \cdot M \cdot [1 - \frac{[N]}{[N]_f}(1 - \frac{k_n(S)}{k_m(S)})] \quad [1]$$

$$\frac{dN}{dt} = -k_n(S) \cdot N + k_a(S) \cdot (1 - \frac{[N]}{[N]_f}) \cdot M \quad [2]$$

where M and N are the total mass and N amounts remaining in the dowel (g), [N] = N/M is the N concentration in the dowel at any time (g of N per g of mass), $[N]_0$ and $[N]_f$ are the initial and final N concentrations; $k_m(S)$, $k_n(S)$ and $k_a(S)$ are state-dependent functions (S: state) to respectively evaluate the rate of mass loss, N mineralization, and soil-to-wood N transference as affected by, e.g., changing moisture and temperature conditions. With these formulations, the rate of decay is proportional to the amount of original mass remaining (first term of Eq. 1) and to the extent that the current N concentration approaches its hypothesized final value $[N]_f$ (second term of Eq. 2). In addition, the rate of net N loss and gain is assumed to be proportional to the current N content (first term in Eq. 2), and by the extent of soil-wood N transference. This transference is assumed to be proportional to the remaining mass and to the difference between [N] and $[N]_f$ (second term of Eq. 2). For the early phase of wood decay, the rate of decay is assumed to be proportional to the amount of wood and N already present, while the initial rate of N mineralization would depend on the initial N concentration or alternatively, the initial C/N ratio of the wood.

Based on the above, and after combining Eq.1 with Eq. 2, the change in d[N]/dt within the decaying wood can be expressed as

$$\frac{d[N]}{dt} = \{[N] \cdot [k_m(S) - k_n(S)] + k_a(S)]\}\,(1 - \frac{[N]}{[N]_f}) \qquad [3]$$

which suggests that [N] increases, stays the same, or decreases depending on whether $k_m(S) - k_n(S) + k_a(S)$ is > 0, = 0, or < 0, respectively. For example, if $k_m(S) > k_n(S)$ (rate of mass loss greater than rate of N mineralization) and $k_a(S) = 0$ (no exogenous uptake of N to the wood from the soil or the atmophsere), than [N] should increase as the decay process proceeds. Also note that, as t approaches infinity ($t \rightarrow \infty$):

1. dM / dN becomes equal to M/ N which then becomes $[N]_f$;
2. both N and M approach 0;
3. both exogenous N absorption (2nd term of dN/dt) and N mineralization (1st term of dN/dt) approach 0.

In principle, the state-dependency of the $k_m(S)$, $k_n(S)$ and $k_a(S)$ parameters needs to reflect location-specific moisture (MC) and temperature (T) conditions of the air- and soil- exposed dowel parts. To simplify, we set

$$k_m(S) = k_m\, f(MC, T),\ k_n(S) = k_n\, f(MC, T),\ \text{and}\ k_a(S) = k_a f(MC,T) \qquad [4]$$

with f(MC,T) determining the moisture- and temperature-dependent part of $k_m(S)$, $k_n(S)$ and $k_a(S)$ functions, and with k_m, k_n and k_a becoming moisture and temperature independent coefficients. For convenience, other state-dependent factors such as microbial composition, soil acidity, and wood composition are ignored for lack of site- and wood-specific information. Also for convenience, we further simplify by setting f(MC,T) = f(MC) f(T), thereby assuming that changes in moisture and temperature affect the decay process independently of one another. Since the actual moisture and temperature conditions within the LIDET dowels are unknown, we proceed by formulating f(MC,T) as follows (Zhang *et al.* 2007):

$$f(MC,T) = \left(\frac{ppt}{ppt_0}\right)^{p1} [1 - p_2 \min(0, \frac{T_{Jan}}{abs(T_{July} - T_{Jan})})] \exp[-\frac{Ea}{R}(\frac{1}{T_{July}} - \frac{1}{T_{Ref}})] \qquad [5]$$

where the annual precipitation rate (ppt, in mm) and mean monthly air temperatures for January (T_{Jan}) serve as surrogate variables to capture the effect of local moisture and frost conditions on the annual rate of wood decay in each dowel. The mean July temperature (T_{July}) serves as a surrogate for the temperature above and below the ground, with Ea representing the activation energy of the wood decay process, and with R as the universal gas constant (= 8.31 J $mole^{-1}$ K^{-1}). The p1 and p2 entries are to be kept the same across all sites, while ppttref and Tref serve as reference values for precipitation and temperature, set at 1000 mm and 15° C, respectively. The default values for p1 and p2 are 1 and 1. Altogether, f (MC, T) is set to become 1 when ppt = 1000 mm, T_{Jan} = 0 °C, and T_{July} = 15 °C.

A simple alternative to using the above f(MC,T) formulation for specifying local climate conditions (Meentemeyer 1978; McClaugherty *et al.* 1985) is obtained by setting

$$f(MC,T) = AET/AET_{ref} \qquad [6]$$

where AET is the mean annual actual evapo-transpiration rate at each LIDET location, and AETref as a reference value so that the AET-based f(MC,T) formulation would generate the same common k_m value for the upper dowel part across all LIDET locations.

Generally, wood decay is portrayed as a first-order reaction process, involving one or two wood compartments: a decay resistant component and a component that is less resistant (see, e.g., Hale & Pastor 1998, Romero *et al.* 2005). The simple one-compartment first-order reaction model is synonymous with exponential decay (Scheu & Schauermann 1994). The above approach retains the single-compartment formulation, but accounts for a gradual, non-exponential change in the rate of decomposition over time by making this rate dependent on the N concentration within the wood. At the same time, the rate of N mineralization and potential exogenous N uptake is back-linked to the rate of mass loss as well.

To emphasize the overall state-dependency of the above formulation, it is useful to relate the relative rate of N change to the relative rate of mass change in the dowels, as follows:

$$\frac{dN}{N} = \frac{k_n}{k_m} \frac{1 + k_a \left(\frac{1}{[N]} - \frac{1}{[N]_f}\right)}{1 - \left(1 - \frac{k_n}{k_m}\right)\frac{[N]}{[N]_f}} \; \frac{dM}{M} \qquad [7]$$

This expression shows that, for wood with low initial N content and no exogenous N uptake, the initial relative change in N content is simply proportional to the initial relative change of dowel mass, with k_n/k_m as the proportionality coefficient.

Together, Eqs. 1 to 7 constitute the Wood Decomposition Model (WDM). This model differs from the earlier leaf litter decomposition model FDLM by assuming that only one mass and one N compartment rather than three mass and N compartments are needed to model mass loss and N remaining in decaying wood. For leaf litter, the compartments refer to organic matter components for which mass and N loss is fast, slow, and very slow. The expectation is that wood generally decomposes completely, whereas decaying leaf litter adds to the accumulation of humic substances on and within soils.

COMPUTATIONAL METHODS

The LIDET data (oven-dry weight of mass remaining, total N remaining, and total N concentrations), as compiled and organized above by location, year of dowel placement, time in the field, and dowel part (upper versus lower) were extended by calculating % mass and N remaining. The mass and N data were averaged by location, time-in-field, and dowel part. Prior to averaging, the mass and nitrogen data were examined in terms of consistency using several quality checks involving (i) typographical errors; (ii) ascertaining data feasibility by plotting each variable against the other, and noting unusual differences relative to the overall inter-variable trends; (iii) checking that the average N concentration by location and by time-in-field was consistent with the corresponding average for N remaining over average of mass remaining. Outliers were subsequently categorized as feasible, or not. The latter were removed, the former were retained. The resulting data contained 224 rows, with inconsistent data entries removed where these occurred.

ModelMaker software (ModelMaker 1999) was used to calibrate the above formulation with the % M and N remaining and [N] averages by location and dowel part over time-in-field. This was done with the built-in Marquardt and Simplex least-squares routines, used for minimizing the residuals between the estimated and actual M, N and [N] values of the two dowel parts, and for obtaining the best-fitted least-squares estimates for the k_m, k_n, k_a, Ea, p1, and p2 parameters. Mean annual entries for ppt, T_{jan} and T_{jul} for each LiDET location (Table 1) were used as model input. To address the effect of the differential moisture and temperature conditions on wood decay and N mineralization, it was necessary to determine k_m, k_n and k_a for the two dowel parts in two steps:

Step 1: keeping the k_m, k_n and k_a values for the upper and lower dowel parts constant across all LIDET sites,

Step 2: adjusting these values to account for site-specific differences in wood decay and N mineralization and uptake where needed.

To balance the simultaneous minimization of the residuals for mass and N remaining and for the N concentrations across all locations, it was necessary to transform the latter from percent (%) to per thousand (‰) so that the extent of the regression residuals for mass remaining, N remaining, and the N concentrations were similar.

Table 3. Model Formulation for the mass and N dynamics in the air- and soil-exposed portions of the LIDET dowels: data sources, values, and units.

Symbol	Definition	Data source / Values	Units	Eq(s).
M	Total mass remaining in the litter bag at time t	Data and model output	gram	1
N	Nitrogen mass remaining at time t	Data and model output	gram	2
[N]	Nitrogen concentration at time t	Data and model output	%	1, 2, 3, 7
f(MC,T)	Climate influence factor for litter decomposition and nitrogen mineralization	Model output		5, 6
ppt	Mean annual precipitation	Table 1	mm	5
ppt_0	Precicipation reference	1000	mm	5
T_{Jan}	Mean monthly January temperature	Table 1	^oC	5
T_{July}	Mean monthly July temperature	Table 1	^oC	5
T_0	July reference temperature	15	^oC	5
AET	Mean annual evapo-transpiration	Table 1	mm	6
AET_0	AET reference	373	mm	6
$[N]_f$	Final nitrogen concentration in well decomposed wood	2.4	%	2,3
k_m	Parameter for mass loss from decaying wood	air-exposed: **0.0304** ± 0.0018**,** soil-exposed: **0.0457** ± 0.0016	y^{-1}	1,2,5,6
k_n	Parameter for N loss from decaying wood, derived from the best-fitted k_m and k_n/k_m estimates	air-exposed: 0.0259 ± 0.0036, soil-exposed: 0.0157 ± 0.0018	y^{-1}	5,6
k_n/k_m	Lumped parameter relating N mineralization to mass loss	air-exposed: **0.852** ± 0.067**,** soil-exposed**: 0.343** ± 0.028		7
k_a	Parameter for exogenous N transference into wood	**0.0088** ± 0.0015	y^{-1}	3
$k_{m,adj}$	Location-specific multiplier adjustment for k_m	Table 3		
$k_{n,adj}$	Location-specific multiplier adjustment for k_n	Table 3		
$(k_n/k_m)_{adj}$	Location-specific adjustment for k_n/k_m	Table 3		
p_1	Parameter to adjust the precipitation influence on f(MC, T)	**0.678** ± 0.031		5
p_2	Parameter to adjust the T_{Jan} influence on f(MC, T)	air-exposed: -1, soil-exposed: 1		5
Ea	Activation energy for wood decay	**60,870** ± 3,250	J $mole^{-1}$	5
R	Universal gas constant	8.31	J $mole^{-1}$ $°C^{-1}$	5

Note: Symbols and numbers in bold represent best-fitted parameters through simultaneous calibration of the averaged mass and N remaining and N concentration data by location and by time-in-field are adjustable parameters, for upper dowels and lower dowels.

RESULTS

The data for mass and N remaining, and for the N concentrations within the LIDET dowels are presented in Fig. 3 by way of box-and-whisker plots in the order of increasing AET by ecosystem type, from forests, grasslands and wetlands to tundra. These plots display the 10, 25, 50, 70 and 90th percentiles of the data for each location. The outliers below the 10th percentile for N and mass remaining generally refer to wooden dowels with advanced decay. The portions of boxes, whiskers and outliers above the 100% line for N remaining suggest exogenous N uptake. There are, however, only four forest locations where this may have taken place in a systematic fashion, namely MTW, BCI, LUQ, LBS. For the grasslands, exogenous uptake would have occurred at KBS, KNZ, CPR and SMR, but only in a minor way. Elsewhere, the uptake of exogenous N was mostly sporadic and fairly dowel specific.

The data for mass and N remaining and for the total N concentrations, averaged by dowel location and year-in-field, are presented in Fig. 4 for the upper and lower dowel parts across the 27 locations, over time. The following can be observed:

1. The data for mass remaining show clear and unambiguous decreasing trends at each location over the time of dowel retrieval; the rate of decline, however, depends on location, with mass losses generally occurring faster in the soil-exposed than in the air-exposed dowel parts, except at the arctic (ARC) and the two wetland (VCR, NIN) locations.

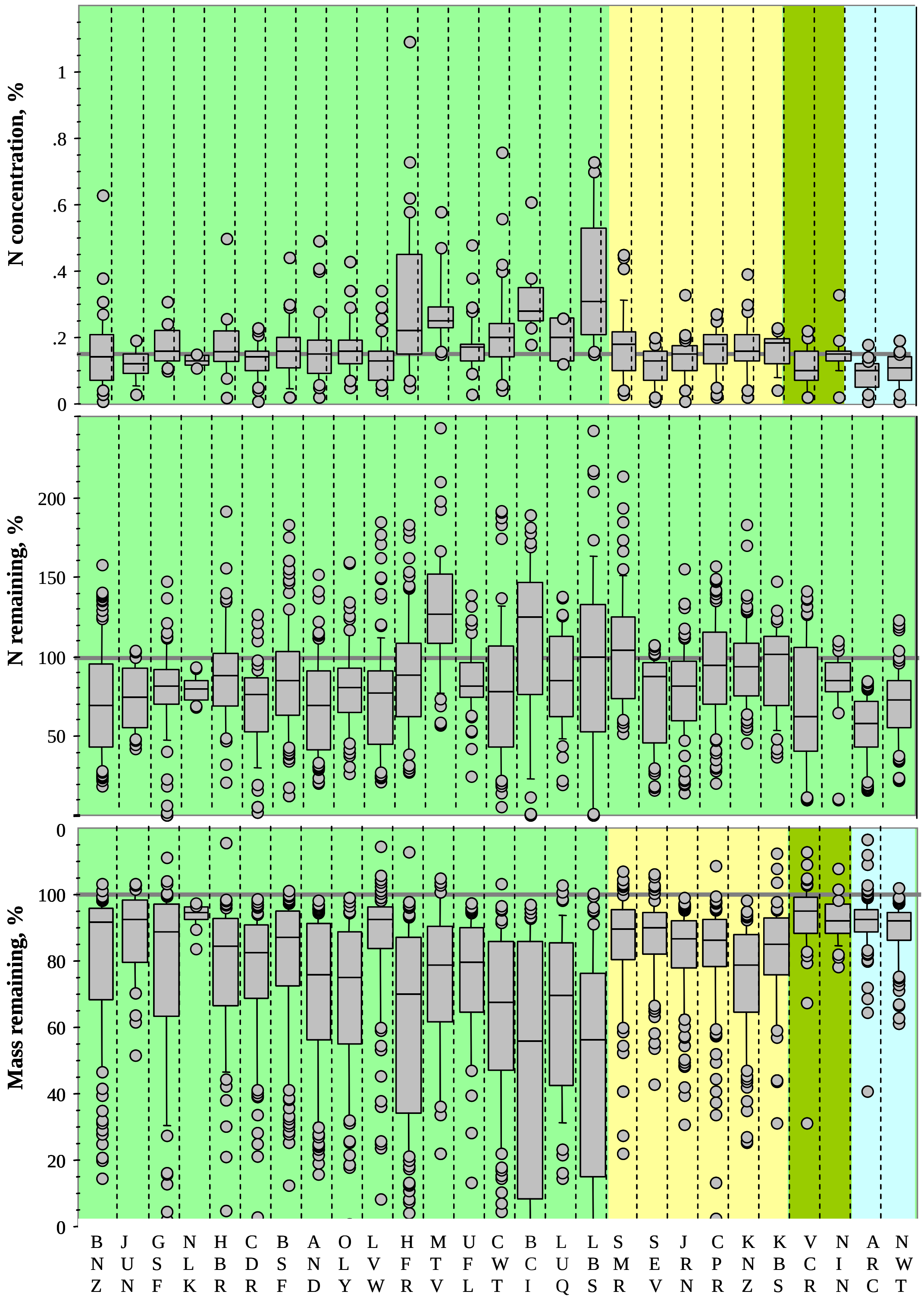

Fig. 3. Box-and-whisker plots for the mass and N remaining and N concentration data in dowels placed at 27 LIDET locations across North America (Table 1). Shown are the 10, 25, 50, 75, and 90th percentiles of the original data, collected over a period of up to 10 years at each location.

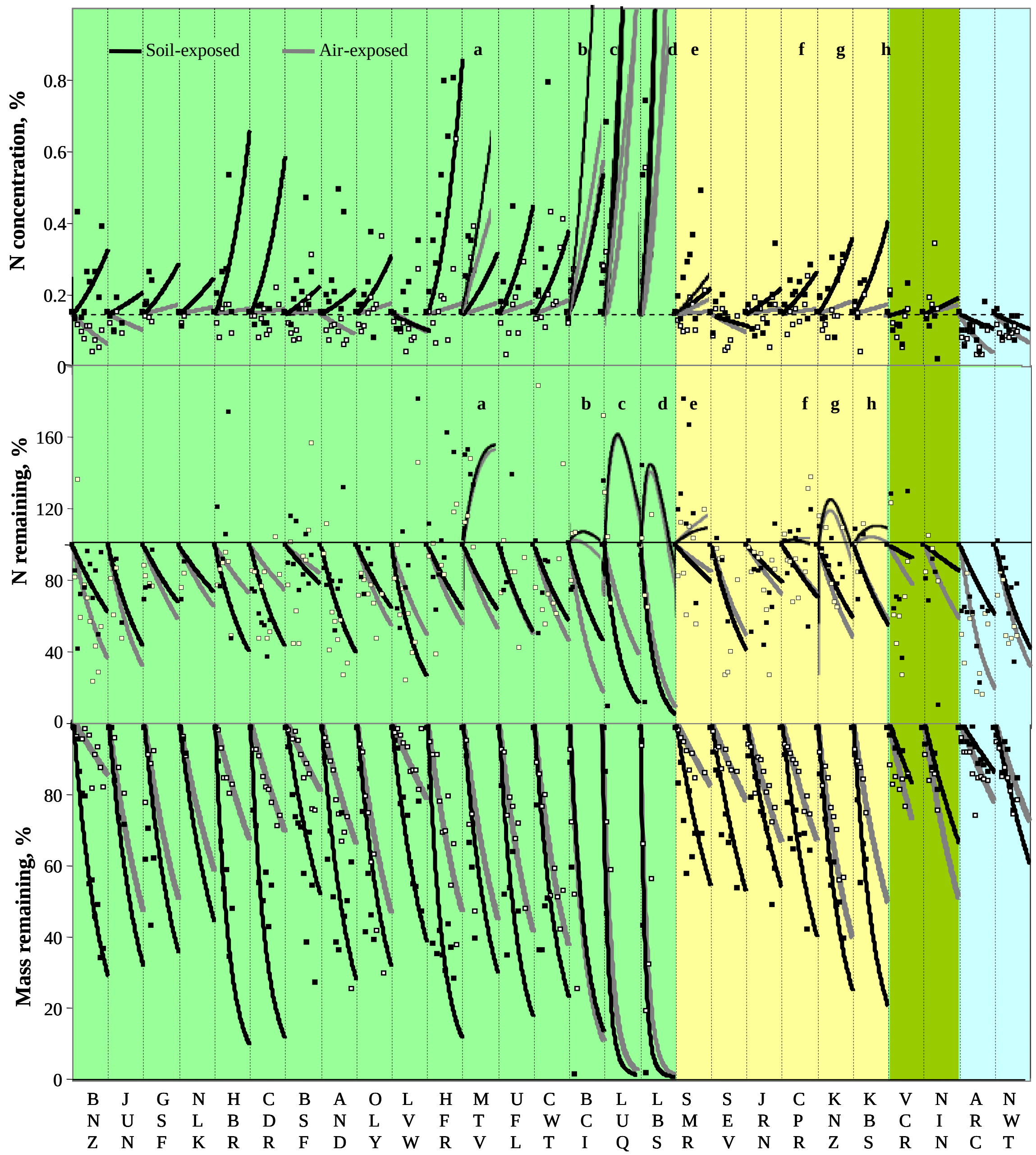

Fig. 4. Time series plots from 0 to 10 years for modeled (lines, Table 4 and 5 specifications) and actual N concentrations, and N and mass remaining for the air- (open dots) and soil- exposed (filled dots) dowel parts at each LIDET location assuming $k_a = 0$ no exogenous N uptake) everywhere. Dots represent average values for each time-in-field year at each location. The alternative calibration outcome for the N concentrations and N remaining where significant exogenous N uptake occurs are also shown for the locations with $k_a > 0$, marked a, b, c …h. Light green is forest cover, yellow is grassland, dark green is wetland and blue is tundra.

2. The mass losses (averaged replicates per location and per time in field, but not combined by placement year) between the upper and lower dowel parts were correlated such that mass loss (soil-exposed) = 1.90 mass loss (air exposed), but only 18% of the mass loss variations for the lower dowel part could be related to the mass loss variations of the upper parts (R^2 = 0.18; Fig. 5). In general, the mass loss from the soil-exposed dowels was generally faster than mass loss from the air-exposed dowels, except for the wetland (VCR, NIN) and tundra (ARC, NWT) locations.

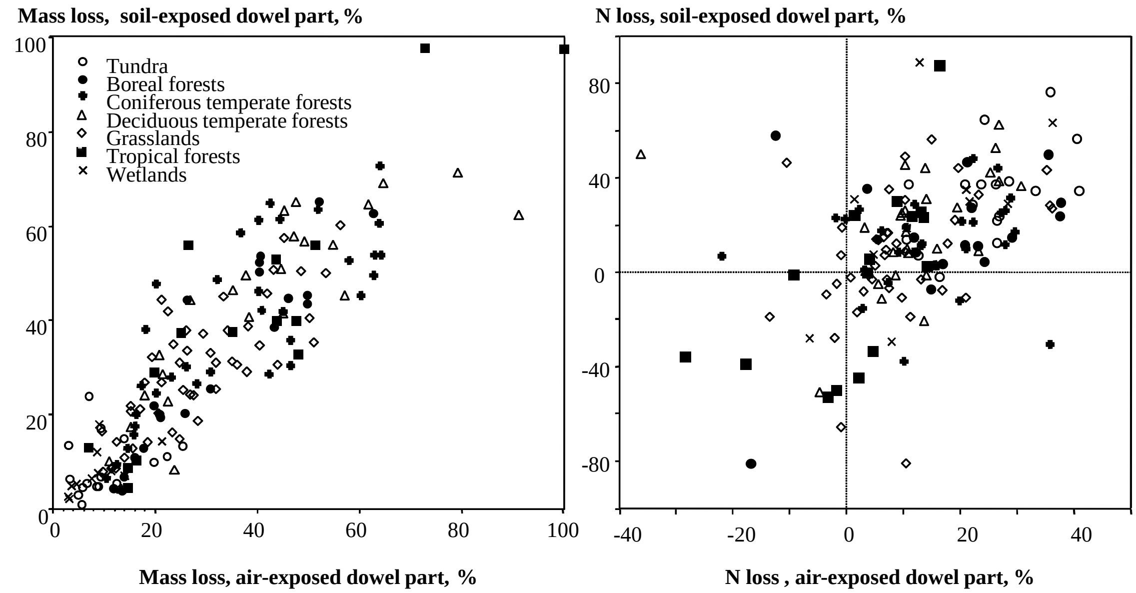

Fig. 5. Soil-exposed versus air-exposed mass (left) and N (right) losses from the upper and lower dowel parts, respectively. Note that the extent of mass loss depends on ecosystem type, but the corresponding N loss predictions do not. Also, the soil- and air-exposed mass losses correlate more closely to one another than the soil- and air-exposed N losses.

3. Mass loss from the air-exposed dowel part generally increased with increasing moisture and air temperature conditions, being lowest at the arctic (ARC) and boreal locations (BNZ, LVW), and highest at the tropical locations (BCI, LUQ, LBS). The low mass loss from the upper dowel part for the temperate conifer location in California at

BSF was somewhat exceptional, but could be due to fairly dry interior forest conditions. For the grassland locations, mass loss increased in direct proportion with increasing precipitation and actual-transpiration, being lowest at SMR, and highest at KNZ.

4. The averaged data for N remaining were quite variable across locations, by time--in-field, and by dowel part. The overall N losses from the lower dowel parts (averaged replicates per location and per time-in-field, but not combined by placement year) were positively correlated to but lower than the corresponding N loss averages from the upper dowel parts such that N loss (soil-exposed) = 0.53 N loss (air-exposed), and $R^2 = 0.25$.

5. Generally, N losses were faster from the air-exposed than the soil-exposed dowel parts. As a result, N concentrations increased to higher values in the soil-exposed than the air-exposed dowel parts in most cases.

6. The N concentrations in the upper dowel part dropped and tended to stay below the initial value for the two tundra locations (ARC, NWT), the two boreal locations (BNZ, LVW), the two temperate conifer locations (AND, JUN), and one grassland location (SEV).

Fitting the above model with the location-averaged data shown in Fig. 4 led to the results listed in Table 4 for the best-fitted common values k_m, k_n and k_a coefficients overall, and in Table 5 with and without their location-specific multiplier adjustments, by dowel part. Note that the k_m values and their adjustments generally remained within a factor of two in reference to the best-fitted k_m values across all locations, with the two wetland locations (NIN, VCR) being exceptional by requiring a factor of 0.2 for the lower dowel part. This is undoubtedly due to the persistently wet and generally anaerobic soil conditions at these locations. In contrast, the upper dowel parts required a multiplier adjustment of 0.5 for both wetlands, likely due to drier conditions than captured by the f(MC,T) for these locations. Drier than f(MC,T)-projected conditions would generally exist in some of coniferous forest interiors, as inferable from the downward k_m adjustments for the upper dowels at the coniferous CDR, BSF, AND and LVW locations, with BSF requiring a particularly low k_m adjustment. Consistently moister than the f(MC,T) projected conditions are indicated by the upward k_m adjustments for the upper dowels parts at the tropical LUQ, BI, and LBS forest locations. Upward k_m adjustments were also needed for the lower dowel parts at the deciduous HBR, CDR, HFR, LUQ and LBS locations, and at the two drier grassland locations (SMR, SEV).

Table 4. Best-fitted calibration results, including R^2 and RMSE values, using two formulations for the climate conditions at all LIDET locations [f(MC,T), Eqs. 5 and 6], and two calibration steps: (i) keeping the k_m and k_n coefficients common across all locations, with k_a = 0 (Step 1), (ii) adjusting k_m, k_n and k_a by location (Step 2). The location-specific adjustments are listed in Table 5.

	Dependent variables	Table 5 adjustments	Parameters	Air-exposed dowel portions		Soil-exposed dowel portions		R^2	RMSE
f(MC,T), Eq. 5	Mass & N remaining, [N]	yes	k_m	**0.030**	0.002	**0.045**	0.002	NA	NA
			k_m/k_n	**0.760**	0.060	**0.350**	0.030		
			p_1	**0.66+/-0.03**					
	Mass remaining	yes	k_m	**0.029**	0.001	**0.045**	0.001	0.77	9.0
		no	k_m	**0.023**	0.001	**0.052**	0.002	0.49	9.3
f(MC,T), Eq. 6	Mass & N remaining, [N]	yes	k_m	**0.022**	0.001	**0.039**	0.001	NA	NA
			k_m/k_n	**0.730**	0.060	**0.320**	0.030		
			p_{AET}	**3.68**					
	Mass remaining	yes	k_m	**0.021**	0.001	**0.038**	0.001	0.76	13.5
		no	k_m	**0.017**	0.001	**0.039**	0.002	0.43	14.2

Table 5. Best-fitted km values (a-1) by location, by ecosystem type, and held in common across all locations, together with best-fitted common k_n/k_m and k_a (a^{-1}) values, and their multipliers for all locations. Also shown are the standard errors of estimate for (i) the common k_m, k_n/k_m and k_a value, and the k_m values by ecosystem type.

Ecosystem	Location	Location-calibrated k_m				k_m by ecosystem, with standard error of estimated				k_n/k_m multiplier		k_a multiplier	
		Air		Soil		Air		Soil					
		Eq. (5)	Eq. (6)	Eq. (5)	Eq. (6)	Eq. (5)	Eq. (6)	Eq. (5)	Eq. (6)	Air	Soil	Air	Soil
Boreal Forest	BNZ	0.010	0.016	0.343	0.138	**0.011**	**0.009**	**0.167**	**0.048**	10	1	0	0
	LVW	0.012	0.010	0.107	0.039	*0.003*	*0.003*	*0.017*	*0.004*	6	4	0	0
Temperate Conifer Forest	JUN	0.020	0.037	0.079	0.077	**0.018**	**0.022**	**0.057**	**0.059**	4	2	0	0
	BSF	0.009	0.015	0.036	0.059	*0.002*	*0.002*	*0.004*	*0.004*	1	1	0	0
	AND	0.019	0.026	0.048	0.065					4	2	0	0
	OLY	0.069	0.060	0.121	0.106					1	1	0	0
	UFL	0.019	0.027	0.049	0.070					1	1	0	0
Temperate Deciduous Forest	NLK	0.024	0.025	0.058	0.028	**0.026**	**0.026**	**0.109**	**0.081**	1	1	0	0
	HBR	0.017	0.027	0.141	0.116	*0.002*	*0.002*	*0.008*	*0.005*	1	1	0	0
	CDR	0.015	0.023	0.129	0.088					3	3	0	0
	HFR	0.028	0.026	0.162	0.123					1	0.5	0	0
	CWT	0.033	0.036	0.094	0.104					1	1	0	0
Tropical Forest	GSF	0.042	0.049	0.124	0.289	**0.060**	**0.072**	**0.121**	**0.140**	1	1	0	0
	MTV	0.071	0.064	0.100	0.090	*0.006*	*0.006*	*0.010*	*0.012*	*1*	1	3	10
	LUQ	0.072	0.136	0.134	0.251					1	1	1	1
	BCI	0.054	0.069	0.121	0.154					1	1	1	1
	LBS	0.058	0.097	0.120	0.200					1	1	1	1
Grasslands	SMR	0.023	0.039	0.082	0.138	**0.020**	**0.030**	**0.051**	**0.071**	1	1	1	1
	SEV	0.013	0.034	0.049	0.126	*0.002*	*0.003*	*0.004*	*0.004*	4	4	0	0
	JRN	0.019	0.050	0.036	0.096					1	4	0	0
	CPR	0.020	0.033	0.064	0.081					1	1	1	3
	KNZ	0.020	0.039	0.044	0.070					1	1	1	3
	KBS	0.023	0.035	0.080	0.086					1	1	1	1
Wetlands	VCR	0.014	0.020	0.007	0.010	**0.013**	**0.015**	**0.008**	**0.009**	6	12	0	0
	NIN	0.014	0.022	0.009	0.015	*0.008*	*0.003*	*0.003*	*0.003*	1	1	0	0
Tundra	ARC	0.026	0.028	0.089	0.021	**0.031**	**0.017**	**0.113**	**0.021**	12	10	0	0
	NWT	0.033	0.024	0.118	0.020	*0.007*	*0.004*	*0.032*	*0.004*	5	5	0	0
Common across all locations[b]		0.022	0.025	0.062	0.056					“Common” k_n/k_m value[c]		“Common” k_a value[d]	
±Standard error of estimate		0.001	0.002	0.003	0.002					0.85 ± 0.04	0.35 ± 0.02	0.0188 ± 0.0030	

[a] Averages by ecosystem **bold**, coefficients of variation *italic*.

[b] Averages and coefficients of variation across ecosystems weighted by number of locations per ecosystem type.

[c] Common kn/km, value: computed for all locations, assuming $k_a = 0$.

[d] Common k_a value: for locations with k_a multipliers > 0 only.

Comparing the k_m adjustments between the upper and lower dowel parts across all locations produced no correlations. In contrast, the lower dowel parts would be strongly affected by, e.g., soil aeration, soil water retention, depth-to-water below the soil surface, and the extent and length of soil frost. In contrast, the k_n/k_m adjustments were highly correlated between the upper and lower dowel parts, with BNZ being an exception. This correlation is likely due to synchronization of N mineralization relative to mass loss along the length of the dowel, possibly due to the natural extension of the same wood-consuming organisms over the entire dowel length, regardless of moisture and temperature changes along this length. Location-specific k_n/k_m adjustments were needed for the tundra (ARC, NWT) and boreal (JUN, AND, BNZ, LVW) locations, and for one grassland location (SEV).

As seen in Fig. 4, exogenous N transfer into the dowels occurred at the tropical locations (BCI, LUQ, LBS, MTV) and at 4 of the 6 grassland locations (CPR, KBS, KNZ, SMR) in a readily discernible manner, i.e., N remaining > 100%. The related k_a values and their location-specific k_a multipliers are listed in Tables 4 and 5, respectively. On the whole, the large and sporadic N remaining variations do not always allow for $k_a > 0$ derivations, as can be observed from Fig. 4, showing the calibrated plots for the N concentrations and N remaining with $k_a = 0$ for all locations, and the alternative plots indicating exogenous N uptake (i.e., $k_a > 0$) for the 8 locations marked a, b, c, … h with. Note that the $k_a = 0$ modelled lines for the upper and lower dowel parts in Fig. 4 capture most of the dowel-to-dowel data divergence for M remaining, N remaining and the N concentrations, with two exceptions: for the MTV location, k_a is most clearly > 0, while the best-fitted $k_a > 0$ adjustment at SMR is not sufficient to reflect the wide variations in N remaining and in the N concentrations for the upper and lower dowel parts.

The location-specific ambiguity in the N data also affects the calibration of the finalized k_n values, because a change in k_a influences k_n and therefore k_n/k_m as well (Eqs. 3 and 7). For that reason, k_n/k_m was set at 1 for the 8 locations with $k_a > 0$. Elsewhere, k_a was set to 0. As formulated, any k_a and k_n adjustments affect the mass loss calculations from the dowels as well. However, the resulting changes were small because $[N] << [N]_f$, and were masked by the overall data variations.

The best-fitted values for mass and N remaining ($N_{remaining}$), and for the N concentrations ([N]) followed this order (Fig. 6):

$M_{remaining}$ ($R^2 = 0.87$) >> [N] ($R^2 = 0.55$) >> $N_{remaining}$ ($R^2 = 0.29$)

for the air-exposed dowel parts, and

$M_{remaining}$ ($R^2 = 0.76$) >> [N] ($R^2 = 0.42$) >> $N_{remaining}$ ($R^2 = 0.40$)

for the soil-exposed dowel parts. These results are, apart from outlier exclusion and the above comments about the variations in exogenous N uptake, also affected by error propagation, because the unaccounted variations for $M_{remaining}$ carry into the modelled values for [N], i.e. $[N]_{modelled}$, as follows:

$[N]_{modelled} = N_{remaining}$ (as modelled) / $M_{remaining}$ (as modelled).

While the best-fitted common values for k_m double from about 0.02 to 0.04 y^{-1} for the upper to lower dowel parts, respectively (Table 2), there is a much wider range associated with the location- and climate-adjusted $k_m(S)$ and $k_n(S)$ values in the plots of Fig. 7. These plots show $k_n(S)$ to be generally smaller than $k_m(S)$, thereby indicating that the dowel wood is more conservative with respect to N loss than mass loss. Also, the soil-exposed dowel parts tend to be more conservative with respect to N loss than the air-exposed dowel parts, but the reverse tends be the case for mass loss.

The $k_m(S)$, $k_n(S)$ and $k_a(S)$ results obtained via Eq. 5 or 6 are fairly comparable with one another, as illustrated in Fig. 8 (left), which shows a logarithmic relationship between the two f(MC,T) estimates for the upper and lower dowel parts. Consequently, the best-fitted k_m values and their adjustments obtained with Eq. 5 or with Eq. 6 are also related to one another as follows (Fig. 8, right):

$$k_m\text{-adjustment (Eq.6)} = 1.02\ k_m\text{-adjustment (Eq.5)},\ R^2 = 0.48, \qquad [8]$$

for the upper dowel parts, and

$$k_m\text{-adjustment (Eq.6)} = 0.90\ k_m\text{-adjustment (Eq.5)},\ R^2 = 0.40 \qquad [9]$$

for the lower dowel parts.

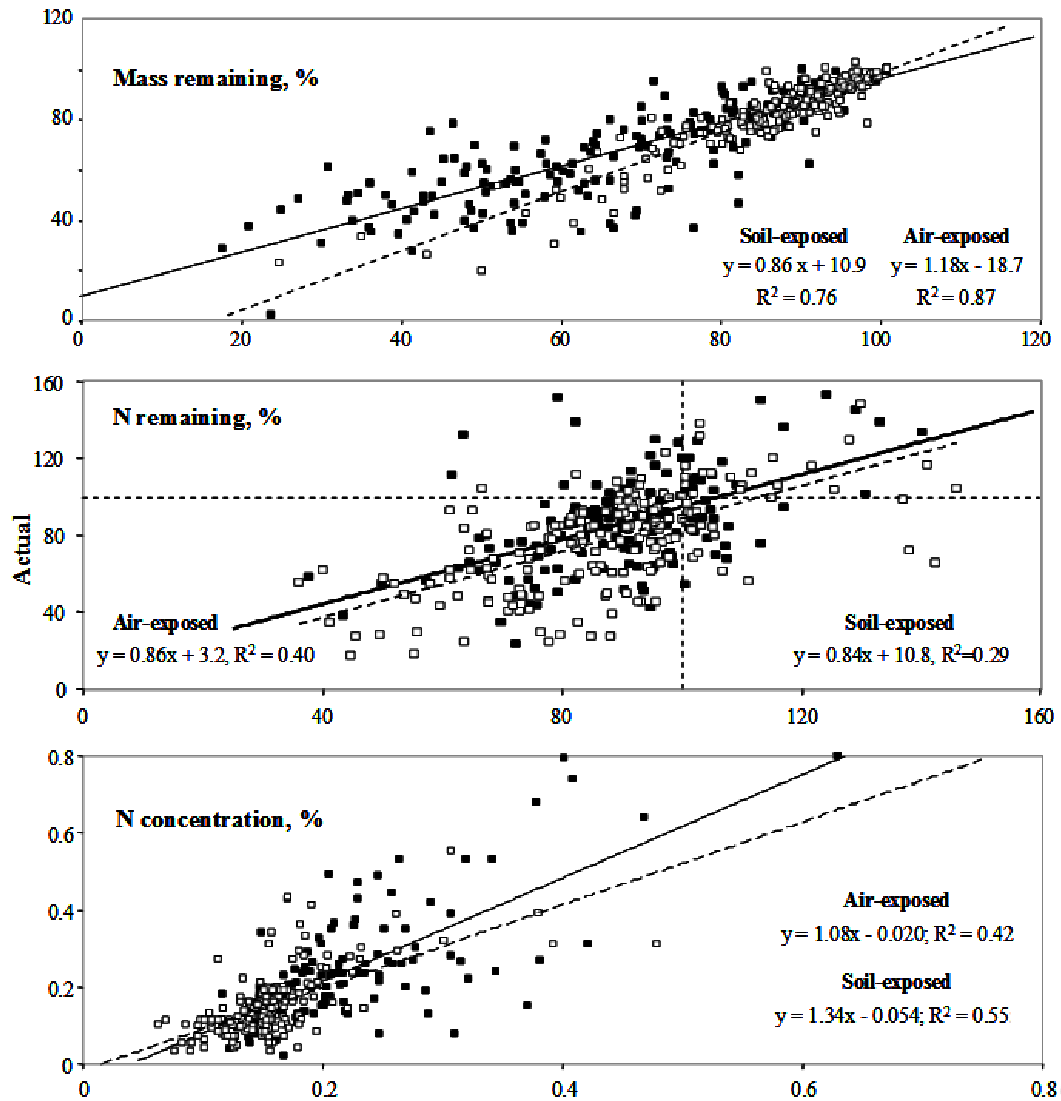

Fig. 6. Scatter plots of actual versus model-calibrated, (or predicted) values (averaged by location) for mass (top) and N remaining (middle), and N concentrations (bottom) in the air-exposed (open dots) and soil-exposed (filled dots) parts of the LIDET dowels, together with best-fitted regression lines (climate formulation based on Eq. 8, parameters specified in Tables 2 and 5).

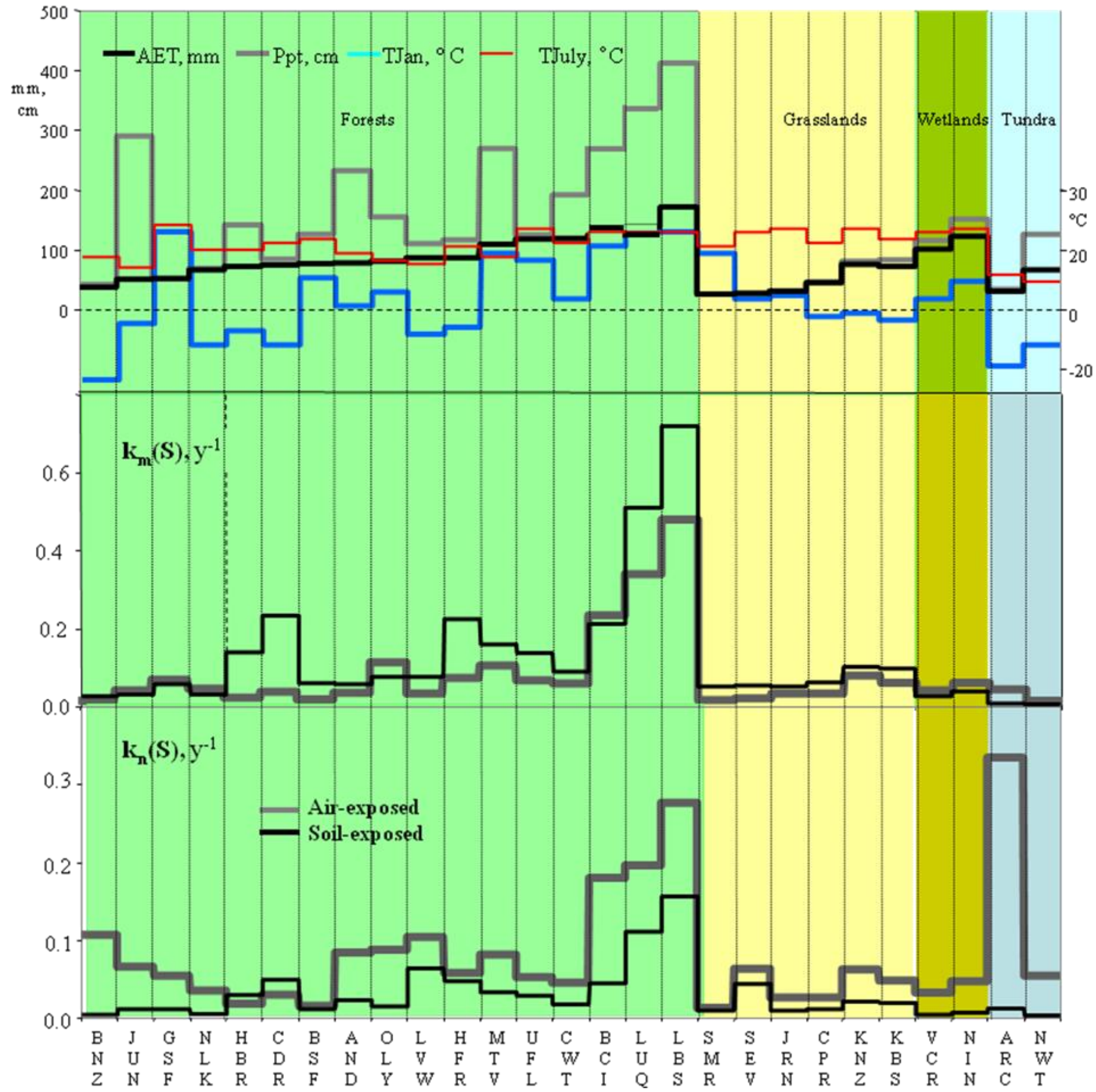

Fig. 7. Mean annual actual -transpiration (AET), mean annual precipitation, and mean monthly January and July temperatures for the 27 LiDET locations (top); best-fitted values for the mass (middle) and N loss (bottom) parameters $k_m(S)$ and $k_n(S)$ for the air- and soil-exposed dowel parts at each LIDET location.

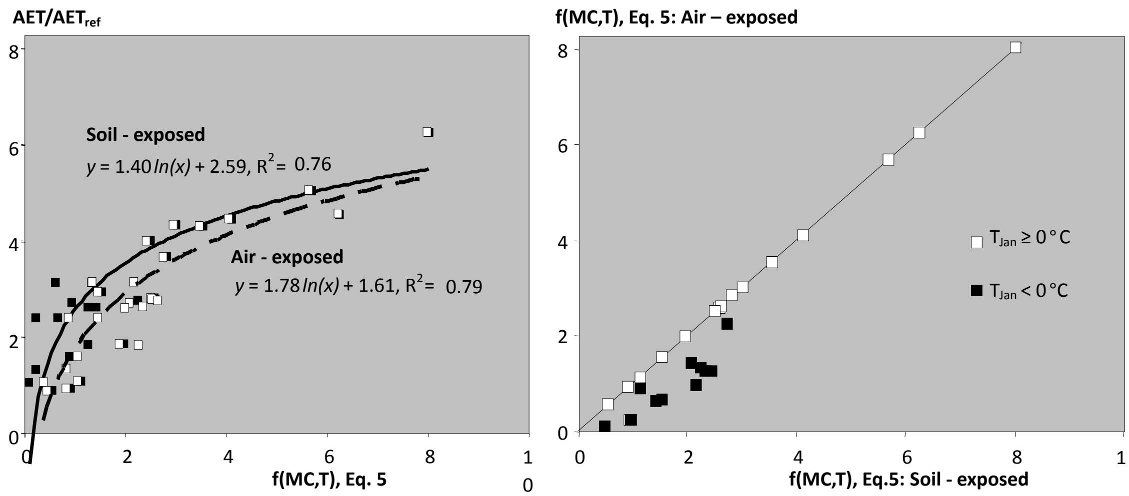

Fig. 8. Comparing the best-fitted values for the climate component of the mass loss parameter function km(S) at each LIDET location: AET/AETref versus best-fitted f(MC,T) based on Eq. 5 for the soil- and the air-exposed dowel parts (**left**); f(MC,T) derived with Eq. 5 for the soil- versus the air-exposed dowel parts (**right**). These plots reveal that the f(MC,T) component of the wood decay function differs for soil and air-exposed wood when the ground is frozen, and when it is not.

The plots in Fig. **Error! Reference source not found.** provide an overview summary of the best- fitted $k_m(S)$ and $k_n(S)$ values (Eq.6) by location (dots) and by ecosystem type (polygons) in relation to the Table 1 entry for mean annual AET. The extent of conformance and non-conformance to the general wood decay and N mineralization expectation with increasing mean annual AET is reflected by the orientation and shape of the polygons. This conformance increases with increased polygon elongation along the 1:1 line, while the width of these polygons reflects the extent that the wood decay and N mineralization rates cannot be captured by mean annual AET specifications alone. Since the polygons for the tropical forests are the largest and least narrow, this means that there are greater uncertainties in relating wood decay and N mineralization in topical forest biomes to simple climate indicators than what appears to be the case for the other biomes of thi study.

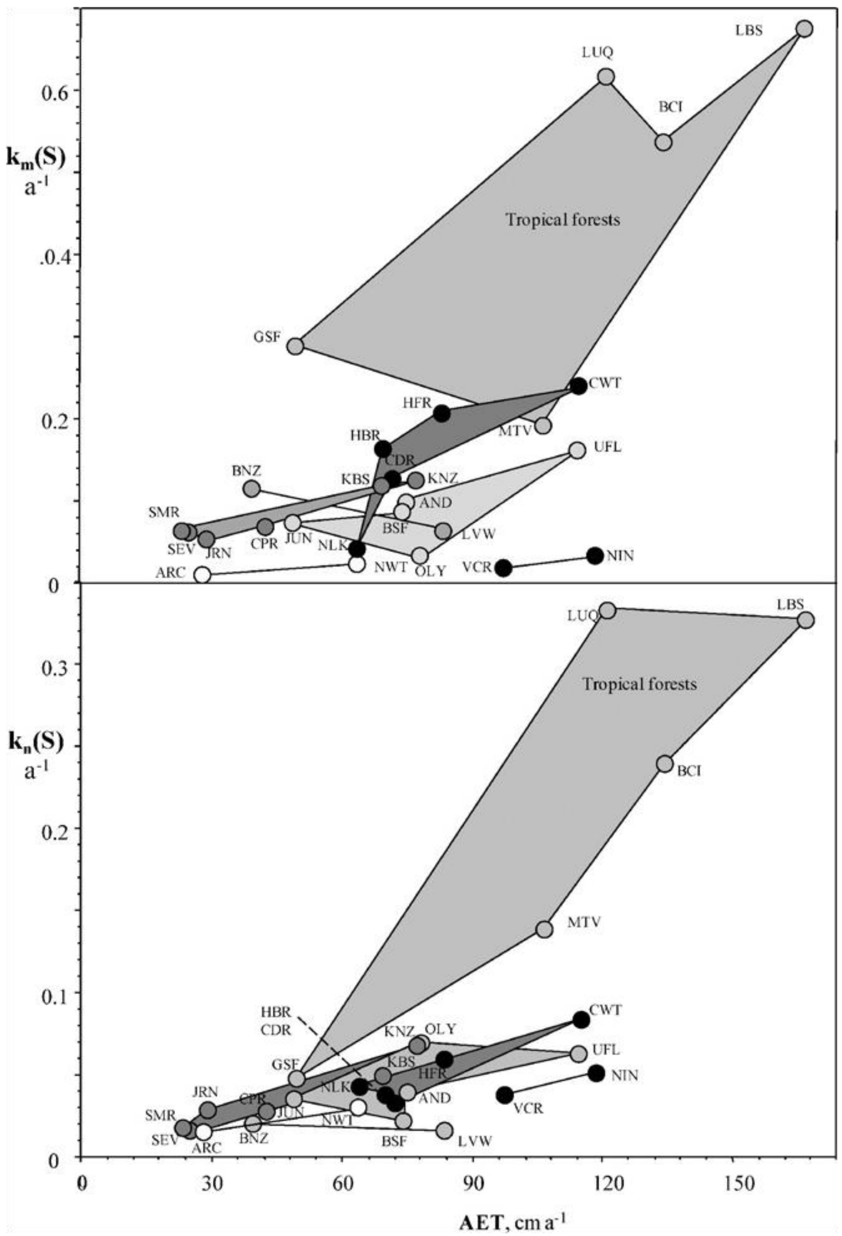

Fig. 9. Plot of the best-fitted $k_m(S)$ and $k_n(S)$ values versus AET, by location (dots) and ecosystem type (polygons).

However, employing Eq. 5 instead of Eq. 6 to derive the common $k_m(S)$ and $k_n(S)$ values and their location-specific adjustments (i) is statistically more robust across the LIDET locations (note the RMSE values listed in Table 4 in reference to Eq. 5 and 6), (ii) is empirically more direct in terms of using existing mean annual precipitation and mean monthly January and July temperatures records rather than using model-generated AET projections as input variable. The main advantage of using the Eq. 5 rather than Eq. 6 stems from explicitly addressing (i) the extra mass and N losses from the air- and therefore wind-exposed dowel parts under sub-zero temperature regimes, and (ii) accounting for low to no mass and N losses from the soil-exposed dowel parts when the soil is frozen.

DISCUSSION

Mass and N loss dynamics in decaying LIDET dowels appear to be similar to the reported mass and N loss dynamics of leaf litter bags (Parton *et al.* 2009). However, as formulated by way of Eqs. 1 to 7, only one mass and one N model compartment are needed for quantifying the overall mass and N losses from the decaying wood for achieving a general model-data conformance for mass loss of 70% or greater. To achieve this conformance, it was sufficient to specify (i) the mean annual precipitation rates and the mean annual July and January air temperatures at each location, and (ii) whether the dowel part was air- or soil-exposed. Substituting the precipitation and air temperatures specifications with mean annual actual evapotranspiration estimates brought about a similar conformance, but this substitution would be too simplistic to address wood decay in areas with extensive snow and frost occurrence.

Relating wood decay to simple climate index functions such as f(MC,T) across North America accounts for about 80% of the observable mass losses from the wooden dowels. This number drops to about 50% without location-specific adjustments (Table 6). Multiplying the common k_m value by a factor of (i) 0.5 for the upper dowel parts in coniferous forest interiors and on the two wetland locations, and (ii) 2 and 0.2 for the lower dowel parts for the deciduous forest (temperate and tropical) and wetland locations, respectively, led to an intermediate result (R^2 = 65%, details not shown). These generic adjustments reflect, respectively, (i) the generally dry conditions underneath coniferous forest canopies and open-field wetland conditions, and (ii) the generally higher levels of microbial activities within deciduous forest soils (Venterea *et al.* 2003). A more detailed approach, however, would be needed to directly relate wood decay to the changing moisture and temperature conditions within the wood, as these vary seasonally, by month and perhaps even by day. Doing so would undoubtedly reveal more details about the wood decay and N transfer and mineralization processes. In general, exogenous N transfer into the dowels would depend on (i) type, intensity and persistence of N-carrying organisms that invade the wood, and (ii) availability of external N sources as these would vary from location to location, and from time to time. Perhaps, the initial N concentration of the dowels (0.15%) may already be sufficient to support the wood-digesting activities of most wood-consuming organisms as these grow, mature and exit the dowels over the course of time, as, on average, could be the case for all the LIDET locations listed in Table 5 with k_a = 0.

The multiplicative aspect of changing moisture and temperature conditions on the decay process within wood as formulated by way of Eq. 5 has also been examined by Brischke and Rapp (2008) at 23 European field locations, where they monitored the in-wood moisture and temperature conditions over the course of 7 years. The field specimens (500 x 50 x 25 mm^3) consisted of Scots pine sapwood (*Pinus sylvestris* L.) and Douglas-fir heartwood (*Pseudotsuga menziesii* (Mirb.) Franco), stacked in multiple layers on foil or on pavement, thereby exposing the blocks to atmospheric conditions only. For the climate function, they formulated a multiplicative temperature and moisture function that varied between 0 and 1, with an operational temperature range from 0 to 50 °C, and an operational moisture content range from 25 to 100 %, with optimal values set at 30 °C and 50 %, respectively. They then accumulated the product of these functions on a daily basis, and correlated the results with the corresponding decay rating for each location, based on the following rating scale: 0 (sound), 1 (slight attack), 2 (moderate attack), 3 (severe attack) or 4 (failure), with failure occurring at all locations within 3 to 7 years. Through least-squares fitting using their cumulative temperature x moisture "dose" function, they obtained a polynomial model for the decay of the Scots pine sapwood. For the Douglas-fir heartwood data, a corresponding function was not generated on account of reduced moisture entry into the wood, thereby keeping the wood below the fiber saturation point, i.e., below the moisture content for decay initiation. This study therefore underscores that wood type as well as wood moisture absorption and retention is critical for initiating and sustaining wood decay. Unfortunately, the European study did not produce mass loss data, so direct comparisons with the above LIDET results cannot be made.

For leaf litter decay, the common and location-independent k_m values vary by leaf litter type (lignin content in particular), and also vary from about 8 to 0.4 and 0.1 y^{-1} for the fast, slow and very slow fractions of leaf litter decay (Zhang *et al.* 2007, 2008). In comparison, the ramin wood of the LIDET dowels would decay more slowly, and this would include the very slow component of leaf litter decay. Note that the location- and climate-adjusted $k_m(S)$ values in Fig. 7 for the coniferous locations are generally in good agreement with the $k_m(S)$ equivalent 0.0025 to 0.07 y^{-1} compilations for coarse woody debris in northern coniferous forests by Laiho and Prescott (2004). In comparison, Onega and Eickmeyer (1991) derived $k_m(S)$-equivalent values 0.06 and 0.11 y^{-1} for standing dead and fallen sugar maple logs at a deciduous location in Tennessee, USA. For dry and tropical conditions in Yucatan, Harmon *et al.* (1991) determined $k_m(S)$ values from 0.15 to 1.02 y^{-1} for fine woody debris, and from 0.008 to 0.615 y^{-1} for coarse woody debris. All of this confirms that the rate of wood decomposition is - for the most part - affected by location and local climate in particular. Type of wood, however, contributes to the variations in local rates of wood decay as well, because coniferous wood generally decomposes more slowly than deciduous wood as reported by, e.g., Harmon *et al.* (2000).

With respect to N, there was a greater loss of N from the air-exposed than the soil-exposed dowel parts across most of the LIDET locations. This suggests active N retention in soil-placed wood because soil-exposed wood is. For the most part, (i) soil-exposed wood is generally more aggressively digested than above-ground wood, and (ii) is also better sheltered against wetting and drying and freezing and thawing. For example, accelerated N leaching from the wood on account of severe freezing-thawing and drying and wetting cycles, including physical abrasion and desiccation, has been noted by Sonesson & Callaghan (1991). In contrast, increased N concentrations with increased wood decay have been reported by, e.g., Torres (1997), Holub *et al.* (2001), Laiho & Prescott (2004), and Sarjubala & Yadava (2007).

The k_n/k_m value of 0.35, pertinent to relating N mineralization to the rate of wood decay in the soil-exposed dowel parts, however, falls into the corresponding 0.1 to 0.4 k_n/k_m range for leaf litter N mineralization (Zhang *et al.* 2007). In contrast, the k_n/k_m value of 0.8 for the air-exposed dowel parts suggests that these parts are less N conservative than the soil-exposed wood underneath, and that these parts are also less N conservative than decaying leaf litter in general. There were only two LIDET locations where the upper dowel parts would be more N conservative than the lower dowel parts, namely the temperate deciduous forests at HBR and CDR (Fig. 7, bottom). Here, the further transformation of mineralized N into nitrate-N (Robertson 1987, Ventera *et al.* 2003) likely contributes to the overall N loss from soil-exposed ramin wood.

Ecosystem-level controls on decay and N dynamics also include topographic and antecedent disturbance effects on wood litter decay. For example, in a detailed grasslands study with ramin dowels placed into the soil of an annually burned and unburned tall grass prairie, at upland, mid slope and lowland sites, O'Lear *et al.* (1996) reported that dowel mass loss was faster on the shallow upland and slope sites than on the deeper lowland sites, while the accompanying N concentrations were unaffected by topographic position. The initial N concentration of the dowels and the generally N limiting growth conditions of the adjacent grassland soils likely contributed to the overall lack of net exogenous N transfer from the soil into the wood. O'Lear *et al.* (1996) also found that dowels showed higher mass loss and N concentration increases when placed on annually burnt sites than the dowels placed on the un-burnt or occasionally burnt sites. This was attributable to differences in soil microflora induced by regular fire recurrence rather than to local differences in moisture and temperature conditions. In fact, average May-August soil temperatures at 10 cm depth were the same for the burned and unburned plots.

Wood that is buried in wet soils generally decays more slowly than surface-placed wood as reported for a wood placement experiment in a Florida mangrove forest of Florida (Romero *et al.* 2005). Here, net N retention within the decaying wood varied by species [*Laguncularia racemosa* (+), *Avicennia germinan* and *Rhizophora mangle* (-)] and with wood placement [surface placed (+), buried (-)], where (+) and (-) refer to initial N gains and losses, respectively. The resulting N concentrations, however, increased in the wood for all three species and for both placement conditions.

Placing wood in the form of wood chips derived from alder [*Alnus rugosa* (L.) Moench], paper birch (*Betula papyrifera* Marshall), trembling aspen (*Populus tremuloides* Michx), balsam fir [*Abies balsamea* (L.) Mill.], and black spruce (*Picea mariana* Mills. BSP) directly into streams systematically increased the overall transference of exogenous N into the wood, thereby increasing N remaining from about 200% (alder) up to 1200% (black spruce), in direct relation to the lignin content of the wood (Melillo *et al.* 1983). Such increases are not seen to occur systematically across the LIDET locations presumably due to direct transference of mineralized N out of the wood through leaching as expedited by repeated drying and wetting and freezing and thawing cycles. This is underscored by the study of Boulanger and Sirois (2006) who reported no significant increases in the N content of post-fire coarse woody debris of black spruce (logs and snags) over the course of 30 years. Similarly, Fahey *et al.* (1991) reported only modest N content increases in post-harvest Sitka spruce wood residues.

The tendency of exogenous N uptake by leaf litter during the initial stage of decay (Parton *et al.* 2007) is also reflected by decaying wood at some of the LIDET locations. However, the extent of this uptake appears to depend on (i) local sporadic on-site conditions as affected by presence, type and activity of wood-consuming organism, and (ii) the changing N concentrations or C/N ratio within the decaying substrate, as formulated above and elsewhere (Parton *et al.* 2007; Zhang *et al.* 2008). Consequently, the k_a and k_n coefficients remain, at least in part, site if not dowel specific for the purpose of quantifying exogenous N uptake and mineralization in general.

The extent to which exogenous nutrients such as N may be required for the decay process to be initiated and become fully effective can be expected to vary with wood type and size as well. For example, van de Wal (2007) reported that nutrient additions to soil next to surface-placed and buried birch sawdust and wood blocks (3 x 0.5 x 0.5 cm) do increase the overall decay process, but on upland soils only. In reference to wooden pieces other than dowels, one would expect that wood decay would require incubation periods that may vary from monthly to annual time scales, and this would further depend on whether the wood is buried or fully exposed, as well as piece size and type, including lignin type (Syafii *et al.* 1988), as discussed by Harmon *et al.* (2000) and Laiho and Prescott (2004). In this regard, it may be necessary to decrease the k_m value in Table 5 to accommodate larger ramin wood dimensions. In addition, a re-parameterization of k_m and an improved assessment of k_a values would be needed to accommodate wood type differences by lignin content as already done for leaf litter (Meentemeyer 1978, Zhang *et al.* 2008), with deciduous wood generally decomposing faster than coniferous wood (Zhang *et al.* 2008).

Recently, Manzoni & Porporato (2009) reviewed about 250 organic matter decomposition models, spread across a wide range of scales, applications, and intrinsic model formulations. The above FLDM-derived formulation may serve within this wider context as a means to parameterize N-limited wood decay across a wide range of climate and terrestrial ecosystem conditions ranging from arctic to tropical. A five-model comparison (Zhang *et al.* 2008) revealed the FLDM formulation to be effective and efficient in quantifying the rate of decay and N dynamics in leaf litter bags in relation to varying leaf litter content for 21 locations across Canada over a time period of 10 years. Further testing should address quantifying the effect of varying lignin content and increased N availability on wood decay and on N transference into wood.

CONCLUDING REMARKS

Examining the mass and N loss data within the air- and soil exposed dowel parts across the 27 North American LIDET locations in the context of the above model formulation for wood decay and associated N dynamics revealed a number of patterns, namely:

1. About 50% of the mass loss variations can be represented by simple yet location-specific climate representations in terms of actual evapotranspiration, or a parameterized combination of mean annual precipitation and mean monthly January and July temperatures. The latter formulation allows for slightly better if more easily generalized calibrations across the LIDET locations.

2. Up to about 80% of the mass loss variations can be accounted for by making location-specific adjustments to the k_m, k_n and k_a coefficients, i.e., by considering micro-climate differences on above- versus below-ground wood decay and N mineralization and related transferences as influenced by type of adjacent soil and type and extent of vegetation cover.

3. On average, soil-exposed dowel parts lost mass about twice as fast as air-exposed parts; in contrast, the latter lost N twice as fast as mass. However, only up to 40% of the N losses and 55% of the N concentration variations following outlier exclusion could be accounted for by site-specific k_n and k_a parameter adjustments. This would in part be due to a generally sporadic nature of exogenous N transfers into the wood at most locations.

4. For wood decay modeling, a one-compartment model is sufficient to model mass and N remaining in wooden dowels over the course of 10 years across biomes; this can be done using (i) annual precipitation and mean July and January temperatures,

or (ii) model estimates for annual rate of actual-evapotranspiration as wood decay predictors.

5. The quality of the best-fitted model calculations improves by rendering the wood decay estimates biome and site specific. Hence, wood decay and N retention in wood is somewhat affected by biome- and site-specific differences. In part, these differences may be due to differences in biome- and site-specific differences for ground level temperature and moisture conditions. They may also be due to other factors such as biome and site specific edaphic conditions and the composition of the decay causing agents.

6. There is greater uncertainty in quantifying N remaining than mass remaining within the decaying dowels. In part, this is due to site-specific regarding the variations of exogenous N into the decaying wood. In contrast to mass loss, these variations are site specific, but not biome specific.

Further wood decomposition modeling research work is required to discern (i) how other factors such as dowel size, wood type (species, density, lignin and cellulose content), whole logs or branches, soil nutrient regime and presence of preservatives influence the overall decay dynamics, (ii) how to extrapolate the WDM parameterization results gleaned from the manufactured LIDET dowels to projecting the decay and rate of N mineralization in coarse woody debris (Laiho & Prescott, 2004). Yet another challenge is to generalize the results of this study to ecosystem-level biomass, with the C and N content of coarse woody debris as a decay factor from arctic to tropical conditions, and from uplands to lowlands and wetlands within these systems (Boulanger

& Sirois 2006). The above WDM formulation could also be expanded to serve as a guideline for capturing Ca, Mg, K, and P mineralization trends above and below the ground.

A direct application of the numerical results of this study would involve making climate-related carbon and N loss projections from the wood compartment forest ecosystems. For coniferous wood, further information may become available for the case of wooden western hemlock blocks [*Tsuga heterophylla* (Raf.) Sarg], left on the ground or buried 30 cm into the soil below for up to about 10 years at 21 CIDET locations across Canada. Finally, the mean annual WGM input formulation could be changed to account for monthly if not weekly or daily changes within the mass and nutrient status of the decaying wood above and below the ground.

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