1 Linking Short-term Soil Carbon and Nitrogen Dynamics: Environmental and Stoichiometric
2 Controls on Fresh Organic Matter Decomposition in Agroecosystems

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Abstract

A continuous, nonlinear model (FLOG-CN) linking carbon mineralization and nitrogen mineralization-immobilization with respect to time was developed that successfully reproduced the complex CO_2 -C and SMN dynamics for a collection of 70 paired C and N soil datasets. Application of the model to diverse C and N datasets showed that incorporating latency into the model of C mineralization, and using C to drive N dynamics, allows heterogeneous data from many different soil amendments to be described by the same model. We successfully modelled complex CO_2 -C and SMN dynamics of widely different shapes and from a variety of soil amendments containing plant and animal residues. The re-interpretation of these datasets with the FLOG-CN models improved the quantitative analysis of C and N dynamics, yielding new insights into how amendment characteristics and experimental conditions influence the timing and quantity of C and N mineralized. Model parameters were responsive to varying soil characteristics (pH, C, N, C:N), amendment N:C, amendment rate, incubation temperature, and N additions. Stepwise regression was used to predict model parameters using metadata available for 56 of these datasets. Significant relationships were developed to estimate model parameters independently using measured system properties or other model parameters that could be independently estimated. Estimates of C and N dynamics both fell along a 1:1 line indicating that the model parameters could be adequately described by the measured properties, but the available metadata was not able to describe C dynamics with high precision. Nitrogen mineralization-immobilization was strongly related to amendment N:C, and switched between the two processes at an amendment N:C between 0.077 to 0.085 (C:N between 11.7 to 12.9). We believe that the modelling approach described here will allow quantitative and objective

43 comparisons of diverse C and N datasets that have been hindered by subjective descriptions of
44 the past.

1. Introduction

Global soil biogeochemical cycles (C, N, P, S) are intricately linked with aboveground terrestrial productivity and atmospheric gas concentrations (Fontaine et al., 2007; Wardle et al., 2004). Agricultural practices in particular, representing approximately 38% of the Earth's land area (FAO STAT, 2013), with respect to soil management have led to significant soil organic matter losses and subsequent land degradation (Koch et al., 2013). Soil conservation practices have promoted additions of agricultural residues in soil to maintain primary productivity in these systems through improved soil structure and building of soil organic matter pools (Lal, 2004). The rates of soil carbon and nitrogen turnover from organic matter additions are intimately linked to substrate quality and quantity, as well as to abiotic factors such as climate and soil type (Voroney et al. 1989). Several studies have reported C losses in excess of 85% from field soils receiving amendments, e.g. plant residues, with the majority being lost within the first year (Jenkinson and Rayner, 1977; Voroney et al., 1989). High variability in the composition of organic amendments limits current quantitative models to making generalized predictions of decomposition (Gras et al., 2011; Morvan and Nicolardot, 2009).

Current approaches for determination of organic matter decomposition dynamics, specifically for carbon and nitrogen, are typically based around environment controlled soil incubation studies. Carbon and nitrogen dynamics are clearly linked through the chemical composition and stoichiometry of biomolecules. The aerobic dynamics of carbon mineralization (CO₂ evolution) are typically less complex than for soil mineral nitrogen, which has a number of interrelated intermediate forms. Carbon mineralization from soils is often described using first-order kinetic models, similar to those used to fit nitrogen mineralization data. When first-order models are unable to adequately describe empirical data, modifications including the first order

plus linear or double first order models have been used (Bernal and Kirchmann, 1992; Murwira et al., 1990; Voroney et al., 1989). Inclusion of two exponential equations to represent ‘fast’ and ‘slow’ pools has been used to provide limits on mineralization based on substrate quantity or quality (Gordillo and Cabrera, 1997). However, there is an implied assumption that the fastest mineralization rate for ‘recalcitrant’ organic matter is at $t = 0$, which is not the case for polymerized substrates that are utilized microbially later in time (Cayuela et al., 2009). An alternative model for C mineralization proposed by Gillis and Price (2011) uses a first order exponential plus logistic function (FLOG) which allows for a delay between peak mineralization rates of the two pools. The logistic function limits the quantity of potentially mineralizable substrate by assuming that the mineralization rate from the logistic pool is proportional to both the fraction of substrate remaining (representing resource depletion) but also to the amount of substrate C mineralized to $\text{CO}_2\text{-C}$. This assumes a process of either microbial growth or increased metabolic activity as the more complex substrates are degraded.

Modeling the dynamics of soil mineral nitrogen (SMN), on the other hand, is complicated by the rapid transformations into different soluble ion forms (Nannipieri and Paul, 2009; Schimel and Bennett, 2004), which has been viewed as a substrate-specific phenomenon (Jensen, 1929; Jensen et al., 2005; Morvan et al., 2006; Peters and Jensen, 2011; Trinsoutrot et al., 2000). Jensen (1929) noted that “the proportion between the supplies of energy material and nitrogenous food” determines whether mineralization or immobilization of SMN will occur. Modelling soil responses with traditional zero- or first-order kinetic equations generates unrealistic parameters, and parameter estimates can be dependent on the initial values during nonlinear regression. Challenges continue to exist relating the model parameters to measurable soil and substrate characteristics (Morvan and Nicolardot, 2009). Moreover, the variability

associated with SMN dynamics along the continuum of mineralization to immobilization often precludes the use of first-order kinetic equations for many datasets. Schimel and Bennett (2004) propose a modified soil nitrogen cycle paradigm emerging from empirical observations, where plants and microbes compete for mineral N, as well as organic monomers containing N. Nitrogen mineralization is dependent on extracellular depolymerizing enzymes producing monomers from complex polymerized organic forms (Schimel and Bennett, 2004). Competition from plants is excluded in aerobic soil incubation studies and competition for SMN is assumed to be solely microbial, assuming gaseous N losses are minimal. In previous work, we postulated that the timing of the delayed logistic pool from the FLOG model of carbon mineralization is related to SMN availability (Gillis and Price, 2011), since depolymerisation by exoenzymes is thought to be a rate-limiting step in the soil microbial decomposition of both C and N (Fontaine et al., 2003; Schimel and Bennett, 2004).

The scientific literature is populated with individual studies on C and N dynamics from the decomposition of organic materials in soil (e.g. Bernal and Kirchmann, 1992; Giacomini et al., 2007; Hadas et al., 1996; Honeycutt et al., 1988; Huang and Chen, 2009; Kirchmann and Lundvall, 1993; Parnaudeau et al., 2004, 2008; Petersen et al., 2005; Pita et al., 2010; Sall et al., 2007; Van Kessel et al., 2000), but efforts to aggregate, analyze, and interpret organic matter decomposition studies in a comprehensive manner are less common (e.g. Nicolardot et al., 2001; Manzoni et al. 2008, 2010; Sinsabaugh et al., 2013). Work by other authors suggests that there should be underlying patterns in the decomposition behaviour of organic matter additions to soil that are conserved across different soil and amendment types, and the patterns should be quantifiable based on differences in the observed C and N dynamics versus measurable properties of the system (Manzoni et al., 2008, 2010; Sinsabaugh et al., 2013). The first objective

of this study was to quantify patterns in soil organic matter decomposition dynamics observed across widely varying organic amendment properties, soil types, and environmental conditions. To facilitate direct comparison between all datasets, a secondary objective was to evaluate a model (FLOG-CN) linking short-term changes in carbon mineralization to synchronistic changes in SMN pools using a large and diverse collection of datasets.

2. Materials and Methods

2.1. Model development

The compartmental model (FLOG-CN) presented in Fig. 1 describes the decomposition of fresh organic matter inputs to soil by dividing the organic matter into two pools, labile and latent, that are available to microorganisms. Gillis and Price (2011) previously outlined a model for carbon mineralization, FLOG-C, with five parameters that describe $C(t)$, the amount of CO_2 -C evolved at time t . The equations are as follows:

$$[1] \quad C(t) = C_{labile}(t) + C_{latent}(t)$$

$$[2] \quad \begin{aligned} \frac{dC_{labile}(t)}{dt} &= k_1 \cdot [C_{labile} - C_{labile}(t)] \\ C_{labile}(0) &= 0 \end{aligned}$$

$$[3] \quad C_{labile}(t) = C_{labile} \cdot (1 - e^{-k_1 t})$$

$$[4] \quad \begin{aligned} \frac{dC_{latent}(t)}{dt} &= \frac{1}{k_3} \cdot C_{latent}(t) \cdot \left[1 - \frac{C_{latent}(t)}{C_{latent}} \right] \\ C_{latent}(k_2) &= \frac{C_{latent}}{2} \end{aligned}$$

$$[5] \quad C_{latent}(t) = \frac{C_{latent}}{1 + e^{-\frac{t-k_2}{k_3}}}$$

Parameters C_{labile} and C_{latent} (mg C mineralized g⁻¹ C added) are the fractions of mineralizable carbon in the labile and latent pools, respectively, which together determine $C(t)$ the cumulative amount of C mineralized. For clarity in our terminology, it is important to note that we use $C_{labile}(t)$, for example, to refer to the variable with respect to time, while C_{labile} is the model parameter which is fitted by nonlinear regression. The dynamics in the labile pool of organic matter are characterized by a first order rate constant k_1 (day⁻¹). The dynamics in the latent pool of organic matter follow a bell curve characterized by parameters k_2 and k_3 . Parameter k_2 (latency, days) is the inflection point in the logistic function and where the maximum mineralization rate of the latent pool occurs, and k_3 (latent period, days) is a scaling factor approximately equal to the time interval between $C_{latent}(t)$ at 50% and 75% maximum height (Fig. 1). The rate of mineralization from the latent pool of organic matter is controlled by the latent period (k_3 , days) and is comparable to the half-life derived from the first-order rate constant ($\ln[2]/k_1$, days).

The model of $SMN(t)$ is structured the same as $C(t)$, with parameters SMN_{labile} , SMN_{latent} , k_4 , k_5 , and k_6 . The equations are as follows:

$$[6] \quad SMN(t) = SMN_{labile}(t) + SMN_{latent}(t)$$

$$[7] \quad \frac{dSMN_{labile}(t)}{dt} = k_4 \cdot [SMN_{labile} - SMN_{labile}(t)]$$

$$SMN_{labile}(0) = 0$$

$$[8] \quad SMN_{labile}(t) = SMN_{labile} \cdot (1 - e^{-k_4 \cdot t})$$

$$[9] \quad \frac{dSMN_{latent}(t)}{dt} = \frac{1}{k_6} \cdot SMN_{latent}(t) \cdot \left[1 - \frac{SMN_{latent}(t)}{SMN_{latent}} \right]$$

$$SMN_{latent}(k_5) = \frac{SMN_{latent}}{2}$$

$$[10] \quad SMN_{latent}(t) = \frac{SMN_{latent}}{1 + e^{-\frac{t-k_5}{k_6}}}$$

Parameters SMN_{labile} and SMN_{latent} (mg SMN mineralized or immobilized g⁻¹ C added) are the quantities of mineralizable or immobilizable nitrogen relative to mineralizable carbon in the labile and latent pools respectively, while k_4 , k_5 , k_6 , are functionally similar to k_1 , k_2 , and k_3 . In this case, the parameters controlling SMN mineralization or immobilization are independent of C, and differences between the timing of C and SMN dynamics can be accounted for in the model. The model with Equations 8 and 10 can be applied to SMN datasets if there are sufficient degrees of freedom for modelling, and also can be used in situations where CO₂-C evolution was not measured. To reduce the number of fitted parameters for datasets with fewer time points, SMN dynamics can be linked to carbon mineralization under the assumptions that SMN transformations are microbially-mediated and CO₂-C evolution is a proxy for this activity. The utilization and release of N is a microbially-mediated process driven by substrate and microbial stoichiometry (Manzoni et al., 2008; Sinsabaugh et al., 2013), so we assumed that the transfer rate of mineral N to or from each SMN pool is proportional to the rate of carbon mineralization from each pool as follows:

$$[11] \quad \frac{dSMN_{labile}(t)}{dt} = r_{labile} \cdot \frac{dC_{labile}(t)}{dt}$$

$$[12] \quad \frac{dSMN_{latent}(t)}{dt} = r_{latent} \cdot \frac{dC_{latent}(t)}{dt}$$

Two proportionality constants are introduced: r_{labile} , which is the ratio of N immobilized or mineralized to C mineralized from the $C_{labile}(t)$ pool, and r_{latent} , which is the ratio of N immobilized or mineralized to the C mineralized from $C_{latent}(t)$ pool. The amount of SMN (per unit of C added), either immobilized from each pool to meet microbial demands during

decomposition or mineralized in excess of microbial requirements, is expressed as $SMN_{labile} = r_{labile} \cdot C_{labile}$ and $SMN_{latent} = r_{latent} \cdot C_{latent}$, respectively. The constants r_{labile} and r_{latent} can be calculated from the fitted parameters in the case where all C and SMN model parameters are fitted separately (as opposed to SMN linked with C). The resulting equations describing $SMN(t)$ as a function of $C(t)$ are as follows:

$$[13] \quad SMN_{labile}(t) = r_{labile} \cdot C_{labile} \cdot (1 - e^{-k_1 \cdot t})$$

$$[14] \quad SMN_{latent}(t) = r_{latent} \cdot \frac{C_{latent}}{1 + e^{-\frac{t - k_2}{k_3}}}$$

In this case, the timing of SMN mineralization or immobilization is dependent on C dynamics, and requires a paired CO₂-C evolution dataset. Using Equations 13 and 14 can be useful to reduce the number of fitted parameters if the number of SMN time points is fewer than 11 (as discussed in Section 2.2), with a consequence of reduced freedom in the range of possible curve shapes for SMN as they are dictated by C parameters.

In our model, the transfer of carbon from each compartment to the atmosphere is a unidirectional process that is described for each pool, as shown in Fig. 1. Soil mineral nitrogen dynamics differ from carbon in that microbes can either mineralize or immobilize mineral N to or from the soil solution depending on stoichiometric requirements during decomposition (Manzoni et al., 2008; Manzoni and Porporato, 2009; Sinsabaugh et al., 2013). The two processes take place simultaneously in different soil microsites (Schimel and Bennett, 2004), but the existing datasets only permitted observation of the most dominant process. We represent the SMN mineralization or immobilization rate with two unidirectional arrows from both the labile and latent pools in Fig. 1, and describe the process mathematically by either a positive (mineralization) or negative (immobilization) transfer rate for each SMN compartment. When

applied to empirical datasets, negative values for SMN should only arise through subtraction of background and/or time-zero values. If SMN data is not time-zero subtracted, an additional parameter is required to account for the amount of SMN present at time zero.

Our objective was to describe a wide range of datasets with the same model, and since a number of the SMN datasets we examined lacked sufficient degrees of freedom to fit all of the parameters, we elected to use the SMN model linked with C to describe the data (Equations 13 and 14). Model parameters for $C(t)$ and $SMN(t)$ were fitted separately using nonlinear regression. CO_2 -C evolution curves were first modelled with Equations 3 and 5 to estimate C_{labile} , k_1 , C_{latent} , k_2 , and k_3 . Parameters C_{labile} , C_{latent} , k_1 , k_2 , and k_3 were then fixed at their estimated values in Equations 13 and 14 to fit r_{labile} and r_{latent} using SMN curves. Nonlinear regression was performed on CO_2 -C and SMN data in SAS ver. 9.3 (SAS Institute Inc., Carey, NC) using the PROC NLIN procedure, with the boundary conditions for FLOG-C of C_{labile} , k_1 , C_{latent} , k_2 , and k_3 all >0 if the model did not initially converge.

2.2. Carbon and Nitrogen Data

The FLOG-CN model was initially tested on an empirical dataset representing a soil incubation study based on increasing rates of an alkaline treated biosolid applied as a liming amendment to an acidic sandy loam soil (Gillis, 2010). Subsequently, a survey of the literature was conducted to identify datasets from aerobic soil incubations covering a wide range of organic amendments, soil types, and experimental conditions. Data was extracted from individual figures in the manuscripts using Plot Digitizer (<http://plotdigitizer.sourceforge.net/>). Where two or more points partially or completely overlapped, a best estimate of the center of

each point was selected based on visible portions of the symbols and the trajectory of connecting lines if available.

Criteria for data selection were: 1. organic amendments were incorporated into the soil, 2. CO₂-C with NH₄-N and NO₃-N or total SMN (destructively sampled, not leached) were measured at each time interval, and 3. an unamended soil control was present for background subtraction, or the data was already background-subtracted. Background-subtraction ignores any priming effects or other interactions caused by the addition of organic matter to soil, but it was necessary to standardize the datasets for comparison of model parameters. Datasets having eleven or more CO₂ data points were identified for nonlinear regression parameter fitting to ensure enough degrees of freedom for error since the FLOG-C model has five fitted parameters. Some datasets with fewer time points were also modelled (e.g. Hadas et al., 1996), which affected the precision of their parameter estimates. Since only two parameters were fitted using SMN datasets, as few as six data points were modelled. Nitrogen data was converted to total SMN (NH₄ + NO₃) and *SMN(0)* was subtracted if not already in that form. Studies with an experimental aspect (varying temperature, soil type, amendment rate, N addition) were also included to investigate their effect on parameter estimates. Amendment rates and units for reporting C and N varied between studies, so data were background-subtracted and standardized to g C kg⁻¹ C added and g N kg⁻¹ C added before modelling. A range of organic amendments were selected, encompassing different physical and chemical properties to isolate possible effects of substrate composition on C and N dynamics, including plant residues (Giacomini et al., 2007; Petersen et al., 2005; Sall et al., 2007; Van Kessel et al., 2000), animal manures (Bernal and Kirchmann, 1992; Kirchmann and Lundvall, 1993), composts (Hadas et al., 1996; Huang and Chen, 2009), and municipal sludges and biosolids (Honeycutt et al., 1988; Parnaudeau et al.,

2004; Parnaudeau et al., 2008; Pita et al., 2010). These datasets included nitrogen dynamics ranging from continuous mineralization of N for the entire incubation, to N immobilization followed by a period of mineralization, to immobilization of N throughout the incubation.

2.3. Predicting Model Parameters Using Measured Properties

After modelling each dataset with FLOG-CN, relationships were developed to predict model parameters using 56 of the 70 extracted datasets. Compost datasets and the ADF fraction dataset were not included in the analysis since the materials generated parameters that were too dissimilar to the plant residues, manures, and municipal sludges and biosolids. The FLOG-CN parameters were regressed against each organic amendment variable of N:C and C:N, and environmental variables including incubation temperature ($^{\circ}\text{C}$), soil pH, and soil C concentration (g kg^{-1}) which were available for all 56 of the datasets examined. Direct relationships with the amendment N:C were established for r_{labile} and $r_{labile} \cdot C_{labile}$ using nonlinear regression with a four parameter logistic function. Stepwise regression was used to identify the best predictors of parameters k_1 , k_2 , k_3 , C_{labile} , C_{latent} , and r_{latent} for multiple linear regression analysis. In some cases (e.g. k_2), a parameter could only be described by other model parameters, so model parameters for which a significant relationship was established were included in the stepwise regression of subsequent parameters. Transformations of the parameters and measured properties were used to induce normality and constant variance of the error terms where necessary.

3. Results and Discussion

3.1. Overall Model Performance

Linking SMN dynamics to soil carbon mineralization, i.e. microbial respiration, using the combined FLOG-CN model generated good estimates for most organic amendments evaluated. In three datasets, removal of one or two outlying points allowed additional modelling of CO₂-C changes over time (B2, B3, and B6, Figure 3). Initial lag periods before the peak in C mineralization at low incubation temperatures (5 to 10°C) were also problematic for the current model, leading to unrealistic latency values (not shown).

A particularly strong fit was obtained with C datasets containing inflection points. Zero- and first-order equations often give a poor representation of these types of datasets. The strength of the FLOG-C component in the model is its ability to estimate and directly compare more diverse soil respiration curve shapes with the same model. The FLOG-N component of the model provides more accurate representations of SMN dynamics, quantifying mineralization or immobilization and accounting for temporal fluctuations in SMN values from the organic amendments tested in the different soils. The meta-data was divided into categories of organic amendments based on composition and modelled using FLOG-CN. Two of the modelled categories (plant residues and municipal sludges and biosolids) and two N-addition experiments with curve shapes representative of typical soil amendments are presented here, while the remaining organic amendment datasets modelled by FLOG-CN are included in the Supplemental Information (Figs. S1 to S8).

3.2. Plant Residues

Van Kessel et al. (2000) presented C and N data from the incubation of different plant-based components of animal feed added to soil, representing plant components considered to be either more highly labile or recalcitrant, and a range of different curve shapes were exhibited

(Fig. 2, Table S1). In all cases, the C and SMN dynamics were closely described by the FLOG-CN model, representing two pools of organic C and N decomposing over the 100 day incubation. Parameter r_{labile} changed from +0.014 to -0.220 between immature and mature orchardgrass, but increased slightly from 0.08 to 0.13 between immature and mature alfalfa. This indicates the role of substrate composition in driving parameter values. Alfalfa had a lower C:N than orchardgrass (immature: 11 vs. 14, mature: 15 vs. 22), but alfalfa also had a lignin C content (recalcitrant C) that was almost twice as high (immature: 56 vs. 36, mature: 82 vs 42 g kg⁻¹). Van Kessel et al. (2000) used the first order plus linear model for CO₂-C evolution, and the parameter estimates for the rate constant did not decrease for mature alfalfa, as expected for a more recalcitrant substrate. In the FLOG-C compartment of the model, rate constants drop by approximately half between immature and mature forages in both cases (Table S1). Soybean meal (SBM) had lower CO₂-C evolution than roasted soybean meal (RSBM), but mineralized more N throughout the incubation. This effect is captured in the FLOG-CN parameters C_{labile} and C_{latent} which are lower for SBM and parameters r_{labile} and r_{latent} which are both higher (Table S1). Decomposition of neutral and acid detergent fiber (NDF and ADF) fractions of soybean meal led to the lowest soil respiration of all the amendments tested by Van Kessel et al. (2000). Cobo et al. (2002) found a negative linear relationship ($R^2 = 0.92$) between the decomposition rate of plant residues and the size of the NDF fraction. These fractions represent insoluble substrates and our data suggest they are much more resistant to decomposition than the whole plant material. In particular, only about 35% of the added C in ADF fraction was mineralized (compared to about 68% for RSBM), and N was immobilized throughout the incubation (r_{labile} and r_{latent} were both negative). However, a small lag phase in the NDF and ADF data, before the initial peak in C mineralization, was not captured using first-order kinetics for the labile pool. This reflects the complex nature of organic

matter fractions. Overall, the FLOG-CN parameters quantified many of the interesting features of the datasets for plant residues.

3.3. Municipal Sludges and Biosolids

An extensive C and N dataset from Parnaudeau et al. (2004) on different municipal sludges and biosolids incubated in soil was also modelled (Fig. 3). In their study, mineral N (as KNO_3) was added to obtain an initial soil $\text{NO}_3\text{-N}$ concentration of 60 mg kg^{-1} to minimize N-limited decomposition, although the amount of mineral N added in each case was not presented. A total of thirteen diverse C and N datasets were analyzed using the FLOG-CN models. Mineralization of N throughout the entire incubation (r_{labile} and r_{latent} both positive) was observed in nine datasets, suggesting that the microbial N requirements were not met by the addition of mineral N in the other four sludges. The composition of the municipal sludges were highly variable (Parnaudeau et al., 2004), and a wide range in observed parameters (Table S4) highlights the substrate-quality dependence of C and N dynamics. Although varied in shape, many commonly observed patterns of C and N dynamics for organic amendments are represented in these datasets (Morvan et al., 2006; Peters and Jensen, 2011; Trinsoutrot et al., 2000), and the features were quantified using the FLOG-CN model.

3.4. Inorganic and Organic N Additions

Addition of mineral N (as $^{15}\text{NH}_4^{15}\text{NO}_3$) strongly influenced the decomposition of corn straw in the data presented by Giacomini et al. (2007) from the original study by Recous et al. (1996). Low levels of N addition (6 and $18 \text{ mg N g}^{-1} \text{ C}$) had lower soil respiration than addition of 34 , 46 , and $57 \text{ mg N g}^{-1} \text{ C}$ which were all similar. Parameter C_{labile} increased with N addition,

but there was no clear trend in C_{latent} . Kinetic parameter k_1 increased while k_2 and k_3 decreased, indicating a faster decomposition of corn straw with higher levels of added N. Nitrogen was immobilized throughout the incubation at the two lowest levels of N addition (r_{labile} and r_{latent} both negative), while the three higher N levels mineralized N from the latent pool (r_{latent} positive). Parameter r_{labile} was negative in all cases and also decreased with N addition, showing that a larger amount of N was immobilized per unit of C mineralized when additional SMN was available to microorganisms. An increase in the fraction of labile C mineralized and an increased immobilization of N per unit of labile C mineralized both suggest an altered microbial efficiency in response to N availability, as proposed by Manzoni et al. (2008), but without measured microbial biomass pools we can only speculate on possible mechanisms.

In modelling data from Aita et al. (2012), substrate modification (adding low C:N organic matter) significantly affected the dynamics of both C and N during wheat straw decomposition (Fig. 5). The size of the latent pool ($\text{g C kg}^{-1} \text{C}$) decreased by almost half when pig slurry was added, and the amount of N mineralized per unit of C from this pool doubled (Table S1). Based on the parameters modelled through the FLOG-C compartment of the model, this suggests that less organic C was depolymerized and mineralized to $\text{CO}_2\text{-C}$ by microorganisms. Decreased mineralization of native soil organic matter has been previously observed with higher N inputs, since a higher microbial N demand can be met by the substrate (Hagedorn et al., 2003). However, it is not possible to separate the mineralization of added fresh OM and native SOM from these datasets. Another possible explanation is that the depolymerized organic matter was utilized by microorganisms more efficiently in the added N treatment, with more carbon incorporated into microbial biomass and less evolved as $\text{CO}_2\text{-C}$. Manzoni et al. (2008) suggest that microbial carbon use efficiency increases exponentially with the N:C ratio of litter, meaning

that the carbon from higher N:C (lower C:N) substrates is incorporated much more efficiently into microbial biomass.

3.5. Linking Model Pools to Measurable Properties

While details of the experimental conditions or organic amendment properties were not always consistent across the modelled datasets, we were able to extract organic amendment N:C, incubation temperature, soil pH, and soil C content. These extracted parameters were sufficient to estimate all model parameters, either directly or in relation to other model parameters with direct relationships to the measured properties. Nitrogen mineralization-immobilization from the labile pool (r_{labile} and $r_{labile} \cdot C_{labile}$) was strongly related to amendment N:C (Fig. 6), and logistic curves were used to describe the relationship in both cases:

$$[15] \quad r_{labile} = \frac{0.273}{1 + e^{\frac{N:C_A - 0.104}{0.028}}} - 0.076$$

$$[16] \quad r_{labile} \cdot C_{labile} = \frac{96.7}{1 + e^{\frac{N:C_A - 0.109}{0.023}}} - 25.5$$

Multiple linear regression relationships describing the remaining parameters (or $t_{1/2} = \ln[2]/k_1$) in terms of T (incubation temperature, °C), C_s (soil carbon, mg g⁻¹), pH_s (soil pH), N:C_A (amendment N:C), or other model parameters are summarized in Figure S9 (closed circles), and are outlined below:

$$[17] \quad t_{1/2} = 5.163 - 0.5155 \cdot T + 0.1403 \cdot C_s + 0.9972 \cdot pH_s + 0.2327 \cdot N : C_A^{-1} - 0.001812 \cdot N : C_A^{-2}$$

$$R^2_{adj.} = 0.722$$

$$[18] \quad k_2 = 25.808 - 4.2147 \cdot t_{1/2}$$

$$R^2_{adj.} = 0.521$$

372 [19] $k_3 = 0.793 + 0.4643 \cdot T + 0.0009696 \cdot N : C_A^{-2} - 3.125 \cdot N : C_A^{-1/3} - 20.210 \cdot r_{labile} + 0.1907 \cdot k_2$
 $R^2 adj. = 0.494$

373 [20] $C_{labile} = 364.7 - 59.53 \cdot pH_S + 3612.8 \cdot N : C_A^2 + \frac{997.1}{k_3} - 1665.7 \cdot r_{labile}$
 $R^2 adj. = 0.466$

374 [21] $C_{latent} = \left(-1.685 - 103.73 \cdot N : C_A^2 + 0.007994 \cdot C_{labile} + \frac{193.81}{k_2} + 0.4577 \cdot k_3 \right)^2$
 $R^2 adj. = 0.401$

375 [22] $r_{latent} = 0.1710 + 0.007765 \cdot C_S - 0.008547 \cdot t_{1/2} + 0.0002981 \cdot C_{labile} - 0.01941 \cdot C_{latent}^{1/2}$
 $R^2 adj. = 0.685$

376 Parameter k_1 (expressed as $t_{1/2}$, $\ln[2]/k_1$) was described by T, soil C, soil pH, N:C⁻¹, and
377 N:C⁻², independent of any other model parameters. The remaining parameters (k_2 , k_3 , C_{labile} ,
378 C_{latent} , and r_{latent}) were described by relationships containing measured properties and/or other
379 parameters. These relationships allowed parameterization of the FLOG-CN models using just the
380 measured T, N:C, soil pH, and soil C, and these calculated parameter values are also summarized
381 in Fig. S9 (open circles). Differences between the regression and calculated values for k_2 , k_3 ,
382 C_{labile} , C_{latent} , and r_{latent} (Fig. S9) are due to additional error associated with dependencies
383 between the parameters in the calculation of the values. Overall model performance using the
384 calculated parameters was tested by generating predictions for all observations of CO₂-C and
385 SMN across the 56 datasets (Fig. 7).

386 Parameterization of FLOG-CN using N:C, T, soil pH, and soil C, yielded predictions of
387 CO₂-C values centered around the 1:1 line, but very low CO₂-C values were over-predicted and
388 the variability increased at higher CO₂-C values (Fig. 7). While the relationships based on
389 measured properties adequately estimated parameters of the C(t) compartment of the model for
390 most datasets, some datasets were difficult to predict CO₂-C dynamics with high precision.

Estimates from the SMN(t) compartment of the model were much closer to the observed values over the entire range of observations (Fig. 7). We believe this is due in part to the strong relationship directly between $r_{labile} \cdot C_{labile}$ and N:C used in SMN(t), rather than the relationship for C_{labile} (dependent on three other parameters) on which C(t) predictions are based. In future studies, additions of more detailed amendment composition data, such as lignin, cellulose, protein, NDF, hydrolysable C and N, would improve predictions of C mineralization, particularly the sizes of C_{labile} and C_{latent} . Additional sources of variability, including soil texture and moisture content, may further improve the FLOG-CN model estimates.

3.6. Theoretical Considerations

We hypothesized that the labile pool is composed of low molecular weight monomers and dimers that are soluble and immediately available, and the latent pool is composed of polymerized organic matter that must first be solubilized by depolymerizing exoenzymes. The recognition of depolymerization as a critical step in organic matter decomposition has led to fundamental shifts in the understanding of soil carbon and nitrogen dynamics (Chapin et al., 2002; Fontaine et al., 2003; Ratledge, 1994; Schimel and Bennett, 2004; Sinsabaugh and Follstad Shah, 2012). Significant evidence of a functional hierarchy of soil microorganisms being active during different stages of decomposition is emerging (Allison, 2005; Allison and Martiny, 2008; Bottomley et al., 2012; Moorhead et al., 2013; Rinkes et al., 2011). At the same time, work has demonstrated that the size of the microbial biomass pool or activities of depolymerizing enzymes do not appear to control the rate of carbon mineralization in laboratory soil incubation studies with unamended soil or with additions of plant biomass (Birge et al. 2015, Kemmitt et al. 2008). Other factors that control the rate at which substrate becomes available to the microbial

populations in the soil solution may be limiting, including sorption and desorption of substrates, diffusion, chemical hydrolysis, or shifts in the microbial community without changing in total biomass (Birge et al. 2015, Erhagen et al. 2015, Kemmitt et al. 2008). While our model was constructed with depolymerization and solubilization in mind, it does not describe a specific process and it may be any combination of processes that ultimately lead to the observed soil respiration and N-mineralization or immobilization patterns. A lack of soil respiration dependence on microbial biomass or enzyme concentrations (Birge et al. 2015, Kemmitt et al. 2008) is in agreement with our description of the system based on substrate, soil, and environmental properties.

The use of a logistic model, which approaches but never actually reaches zero, introduces an error which is equal to $C_{latent} / (1 + \exp(k_2/k_3))$, or approximately 4% of the C in the latent pool depending on k_2 and k_3 . Consequently, estimates of SMN at time zero generate either positive or negative errors depending on the value of r_{latent} . The FLOG-CN model predictions are only minimally affected, especially given the high variability in organic amendment or soil composition in the 56 datasets analyzed, and the model is able to successfully link C and N dynamics over several months. Exponential models with a rate constant modified by a sigmoidal function, as described by Rovira and Rovira (2010), were also attempted to model C and N dynamics across the 56 datasets, but in the organic matter amendment datasets modelled convergence was not reached during nonlinear regression. The sigmoidal modified rate constant in nonlinear regression resulted in some parameters becoming confounded with each other, preventing the independent estimation of those parameters. The complexity of the logistic model requires additional time points for a robust analysis compared to a purely exponential model, but

the logistic model was applied successfully in the majority of datasets modelled despite the high variability in experimental conditions and organic amendments used.

Relating organic matter stoichiometry to microbial carbon use efficiency (CUE) and nutrient mineralization or immobilization in decomposition has been the objective of a number of recent modelling approaches (Manzoni et al. 2008, 2010; Manzoni and Porporato 2009; Sinsabaugh et al., 2013). Sinsabaugh et al. (2013) reviewed how CUE is related to substrate stoichiometry in the context of nutrient-limited microbial growth. They define the threshold element ratio ($TER_{C:E}$) as the ratio of carbon to element E required in a substrate for optimum growth of microorganisms. In some situations (e.g. immobilization of SMN), nutrients can be obtained externally to meet microbial growth requirements. The $TER_{C:N}$ was estimated by Sinsabaugh et al. (2013) to be between 12.1 to 14.3 (N:C of 0.070 to 0.083) using two different models and a dataset with materials of C:N ranging between 10 to 1000. In our study, mineralization-immobilization of N from the labile pool was very strongly related to organic amendment N:C (Figure 6), and $TER_{C:N}$ was estimated by assuming the organic amendment C:N ratio at the point when the system switches between mineralization and immobilization. Based on the equations from Figure 6, the $TER_{C:N}$ is estimated to be between 11.7 to 12.9 (N:C of 0.077 to 0.085), which is in agreement with Sinsabaugh et al. (2013). Manzoni et al. (2008) described the aboveground decomposition of woody materials (C:N 17 to 1400) in litterbag studies with a model describing N concentration as a function of C mineralization, similar to the FLOG-CN model. The model contains litter and microbial stoichiometry as constants, and a single fitted parameter (CUE) that was related to litter N:C by a power law. The model could account for much of the variability in litter N concentration during decomposition. The product of CUE and microbial biomass N:C (which has a narrow range around 0.1) determines the

critical litter N:C, where sufficient N is available to decomposers (Manzoni et al. 2008). Under the same assumption that the $TER_{C:N}$ of decomposing organic matter occurs where the system switches between mineralization and immobilization of N (litter N:C = critical N:C), we estimated $TER_{C:N}$ from their equations to occur at a litter C:N of 27.8 (N:C of 0.036), higher than the estimates from Sinsabaugh et al. (2013) and in this study. This may reflect additional metabolic requirements or a different efficiency in microbial groups accessing wood-based organic matter located aboveground. The models in each case, though different, are suited to the system under study, and quantify how proportions of energy material and nitrogen sources (Jensen 1929) control N mineralization-immobilization.

The FLOG-CN model was an attempt to interpret short-term soil organic matter decomposition based on ecological principles (microbial succession and r-K selection) using a soil biogeochemical model of carbon and nitrogen mineralization. However, we were not able to conclude a specific mechanistic driver (e.g. microbial biomass, exoenzymes, diffusion, sorption/desorption) for the observed C and N dynamics reproduced with this model. In effect, our model summarized the various competing factors contributing to C and N dynamics into two pools of activity (labile and latent) separated in time. Although microbial parameters, such as biomass or enzyme concentrations, are not explicitly included in the model, the latent pool was conceived as a way to improve the representation of microbial succession in decomposition models. Improvement of the model may come through coupled microbial biomass or enzyme data to incorporate Michaelis-Menten, Monod, or multiplicative-type models of organic matter decomposition. We have demonstrated that over 1500 C and 900 N data points in the 70 datasets modelled can be reduced to seven parameters by coupling soil mineral nitrogen cycling to soil respiration in two consecutive phases of activity (labile and latent pools). Characterizing

decomposition dynamics with the numerical values for these seven parameters allows a large amount of the variability in C and N dynamics to be accounted for (in 56 of 70 datasets) using just four measured environmental and organic amendment variables.

The versatility of the FLOG-CN model becomes apparent when we consider that nearly all commonly reported responses of short-term SMN dynamics (e.g. Morvan et al., 2006; Peters and Jensen, 2011; Trinsoutrot et al., 2000), are also reproduced here. The FLOG-CN model parameters are responsive to soil type, incubation temperature, inorganic and organic N addition, as well as organic amendment type and rate. It provides an interpretive and predictive framework for CO₂-C and SMN dynamics, and suggests that a large amount of variability in soil biogeochemical processes may be predictable by accounting for the underlying ecological principles of the system (Fierer et al., 2009). Further modifications to the model, including adjustments based on temperature (Desserault-Rompré et al., 2011a) or water-filled pore space (Desserault-Rompré et al., 2011b, Georgallas et al., 2012), may also prove useful to account for additional variability.

3.7. Opportunities for Improvement

A constraint on the work presented is the inconsistency in which data is reported between different studies. Although some authors document soil type, environmental conditions, and amendment characteristics in detail (e.g. Parnaudeau et al., 2004, 2008), many others do not. In addition, degrees of freedom requirements for nonlinear regression modelling excluded a number of potentially informative datasets with too few time points. Some fields of science are developing reporting standards or minimum required information about an experiment to provide guidance when designing and executing research in these areas (Brazma et al., 2001; Fiehn et al.,

2007; Taylor et al., 2007). Such standards are intended to make information on generally accepted practices easily accessible, with the goal of generating consistent, high-quality, and compatible data that can be easily shared. There is much to gain from reviewing published data, to confirm current beliefs or generate new hypotheses (Fiehn et al., 2007). Efforts directed towards standardizing the reporting of results and development of a data repository for terrestrial organic matter decomposition experiments would be of great service to the modelling community and the field of biogeochemistry.

4. Conclusion

A synchronous model of coupled carbon mineralization and nitrogen mineralization-immobilization (FLOG-CN) with respect to time was developed and validated using a collection of 70 paired C and N soil incubation datasets. Application of the model to these diverse C and N datasets showed that incorporating latency allows heterogeneous data from many different organic amendments added to soil and varying experimental conditions to be described. The FLOG-CN model parameters were all predictable using amendment C:N, soil C, soil pH, and incubation temperature, or in relation to other model parameters. Nitrogen dynamics switched between mineralization and immobilization at an amendment C:N between 11.7 to 12.9 (N:C of 0.077 to 0.085), agreeing with other estimates of the threshold element ratio of C:N for soil microbial N cycling. Further work is necessary to identify the factors controlling C and N dynamics which lead to the observed responses, and to determine if additional amendment composition metadata can predict FLOG-CN parameters with greater precision. The FLOG-CN models provide an interpretive and predictive framework to quantify C and N dynamics following fresh organic matter additions to soil.

528

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539

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Figure Titles

Fig. 1. Compartmental model (A) of fresh organic matter decomposition incorporating two hypothetical pools of organic carbon and nitrogen: a ‘labile’ pool of low molecular weight organic monomers described by first order kinetics, and a ‘latent’ pool of polymerized organic matter that is described by a logistic model (B and C) to delay the peak mineralization rate. Carbon mineralization is a one-way process, while nitrogen can either be mineralized to or immobilized from the SMN pool at a rate that is proportional to the rate of carbon mineralization, a proxy for microbial activity (A). The latent pool dynamics are controlled by k_2 (latency) which determines the center of the logistic function, and k_3 (latent period) which dictates the slope (C).

Fig. 2. Extracted C and N data from Van Kessel et al. (2000) modelled with FLOG-CN. Soil was incubated with various animal feed components at 25°C. Amendment rates were such that 117 mg N kg⁻¹ soil was applied from each amendment.

Fig. 3. Carbon and nitrogen data presented in Parnaudeau et al. (2004) from soil incubations with a variety of different wastewater sludges at 28°C. Sludge types are indicated in the legend. Three sludges could not be modelled since the cumulative CO₂-C decreased substantially in later time periods (preventing model convergence) and were not included.

Fig. 4. Extracted C and N data from Giacomini et al. (2007) modelled with FLOG-CN. Soil was amended with corn straw at 4 mg g⁻¹ with additional mineral N supplied at rates indicated in the legend. Addition of N increased soil respiration and the amount of N immobilized, but led to re-mineralization of N by the latent pool.

Fig. 5. Extracted C and N data from Aita et al. (2012) modelled with FLOG-CN. Soil was incubated with 5 g kg⁻¹ wheat straw alone or mixed with 1 g kg⁻¹ pig slurry.

Fig. 6. Logistic relationships between both the amount of N mineralized or immobilized per unit of C mineralized (left) or C added (right) and the amendment N:C. Based on the estimate for $y = 0$ from each relationship, SMN dynamics switch between immobilization and mineralization at an amendment N:C between 0.077 to 0.085 (C:N between 11.7 to 12.9).

Fig. 7. Predicted vs. observed values for CO₂(t) (left) and SMN(t) (right) parameterized using the relationships described in the text. With a few datasets as exceptions, estimates generally fall along the 1:1 line for both CO₂ and SMN dynamics. There is greater variability in CO₂(t) estimates that is more pronounced at higher CO₂ values, likely resulting from the uncertainty associated with parameters C_{labile} and C_{latent} in particular. Estimates from SMN(t) are more precise and variability is generally more consistent across the range of SMN dynamics. This may be due to the direct relationship between $r_{labile} \cdot C_{labile}$ and N:C used in SMN(t) predictions.

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

Figure 7