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Abstract. Microbial decomposition of plant litter is a crucial process for the land carbon (C) cycle, as it directly controls the partitioning of litter C between CO_2 released to the atmosphere versus the formation of new soil organic matter (SOM). Land surface models used to study the C cycle rarely considered flexibility in the decomposer C use efficiency (CUE_d) defined by the fraction of decomposed litter C that is retained as SOM (as opposed to be respired). In this study, we adapted a conceptual formulation of CUE_d based on assumption that litter decomposers optimally adjust their CUE_d as a function of litter substrate C to nitrogen (N) stoichiometry to maximize their growth rates. This formulation was incorporated into the widely used CENTURY soil biogeochemical model and evaluated based on data from laboratory litter incubation experiments. Results indicated that the CENTURY model with new CUE_d formulation was able to reproduce differences in respiration rate of litter with contrasting C : N ratios and under different levels of mineral N availability, whereas the default model with fixed CUE_d could not. Using the model with flexible CUE_d, we also illustrated that litter quality affected the long-term SOM formation. Litter with a small C : N ratio tended to form a larger SOM pool than litter with larger C : N ratios, as it could be more efficiently incorporated into SOM by microorganisms. This study provided a simple but effective formulation to quantify the effect of varying litter quality (N content) on SOM formation across temporal scales. Optimality theory appears to be suitable to predict complex processes of litter decomposition into soil C and to quantify how plant residues and manure can be harnessed to improve soil C sequestration for climate mitigation.

1 Introduction

Plant litter decomposition plays a key role in the global carbon (C) cycle and thus needs to be well represented in land surface models. The decomposition and transformation processes of plant litter control the formation of soil organic matter (SOM) (Prescott, 2010; Schmidt et al., 2011; Walela et al., 2014; Cotrufo et al., 2015) and associate immobilization and mineralization of essential plant nutrients (Moorhead and Sinsabaugh, 2006; Parton et al., 2007; Manzoni et al., 2008; Manzoni and Porporato, 2009). Hence, a reliable litter decay model is necessary for estimating soil C balance and turnover of ecosystem C (Allison, 2012; Bonan et al., 2013; Wieder et al., 2013; Campbell and Paustian, 2015). In particular, a realistic representation of litter decomposition in land surface models is helpful to decrease the uncertainties in predicted effects of climate change and anthropogenic management on ecosystems (Gholz et al., 2000; Campbell and Paustian, 2015; Luo et al., 2016). As litter decomposition is a very complex process determined by climate (e.g., temperature and moisture), litter quality (e.g., nitrogen (N) concentration), soil nutrients and the physiological characteristics of microorganisms (Lekkerkerk et al., 1990; Prescott, 2010; Manzoni et al., 2012; Frey et al., 2013; Sinsabaugh et al.,

2013; García-Palacios et al., 2016), there remain large uncertainties in existing litter decay models (Zhang et al., 2008; Bonan et al., 2013; Campbell and Paustian, 2015). Many litter decay models, especially those incorporated in global land surface models, have ignored stoichiometric constraints to microbial processes (Bonan et al., 2013; Cotrufo et al., 2013; Wieder et al., 2013, 2015).

Microbial carbon use efficiency (CUE), defined as the ratio of microbial biomass production to material uptake from substrates (Lekkerkerk et al., 1990; Manzoni et al., 2012), is an important parameter constraining litter decay, but it has rarely been represented as a flexible quantity in land surface models. During litter decomposition, only a part of the decomposed litter C is being transferred into SOM, while the remaining C is being released as CO_2 to the atmosphere by microbial respiration (Campbell and Paustian, 2015; Cotrufo et al., 2015). While CUE is a physiological property of each decomposer community, it also determines the ecosystem-level efficiency at which litter C is transferred into SOM a step further from simple microbial incorporation. We denote this efficiency as carbon use efficiency of litter decomposition (CUE_d). With higher CUE_d, more plant-produced litter is transformed biologically into SOM, and soil C storage can reach higher values (Six et al., 2006; Sinsabaugh et al., 2013). In most existing soil biogeochemical models, CUE_d is assumed to be the same as microbial CUE and considered as a fixed parameter. The Verberne model (Verberne et al., 1990) assumes, for instance, $CUE_d \approx 0.25$. In the Yasso model (Liski et al., 2005), the CUE_d is set to 0.2. The CENTURY model sets the CUE_d for decomposition of surface and belowground metabolic litter to 0.55 and 0.45, respectively (Parton et al., 1988). In Daisy (Hansen et al., 1991), NCSOIL (Molina et al., 1983) and ICBM (Kätterer and Andrén, 2001), $CUE_d = 0.6$ for the labile litter pools and takes a lower value for recalcitrant substrates. Only a few models account for variable CUE, letting it vary in response to substrate stoichiometry (Schimel and Weintraub, 2003) or temperature (Allison et al., 2010).

The increasing evidence for a variable microbial CUE leads to a conceptual CUE model which can explain trends in CUE of microorganisms along stoichiometric gradients (Manzoni et al., 2017). The values of CUE_d used in existing litter decay models are mostly derived from CUE obtained in laboratory studies on microbial physiology or limited observations in certain ecosystems and thus show large variations without a dynamic link to environmental conditions (Parton et al., 1988; Verberne et al., 1990; Hansen et al., 1991; Liski et al., 2005; Manzoni et al., 2012). Recent studies (Manzoni et al., 2008, 2012) suggested that the microbial CUE in terrestrial ecosystems ranges from less than 0.1 for wood decomposers to about 0.5 for decomposition of N-rich and high-quality litter. To explain those differences, Manzoni et al. (2017) proposed a conceptual model of microbial CUE based on the assumption that decomposers adapt their metabolism (and hence CUE) to maximize their growth rate. This model based on optimality theory links CUE to substrate and decomposer stoichiometry, where the optimal CUE decreases with increasing substrate C-to-nutrient ratio and increases with soil nutrient availability. The predictions of this theoretical model have been verified by empirical evidence from CUE estimates for different microorganisms in both aquatic and terrestrial ecosystems (Manzoni et al., 2017).

Besides variable CUE_d, many previous studies have also indicated the necessity for litter decomposition models to consider soil mineral N availability as a driver of litter decomposition rates, in particular under low N availability (Wieder et al., 2015; Luo et al., 2016; Averill and Waring, 2018). Microbial biomass is nearly homeostatic (Cleveland and Liptzin, 2007; Franklin et al., 2011; Allison, 2012). When the supply of N from substrates is lower than the demand of microbes to fulfill their specific stoichiometric C : N ratio, microbes will utilize mineral N (immobilization) (Manzoni et al., 2012). Thus, low availability of mineral N can limit microbial activity and in turn litter decay rate (Manzoni and Porporato, 2009; Fujita et al., 2014). Although there are fertilization experiments reporting insignificant or even negative impacts of added N on litter decay rate (Fog, 1988; Hobbie and Vitousek, 2000; Finn et al., 2015), many incubation experiments showed a significant decrease of litter decomposition rate with declining mineral N availability (Recous et al., 1995; Hobbie and Vitousek, 2000; Guenet et al., 2010). Moreover, recent modeling studies have indicated that including the limiting effect of low mineral N on decomposition improved predictions of C and N fluxes (Bonan et al., 2013; Fujita et al., 2014). Therefore, soil mineral N can alter litter C flux by affecting both the litter decay rate and the partition of decayed litter C (via flexible CUE_d).

Some detailed microbial decomposition models actually have included variable microbial CUE and the limitation of low mineral N availability on litter decay rate (Ingwersen et al., 2008; Pagel et al., 2013; Campbell et al., 2016; Huang et al., 2018); however, the parameterization and evaluation of these models pose significant challenges due to their complexity and limited verification data (Wieder et al., 2013; Campbell and Paustian, 2015). There is still scope for implementing the effects of litter stoichiometry and soil mineral N availability on litter decomposition in litter decay models with more generalizable structure. In particular, it is important to test the role of these effects in models that have already been incorporated into land surface models for long-term and large-scale applications (e.g., CENTURY; Parton et al., 1988). In this study, we incorporated flexible CUE_d based on substrate C : N ratios and mineral N limitations into a soil biogeochemical model based on the CENTURY equations to simulate the decomposition and transfer processes of litter C. The study was organized as follows. First, the new model was calibrated and tested against data from laboratory litter incubation experiments for its ability to capture the effect of variable litter quality and soil mineral N

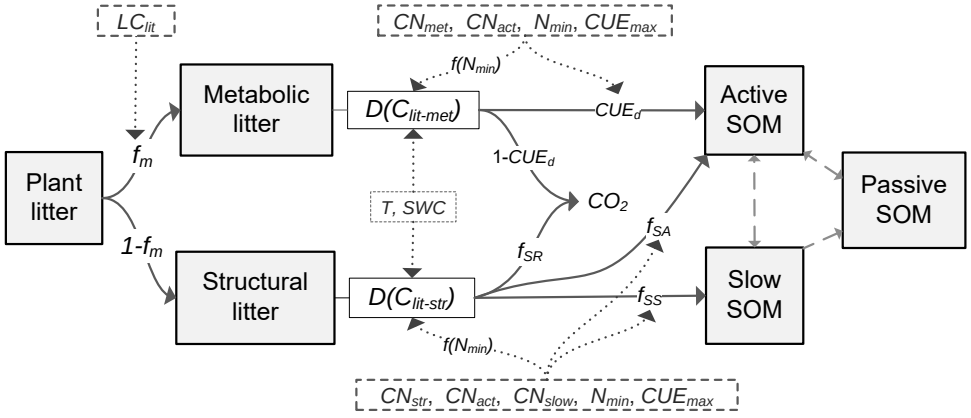

Figure 1. Schematic diagram of the C flows in the litter decay model used in this study. f_{m} is the fraction of metabolic compounds in plant litter. $D(C_{\text{lit-met}})$ and $D(C_{\text{lit-str}})$ are the decomposition rates ($\mathrm{g\,C\,kg^{-1}\,day^{-1}}$) of metabolic or structural litter, respectively. $\mathrm{LC_{lit}}$ is the lignin-to-C ratio (on a mass basis) of plant litter; $\mathrm{CN_{met}}$, $\mathrm{CN_{str}}$, $\mathrm{CN_{act}}$ and $\mathrm{CN_{slow}}$ are the C : N ratio of metabolic litter pool, structural litter pool, active SOM pool and slow SOM pool, respectively; $\mathrm{N_{min}}$ is the concentration of mineral N in solution ($\mathrm{g\,N\,kg^{-1}}$ soil); $f(\mathrm{N_{min}})$ is a factor reducing litter decay rate when soil mineral N availability is limiting; T (°C) and SWC (%) are temperature and soil water content, respectively; $\mathrm{CUE_d}$ is C use efficiency of the transformation from litter to soil organic matter (SOM); $\mathrm{CUE_{max}} = 0.8$ is the maximum microbial CUE (dimensionless) when growth is limited by C from the organic substrate; f_{SA}, f_{SS} and f_{SR} are the fractions of decomposed structural litter C that is transferred to active SOM pool, slow SOM pool and released to atmosphere in forms of $\mathrm{CO_2}$, respectively. As in the algorithms in the CENTURY model (Parton et al., 1988), here $f_{\mathrm{SA}} = \mathrm{CUE_{d\_SA}} \times (1 - f_{\mathrm{lig}})$, $f_{\mathrm{SS}} = \mathrm{CUE_{d\_SS}} \times f_{\mathrm{lig}}$, $f_{\mathrm{SR}} = 1 - (f_{\mathrm{SA}} + f_{\mathrm{SS}})$, where f_{lig} is the lignin fraction (0–1, dimensionless) in the structural litter pool, and $\mathrm{CUE_{d\_SA}}$ and $\mathrm{CUE_{d\_SS}}$ are the CUE of C transformation from structural litter pool to active and slow SOM pools, respectively.

on litter respiration rates (short-term simulations). Second, the model parameterized assuming flexible $\mathrm{CUE_d}$ and mineral N limitations was used to explore the consequences of such stoichiometric constraints on the production of soil organic carbon (SOC) (long-term simulations). With these two modeling analyses, we aimed at linking stoichiometric constraints acting on short-term (months to years) decomposition dynamics to their consequences on SOC accumulation occurring at decadal to centennial timescales.

2 Materials and methods

2.1 The CENTURY decomposition model

The basis of the litter decay model used in this study is the CENTURY model (Fig. 1), a first-order decay model that describes decomposition as a function of substrate availability and quality, clay content, soil moisture and soil temperature (Parton et al., 1988). Most land surface models (e.g., Kucharik et al., 2000; Sitch et al., 2003; Krinner et al., 2005) adopted a similar structure to simulate the litter and soil biogeochemical processes. Dead organic matter in CENTURY is separated into structural and metabolic litter and three SOM pools (active, slow, passive) with different turnover times. There is no explicit representation of microbial biomass in CENTURY; instead, the biomass of microbes is assumed to be in equilibrium with labile SOM and thus implicitly included in the active SOM pool. When litter is being decomposed, a fraction of the decomposed C is respired to the atmosphere and the remaining fraction ($\mathrm{CUE_d}$ conceptually equal to microbial CUE) enters the acceptor SOM pool. Three of such fractions are defined to characterize the transfer of C from litter to SOM: $\mathrm{CUE_{ma}}$ for transfer of the metabolic litter to the active SOM pool, and $\mathrm{CUE_{sa}}$ and $\mathrm{CUE_{ss}}$ for transfer of structural litter to active and slow SOM pools, respectively (Fig. 1). These fractions are set to be time invariant in the original version of CENTURY, so that a fixed fraction of decomposed C is retained in the acceptor pool regardless of environmental conditions and changes in the quality of the donor pool. The N flows in CENTURY follow the C flows and are equal to the product of C flow by the N : C ratio of the acceptor SOM pool. N mineralization is defined as the difference between N obtained from the donor pools and N stoichiometric demand of the acceptor pool (Parton et al., 1988; Metherell et al., 1993). In this way, net N mineralization occurs when the donor pool has a low C : N ratio, but N is immobilized (taken up by microbes) when the donor pool has a high C : N ratio.

2.2 Optimal CUE

To quantify how microbial CUE varies along gradients of nutrient availability, it can be hypothesized that microorganisms maximize their growth rate, and hence their ecological competitiveness, by adapting resource (C and nutrients) use efficiencies. This follows the growth maximization hypothesis (Mooshammer et al., 2014; Manzoni et al., 2017). Based

on this hypothesis, Manzoni et al. (2017) formulated a theoretical model expressing microbial CUE as a function of the stoichiometric difference between decomposers and their substrate. The CUE for which growth rate is maximized is the optimal CUE (CUE_{opt}) given by

$$CUE_{opt} = CUE_{max} \times \min\left[1, \frac{CN_D}{CUE_{max}} \times \left(\frac{1}{CN_S} + \frac{I_N}{U_0}\right)\right], \quad (1)$$

where CUE_{max} is the maximum microbial CUE (dimensionless) when growth is limited by C from the organic substrate. CN_D and CN_S are the C : N ratio (in mass, dimensionless) of decomposer and their substrate, respectively. Although Manzoni et al. (2017) indicated that mineral phosphorus (P) could also affect optimal CUE, we only considered N as a limiting nutrient. I_N ($g\,N\,kg^{-1}$ soil) is the maximum rate at which mineral N can be taken up by microbes, and U_0 ($g\,C\,kg^{-1}$ soil) is the C-limited uptake rate (corresponding to the decomposition rate at optimal mineral N concentration). When litter C : N is low or soil mineral N is in excess, the second term in the minimum function (Eq. 1) is higher than 1, and $CUE_{opt} = CUE_{max}$ (C-limited conditions, as in nutrient-rich litter). In contrast, when mineral N is scarce, CUE_{opt} decreases with increasing substrate C : N ratio (N-limited conditions, N-poor litter). Lack of N in the organic substrates can be compensated by mineral N being immobilized by microorganisms from the soil solution. Immobilization meets the nutrient demands as long as it is lower than the maximum supply rate I_N, at which point microbial CUE starts being downregulated. Thus, for any given C : N ratio in the substrate, CUE_{opt} increases with inorganic N concentration in the soil solution until CUE_{max} is reached. It should also be noted that Eq. (1) is interpreted at the microbial community scale, not for individual organisms.

2.3 Adaption of the optimal CUE model in the CENTURY model

CUE of decomposition (CUE_d) is also assumed to be equivalent to microbial CUE in this study. Then we followed the theory from Manzoni et al. (2017) (Eq. 1) to parameterize CUE_d during litter decomposition into CENTURY (Fig. 1). Due to the implicit representation of microbial growth in CENTURY, we replaced the original optimality CUE model (Eq. 1) by a simpler equation that involves the C : N ratios of the donor and acceptor pools, rather than microbial C : N ratios:

$$CUE_{opt} = CUE_{max} \times \min\left[1, \left(\frac{CN_{lit}}{CN_{SOM}}\right)^a\right], \quad (2)$$

where CN_{lit} and CN_{SOM} are the C : N ratio (dimensionless) of litter (metabolic or structural) and SOM pools (active, slow or passive), respectively. The C : N ratio of SOM (around 9 : 1 on a mass basis in CENTURY) is representative of the decomposer biomass, its value being between the average C : N ratio of soil microbial communities including fungi and bacteria (7.4 : 1 in Cleveland and Liptzin, 2007) and the C : N ratio of soil fungi (13.4 : 1 in Zhang and Elser, 2017), which are probably largely responsible for fresh litter decomposition. CUE_{max} (dimensionless) is the maximum CUE_d achieved when nutrients are not limiting, and it is set to 0.8 based on a synthesis of observed CUE of soil microbes (Manzoni et al., 2012). The exponent a ($g\,N\,kg^{-1}$ soil) captures the effect of mineral N uptake by microbes on CUE_d. Because CUE_d is expected to increase with mineral N availability (Eq. 1), a is assumed to be a linear function of the mineral N concentration (N_{min}, $g\,N\,kg^{-1}$ soil):

$$a = m_1 \times (N_{min} - n_1), \quad (3)$$

where m_1 ($kg\,g^{-1}\,N$) and n_1 ($g\,N\,kg^{-1}$ soil) are two coefficients that need to be calibrated. Equations (2) and (3) modulate the decrease in CUE_d with decreasing litter quality when mineral N availability changes: the exponent a increases with increasing mineral N availability, causing an increase in CUE_d at any given litter C : N ratio. Hence, increasing a mimics an increase in I_N in Eq. (1). Figure 2a illustrates how CUE_d from Eq. (2) varies as a function of mineral N concentration for different values of litter C : N.

Equations (2) and (3) were implemented in CENTURY to modify the originally fixed CUE_d (Fig. 1). With this change, the fractions of C from litter that remain in SOM are mediated by stoichiometric constraints and mineral N availability, at the expense of additional parameters to fit. The CUE_d values for C transfers between SOC pools (active, slow and passive) are not modified.

2.4 Constraint of soil nutrient availability on litter decomposition rate

CENTURY is a first-order decay model in which decomposition rates of metabolic and structural litter are modulated by scaling factors of soil temperature (f(tem)) and moisture (f(water)) (Parton et al., 1988). Here, we introduced an additional mineral N scaling factor ($f(N_{min})$, 0–1, dimensionless) to account for the limitation imposed by low mineral N availability on litter decay rate ($D(C_{lit})$):

$$D(C_{lit}) = C_{lit} \times k \times f(\text{tem}) \times f(\text{water}) \times f(N_{min}), \quad (4)$$

where C_{lit} is the C ($g\,C\,kg^{-1}$ soil) in the litter pool (metabolic or structural) and k is the potential maximum turnover rate (day^{-1}) at optimal soil temperature, moisture and nutrient conditions.

In this study, we assumed that the scaling factor of mineral N increases linearly with increasing soil mineral N concentration (N_{min}; Eq. 5) below a threshold value of $1/m_2\,g\,N\,kg^{-1}$ soil, where m_2 is a positive coefficient which needs to be calibrated (Fig. 2b). The inhibition effect of mineral N only occurs in the case of immobilization ($1/CN_{lit} < CUE_{opt}/CN_{SOM}$). The specific function $f(N_{min})$ can be ex-

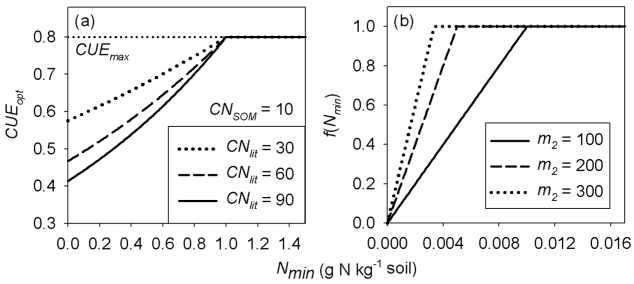

Figure 2. Schematic plot of **(a)** the optimal carbon use efficiency ($\mathrm{CUE_{opt}}$) as a function of soil mineral nitrogen for different litter C : N ratios (from Eq. 2) in the main text (with $m_1 = 0.3, n_1 = 1.0$) and **(b)** the N limitation function $f(\mathrm{N_{min}})$ applied to litter decomposition rates (from Eq. 5) in the main text. $\mathrm{CN_{lit}}$ and $\mathrm{CN_{SOM}}$ are the C : N ratios of the litter and SOM pools, respectively. $\mathrm{CUE_{max}} = 0.8$ is the maximum CUE under optimal nutrient condition (C limitation only). m_1 and n_1 are the parameters of Eq. (3) and m_2 is the parameter of Eq. (5).

pressed as

$$f(\mathrm{N_{min}}) = \begin{cases} \min(1, m_2 \times \mathrm{N_{min}}), & \dfrac{\mathrm{CUE_{opt}}}{\mathrm{CN_{SOM}}} - \dfrac{1}{\mathrm{CN_{lit}}} > 0 \\ 1, & \dfrac{\mathrm{CUE_{opt}}}{\mathrm{CN_{SOM}}} - \dfrac{1}{\mathrm{CN_{lit}}} \le 0 \end{cases}. \quad (5)$$

Existing studies have adopted approaches that differ from our definition to explicitly represent the N inhibition effects on microbial processes (Manzoni and Porporato, 2009; Bonan et al., 2013; Fujita et al., 2014; Averill and Waring, 2018). In these previous studies, $f(\mathrm{N_{min}})$ was assumed equal to the ratio between immobilized mineral N and the N deficit for maintaining a stable C : N of decomposer biomass or other receiver pools. Using the notation of Sect. 2, this definition of $f(\mathrm{N_{min}})$ can be expressed as

$$f(\mathrm{N_{min}}) = \begin{cases} \min\left(1, \dfrac{m_3 \times \mathrm{N_{min}}}{U_0 \times \left(\frac{\mathrm{CUE_{opt}}}{\mathrm{CN_{SOM}}} - \frac{1}{\mathrm{CN_{lit}}}\right)}\right), \\ \quad \dfrac{\mathrm{CUE_{opt}}}{\mathrm{CN_{SOM}}} - \dfrac{1}{\mathrm{CN_{lit}}} > 0 \\ 1, \quad \dfrac{\mathrm{CUE_{opt}}}{\mathrm{CN_{SOM}}} - \dfrac{1}{\mathrm{CN_{lit}}} \le 0 \end{cases} \quad (6)$$

where m_3 is a coefficient that needs to be optimized. U_0 ($\mathrm{g\,C\,kg^{-1}\,soil\,day^{-1}}$) is the C uptake rate (equivalent to the litter decomposition rate in absence of leaching) when soil mineral N is fully adequate for litter decay (i.e., $f(\mathrm{N_{min}}) = 1$) and can be calculated from Eq. (7) as

$$U_0 = C_{\mathrm{lit}} \times k \times f(\mathrm{tem}) \times f(\mathrm{water}). \quad (7)$$

In this study, we also tested this formulation in the CENTURY-based model, in addition to Eq. (5) (see model M4 in Table A3).

2.5 Model parameterization and validation

To determine the respective impacts of including flexible $\mathrm{CUE_d}$ and N availability constraining decay rates, we built four conceptual litter decay models (Table 1). Model M0 corresponds to the default CENTURY parameterization of a fixed $\mathrm{CUE_d}$ and no constraints of N availability on litter decay rates ($f(\mathrm{N_{min}}) = 1$). Model M1 accounts for flexibility in CUE from Eq. (2) and N constraints on decay rates by Eq. (5). Model M2 has flexible $\mathrm{CUE_d}$ but no N constraints on decay rates ($f(\mathrm{N_{min}}) = 1$). Model M3 has N constraints on decay rates but a fixed $\mathrm{CUE_d}$ (Table 1). All of these four models are run at a daily time step. Finally, model M4 also accounts for flexibility in CUE and N constraints on decays (Table A3), but it uses Eq. (6) to represent the N constraints on decays rate rather than Eq. (2). Results from model M4 are presented in the main text, but only shown in the Appendix. This range of models allows identifying which mechanisms are at play during decomposition: flexible $\mathrm{CUE_d}$ only (M3), mineral N limitation only (M2), both mechanisms (M1, M4), or none (M0).

For calibrating model parameters and evaluation of their results, we collected data of laboratory litter incubation experiments from Recous et al. (1995) (five experiments) and Guenet et al. (2010) (nine experiments; Table A2). The incubation experiments of Recous et al. (1995) and Guenet et al. (2010) continued 80 and 124 days, respectively. Recous et al. (1995) used corn residues (C : N ratio of 130) and Guenet et al. (2010) used wheat straw (C : N ration of 44) in their incubation experiments. The C : N ratios of the corn residue and wheat straw span the range of litter C : N ratios among different ecosystems (Harmon et al., 2009; Brovkin et al., 2012; Manzoni et al., 2010). In the incubation experiments, plant litter was firstly cut into fine fragments before it was mixed with mineral soil. Soil temperature and moisture condition were kept constant during the experiment. Respired C from the incubated litter and SOC as well as the soil mineral N concentrations were measured continuously across the incubation period. To distinguish the litter- and SOC-derived CO_2 flux, Guenet et al. (2010) used straw from wheat grown under ^{13}C labeled CO_2, and they were therefore able to track the CO_2 coming from litter and the CO_2 coming from soil. In the experiments by Recous et al. (1995), litter-derived CO_2 flux is calculated as the difference in CO_2 flux between the incubation samples with both soil and litter, and the control samples without added litter. More detailed information about the incubation experiments of Recous et al. (1995) and Guenet et al. (2010) can be found in Table A2.

The initial C storage and C : N ratios of litter and SOM pool, as well as soil temperature and moisture conditions for decomposition in all of the five versions of the model (M0–M4), were set based on observations (Table A2). Plant litter was firstly separated into metabolic and structural litter pools based on its lignin-to-C ratio ($\mathrm{LC_{lit}}$, dimensionless). The fraction of metabolic litter C (f_{m}, 0–1, dimensionless) is

Table 1. Optimized parameter values for the five versions of the litter decomposition model used in this study. cue_{fit} is the optimized value of CUE, m_1 and n_1 are the coefficients in Eq. (3), m_2 is the coefficient in Eq. (5), and m_3 is the coefficient in Eq. (6). Values in brackets following each parameter are the means (± standard deviations) of the fitted parameter values based on "leave-one-out" cross-validation (see Sect. 2.5 for more details).

Version	CUE	$f(N_{min})$	Parameters
M0	Fixed	1	cue_{fit} (0.57 ± 0.004)
M1	Eqs. (2), (3)	Eq. (5)	m_1 (0.61 ± 0.34), n_1 (0.53 ± 0.21), m_2 (297.4 ± 38.0)
M2	Eqs. (2), (3)	1	m_1 (0.11 ± 0.01), n_1 (1.96 ± 0.13)
M3	Fixed	Eq. (5)	cue_{fit} (0.54 ± 0.01), m_2 (396.9 ± 23.6)
M4	Eqs.(2), (3)	Eq. (6)	m_1 (0.13 ± 0.07), n_1 (1.91 ± 0.37), m_3 (0.58 ± 0.12)

calculated by

$$f_m = f_{max} - m_4 \times LC_{lit}, \tag{8}$$

where m_4 is a coefficient to be calibrated; $f_{max} = 0.85$ is the maximum fraction of metabolic litter (i.e., the default value in CENTURY; Parton et al., 1988). The fraction of structural litter C is thus $1 - f_m$. The C : N ratios of both metabolic and structural pools are assumed to be equal to the C : N ratio of litter input.

In the M1 and M3 models, the observed mineral N concentrations across the incubation period were used to calculate the daily N inhibition effect (Eq. 5). The observed cumulative respired litter C ($g\,C\,kg^{-1}$ soil) measured in the incubation experiments was used to calibrate the model parameter values. Moreover, to quantify the simulated CO_2 flux derived from the litter, we also performed a set of control simulations with only SOM (initial litter pools were set to $0\,g\,kg^{-1}$ soil) using the four model versions. The simulated litter-derived CO_2 flux is calculated as the difference in CO_2 flux between the simulation with both litter and SOM inputs and the simulation with only SOM input.

Parameter calibration was performed for each model with the shuffled complex evolution (SCE) algorithm developed by Duan et al. (1993). The SCE algorithm relies on a synthesis of four concepts that have proved successful for global optimization: combination of probabilistic and deterministic approaches; clustering; systematic evolution of a complex of points spanning the space in the direction of global improvement and competitive evolution (Duan et al., 1993). A more detailed description of this SCE optimization method can be found in Duan et al. (1993, 1994). In this study, the RMSE (root mean square error; Eq. 9) between simulated and measured cumulative respired litter C (%) on all observation days (Table A2) of each incubation experiment was used as the objective function, and the parameters minimizing RMSE between simulated and observed cumulative respired litter C were regarded as optimal parameter values.

$$RMSE = \sqrt{\left(\frac{\sum_{i=1}^{n}(Sim_i - Obs_i)^2}{n}\right)}, \tag{9}$$

where n is the number of observation days, and Sim_i and Obs_i (%) are the simulated and observed percent of cumulative litter-C flux on day i, respectively.

We used leave-one-out cross-validation (Kearns and Ron, 1997; Tramontana et al., 2016) to evaluate each of the four models (i.e., M0–M3), a cross-validation method used when data are scarce. The number of cross-validations corresponds to the number of incubation experiments (14). Each time, one of the 14 incubation experiments was left out as the validation sample, and the remaining 13 experiments were used to train model parameters. In addition to RMSE, we also adopted the Akaike information criterion (AIC; Bozdogan, 1987; Eq. 10) to determine the relative quality of the four version models on estimating cumulative respired litter C.

$$AIC = n \times \ln\left(\frac{\sum_{i=1}^{n}(Sim_i - Obs_i)^2}{n}\right) + 2n_p, \tag{10}$$

where n_p is the number of model parameters. The evaluation of AIC is important here because depending on the model version, different numbers of parameters have to be determined (Table 1), requiring us to weigh both model accuracy and robustness.

Note that the turnover times of SOM pools (active, slow and passive) used in this study are obtained from Organising Carbon and Hydrology In Dynamic Ecosystems – aMeliorated Interactions between Carbon and Temperature (ORCHIDEE-MICT v8.4.1; Guimberteau et al., 2018). The turnover times of litter pools (metabolic and structural), as well as the coefficient m_4 in Eq. (8), were optimized against the observed cumulative respired litter C from all of the 14 incubation experiments using the M0 and M1 models (Table A3). A previous study has shown that litter decomposability is negatively correlated to its physical size (for example, Tuomi et al., 2011). Therefore, the turnover times of the fine litter fragments used in the incubation experiments of Recous et al. (1995) and Guenet et al. (2010) are expected to be shorter than the values set in ORCHIDEE-MICT, which are representative of the turnover times of natural plant residues. In addition, the mixing of soil and litter particles in the incubation experiment likely enhances decomposition as spatial disconnection of decomposer and sub-

strate, which can occur under natural soil conditions (Barnes et al., 2012; Hewins et al., 2013), is prevented. The calibrated turnover times of the metabolic and structural pools and the value of m_4 in Eq. (8) are 3.5 and 30 days and 0.5, respectively.

2.6 Impacts of litter stoichiometry and mineral N availability on SOM accumulation

We used model M1, with flexible CUE_d and decomposition rate function of available N to study the impacts of litter stoichiometry (C : N ratio) and soil mineral N availability on the formation and accumulation of SOM. In total, 24 idealized simulation experiments with different values of litter C : N ratios and soil mineral N availabilities were conducted (Table A4). The assumed litter C : N ratios (CN_{lit}) of 10, 15, 30, 60, 120 and 200 span the variation among most natural substrates and soil amendments from organic matter input in agriculture (Harmon et al., 2009; Brovkin et al., 2012; Manzoni et al., 2010). The assumed range of mineral N availability (N_{min}) of 0.001, 0.005, 0.01 and 0.05 g N kg^{-1} soil spans the observed concentrations of soil mineral N in major terrestrial ecosystems (Metherall et al., 1993).

In each simulation experiment, model M1 was run for 5000 years to bring the litter and SOM pools in equilibrium with the prescribed litter input flux. The daily input rate of plant litter was set to 0.006 g C kg^{-1} soil day^{-1}, and the initial C stock of litter and SOM pools was all set to be 0 g C kg^{-1} soil. During the simulation, soil temperature and soil water content were assumed to be 25 °C and 60 % of water holding capacity, respectively. We emphasized that our goal with this simplified scenario was to single out the effects of stoichiometric constraints, not to simulate the effects of a realistic climatic regime. Parameter values for M1 (with $m_1 = 0.54$, $n_1 = 0.50$ and $m_2 = 296.8$) used here were optimized based on all of the 14 incubation experiments from Recous et al. (1995) and Guenet et al. (2010) (see above). More detailed information about the specific settings of our simulation experiments can be found in Table A4.

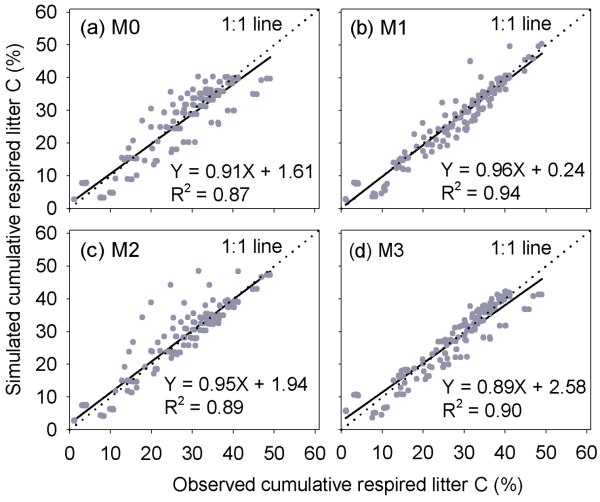

Figure 3. Comparison of the predicted cumulative respired litter C to observed values at different times during the litter decomposition process. Each dot denotes an observation of cumulative respired litter C on a certain day. In total, there are 149 points. M0–M3 are the four versions of litter decay models tested in this study (Table 1).

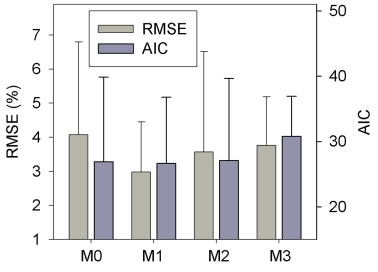

Figure 4. The RMSE and AIC of the simulated cumulative respired litter C from the four versions of litter decay model used in this study. Error bars denote the standard deviation of RMSE or AIC for different incubation experiments. M0–M3 denote the four models tested in this study (Table 1).

3 Results

3.1 Evaluation of different models

Results of leave-one-out cross-validation suggest that model M1 provides more accurate prediction of cumulative respired litter C than other models (Fig. 3). The differences between simulated and observed cumulative respired litter C from M1 are mostly less than 6 % for over 93 % of the data (Fig. A1b). The average RMSE of predicted cumulative respired litter C from M1 (3.0 %) is lower than that of model M0 (4.1 %). Models M2 and M3 have slightly lower RMSE values than M0 (3.7 % and 3.8 %, respectively) but perform worse than M1 (Fig. 4). However, the average AIC values of all the models are comparable, suggesting that models with more fitted parameters do not overfit the observations (Fig. 4).

Model M1 captures the differences in respiration rates due to different C : N ratios of substrate and varying levels of mineral N availability across the 14 incubation experiments (Fig. 5). While model M3 can reproduce the observed effect of soil mineral N availability on litter respirations rates (Fig. 5d), it underestimates the cumulative respired CO_2 from low quality litter ($CN_{lit} = 130$) at high mineral N concentrations (> 0.04 g N kg^{-1} soil). Models M0 and M2 cannot represent the effects of soil mineral N on litter respiration rate (Fig. 5a, c), and their predictions are more biased from the observed values compared to M1. Model M4, which uses the alternative formulation for N constraints on litter decay (Eq. 6), reproduces the different respiration rates of substrates with contrasting C : N ratios and at different levels of

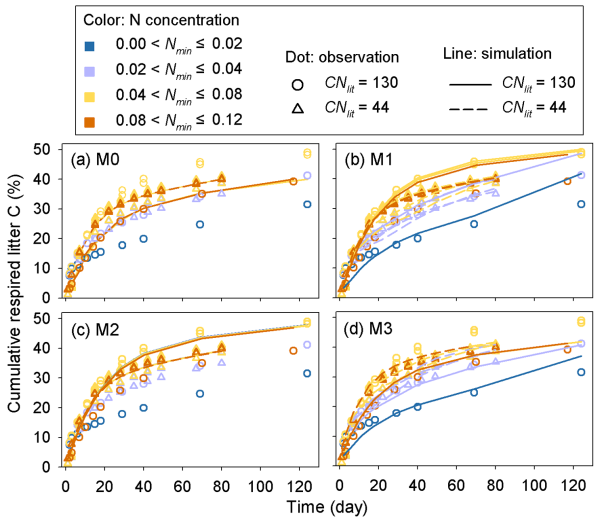

Figure 5. Time series of the simulated (lines) and observed (dots) cumulative respired litter C (% of initial litter C) at four different levels of soil mineral N availability (N_{min}, g N kg^{-1} soil). CN_{lit} is the C : N ratio of plant litter. M0–M3 denote the four models tested in this study (Table 1). Here, the simulation results of each model were calculated with parameters optimized based on all of the 14 samples of incubation experiments (Table A2).

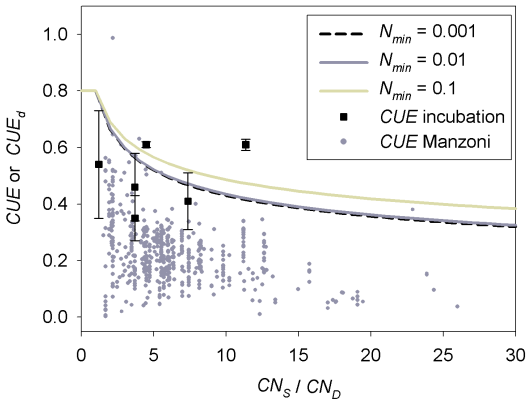

Figure 6. Comparison of CUE_d (lines) predicted by Eq. (2) with parameter values ($m_2 = 0.54$, $n_1 = 0.50$) calibrated based on the incubation experiments (Table A2) of Recous et al. (1995) and Guenet et al. (2010) to observed CUE of terrestrial microorganisms along a gradient of CN_S/CN_D. For observed CUE (dots), CN_D and CN_S are the C : N ratio of decomposers and their substrates, respectively. For simulated CUE (lines), CN_S and CN_D correspond to the C : N ratio of donor (litter pool) and acceptor (the active SOM pool of the CENTURY), respectively. Gray dots are the estimated microbial CUE of litter decomposition in natural terrestrial ecosystems from Manzoni et al. (2017). Black squares are the microbial CUE measured via laboratory incubation experiments of Gilmour and Gilmour (1985), Devêvre and Horwáth (2000) and Thiet et al. (2006). Error bars represent the standard deviations. N_{min} (g N kg^{-1} soil) is the concentration of soil mineral N.

mineral N availability (Fig. A2) but with a slightly higher average RMSE of cumulative respired litter C than model M1.

The predicted CUE_d and the limitation effects of soil mineral N availability on litter decay rate ($f(N_{min})$ function; Eq. 5) are different among the four tested models (Fig. A3). In models M0 and M3, which used a fixed CUE_d, the fitted values of CUE_d calculated with optimized parameters during the incubation period are about 0.57 and 0.54, respectively (Fig. A3a, d). In models M1 and M2, the CUE_d varies with the C : N ratios of plant litter and is only slightly affected by soil mineral N concentrations (Fig. A3b, c). For very low quality litter with a C : N ratio of 130, the CUE_d values in models M1 and M2 are 0.40 and 0.44, respectively, which are lower than for better-quality litter with a C : N ratio of 44 (approximately 0.55 and 0.56 in M1 and M2, respectively). Models M0 and M2 do not include the N inhibition effects on litter decay rate; thus, the $f(N_{min})$ in these two models is always 1 (Fig. A3e, g). In M1 and M3, the N inhibition effect changes with both the litter C : N ratio and the mineral N availability (Fig. A3f, h).

CUE_d from Eq. (2), calibrated with the data of the two incubation experiments, decreases with increasing CN_{lit}/CN_{SOM} (Fig. 6). The average CUE_d value is larger than the average of data compiled for microbial CUE of litter decomposition in terrestrial ecosystems by Manzoni et al. (2017). This is shown by the gray circles in Fig. 6. Our optimized values of CUE_d for a given C : N ratio are more comparable with microbial CUE observed in incubations of soil mixed with litter (Gilmour and Gilmour, 1985; Devêvre and Horwáth, 2000; Thiet et al.,2006), shown as black squares in Fig. 6.

3.2 The effect of litter quality vs. quantity on equilibrium SOM stocks

Model M1 predicts that the size of the SOM pool at equilibrium is mainly determined by litter stoichiometry, with a minor effect of soil mineral N (Fig. 7). The lower the C : N ratio of litter is, the higher the equilibrium SOC stock. For litter with a specific C : N ratio, high soil mineral N concentration (e.g., above 0.05 g N kg^{-1} soil) generally produces a slightly larger equilibrium SOC stock than a low mineral N concentration (Fig. 7). Further analysis suggests that the SOC at equilibrium increases with decreasing litter C : N because the SOC pool is positively related to the CUE_d; however, the limitation of soil mineral N on litter decomposition rate almost shows no impact on SOC (Fig. A4).

4 Discussion

We hypothesized that stoichiometric constraints (flexible CUE_d or inhibition of decomposition under N-limited conditions) played a role in shaping the trajectory of litter decomposition, with potential consequences on predicted SOC

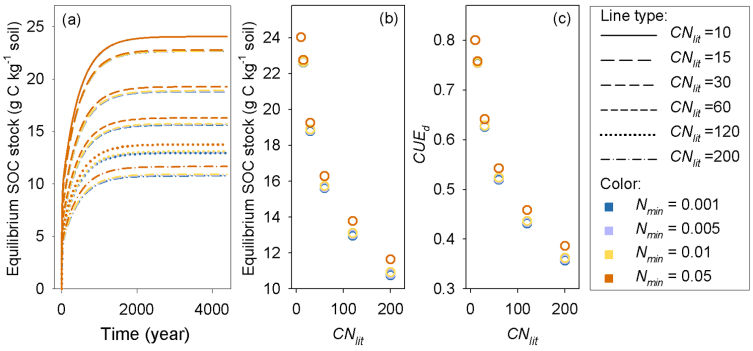

Figure 7. (a) Accumulation of soil organic carbon (SOC) for constant substrates input (plant litter) with different C : N ratios (CN_{lit}) at different levels of soil mineral N concentrations (N_{min}, g N kg^{-1} soil), **(b)** change trends of equilibrium SOC stock and **(c)** carbon use efficiency of decomposed litter (CUE_d) with increasing litter C : N ratio.

stocks. Our results suggest that flexible CUE_d and inhibition effects of soil mineral N on litter decay rate improve prediction of litter decomposition when using a modified version of the CENTURY model (denoted as M1). Evaluation of model M1 using data from incubation experiments indicates that this modified model captures the effects of both variable litter quality (stoichiometry) and mineral N availability on respiration rates (Fig. 5), without strongly inflating the complexity of CENTURY (Table 1). As the stoichiometric constraints are implemented in the generalizable and widely used structure of CENTURY and require only three parameters to be calibrated, they can also be easily implemented into land surface models for large-spatial-scale applications.

Accurately representing N control of microbial processes during litter decomposition has been suggested to be important for modeling the connection between the litter inputs, CUE_d and soil C dynamics (Gerber et al., 2010; Manzoni et al., 2012; Cotrufo et al., 2013; Sinsabaugh et al., 2013). In model M1, soil mineral N affects the litter-C flux via two mutually different pathways: (1) mineral N availability affects the litter decay rate and (2) flexible CUE_d determining the partition of decomposed C into SOC products and respired CO_2 (Fig. 1). Therefore, an increase in soil mineral N concentration enhances litter decay rates, which alone will increase the flux of litter-derived CO_2 (Eq. 5 and Fig. A5). However, as higher N concentration also results in a higher CUE_d (Eq. 2), more C is transferred to SOC and less C is respired. In this way, SOC is predicted to accumulate with increasing mineral N availability when using model M1 (Fig. 7). In addition, model M4, which is comparable to model M1 but uses an alternative formulation for N effects on the decomposition rate (Eq. 6), performed slightly worse than model M1 (Fig. A2). Arguably, Eq. (6) represents the underlying mechanisms of N inhibition effects (Manzoni and Porporato, 2009, Bonan et al., 2013; Fujita et al., 2014; Averill and Waring, 2018) better than Eq. (5) and due to the minor differences in RMSE and AIC (Fig. A2b) between these formulations it can serve as an alternative to M1.

Our results indicate that the observed diversity of responses of litter respiration rate to mineral N additions (Hobbie and Vitousek, 2000; Guenet et al., 2010; Janssens et al., 2010) is likely due to the combined effects of changes in litter decay rate and CUE_d (Fig. A5). Thus, N addition effects can differ among fertilization experiments if litter quality and background N availability vary. In addition to altering litter decay rate and CUE_d, mineral N addition can induce abiotic formation of compounds that resist microbial attack, inhibit oxidative enzymes involved in lignin degradation, stimulate microbial biomass production early in decomposition or lead to the accumulation of microbial residues that are resistant to decay (Fog, 1988; Hobbie, 2015). All these effects might decrease litter respiration rate by inhibiting the decomposition process but have not been considered in our current model.

This study provides insights on processes leading to increased SOM sequestration. Enhancing the efficiency at which plant residuals are transformed into stable SOM has been suggested as an effective strategy to sequester C in soil (Prescott, 2010; Cotrufo et al., 2013). Simulation results from our model suggest a positive linear relationship between equilibrium SOC stock and CUE of decomposed litter (Fig. A4), in line with the earlier findings with a similar model (for example, Frey et al., 2013). In fact, with linear models such as CENTURY it can be shown that the steady-state SOC scales linearly with CUE, different from nonlinear models predicting that higher CUE can trigger SOC loss (Allison et al., 2010). Our model goes beyond earlier attempts (Bonan et al., 2013; Fujita et al., 2014; Averill and Waring, 2018) by adapting the optimal metabolic regulation hypothesis of Manzoni et al. (2017) to link CUE, litter quality and SOM formation in a process-oriented way.

The importance of litter quality for SOM formation as found here is in line with recent experiments (Bahri et al., 2008; Rubino et al., 2010; Walela et al., 2014) and modeling studies (Grandy and Neff, 2008; Cotrufo et al., 2013). SOM is mainly formed though the partial decomposition of plant debris by microorganisms (Paul, 2007; Knicker, 2011;

Cotrufo et al., 2013). The conceptual model developed by Cotrufo et al. (2013) suggested that although labile litter was decomposed faster than recalcitrant litter, a higher fraction of this labile litter C would be incorporated into microbial biomass and subsequently incorporated into SOM pool (corresponding to a higher CUE_d). Therefore, labile litter inputs tend to form a larger SOM pool than the poor-quality (high C : N ratio) litter that is generally used by microbes at lower efficiency. Our simulations of decomposition process of plant litter with different C : N ratios also suggest that litter of good quality (with low C : N ratio) can induce a larger SOM pool than the poor-quality litter (Fig. 7). CUE_d plays a more important role than the inhibition effect of low mineral N concentration in determining the size of the stable SOM pool (Fig. A4).

The predictions from Cotrufo et al. (2013) and this study contrast with the conventional hypothesis whereby the poor-quality litter with low decay rate and small CUE_d are preferential to be accumulated in SOM (Berg and Mcclaugherty, 2008; Walela et al., 2014). This view of SOM stabilization, however, seems to apply to N-limited systems with high C : N litter and where microbial remains are recalcitrant to decomposition (e.g., boreal forests); in these systems, SOC does accumulate despite its low quality (Kyaschenko et al., 2017). Moreover, one could argue that higher CUE_d implies larger microbial biomass, allowing faster decomposition (Allison et al., 2010). These feedbacks between microbial biomass and decomposition rate were not implemented in the current model, but could offer additional flexibility – again at the expense of more difficult model parameterization.

The CUE_d formulation from Eq. (2) with parameters calibrated from the two sets of incubation experiments might underestimate the impacts of litter quality on microbial CUE under natural conditions, in particular in the case of SOM decomposition. In both incubation experiments, litter is firstly cut into fine fragments and then fully mixed with mineral soil (Recous et al.,1995; Guenet et al., 2010). Thus, the nutrient accessibility, air permeability and some other environmental factors (e.g., pH) of incubated litter are different from those of decaying litter in more natural, heterogeneous soil conditions. Those different decomposition conditions might be responsible for the differences observed in Fig. 6 between our CUE estimates and previously reported values. We speculate that more heterogeneous conditions reduce nutrient availability and thus might cause lower CUE. Similarly, CUE of surface litter decomposers may be lower than we estimated (Fig. 6), because litter not mixed with soil is probably subject to stronger nutrient limitation.

Further validation and development of our model are still necessary to decrease the model uncertainties. Soil mineral N which affects both litter decay rate and CUE of decayed litter is seldom monitored in litter incubation experiments (e.g., Walela et al., 2014; Stewart et al., 2015) and field litter decay experiments (e.g., Gholz et al., 2000; Harmon et al., 2009), with few exceptions (Recous et al., 1995; Guenet et al., 2010). An increasing number of land surface models (Wang et al., 2010; Zaehle et al., 2014; Goll et al., 2017) have representations of the terrestrial N cycle. By incorporating our newly developed formulations of CUE_d and $f(N_{min})$ in these land surface models that simulate the dynamics of soil mineral N concentration, it will be possible to test and validate our developments with more extensive data from laboratory and field experiments. Moreover, similar to N, P has also been suggested as another important factor for litter decomposition and SOM formation (Güsewell and Verhoeven, 2006; Talkner et al., 2009; Manzoni et al., 2010; Prescott, 2010), especially in regions with highly weathered soil (Goll et al., 2012, 2017; Yang et al., 2014). So, it might be necessary to include the effects of P on litter decay rate and CUE_d in our model in order to further decrease the simulation uncertainties.

5 Conclusions

By adapting the hypothesis of optimal microbial CUE proposed by Manzoni et al. (2017) for use in a CENTURY-based model and also introducing a N scaling function to represent the limits of mineral N availability on litter decay rate, we developed a simple but effective litter decomposition model that accounts for key stoichiometric constraints during decomposition. Validation using observation data obtained from laboratory incubation experiments indicated that our model could well predict the respiration rates of litter in different qualities at various levels of mineral N availability. Idealized simulations using our model revealed that the quality of litter inputs plays an important role in determining the soil C stock at equilibrium. High-quality litter (i.e., with low C : N ratio) tends to form a larger SOM pool, as it can be more efficiently utilized by microorganisms than recalcitrant litter (e.g., high C : N ratio). Overall, the developed model captures the microbial mechanisms mediating litter stoichiometry and soil mineral N effects on litter decomposition and SOM formation. Due to the simple and generalizable structure of our model, it can be incorporated into existing land surface models for further long-term and large spatial-scale applications.

Code and data availability. The CENTURY-based model used here is programmed in MATLAB language. The source code is available online (https://github.com/hchzhang/CENYUTY_CUE/tree/v1.0 from 8 July 2018). All the data used in this study can be obtained from published literature. Specific references to these data can be found in Sect. 2.5.

Appendix A

Table A1. List of symbols used in this study; stoichiometric ratios are all expressed on a mass basis.

Symbol	Unit	Description
A	g N kg^{-1} soil	Exponent in Eq. (2)
AIC	dimensionless	Akaike information criterion (Eq. 10)
CN_{act}	dimensionless	C : N ratio of active soil organic matter pool
CN_D	dimensionless	C : N ratio of decomposer (Eq. 1)
CN_{met}	dimensionless	C : N ratio of metabolic litter pool
CN_{slow}	dimensionless	C : N ratio of slow soil organic matter pool
CN_{str}	dimensionless	C : N ratio of structural litter pool
CN_S	dimensionless	C : N ratio of substrate (Eq. 1)
C_{lit}	g C kg^{-1} soil	C stock of litter pool (Eq. 4)
CN_{lit}	dimensionless	C : N ratio of litter pool (metabolic or structural; Eq. 2)
CN_{SOM}	dimensionless	C : N ratio of soil organic matter pool
CUE	dimensionless	Microbial carbon use efficiency
CUE_d	dimensionless	Carbon use efficiency of decomposition (C incorporated in SOC over litter C decomposed)
cue_{fit}	dimensionless	Optimized value of fixed CUE in models M0 and M4
CUE_{max}	dimensionless	Maximum CUE_d (Eqs. 1 and 2)
CUE_{opt}	dimensionless	Optimal CUE_d (Eq. 1)
CUE_{d_SA}	dimensionless	CUE of the transformation from structural litter to active SOM pool
CUE_{d_SS}	dimensionless	CUE of the transformation from structural litter to slow SOM pool
$D(C_{lit\text{-}met})$	g C kg^{-1} soil day^{-1}	Decomposition rate of metabolic litter
$D(C_{lit\text{-}str})$	g C kg^{-1} soil day^{-1}	Decomposition rate of structural litter
$f(N_{min})$	dimensionless	Limit factor of soil mineral N on litter decomposition (Eqs. 4 and 5)
f(tem)	dimensionless	Limit factor of soil temperature on litter decomposition (Eq. 4)
f(water)	dimensionless	Limit factor of soil water content on litter decomposition (Eq. 4)
f_m	dimensionless	Fraction of metabolic plant litter
f_{SA}	dimensionless	Fractions of decomposed structural litter C that is transferred to active SOM pool
f_{SR}	dimensionless	Fractions of decomposed structural litter C that is released to the atmosphere
f_{SS}	dimensionless	Fractions of decomposed structural litter C that is transferred to slow SOM pool
I_N	g kg^{-1} soil	Maximum mineral N immobilization rate (Eq. 1)
K	day^{-1}	potential maximum turnover rate (Eqs. 4 and 7)
LC_{lit}	dimensionless	Lignin-to-C ratio of litter input
m_1	kg g^{-1} N	Coefficients in Eq. (3)
n_1	g N kg^{-1} soil	Coefficients in Eq. (3)
m_2	day^{-1}	Coefficients in Eq. (5)
m_3	kg g^{-1} N	Coefficients in Eq. (6)
N_{min}	g N kg^{-1} soil	Soil mineral N concentration (Eq. 5)
RMSE	%	Root mean square error (Eq. 9)
SOC	g C kg^{-1} soil	Soil organic carbon
SOM	g C kg^{-1} soil	Soil organic matter
U_0	g C kg^{-1} soil day^{-1}	C uptake rate when soil mineral N is fully adequate for litter decay (Eqs. 1 and 8)

Table A2. Information about the 14 samples of laboratory incubation experiment used in this study. CN_{lit} and LC_{lit} are the C : N ratio and lignin-to-C ratio of plant litter, respectively. CN_{SOM} is the C : N ratio of SOM pool. N_{min} is the concentration of soil mineral N ($NO_3^- - N + NH_4^+ - N$). For the incubation experiments of Guenet et al. (2010), cumulative respired litter C was measured on days 1, 3, 7, 15, 22, 28, 35, 42, 49, 67 and 80, and N_{min} was measured on days 3, 7, 17, 28 and 80. For the incubation experiments of Recous et al. (1995), both cumulative respired litter C and N_{min} were mostly measured on days 2, 3, 6, 11, 15, 18, 29, 40, 69 and 124.

Sample	CN_{lit}	LC_{lit}	CN_{SOM}	Initial N_{min} ($g\,N\,kg^{-1}$ soil)	Duration (day)	Temperature (°C)	Soil moisture (%, in volume)	Litter type	Reference
1	44	0.26	11	0.035	80	20	50	Crop (wheat)	Guenet et al.
2	44	0.26	11	0.051	80	20	50	Crop (wheat)	(2010)
3	44	0.26	11	0.055	80	20	50	Crop (wheat)	
4	44	0.26	11	0.033	80	20	50	Crop (wheat)	
5	44	0.26	11	0.049	80	20	50	Crop (wheat)	
6	44	0.26	11	0.067	80	20	50	Crop (wheat)	
7	44	0.26	11	0.033	80	20	50	Crop (wheat)	
8	44	0.26	11	0.048	80	20	50	Crop (wheat)	
9	44	0.26	11	0.079	80	20	50	Crop (wheat)	
10	130	0.23	9	0.010	124	15	42	Crop (Corn)	Recous et al.
11	130	0.23	9	0.030	124	15	42	Crop (Corn)	(1995)
12	130	0.23	9	0.060	124	15	42	Crop (Corn)	
13	130	0.23	9	0.080	124	15	42	Crop (Corn)	
14	130	0.23	9	0.100	124	15	42	Crop (Corn)	

Table A3. List of parameters calibrated for two versions of the litter decomposition model (M0, M1): k_{litm} and k_{lits} are, respectively, the turnover rates of metabolic and structural litter pools, m_4 is the coefficient in Eq. (8), cue_{fit} is the optimized value of CUE, m_1 and n_1 are the coefficients in Eq. (3), and m_2 is the coefficient in Eq. (5).

Version	CUE	$f(N_{min})$	Parameters
M0	Fixed	1	cue_{fit}, k_{litm}, k_{lits}, m_4
M1	Eqs. (2), (3)	Eq. (5)	m_1, n_1, m_2, k_{litm}, k_{lits}, m_4

Table A4. Specific setting of litter and SOM properties, and soil conditions in the 16 idealized simulations for exploring the impacts of litter stoichiometry (i.e., C : N ratio) and soil mineral N on SOC accumulation. CN_{lit} and LC_{lit} are the C : N ratio and lignin-to-C ratio of plant litter, respectively. Lit_{inp} ($g\,C\,kg^{-1}$ soil day^{-1}) is the daily input rate of plant litter. CN_{SOM} is the C : N ratio of SOM pool. N_{min} ($g\,N\,kg^{-1}$ soil) is the concentration of soil mineral N ($NO_3^- - N + NH_4^+ - N$). Temp (°C) and SWC (%) are the temperature and soil water content, respectively.

Experiment	CN_{lit}	LC_{lit}	Lit_{inp}	CN_{SOM}	N_{min}	Temp	SWC
1	15	0.2	0.006	12	0.001	25	60
2	30	0.2	0.006	12	0.005	25	60
3	60	0.2	0.006	12	0.01	25	60
4	120	0.2	0.006	12	0.05	25	60
5	15	0.2	0.006	12	0.001	25	60
6	30	0.2	0.006	12	0.005	25	60
7	60	0.2	0.006	12	0.01	25	60
8	120	0.2	0.006	12	0.05	25	60
9	15	0.2	0.006	12	0.001	25	60
10	30	0.2	0.006	12	0.005	25	60
11	60	0.2	0.006	12	0.01	25	60
12	120	0.2	0.006	12	0.05	25	60
13	15	0.2	0.006	12	0.001	25	60
14	30	0.2	0.006	12	0.005	25	60
15	60	0.2	0.006	12	0.01	25	60
16	120	0.2	0.006	12	0.05	25	60

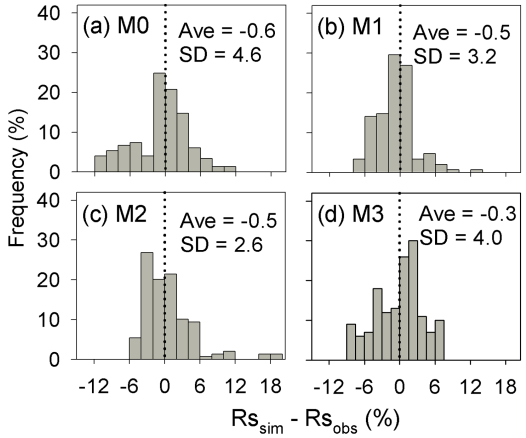

Figure A1. Distribution of the difference between the predicted cumulative respired litter C (Rs_{sim}, %) and the observed values (Rs_{obs}, %) for all experiments and points in time. SD is the standard deviation of the biases. M0–M3 denote the four models tested in this study (Table 1).

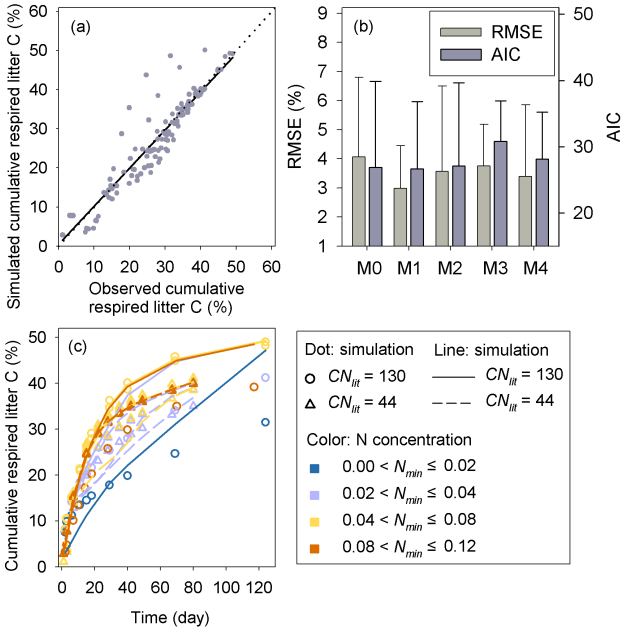

Figure A2. Comparison between simulated cumulative respired litter C with $f(N_{min})$ (inhibition effect of soil mineral N on litter decomposition) calculated by Eq. (6) and the observed results from incubation experiments. In panel **(b)**, M0–M4 denote the five versions of litter decay model in Table 1. M4 denotes the model which used Eq. (2) to calculate the dynamic CUE and Eq. (6) to calculate $f(N_{min})$.

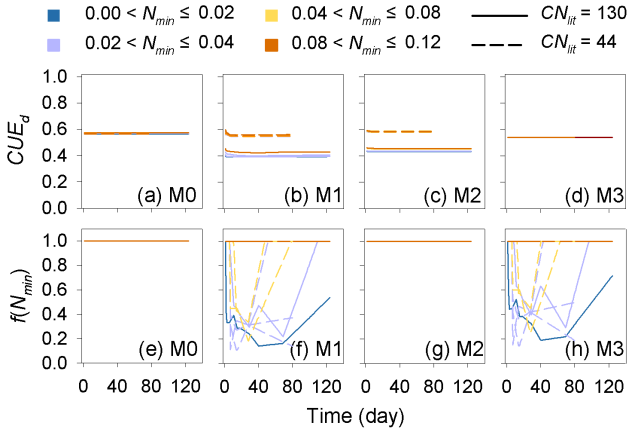

Figure A3. Dynamic of the simulated carbon use efficiency (CUE) and $f(N_{min})$ during the incubation experiments (Table A4). CN_{lit} is the C : N ratio of incubated litter, and N_{min} is the initial soil mineral N concentration (g N kg^{-1} soil). M0–M3 are the four models in Table 1. Here, the simulation results of each model were calculated with parameters optimized based on all of the 14 samples of incubation experiments (Table A2).

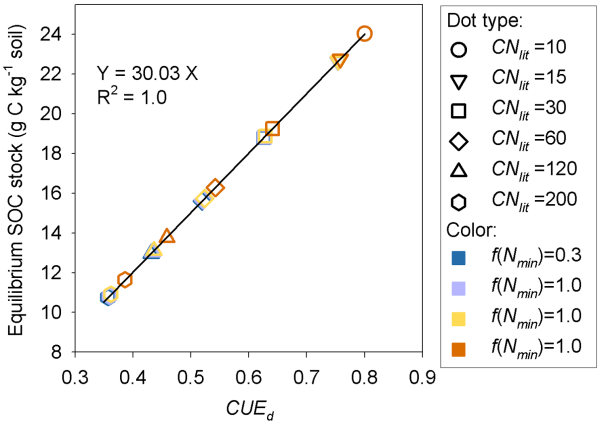

Figure A4. Relationship between C stock of the potentially equilibrated SOM pool and the carbon use efficiency of decomposed metabolic litter (CUE_d) at the dynamic equilibrium stage. $f(N_{min})$ denotes the inhibition factor (0–1) of soil mineral N on litter decomposition.

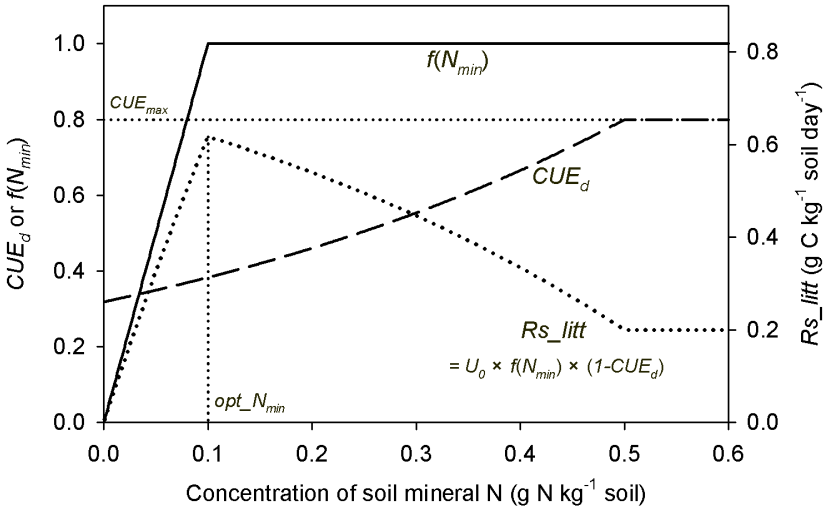

Figure A5. Schematic plot for change trends of f (N_{min}) (inhibition effect of mineral N; Eq. 6), CUE_d (carbon use efficiency of decomposed litter; Eqs. 2, 3) and Rs_litt (litter respiration rate) with increasing concentration of soil mineral N. CUE_{max} (equal to 0.8) is the maximum CUE set in this study. opt_N_{min} denotes the concentration of soil mineral N at which litter respiration is maximized. U_0 is the potential decomposition rate when mineral N is fully adequate for litter decay.

Author contributions. HZ led the model development, calibration and validation, and performed all simulations and analysis. DSG, SM, and PC assisted with the implementation of flexible CUE and the limit of soil mineral N availability on litter decomposition rate in the CENTURY model, and contributed to model validation and result analysis. BG provided a part of the calibration and validation data from his laboratory incubation data. HY provided the original source code of CENTURY model. All authors contributed with their comments to the writing of the paper.

Competing interests. The authors declare that they have no conflict of interest.

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