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Priming and substrate quality interactions in soil organic matter models

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Abstract. Interactions between different qualities of soil organic matter (SOM) affecting their turnover are rarely represented in models. In this study we propose three mathematical strategies at different levels of abstraction for representing those interactions. Implementing these strategies into the Introductory Carbon Balance Model (ICBM) and applying them to several scenarios of litter input show that the different levels of abstraction are applicable at different time scales. We present a simple one-parameter equation of substrate limitation applicable at decadal time scale that is straightforward to implement into other models of SOM dynamics. We show how substrate quality interactions can explain priming effects, acceleration of turnover times in FACE experiments, and the slowdown of decomposition in long-term bare fallow experiments as an effect of energy limitation of microbial biomass. The mechanisms of those interactions need to be further scrutinized empirically for a more complete understanding. Overall, substrate quality interactions offer a valuable way of understanding and quantitatively modelling SOM dynamics.

1 Introduction

The priming effect, i.e. the enhanced or retarded soil organic matter (SOM) decomposition due to amendment of fresh SOM or mineral nitrogen (Jenkinson et al., 1985; Kuzyakov et al., 2000), and the role of microbial biomass controlling decomposition rates have received increasing attention during the last years (Todd-Brown et al., 2012; Treseder et al., 2011; Allison et al., 2010; Guenet et al., 2010; Blagodatskaya and Kuzyakov, 2008; Fontaine et al., 2003) (but see also older works of Löhnis, 1926; Parnas, 1975; Smith, 1979; Panikov, 1995; Ågren and Bosatta, 1996). This is because, first, understanding its causes opens perspectives on SOM decomposition and SOM stabilization and, second, because of its potential relevance for understanding feedbacks to climate warming. Enhanced primary production associated with environmental change may enhance decomposition of the large amount of old carbon stored in soils (Jobbagy and Jackson, 2000), because this fraction is especially vulnerable to priming (Fontaine et al., 2007). Hence, the increase in SOM inputs by plant litter with enhanced primary productivity may lead to net loss of SOM due to and enhanced mineralization due to positive priming effects. The issue highlighted by the priming effect is that the decomposition rate of SOM of one quality is dependent on the amount of SOM of a other qualities, i.e. there are substrate quality interactions.

In contrast to this substrate quality interaction paradigm, all the widely applied SOM dynamic models (e.g. RothC, Century, Yasso, CASA, Q-model) (Jenkinson and Coleman, 2008; Parton et al., 1988; Liski et al., 2005; Potter et al., 1993; Ågren and Bosatta, 1996) assume that SOM of different qualities decomposes independent of each other, i.e. they neglect substrate quality interactions. For a recent overview see (Manzoni and Porporato, 2009). In recent decades, several models have been proposed that explicitly account for cometabolization of different SOM qualities by the microbial biomass of active decomposer to explain substrate interactions and priming effects (Fontaine and Barot, 2005; Fang et al., 2005; Wutzler and Reichstein, 2008; Blagodatsky et al., 2010; Neill and Gignoux, 2006; Moorhead and Sinsabaugh, 2006; Poll et al., 2010). It is now timely to implement those processes into ecosystem models and test whether the SOM quality interactions matter at larger spatial and temporal scales. Implementing the details of active microbial biomass in components of global land-surface models running on large spatial extents, however, will increase uncertainty because of additional uncertain model parameters (Hilborn and Mangel, 1997). Hence, an abstraction of those processes is required, which still captures the main effects of the interactions of different SOM qualities.

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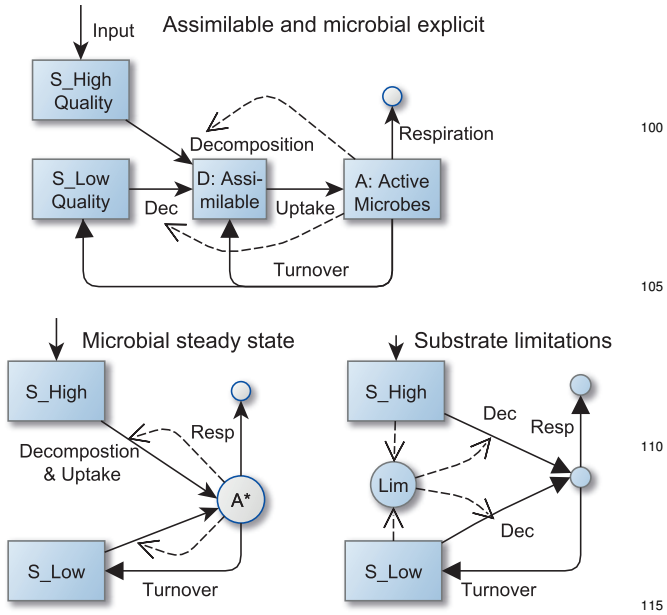

Fig. 1. Basic strategies of implementing substrate interactions. Solid arrows represent carbon fluxes, dashed arrows highlight further controls, boxes represent state variables and circles represent values that are derived from state variables.

The aims of this paper are: first, to propose basic strategies of representing SOM quality interactions in models (Sect. 1.1); second, to exemplify their implementation (Sect. 2.1); and third, to compare their advantages and disadvantages for different modelling purposes and settings (remainder of the paper).

1.1 Basic strategies

The most detailed strategy we propose, explicitly models assimilable organic matter (OM) and active microbial biomass. In contrast, the most abstract strategies lets the decomposition rate of the lower quality SOM, i.e. with slower decomposition, depend on the amount of high quality SOM. An intermediate strategy assumes that microbial biomass dynamics are fast compared to other processes and assumes microbial activity to be in steady state with the mineralization flux (Fig. 1).

1.1.1 Explicit assimiable OM and active microbial biomass representation

Cometabolization of different substrate qualities is hypothesized to be the main mechanism of substrate interactions (Wutzler and Reichstein, 2008). Decomposition of substrate is not only dependent on the amount of substrate but also on the activity of decomposers. Independent decomposition of SOM qualities is coherent with the assumption that each quality of SOM is decomposed by a specific microbial community and that this community is in steady state with the current pool. In contrast, assuming that the microbial community is able to decompose SOM of different qualities, or that there are interactions between the comunities degrading SOM of different qualities, links the decomposition of SOM of one quality to the decomposition of SOM of another quality. When the microbial community is stimulated by increased availability of high quality SOM, also the decomposition of low quality SOM can be enhanced.

Hence, the first strategy to implement substrate interactions is to explicitly model microbial activity (Sect. 4.6), or active microbial biomass as a dynamic state variable. The most detailed model (Fig. 1 top) assumes that different SOM qualities are decomposed into smaller assimilable compounds, and that microbial growth can be modeled with a single substrate (Monod, 1949). Turnover of microbial biomass can be modeled as the difference between uptake of carbon and respiratory carbon requirements for energy and additional turnover by predation or disturbances that usually increase with microbial biomass.

$$\text{substrate:} \quad \frac{\mathrm{d}S_j}{\mathrm{d}t} = i_j + p_j\tau - d_j$$

$$\text{assimilable OM:} \quad \frac{\mathrm{d}D}{\mathrm{d}t} = \sum_j d_j + p_\mathrm{D}\tau - u$$

$$\text{active microbial biomass:} \quad \frac{\mathrm{d}A}{\mathrm{d}t} = u - r_\mathrm{g} - \tau$$

$$\text{decomposition:} \quad d_j = l_{e,j}(t)\, f_d(S_j, A)$$

$$\text{uptake:} \quad u = f_u(D, A)$$

$$\text{growth respiration:} \quad r_\mathrm{g} = (1-\epsilon)u$$

$$\text{microbial turnover:} \quad \tau = f_\tau(A)$$

Where j denotes the quality of a given substrate, i_j is the external input to the system, p_j is the proportion of microbial turnover feeding to pool j, and ϵ is the microbial efficiency or yield. $l_{e,j}(t)$ is a model driver that modifies of decomposition fluxes based on time dependent environemntal conditions such as temperature or moisture.

There are a number of potentially important additional processes that might be required to include in this basic scheme. These include preferential substrate usage, dormancy or sustaining states, and heterogeneity of kinetic parameters between different microbial communities. These will actually drive short term dynamics when monitoring microbial growth over a few days as is commonly done in priming experiments. However, our goal here is to capture the basic dynamics and we seek to obtain abstract understanding instead of including more detail.

1.1.2 Quasi-steady-state active microbial biomass

Another strategy is to successively increase abstraction from details of the microbial explicit model. The assimilable pool quickly approaches a state where its input equals microbial uptake. Hence, we may set uptake $u = \sum_j d_j + p_\mathrm{D}\tau$.

Further, also active microbial biomass approaches a state where growth depending on mineralization fluxes equals its turnover. Hence, we can calculate a quasi-steady-state (Segel and Slemrod, 1989) of the active microbial biomass for given amounts of available substrates $A^* = f(S_j)$ and replace microbial biomass by this steady-state in the equations of respiration, microbial turnover, and decomposition (Fig. 1 bottom left). The resulting microbial steady state model can be reformulated, so that the limitation of decomposition by decomposer activity can be directly expressed by model parameters.

1.1.3 Substrate limitations

A coarse strategy is to directly formulate substrate interactions in the decomposition equations as

$$\text{substrate:} \quad \frac{\mathrm{d}S_j}{\mathrm{d}t} = i_j(t) - d_j + \sum_{i \neq j} a_{ij} d_i$$

$$\text{decomposition:} \quad d_j = l_{e,j}(t) f_j(S_1, \ldots, S_n)$$

Where a_{ij} is the portion of carbon decomposed of pool i that is transferred to pool j.

One specialization of this general decomposition formula d_j is to specify one common limitation factor, l_A, for all substrate qualities j. This factor depends on the amount of all substrate in all qualities or alternatively depends only on the amount of the high quality substrate (Fig. 1 bottom right).

$$\text{decomposition:} \quad d_j = l_A l_{e,j}(t) f_{d,j}(S_j) \qquad (1)$$

$$\text{substrate limitation:} \quad l_A = f_A(S_1, \ldots, S_n) \qquad (2)$$

The substrate interaction strategy can be applied without any considerations of decomposers. Alternatively, it can also be derived as a further level of abstraction of the quasi-steady-state active microbial biomass strategy.

2 Methods

2.1 Implementations to the ICBM

The basic strategies (Sect. 1.1) are exemplified by implementing them into a model of SOM dynamics. We present a series of versions of the Introductory carbon balance model (ICBM) (Andrén and Kätterer, 1997).

The ICBM is a simple two-pool model that shares the basic structure and captures most of the dynamics of more complex pool models for SOM turnover such as RothC and Century. In this study, several variants of the model were developed (Fig. 2), which varied in structural complexity. A more detailed explanation of the model variants and the differential equations are given in Appendix A. Pool names and parameters are described in Table 1. The following text summarizes the main characteristics of the model variants.

AssimExplicit

We started implementing the substrate interactions with the microbial-explicit strategy. Litter input enters the high quality pool, denoted by Y. Decomposition flux of this pool and the decomposition flux of the low quality pool, denoted by O, enters a pool of assimilable carbon, denoted by D. Here, the decomposition was first order with respect to substrate (Y or O) but decreased at low microbial activity, which was expressed by the amount of active microbial biomass A: $f_d(S_j, A) = k_j S_j \frac{A}{m_a + A}$ (Schimel and Weintraub, 2003). Microbial uptake from the assimilable pool was modelled according to Monod-kinetics. In addition to growth respiration, we included also maintenance respiration, which linearly increased with active microbial biomass. As a first approximation, the entire turnover of the microbial biomass was assigned to the low quality pool.

Dependence of decomposition rates for substrate quality j on environmental factors such as temperature and moisture that can very with time were incorporated by the term $l_{\mathrm{e,j}}(t) = f(T, \mathrm{M}, \ldots)$.

MicExplicit

As a first step we abstracted from fast dynamics of the assimilable pool, using the quasi-steady-state assumption. Specifically, we replaced the Monod-uptake kinetics with the influx to the assimilable pool, i.e. the sum of decomposition fluxes.

MicSteady

As a second step we abstract from the short-term dynamics of the active microbial biomass pool. We used the same equations as in the MicExplicit variant, but replaced active microbial biomass by its steady-state formulation, which depended on the current amount of substrates.

LimUptake

Further, we abstracted from several sources of respiration, keeping only an effective growth respiration in the system of equations. Microbial efficiency then, corresponded to the amount of uptake that is transformed to lower quality substrate, i.e. the humification coefficient h in the original ICBM. Further we lumped all microbial parameters into a single parameter a_{A}. The limitation factor l_A for decomposition then could be reformulated based on potential uptake. The potential uptake u_{Pot} corresponds to the uptake with no microbial limitation, i.e. $l_A = 1$, from all substrate qualities (here Y and O).

$$l_A = \max\left(0, 1 - \frac{a_{\mathrm{A}}}{u_{\mathrm{Pot}}}\right) \qquad (3)$$

$$u_{\mathrm{Pot}} = \epsilon \sum_j l_{\mathrm{e,j}}(t) k_j S_j$$

Note that equation 3 is not an ad-hoc formulation but is derived from a simplification of the MicSteady model

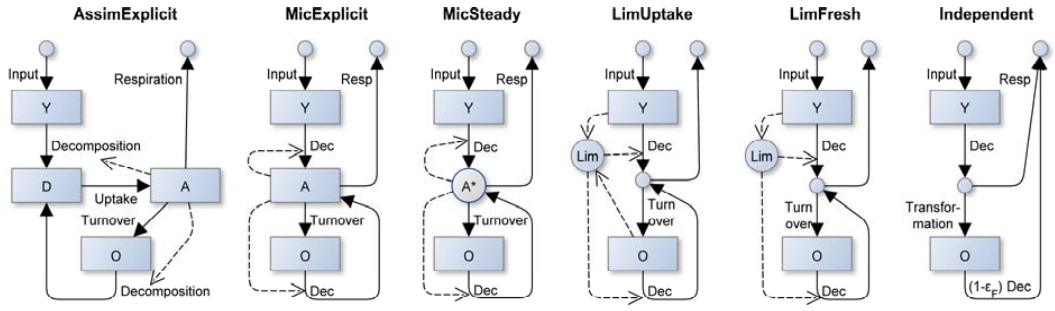

Fig. 2. Structure of the ICBM model variants. Solid arrows denote carbon flows, dashed arrows represent further controls.

Table 1. Parameters of the ICBM model variants. + indicates usage in respective model variant.

	Unit	Description	AssimExplicit	MicExplicit	MicSteady	LimUptake	LimFresh	Independent
State Variables			4	3	2	2	2	2
Y	$\mathrm{gCm^{-2}}$	high quality substrate (young)	+	+	+	+	+	+
O	$\mathrm{gCm^{-2}}$	low quality substrate (old)	+	+	+	+	+	+
A	$\mathrm{gCm^{-2}}$	active microbial biomass	+	+				
D	$\mathrm{gCm^{-2}}$	assimilable organic carbon (dissolved)	+					
Parameters			8	6	6	4	4	3
$\mu_{\max}$	$\mathrm{yr^{-1}}$	maximum growth rate	+					
m_{D}	$\mathrm{gCm^{-2}}$	affinity, i.e. half saturation, of uptake	+					
k_{Y}	$\mathrm{yr^{-1}}$	decomposition rate of high quality pool	+	+	+	+	+	+
k_{O}	$\mathrm{yr^{-1}}$	decomposition rate of low quality pool	+	+	+	+	+	+
ϵ	$0\ldots1$	microbial efficiency	+	+	+	+	+	+
t_{A}	$\mathrm{yr^{-1}}$	turnover rate of active microbial biomass	+	+	+			
s_{A}	$\mathrm{yr^{-1}}$	maintenance rate	+	+	+			
m_{A}	$\mathrm{gCm^{-2}}$	half saturation of decompostion	+	+	+			
a_{A}	$\mathrm{gCm^{-2}yr^{-1}}$	minimum uptake				+	+	
Drivers								
$i(t)$	$\mathrm{gCm^{-2}yr^{-1}}$	litter input flux						
$l_{\mathrm{e,Y}}(t)$	0..1	environmental effects on k_Y						
$l_{\mathrm{e,O}}(t)$	0..1	environmental effects on k_O						

variant. However, it also can be seen as a representation of the substrate limitation strategy (Fig. 1). More details of equation 3 are discussed in section 4.7.

LimFresh

An alternate application of the substrate limitation strategy is to make decomposition depend on the high quality OM only. Hence we implemented another abstraction, where we neglected the contribution of uptake from the low quality organic matter in the formulation of the limitation factor.

Independent

This variant is equivalent to the original ICBM, where decomposition fluxes of SOM of different qualities are independent of each other. Here it is presented as a further abstraction of the LimUptake model variant where we fully neglected the substrate limitation in decomposition equations.

2.2 Simulation scenarios

The model variants presented in Sect. 2.1 have been applied to different scenarios of litter inputs. In all scenarios all model variants started from steady state for a litter input of $400\,\mathrm{gCm^{-2}yr^{-1}}$. Parameters were derived from the following constraints. 1) Prescribed initial carbon stocks in steady state before the change of litter input: Y_0 and O_0, 2) prescribed initial apparent substrate turnover times 3) total microbial biomass of 2 % of organic matter, and 4) prescribed initial activity of microbial biomass as expressed by the microbial limitation factor l_A. Initial microbial

limitation factor was set to 5 % for the LabPriming scenario, 20 % for the FaceLim scenario and 80 % for the other scenarios. The details of litter inputs over time and calculation of parameter values and initial stocks from the constraints above are given in Appendix B. As the scenarios explore consequences of different litter inputs, the environmental limitation factors were kept constant: $l_{e,Y}(t) = l_{e,O}(t) = 0.8$.

LabPriming
Adding half the cumulated yearly litter input at once and no input thereafter. This emulates a laboratory priming experiment, where labelled fresh substrate is added at the beginning of a soil incubation and the label in the respiration flux is monitored over time without any further litter inputs.

FaceAct
Increase of the input by 25 % with an initially active microbial biomass. This simulates a CO_2 enrichment experiment (Norby et al., 2005). With this scenario litter input increased in the first year and thereafter stayed at this level.

FaceLim
Increasing the input by 25 % with an initially energy-limited microbial biomass. This is the same as FaceAct scenario, except that initial microbial limitation factor was set to 20 %.

DeadRoot
Exponential decay of litter input to $8\,\mathrm{gCm^{-2}yr^{-1}}$. This simulates stabilization of organic matter based on the energy-limitation of the decomposers when the supply of high quality organic matter diminishes. This may happen in the subsoil when the rooting system dies and fresh OM input is small because of absense of root exudates.

3 Results of simulation studies

In the course of this paper we discuss the effects of model simplifcations and abstractions by comparing simulated trajectories to predictions of the more detailed model variants. Hence we treat the predictions of the most detailed AssimExplicit model variant as the target to compare to.

3.1 LabPriming scenario

For the priming scenario, the time course of respiration from autochthonous soil carbon, i.e. soil organic carbon present before substrate addition, can be seen in Fig. 3. Respiration from authochonous soil closely follows active microbial biomass (see electronic supplement PrimingMic.pdf). Both the AssimExplicit and the MicExplicit model variants show the typical hump shaped pattern (e.g. Blagodatsky et al., 2010, Fig 2b). The duration of the hump here is longer than in typical priming experiments, because amendment is usually an easily available substrates that are degraded within

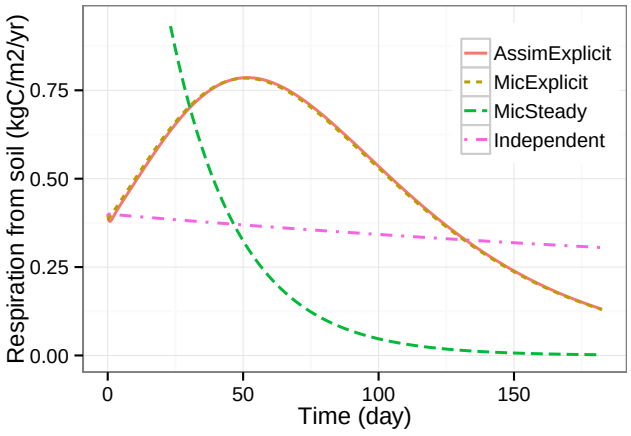

Fig. 3. Time series of respiration from autochthonous SOC, i.e. soil organic carbon present before substrate addition, in the LabPriming scenario.

hours to days. Whereas in the scenario of this paper we simulated addition of litter with a turnover time of one year.

The AssimExplicit model predicted a very short (2 days) phase of negative priming, i.e. decreased respiration from authochthonous soil.

The MicExplict model variant does not represent this negative priming effect. However, the overall dynamics at monthly time scale is described very well with the MicExplicit variant, despite abstracting from the dynamcis of the assimilable pool.

The MicSteady model variant strongly overestimates the initial microbial biomass (see electronic supplement PrimingMic.pdf) and hence also the decomposition of the autochthonous SOM at the beginning of the incubation. Simulations of the LimUptake and LimFresh variants have not been conducted, as the abstraction level was already to high for this scenario.

There was no priming effect in the substrate independent model variant in which the autochthonous SOM decomposes independently from the added label.

3.2 FaceAct and FaceLim scenarios

At longer time scales, with continuous litter inputs that do not change abruptly, there was no discernable difference between predictions of the MicExplicit and the AssimExplicit model variants. There were also no discernable differences between predicitons after 3 years of the MicExplicit and the MicSteady and LimUmptake variants (Figs. 4–6).

All the variants of substrate interactions agreed remarkably well in the FaceAct scenario (Fig. 4). In contrast, the model in which substrates decompose independently predicts higher long-term carbon stocks. This difference became more pronounced when a an more strongly substrate-limited decomposer community was prescribed at the beginning of the incubation with the FaceLim scenario. All the models

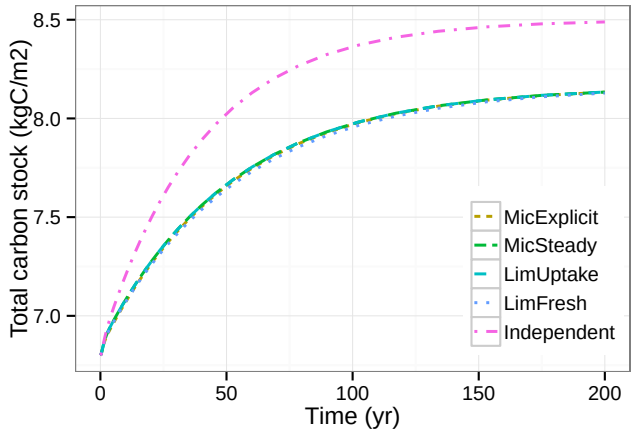

Fig. 4. Time series of total carbon stocks in the FaceAct scenario.

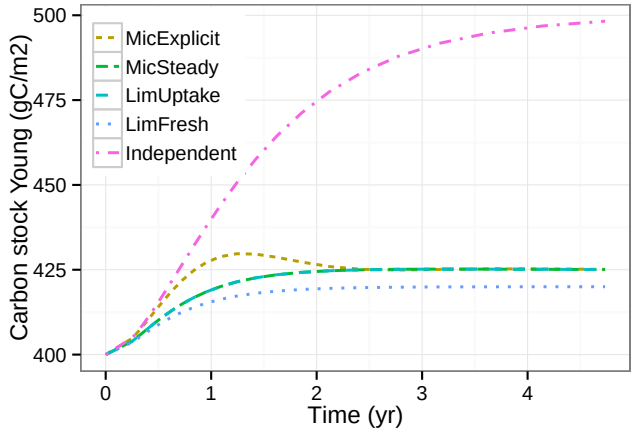

Fig. 5. Time series of carbon in the high-quality pool in the FaceLim scenario.

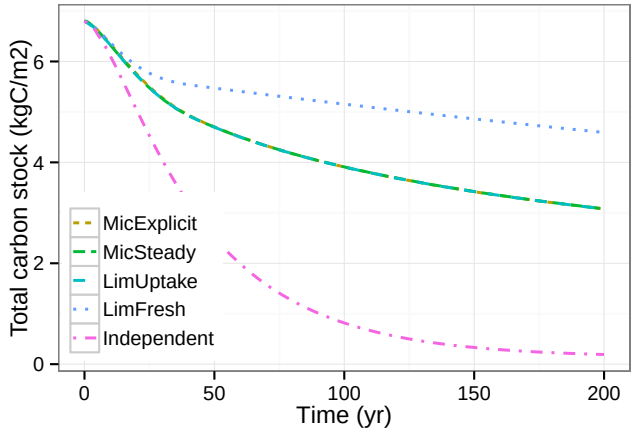

Fig. 6. Time series of total carbon stocks in the DeadRoot scenario.

that account for substrate interactions, predicted a smaller change in carbon stocks. This was because the increased litter input relieved the microbial limitation causing a faster SOM cycling.

In the first year after increasing litter inputs, the microbial activity was transiently smaller than its potential quasi steady state. This effect was not represented with the more simplified models variant. The effect of this transition on predicted carbon dynamics, however, was so small that it was only seen when plotting the first years of the fast carbon stock (Fig. 5).

The slight deviation of the LimFresh variant from the more detailed variants was due to neglecting the uptake of low quality organic matter as explained below.

3.3 DeadRoot scenario

In the DeadRoot simulation scenario (Fig. 6) the assimilation of low quality organic matter became relevant. The high quality substrate was depleted fast, while the stored amounts of low quality substrate were available for a longer time. Hence, the proportion of decomposition and uptake of the low quality pool transiently increased.

The LimFresh model variant, which was based solely on high quality organic matter, predicted lower microbial activity and decomposition.

The substrate independent model did not account for the microbial energy-limitation at all and predicted more rapid decomposition of the substrate.

4 Discussion

This study presents an approach of successively abstracting from detailed fast dynamics in complex models to derive less complex formulations that still capture the important dynamics at a given time scale. Moreover, the derived lumped parameters can be traced back to the underlying more complex mechanisms.

The application of the model variants to different scenarios of changing litter input revealed pronounced differences in their dynamics. Different abstraction levels are appropriate at different settings.

4.1 Timescale

The most important factor for choosing an appropriate abstraction level is time scale. When investigating the dynamics at larger time scales, we assumed that the detailed description of the dynamics of fast processes can be replaced by an approximation based on a quasi-steady-state assumption (QSSA) (Segel and Slemrod, 1989). This is applicable where after an initial fast transient period, the assimilable substrate and the microbial biomass can be regarded in steady-state with respect to the instantaneous values of the available substrate.

The fast dynamics of the assimilable pool is driven by microbial substrate uptake. It is caused a transient period, where the assimilable pools differed from steady state (seen as difference between AssimExplicit and MicExplicit in Fig. 3). The length of this period was of order of 1/(microbial growth rate). In this study we assumed a microbial growth rate of 1/(24 h). This is already a quite slow growth rate compared to priming experiments, where microbial communities responding to glucose with rates of about 1/(5 h) (Wutzler et al., 2012). Hence, we argue that the details of microbial uptake are not important at time scales larger than weeks.

The non-steady-state dynamics of microbial biomass was most important at the daily to monthly scale (Fig. 3) and was still visible over about two years (Fig. 5). With the MicExplicit model, decomposition of substrate is limited by the current activity, which is lagging behind its steady state. The timescale of this transient period is in the order of the turnover time of the changing substrate pool. In the LabPriming scenario where we studied dynamics on daily to monthly timescale the simplified models differed strongly from the microbial explicit model. Note, however, that in this study we used a turnover time of one year for the fastest pool, whereas a big part of the litter turns over faster. With using a shorter turnover time of the fast pool or a more fine-grained resolution of the substrate quality continuum (Ågren and Bosatta, 1996) we expect the differences between the model variants to be smaller.

When looking at decadal to century time scale with assuming continuous change of litter input, the quasi-steady state assumption of microbial activity was a very effective model simplification compared to the more complex microbial explict model varaints (Figs. 4–6).

4.2 Short term environmental fluctuations

An assumption of the used model simplifications is that substrate availability changes continuously. In contrast, substrate availability can change abruptly with fluctuations of environmental conditions. For example during rewetting events, a large amount of high quality substrate can become available in a short time. As seen in Fig. 3 the simplified models overestimate initial microbial biomass and respiration in those cases and underestimate respiration at later times under such conditions. Hence, they give wrong predictions for for short time scale dynamics under these conditions. However, they are intended for application at longer time scales. Hence, we ask: Do errors average out or will they result in a bias in the mean rates on time scales from months to decades?

A thorough answer to this scaling question requires further study and discussion and is beyond the scope of this paper. However, we put forward the following hypothesis. There will be a consistent but negligibly small underestimation of mineralization with the steady-state model. Our rationale in condensed form is as follows. The microbial dynamics in the microbial explicit model variant can be viewed as a smoothed version of dynamics with the simplified variants, because the detailed dynamics lets the actual microbial activity approach the extreme values more slowly than its quasi steady state. Further, the mineralization is a monotonously increasing non-linear function of the active microbial biomass: $dec = f(A/(m_A + A))$. Hence, underestimation of actual microbial biomass leads to an underestimation of mineralization. Similarly, an overestimation of active mirobial biomass leads to an overestimation of mineralization. The overestimation will be consistently smaller than the underestimation, because the mineralization function is concave in A. Within the range of misrepresentation of microbial biomass, however, the deviation of the mineralization function from a linear function is very small, especially for microbial biomass larger than its half-saturation constant m_A. Hence, we expect the bias to be very small too. In addition the effect may be counterbalanced by the observation that abrupt increases of substrate availability, e.g. with rewetting, occur more often than abrupt decreases of substrate availability.

4.3 Proportion of uptake from low quality substrates

Dynamics of microbial activity are usually dominated by the availabiltiy of high quality substrate. This leads to the model simplification of relating microbial activity or substrate limitation of decomposition directly to availability of high quality substrate (e.g. Guenet et al., 2012).

We argue that this simplification is only valid if the proportion of uptake from low quality substrates compared to uptake from high quality substrates is low.

The discussed simplification is represented by the LimFresh model variant. It predicted similar dynamics as the slighly more detailed limUptake variant in all scenarios of high litter inputs. However, predictions for the DeadRoot scenario of diminished litter inputs (Fig. 6) differed considerably. This is because the high-quality OM was consumed and depleted faster than the low-quality OM. If the mineralization of the low-quality OM is sufficiently high, the contribution of low-quality OM to uptake by microbial biomass cannot be neglected during such transient changes.

4.4 OM stabilization by energy limitation

In the DeadRoot scenario, the long-term predictions of the model with substrate interactions differed notably from the predictions of the model with independent substrate decomposition. This is because the substrate interactions can explain OM stabilization by energy limitation of decomposers in subsoil (Fontaine et al., 2007). With decreasing supply of high-quality substrate (young pool in the ICBM) the microbial limitation to decomposition increases. This results in an increase in the apparent turnover time of the low quality substrate (Fig. 7).

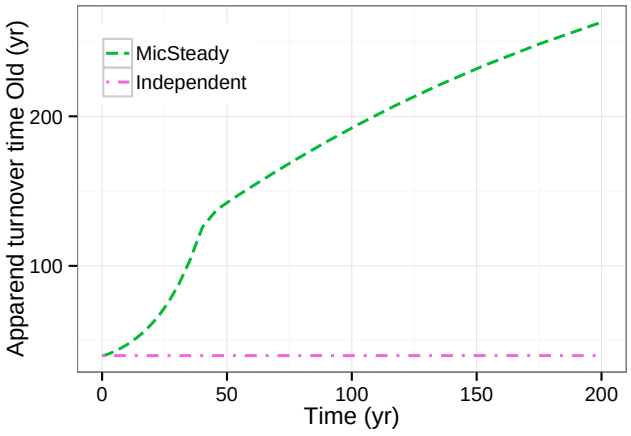

Fig. 7. Increase of apparent turnover time $1/k_{\mathrm{app,\,Old}} = 1/(l_A k_{\mathrm{Old}})$ in the DeadRoot scenario.

In addtion this effects also provides an alternative explanation of the observed decreasing speed of decomposition at long-term bare fallow experiments (e.g. Barré et al., 2010, Fig. 1). Traditionally, additional OM pools with an intrinsically low decomposition rate or quality were included in the SOM models (Manzoni and Porporato, 2009). However, recent studies have shown that the old OM associated with these pools is vulnerable to priming effects (Fontaine et al., 2007). Hence, the emerging view is that the observed long turnover times are properties of the environment instead of being associated to the conceptual OM pools (Schmidt et al., 2011). This is in line with the predictions of those models in this study that included substrate interactions.

While the traditional substrate independent models are quite successful in explaining effects of changing litter inputs under one land-use at one site, they often need to be re-parameterized to other sites. Moreover, data on forest–grassland transition could be modelled much better with a with the redistribution of carbon between different SOM-qualities after the disturbance instead of modifying model parameters (Gottschalk et al., 2010). It will be interesting to test, if changed substrate interactions can explain such kind of data.

4.5 Acceleration of SOM turnover instead of SOM accumulation

A second major difference in dynamics with regard to substrate interactions was seen in the FaceLim simulation scenario (Fig. 5). With the substrate independent model, a 25 % increase of the input led to 25 % increase of the total OM stock, if there were no limitations besides carbon substrate. In contrast, with the substrate interaction models the increased litter input resulted in a release of microbial limitation. This led to an accelerated decomposition, which resulted in only a slight increase in OM stocks. This prediction is in line with several observations from Free air carbon enrichment (FACE) experiments (Cardon et al., 2001; Carney et al., 2007; Heath et al., 2005; Trueman and Gonzalez-Meler, 2005), where the increased net primary productivity and rhizodeposition, especially under nitrogen limitation (Norby et al., 2010; Phillips et al., 2011), was not accompanied by large increases in soil carbon stocks (Drake et al., 2011).

4.6 Microbial activity

The more complex model variants make use of a a pool called the active microbial biomass. Here we discuss why we use this concept instead of soil microbial biomass.

Aside from hot spots of high quality OM, most of the microbes are found in a sustaining state (Panikov, 1995), where they have low energy requirements, i.e. maintenance respiration, and reduced growth and metabolic rates. When substrate supply increases, large parts of the metabolic machinery, need to be resynthesized before growth can take place. This causes a time-lag before exponential growth occurs. The observed time lag can be related to the activity state. Hence, amongst all the methods of measuring soil microbial biomass, the kinetic respiration analysis (Panikov and Sizova, 1996; Blagodatsky et al., 2000; Wutzler et al., 2012) might come most close to the modeled pool of active microbial biomass.

In addition to overall activity, the community structure and competition presumably plays a major role in regulating OM cycling (Fontaine et al., 2003; Treseder et al., 2011; Todd-Brown et al., 2012). Such community effects were not considered even with the most complex model in the current study.

At low growth rates other factors related to the microbial energy budget in addition to microbial substrate use efficiency become important. Maintenance respiration is required also with low or no uptake of substrate (Pirt, 1965; Beeftink et al., 1990; van Bodegom, 2007).

Other factors that potentially influence the dynamics, but were not considered in this study are dynamics of predation (Raynaud et al., 2006), limitation by resources other than carbon (Fontaine and Barot, 2005) and preferential substrate usage (Blagodatskaya and Kuzyakov, 2008), and adaptation (Schmidt et al., 2007).

Further studies can start from models of more complex microbial interactions and use the presented approach of successively abstracting from the details.

4.7 Microbial limitation factor

Results show that the abstraction level in the limUptake model variant is able to account for the effects of microbial activity at time scales of seasons to decades. Therefore we discuss the derived one parameter equation 3 in more detail.

For a single substrate pool the equation is plotted in Fig. 8. Parameter a_A corresponds to the minimum carbon uptake flux that can support active microbial biomass. Below this threshold the microbial community has more carbon costs in sustaining growing compartments than can be obtained from degrading the substrate. With larger amounts of available substrate a bigger decomposition and uptake flux is possible. Hence With more and more available substrate a bigger part of the community can be active.

Note, that the decomposition and uptake flux also depends on current environmental conditions (l_e). Hence, steady state microbial activity also fluctuates with environmental drivers.

4.8 Priming effects

The AssimExplicit model variant simulates a short phase of negative priming in the LabPriming scenario. This is in line with the hypothesis that microbial dynamics cause the priming effect (Blagodatskaya and Kuzyakov, 2008). However, while negative priming is usually attributed to preferential substrate usage, it is caused in this model solely by a dilution of the assimilable pool with the carbon from the amendment. Right after the amendment, microbes take up and respire the same total amount of carbon as before, but a part of this originates now carbon from the amendment instead of the autochthonous soil carbon.

There is a discussion about apparent and real priming effects (see e.g. review Blagodatskaya and Kuzyakov, 2008). The priming effect is defined as the increased or diminished mineralization of soil organic matter after treating soil with an amendment, compared to a control without amendment (Kuzyakov et al., 2000). Apparent priming is an increased respiration originating from increased turnover of microbial biomass without additional mineralization of soil organic matter (Blagodatskaya and Kuzyakov, 2008). We argue that the distinction between apparent and real priming is not as important on longer time scales as on the short term. Microbial biomass is usually only a small fraction of 2–4 % (Anderson and Domsch, 1989) of organic matter. The active part can be again a magnitude smaller (Wutzler et al., 2012). Hence, the turnover of one complete pool of active microbial biomass contributes only a small part to respiration integrated over seasons and years. If we detect significant priming effects over this time scale, the contribution of primed carbon originating from initially present microbial biomass will be small compared to the overall effect.

4.9 Outlook

In order to highlight the energy limitation aspects, this study focused on SOM cycling under constant environmental conditions and no other limitations than carbon substrate. In order to gain a more comprehensive understanding of substrate interactions and to compare model predictions to observations, other aspects need to be considered as well. First, due to the narrow range in the stochiometry of microbial biomass, substrate interactions will be strongly determined by differences in elemental composition of litter and transformed soil organic matter (Fontaine et al., 2003). Second, substrate interactions can influence the temperature sensitivity of decomposition (Thiessen et al., 2012). Third, the availability of substrate and oxygen is strongly influenced by soil moisture (Davidson et al., 2012). Fourth, we discussed several aspects of microbial dynamics such as preferential substrate usage and predation which are not considered in this study.

The DeadRoot scenario showed that it is important to distinguish between hot spots and sites of low organic matter input and the transitions between them. For further model development, we propose to first start accounting for the vertical heterogeneity of the inputs: high in top soil and low at most sites in subsoil (Braakhekke et al., 2013).

Further simulation experiments should be designed to study, whether the bias introduced by the quasi-steady state assumption with rapidly changing environmental conditions is indeed negligible.

A bottom up strategy of successively integrating effects of microbial dynamics into lumped models is the following. First set up more detailed models that include refined processes and compare model predictions to data of short term experiments. The detailed models then can be simplified similarly as it has been done with the assimilable and microbial explicit ICBM of this study.

A complementary strategy is to implement several forms of substrate interactions such as Eq. (3) directly into lumped SOM cycling models that already account for stochiometry and environmental constraints. Model predictions can be compared to data from FACE experiments or long-term experiments of changes in C3/C4 vegetation, or long-term observation of carbon stocks and fluxes at specific sites (Smith et al., 1996).

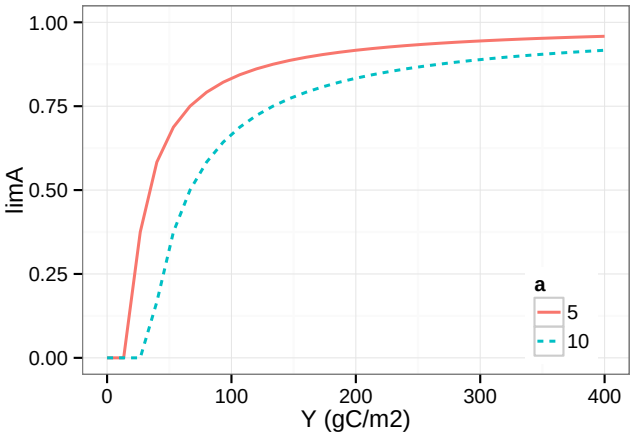

Fig. 8. Microbial limiation l_A as a function of amount of a single substrate Y: $l_A = \max\left(0, 1 - \frac{a_\mathrm{A}}{\epsilon l_{\mathrm{e,Y}} k_Y Y}\right)$. With $\epsilon = 0.3$, $l_{\mathrm{e,Y}} = 1$, and $k_Y = 1 yr^{-1}$.

5 Conclusions

There are several basic strategies of incorporating interactions of SOM qualities into SOM cycling models. Different abstraction levels are appropriate at different time scales and different magnitudes of changes in litter input. For decadal scale application the substrate interaction strategy is appropriate. Out of the 5 model variants presented in this paper, the LimUptake variant is more parsimonious than the LimFresh variant, as it has only one additional parameter, but includes more microbial detail. In contrast, at applications involving fast changes in litter inputs where the transient microbial dynamics and details of microbial energy budget become important, the strategy of explicitly representing microbial dynamics (MicExplicit variant) is appropriate.

The derived simple one-parameter equation of microbial limitation (Eq. 3) can be directly transferred to other SOM cycling models. Incorporating substrate interactions into SOM models, as exemplified by the current study, results in qualitatively different dynamics both on the short as well on the long time scale.

Substrate interactions offer an explanation for the acceleration of SOM cycling instead of extensive SOM accumulation as observed in several FACE experiments. They offer and alternative explanation of the slowing down of decomposition with time in bare fallow long term experiments compared to the explanation of a continuing decrease of substrate quality. Integration of perspective with other aspects of SOM cycling such as other nutrients and environmental influences requires further work both on short-term controlled experiments as well as model data integration with long-term datasets. Overall, consideration of substrate interactions offer a valuable way of understanding and quantitatively modelling SOM dynamics and stabilization.

Appendix A ICBM variants

This appendix describe the model abstraction process in more detail and reports the differential equations used in the variants of the ICBM. State variables and Parameters are explained in Table 1.

A1 AssimExplicit

We started with a detailed assimilable and microbial explicit model similar to several published ones (Blagodatsky and Richter, 1998; Schimel and Weintraub, 2003; Blagodatsky et al., 2010). Carbon input flux i enters the high quality pool Y. Microbial uptake of assimilable substrate was modeled by Monod-kinetics (Monod, 1949; Madigan and Martinko, 2006). Decomposition of non-assimilable substrate was modeled by an equation that was first order to substrate but was a saturating function with active microbial biomass (Schimel and Weintraub, 2003; Wutzler and Reichstein, 2008). This represented the declining probability of enzyme-substrates encounters with decreasing concentration of active microbial biomass. As a first approximation we assumed that all microbial turnover is added to the low quality pool. Microbial turnover was modelled first order to active microbial biomass. Environmental limitations $l_{\mathrm{e,S}}$ of decomposition by cold or drought are treated here as externally

computed model drivers that can change with time.

high quality substrate: $\frac{\mathrm{d}Y}{\mathrm{d}t} = i(t) - d_\mathrm{Y}$

low quality substrate: $\frac{\mathrm{d}O}{\mathrm{d}t} = \tau - d_\mathrm{O}$

assimilable: $\frac{\mathrm{d}D}{\mathrm{d}t} = d_\mathrm{Y} + d_\mathrm{O} - u$

active microbial biomass: $\frac{\mathrm{d}A}{\mathrm{d}t} = u - r_\mathrm{g} - r_\mathrm{m} - \tau$

microbial limitation: $l_A = \frac{A}{m_\mathrm{A} + A}$

decomposition of Y: $d_\mathrm{Y} = l_A l_\mathrm{e}(t) k_\mathrm{Y} Y$

decomposition of O: $d_\mathrm{O} = l_A l_\mathrm{e}(t) k_\mathrm{O} O$

uptake: $u = \mu_\mathrm{max} A \frac{D}{m_\mathrm{D} + D}$

growth respiration: $r_\mathrm{g} = (1-\epsilon) u$

maintenance respiration: $r_\mathrm{m} = s_\mathrm{A} A$

microbial turnover: $\tau = t_\mathrm{A} A$

A2 MicExplicit

First, we abstracted from the fast dynamcis of the assimilable pool. Near its quasi-steady state the change of the pool is small compared to its inflow and outflow. Hence we modeled the microbial uptake as the sum of the inputs to this pool, i.e the sum over all decomposition fluxes. The equations are the same as in the AssimExplicit variant, except for the uptake u.

uptake: $u = d_\mathrm{Y} + d_\mathrm{O}$

A3 MicSteady

Second, we abstracted from the fast dynamics of the active microbial biomass. Again we made use of the quasi steady state approximation. Equations were the ame as in the MicExplicit variant, unless microbial biomass A was replaced by its quasi steady state A^* in all equations.

Quasi steady state of active microbial biomass A^* was derived by setting the derivative to time to zero.

$$\frac{\mathrm{d}A^*}{\mathrm{d}t} = u - r_\mathrm{g} - r_\mathrm{m} - \tau = 0 \quad \text{(A1)}$$

$$A^* = \max\left(0, \frac{\epsilon(l_{\mathrm{e,Y}}(t) k_\mathrm{Y} Y + l_{\mathrm{e,O}}(t) k_\mathrm{O} O)}{s_\mathrm{A} + t_\mathrm{A}} - m_\mathrm{A}\right) \quad \text{(A2)}$$

By substituting the steady state biomass A^* into the other equations, we could express them directly as a function of microbial paraemters. E.g. for the microbial limiation we derived the following equation.

$$l_A = \max\left(0, 1 - \frac{m_\mathrm{A}(s_\mathrm{A} + t_\mathrm{A})}{\epsilon(l_{\mathrm{e,Y}}(t) k_\mathrm{Y} Y + l_{\mathrm{e,O}}(t) k_\mathrm{O} O)}\right)$$

A4 LimUptake

We further abstracted from different kinds of respiration and assumed that respiration could be expressed solely by the microbial efficiency ϵ. This corresponds to including maintenance respiraiton into an effective growth respiration term.

By lumping the microbial parameters into an effective parameter a_A, we reformulated the microbial limiation. This resulted in an expression that was dependent on a minimum potential uptake, rendering microbial mechanisms completely implicit. Decomposition d_Y and d_O were the same as in the AssimExplicit variant.

substrate Young: $\frac{\mathrm{d}Y}{\mathrm{d}t} = i - d_\mathrm{Y}$

substrate Old: $\frac{\mathrm{d}O}{\mathrm{d}t} = \epsilon(d_\mathrm{Y} + d_\mathrm{O}) - d_\mathrm{O}$

respiration: $r = (1-\epsilon)(d_\mathrm{Y} + d_\mathrm{O})$

lumped biomass parameter: $a_\mathrm{A} = m_\mathrm{A}(s_\mathrm{A} + t_\mathrm{A})$

uptake limitation: $l_A = \max\left(0, 1 - \frac{a_\mathrm{A}}{\epsilon(l_{\mathrm{e,Y}}(t) k_\mathrm{Y} Y + l_{\mathrm{e,O}}(t) k_\mathrm{O} O)}\right)$

A5 LimFresh

Usually, the uptake of high qualyity substrate (here Y) is much larger than the uptake of low quaility substrate (here O). Hence, we further explored the simplified model variant that neglected the uptake of low quality substrate in the limitation factor l_A. All other equations were the same as in the LimUptake variant.

uptake limitation: $l_A = \max\left(0, 1 - \frac{a_\mathrm{A}}{\epsilon l_{\mathrm{e,Y}}(t) k_\mathrm{Y} Y}\right)$

A6 Independent

Finally we abstracted the model by neglecting substrate limitations at all and omitted the limitation factor in the decomposition equations. All other equations were the same as in the LimUptake variant. Decomposition fluxes of the substrate qualities were independent of each other.

decomposition of Y: $d_\mathrm{Y} = l_{\mathrm{e,Y}}(t) k_\mathrm{Y} Y$

decomposition of O: $d_\mathrm{O} = l_{\mathrm{e,O}}(t) k_\mathrm{O} O$

By this we derived a model structure that was equivalent to the original ICBM model. The microbial efficiency ϵ structurally corresponded to the humification factor h in the original model. Note, however, that its interpretations differs in terms of what the low quality matter is composed of: microbial turnover versus preserved litter. Similarly, the decomposition rate k'_O in the original model did not take into account recycling of decomposed low quality OM by microbial turnover. It relates to the one in this model by $k'_\mathrm{O} = (1-\epsilon) k_\mathrm{O}$.

Appendix B Model parameterisation

This appendix reports the calculation of parameters used in running the simulation scenarios in Sect. 2.2. Parameters were chosen so that all variants predicted the same steady state carbon stocks before the change of litter input: $Y_0 = 400\mathrm{gC\,m^{-2}}$, $O_0 = 6400\mathrm{gC\,m^{-2}}$. All apparent turnover times corresponded to one and fourty years for the Y and O pool respectively. Other model parameters were derived from these constrained apparent turnover rates, the steady state assumptions, and other reasonable constraints, e.g. that total microbial biomass was 2% of organic matter.

B1 LabPriming

The amount of amendment was in the order of soil microbial biomass: $2\% C_{Tot} \approx 140\mathrm{g\,m^{-2}}$ (Blagodatskaya and Kuzyakov, 2008).

Input: $i(t \geq 0) = 0\,\mathrm{g\,m^{-2}yr^{-1}}$

Average input before the experiment: $i_0 = 400\,\mathrm{g\,m^{-2}yr^{-1}}$

Added label at $t = 0$: $Y_{\mathrm{label}} = \frac{1}{2} i_0 \, 1\mathrm{yr} = 200\mathrm{g\,m^{-2}}$

Independent

Initial apparent decomposition rates:

- $k_{\mathrm{Y,app}} = l_{\mathrm{e,Y}}(0) k_{\mathrm{Y}} = \frac{1}{1\mathrm{yr}}$
- $k_{\mathrm{O,app}} = l_{\mathrm{e,O}}(0) k_{\mathrm{O}} = \frac{1}{40\mathrm{yr}}$

Dividing the apparent decomposition rates by the mean environmental limitation $l_{\mathrm{e,j}}$ resulted in decomposition rates.

Microbial efficiency: $\epsilon = 0.4$ Initial pools then result from steady state:

- $Y_0 = \frac{i_0}{k_{\mathrm{Y,app}}}$
- $O_0 = \frac{\epsilon i_0}{k_{\mathrm{O,app}}}$

MicExplicit and MicSteady

Apparent decomposition rates, and microbial efficiency, and calculation of initial pools were the same as with the Independent model variant.

Initial microbial limitation was set to $l_A(0) = 0.05$ corresponding to low activity due to some time of storage before the exeperiment.

Dividing the apparent decomposition rates by $(l_0 l_{\mathrm{e,j}})$ resulted in decomposition rates k_{Y} and k_{O}

Given an initial active microbial biomass $A_0 = 0.02(Y_0 + O_0) l_0$ the other rates were defined by the initial steady state condition:

Affinity: $m_{\mathrm{a}} = A_0 \left(\frac{1}{l_{\mathrm{A}}(0)} - 1 \right)$

Microbial turnover rate: $t_{\mathrm{A}} = \frac{l_{\mathrm{A}}(0) l_{\mathrm{e,O}}(0) k_{\mathrm{O}_0} O}{A_0}$

Maintenance rate: $\frac{\epsilon l_{\mathrm{A}}(0)(l_{\mathrm{e,Y}}(0) k_{\mathrm{Y}} Y_0 + l_{\mathrm{e,O}}(0) k_{\mathrm{O}} O_0)}{A_0} - t_{\mathrm{A}}$

AssimExplicit

Same as MicExplicit variant. In addition maximum growth rate was set to $\mu_{max} = 1/(24h)$. Typical maximum growth rates in priming experiments are higher than 1/day (Wutzler et al., 2012) but correspond to communities growing on substrates that are mineralized faster. With higher growth rates, microbial dynamics would be even faster near steady state.

Initial assimilable pools was set to $D_0 = 1g/m^2$, which corresponds to 10 mg/l (Borken et al., 2011) for a 40cm deep soil and 25% of the volume occupied by water. Half-saturation m_S was calculated from steady state assumption of the assimilate pool prior to change of litter inputs as $m_S = D_0 \left(\frac{\mu_{max} A_0}{l_{\mathrm{A}}(0)(l_{\mathrm{e,Y}}(0) k_{\mathrm{Y}} Y_0 + l_{\mathrm{e,O}}(0) k_{\mathrm{O}} O_0)} - 1 \right)$.

B2 FaceAct

Soil carbon input increased from steady state values of $i_0 = 400\,\mathrm{g\,C\,m^{-2}yr^{-1}}$ rapidly ($e_{\mathrm{Fold}} = 0.5$ yr) levelling out at $r = 25\,\%$ above i_0 (Phillips et al., 2011).

$$i(t) = i_0 + r i_0 (1 - \exp(-1/e_{\mathrm{Fold}} t))$$

Parameters for Independent, MicExplicit, and MicSteady variants were the same as with the LabPriming scenario, unless initial microbial limitation was set to: $l_0 = 0.8$ assuming high microbial activity adapted to high quality inputs from rhizodeposition.

The LimUptake and the LimFresh model variant neglected maintenance respiration. In order to match the same initial total stocks, the growth respiration had to compensate for this. Hence the effective microbial efficiency was set to 0.7143 times the true ϵ.

The lumped limitation parameters of the LimUptake and the LimFresh variants were calculated from steady state assumption before the change of litter input:

$$a_{\mathrm{A}} = (1 - l_{\mathrm{A}}(0)) \epsilon (l_{\mathrm{e,Y}}(0) k_{\mathrm{Y}} Y_0 + l_{\mathrm{e,O}}(0) k_{\mathrm{O}} O_0)$$

B3 FaceLim

This scnearios was the same as the FaceAct scenario, unless initial microbial limitation were set to: $l_A(0) = 0.2$

B4 DeadRoot

Input decreased from steady state values of $i_0 = 400\,\mathrm{g\,C\,m^{-2}yr^{-1}}$ slowly ($e_{\mathrm{Fold}} = 10$ yr) to a minimum arbitrary low value of $i_{\min} = i_0/50$. The time scale was choosen to match a decomposing coarse root.

$$i(t) = \max(i_{\min}, i_0 \exp(-1/e_{\mathrm{Fold}} t)$$

Parameters were calculated the same way as in the FaceAct scenario.

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