Biogeosciences Discuss., 9, 17167–17201, 2012
www.biogeosciences-discuss.net/9/17167/2012/
doi:10.5194/bgd-9-17167-2012
© Author(s) 2012. CC Attribution 3.0 License.

Biogeosciences Discussions

This discussion paper is/has been under review for the journal Biogeosciences (BG).
Please refer to the corresponding final paper in BG if available.

Priming and substrate quality interactions in soil organic matter models

T. Wutzler and M. Reichstein

Max Planck Institute for Biogeochemistry, Hans-Knöll-Straße 10, 07745 Jena, Germany

Received: 18 October 2012 – Accepted: 21 November 2012 – Published: 6 December 2012

Correspondence to: T. Wutzler (twutz@bgc-jena.mpg.de)

Published by Copernicus Publications on behalf of the European Geosciences Union.

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 on 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, and the role of microbial biomass controlling decomposition rates have received increasing attention during the last years (Allison et al., 2010; Todd-Brown et al., 2012; Treseder et al., 2011). This is because, first, it opens new ways of understanding 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). The new issue highlighted by the priming effect is that decomposition of

BGD
9, 17167–17201, 2012

SOM of one quality is dependent on the amount of SOM of a different quality, i.e. there are substrate quality interactions.

Contrary to this new 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 decomposition of SOM of different qualities is independent of each other, i.e. they abstract from 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 (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 model parameters that may be uncertain (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.

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 active microbial biomass. On the contrary, 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

BGD
9, 17167–17201, 2012

to other processes and includes a general formulation of the microbial limitation in the description of the decomposition function (Fig. 1).

1.1.1 Explicit 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 the amount of substrate but also on the activity of decomposers. When activity of the decomposers that degrade also less quality SOM is stimulated or suppressed by the amount of high quality substrate, then the decomposition of this lower quality SOM is affected by the high quality SOM. Hence, the first strategy to implement substrate interactions is to explicitly model microbial activity, i.e. the physiological state that modifies rates of metabolic transformations and growth (Sect. 4.5), or its biomass as a dynamic state variable. The basic 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.

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

assimilable OM: $\frac{\mathrm{d}F}{\mathrm{d}t} = \sum_j d_j + p_\mathrm{F} t - u$

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

decomposition: $d_j = f(S_j, A)$

uptake: $u = f(F, A)$

BGD
9, 17167–17201, 2012

growth respiration: $r_g = (1 - \epsilon_F)u$

microbial turnover: $t = f(A)$

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_F is the microbial efficiency or yield.

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. Those 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. At larger time scales, the influx to the assimilable pool quickly approaches a state where its input by mineralization equals its turnover by microbial uptake. Hence, we may set uptake $u = \sum_j d_j$. Further, also active microbial biomass approaches a state where growth depending on given substrates 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 and turnover, and the microbial limitation to decomposition (Fig. 1 bottom left). Starting with the limitation based on active microbial steady-state, we may further abstract from details of microbial dynamics and simplify the limitation factor.

BGD
9, 17167–17201, 2012

1.1.3 Substrate limitations

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

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

$$\text{decomposition:} \quad d_j = f(S_1, \ldots, S_n)$$

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 for all substrate qualities j that depends on the amount of all substrate in all qualities or alternatively only on the amount of the high quality substrate (Fig. 1 bottom right).

$$\text{decomposition:} \quad d_j = l k_j S_j$$

$$\text{substrate limitation:} \quad l = f(S_1, \ldots, S_n)$$

The substrate interaction strategy can be applied without any considerations of decomposers. Alternatively, it can also be applied as a further level of abstraction of the decomposer dynamics.

2 Methods

2.1 Implementations to the ICBM model

In order to exemplify the basic strategies of implementing substrate interactions (Sect. 1.1) into a model of SOM dynamics, we present a series of versions of the ICBM model.

BGD
9, 17167–17201, 2012

The ICBM model (Andrén and Kätterer, 1997) 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. The systems of differential equations are given in Appendix A, and parameters are described in Table 1. The following text describes the main characteristics.

Independent
This variant is the original ICBM model. It does not account for substrate interactions. The input enters the high quality pool, denoted by Young. Decomposition flux of this pool is divided into respiration and into a part that is transformed to low quality substrate, denoted by Old. A part of the decomposition flux of the old pool is respired.

MicExplicit
We started implementing the substrate interactions with the microbial-explicit strategy. Here, the decomposition was first order with respect to substrate but decreased at low microbial activity. In addition to growth respiration, we included also maintenance respiration that linearly increased with biomass. We already abstracted from the Assimilable pool and set the uptake flux equal to the sum of decomposed substrate $u = \sum_j d_j$. As a first approximation, the entire turnover of the microbial biomass was added to the low quality pool.

MicSteady
This variant uses the steady-state strategy. It is abstracted from the short-term dynamics in the active microbial biomass pool. We used the same equations as in the MicExplicit variant, but replaced active microbial biomass by its steady-state, which depends on the current amount of substrates.

LimUptake
This variant neglected maintenance respiration, leaving only growth respiration in the system of equations. Microbial efficiency then, corresponded to the amount of uptake

BGD
9, 17167–17201, 2012

that is transformed to lower quality substrate, i.e. the humification coefficient in the original ICBM model. The variant was derived from the MicSteady variant by lumping all microbial parameters into a single parameter a_A. The limitation factor I for decomposition was based on potential uptake. The potential uptake u_{Pot} corresponds to the uptake with no microbial limitation, i.e. $I = 1$, from all substrate qualities.

$$I = \max\left(0, 1 - \frac{a_A}{u_{Pot}}\right) \quad (1)$$

$$u_{Pot} = \epsilon_F \sum_j k_j S_j$$

This variant can be seen as a representation of the substrate limitation strategy (Fig. 1), although here we derived it as a further abstraction of the MicSteady model variant.

LimFresh

An alternate application of the substrate limitation strategy consist of making decomposition only dependent on the fresh energy-rich OM. With this model variant, the limitation factor was based only on the amount of high quality substrate Y. In this study, it was derived from the LimUptake variant by neglecting the uptake from low quality substrate.

$$I = \max\left(0, \frac{Y - a_Y}{Y}\right)$$

The parameter a_Y describes the minimum amount of high energy substrate Y to sustain active microbial biomass. When Y declines towards this value, the decomposition rate slows down.

2.2 Simulation scenarios

The model variants presented in Sect. 2.1 have been applied to different scenarios of litter inputs. In all scenarios the model started from steady state for a litter input of

BGD
9, 17167–17201, 2012

400 g C m^{-2} yr^{-1}. Initial microbial limitation was 5 % for the LabPriming scenario, 20 % for the FaceLim scenario and 80 % for the other scenarios. The detailed parameter values, initial stocks, and litter inputs over time are given in Appendix B.

LabPriming
Adding a 3-fold amount of steady-state Young substrate and no input thereafter. This simulates 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.

FaceActive
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 stays at this level.

FaceLim
Increasing the input by 25 % with an initially energy-limited microbial biomass. This is the same as FaceActive scenario, except that initial microbial activity was only 20 % of potential activity.

DeadRoot
Exponential decay of litter input to 8 g C m^{-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, only by matrix flow instead of root exudates.

BGD
9, 17167–17201, 2012

3 Results of simulation studies

The typical increase in respiration from autochthonous soil carbon with amendment of fresh organic matter in priming experiments can be seen in Fig. 3 with the MicExplicit model. There is no priming effect in the original model where the autochthonous SOM decomposes independent from the added label. The MicSteady model strongly overestimates the initial microbial biomass and hence also the decomposition of the autochthonous SOM at the beginning of the incubation.

At longer time scales, with continuous litter inputs that do not change abruptly, there is no visible difference between the MicExplicit and the MicSteady model at all long-term predictions (Figs. 4–6).

All the variants of substrate interactions agree remarkably well in the FaceAct scenario (Fig. 4). Contrary, the model in which substrates decompose independently predicts higher long-term carbon stocks.

This difference became more pronounced when we assumed an more strongly substrate-limited decomposer community at the beginning of the incubation (Fig. 5). All the models that account for substrate interactions, predict only a smaller change in carbon stocks. This is because the microbial limitation is relieved and the SOM just cycles faster instead of accumulating. The slight deviation of the limFresh variant from the other variants is due to neglecting the uptake of low quality organic matter as explained below.

In the DeadRoot simulation scenario (Fig. 6) the assimilation of low quality organic matter becomes relevant. The proportion of the low quality decomposition and uptake increases. The high quality substrate is depleted fast, while the stored amounts of low quality substrate are available for a longer time. Hence, the LimFresh model variant, which is based solely on high quality organic matter, predicts lower microbial activity and decomposition. The substrate independent model does not account for the microbial energy-limitation at all and predicts more rapid decomposition of the substrate.

BGD
9, 17167–17201, 2012

4 Discussion

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 was time scale. When investigating the dynamics at larger time scales, we assumed that the description of the dynamics of fast processes can be replaced by a quasi-steady-state assumption (QSSA) (Segel and Slemrod, 1989), where after an initial fast transient, the assimilable substrate and the microbial biomass can be regarded in steady-state with respect to the instantaneous values of the available substrate.

The non-steady-state dynamics of microbial biomass was most important at the daily to seasonal scale (Fig. 3) and was still visible over about two years (Fig. 5). With the MicExplicit model, initial decomposition of substrate was limited by the initially low activity. The transient time, required by microbes to increase their activity, was long enough to consume a non-negligible amount of substrate. Hence, with the MicSteady model, the initial activity was strongly overestimated and also the decomposition and respiration was initially too high initially and too low after 20 days.

However, when looking at decadal to century time scale changes with assuming continuous change of litter input, the quasi-steady state assumption was a very effective model simplification (Figs. 4–6).

4.2 High vs. low available energy

A second important factor was available energy. At high supply of fresh litter, the microbial efficiency in substrate uptake dominated the potential microbial activity. At low supply of fresh litter, however, other factors related to the microbial energy budget

BGD
9, 17167–17201, 2012

became 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 physiological states of microbial biomass (Panikov, 1995; Blagodatsky and Richter, 1998), 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). Further work needs to be done to incorporate those effects into the steady state calculations and the decomposition limitation factors.

Moreover, the proportion of uptake of low quality OM compared to high quality OM can be considerable at low fresh organic litter inputs. The LimFresh model, which solely depended on fresh litter, predicted similar dynamics at high litter inputs as the other models, but differed in its predictions for the DeadRoot scenario of diminished litter inputs (Fig. 6). This is because the high-quality OM is 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.

4.3 OM stabilization by energy limitation

In the DeadRoot scenario, the long-term predictions of the model with substrate interactions differed qualitatively 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 model) the microbial limitation to decomposition increases. This results in an increase in the apparent turnover time of the low quality substrate (Fig. 7).

This is an alternative explanation of the observed decreasing decomposition rate at long-term bare fallow experiments (Barré et al., 2010). 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

BGD
9, 17167–17201, 2012

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 the model in this study that included substrate interactions, where stabilization of the low-quality OM depends on fresh litter inputs.

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 event-like redistribution of carbon between different SOM-qualities instead of modifying model parameters (Gottschalk et al., 2010). It will be interesting to test, if changed substrate interactions with changing input distribution also can explain such kind of data.

4.4 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. Contrary, 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).

BGD
9, 17167–17201, 2012

4.5 Microbial activity

The active microbial biomass pool in the microbial-explicit strategy does not correspond to measurements of microbial biomass in soil. 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, but need to synthesize big parts of their metabolic machinery again before growing. Growth and metabolic rates are reduced. The time lag before visible exponential growth can be related to this physiological state of activity. 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., 2011) might come most close to the modeled pool.

In addition to overall activity, the community structure is supposed to play a major role in regulating OM cycling (Fontaine et al., 2003; Treseder et al., 2011; Todd-Brown et al., 2012).

4.6 Priming effects and substrate interactions

We argue that the distinction between apparent and real priming is not as important on longer time scales as on the short term. 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 after amendment originating from increased turnover of microbial biomass without additional mineralization of soil organic matter (Blagodatskaya and Kuzyakov, 2008).

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., 2011). 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

BGD
9, 17167–17201, 2012

originating from initially present microbial biomass will be small compared to the overall effect.

In this paper we rather discuss the underlying interactions between SOM qualities instead of priming effects directly. This is because we want to avoid the comparison to a control. We hypothesize that priming effects after addition of high-quality substrates arise because of the substrate interactions mediated by microbial activity. But the substrate interactions are present also in the control treatments. We argue that it is the absence of a high quality substrate source aside the hot spots of litter input that is one factor of understanding soil carbon stabilization.

4.7 Outlook

In order to highlight the energy limitation aspects, this study focused on very constrained conditions of SOM cycling of 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. 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., 2012).

A bottom up strategy of successively integrating those varying aspects is to include those processes in detailed models and compare model predictions to rich data of short

BGD
9, 17167–17201, 2012

term experiments. The resulting detailed models can be simplified similarly as how it has been done with the microbial explicit ICBM model of this study. A complementary strategy can implement several forms of substrate interactions such as Eq. (1) directly into SOM cycling models that already account for stochiometry and empirical formulations of environmental constraints. Those 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).

5 Conclusions

There are several basic strategies of incorporating interactions of SOM qualities into SOM cycling models. Different abstraction levels are appropriate at different scales and different magnitudes of changes in litter input. For larger scale application the parameterization of uptake limitation 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. Contrary, 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 energy limitation (Eq. 1) can be directly transferred to other SOM cycling models. Incorporating substrate interactions into SOM models, as exemplified by the ICBM model, 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

BGD
9, 17167–17201, 2012

controlled experiments as well as model data integration with long-term datasets. Overall, substrate interactions offer a valuable way of understanding and quantitatively modelling SOM stabilization.

Appendix A

ICBM model variants

This appendix reports the differential equations used in the variants of the ICBM model. Parameters are explained in Table 1.

A1 Independent

substrate Young: $\frac{dY}{dt} = i - d_Y$

substrate Old: $\frac{dO}{dt} = \epsilon_F d_Y - d_O$

decomposition Young: $d_Y = k_Y Y$

decomposition Old: $d_O = k_O O$

respiration: $r = (1 - \epsilon_F) d_Y + d_O$

BGD
9, 17167–17201, 2012

A2 MicExplicit

substrate Young: $\frac{dY}{dt} = i - d_Y$

substrate Old: $\frac{dO}{dt} = t - d_O$

active microbial biomass: $\frac{dA}{dt} = u - r_g - r_m - t$

microbial limitation: $l = \frac{A}{m_A + A}$

decomposition Young: $d_Y = l k_Y Y$

decomposition Old: $d_O = l k_O O$

uptake: $u = d_Y + d_O$

growth respiration: $r_g = (1 - \epsilon_F)u$

maintenance respiration: $r_m = s_A A$

microbial turnover: $t = t_A A$

BGD
9, 17167–17201, 2012

A3 MicSteady

substrate Young: $\frac{dY}{dt} = i - d_Y$

substrate Old: $\frac{dO}{dt} = t - d_O$

steady state microbial biomass: $A^* = \frac{\epsilon_F(k_Y Y + k_O O)}{s_A + t_A} - m_A$

microbial limitation: $l = \frac{A^*}{m_A + A^*}$

decomposition Young: $d_Y = l k_Y Y$

decomposition Old: $d_O = l k_O O$

uptake: $u = d_Y + d_O$

growth respiration: $r_g = (1 - \epsilon_F)u$

maintenance respiration: $r_m = s_A A^*$

microbial turnover: $t = t_A A^*$

A4 LimUptake

substrate Young: $\frac{dY}{dt} = i - d_Y$

substrate Old: $\frac{dO}{dt} = \epsilon_F d_Y - d_O$

lumped biomass parameter: $a_A = m_A(s_A + t_A)$

uptake limitation: $l = \max\left(0, 1 - \frac{a_A}{\epsilon_F(k_Y Y + k_O O)}\right)$

BGD
9, 17167–17201, 2012

decomposition Young: $d_Y = l k_Y Y$

decomposition Old: $d_O = l k_O O$

respiration: $r = (1 - \epsilon_F) d_Y + d_O$

A5 LimFresh

substrate Young: $\frac{dY}{dt} = i - d_Y$

substrate Old: $\frac{dO}{dt} = \epsilon_F d_Y - d_O$

lumped limitation parameter: $a_Y = \frac{a_A}{\epsilon_F k_Y}$

substrate limitation: $l = \max\left(0, \frac{Y - a_Y}{Y}\right)$

decomposition Young: $d_Y = l k_Y Y$

decomposition Old: $d_O = l k_O O$

respiration: $r = (1 - \epsilon_F) d_Y + d_O$

Appendix B

Model parameterisation

This appendix reports the parameters used in running the simulation scenarios in Sect. 2.2.

BGD
9, 17167–17201, 2012

B1 LabPriming

Input: $i(t) = 0\,\mathrm{g\,m^{-2}\,yr^{-1}}$
Average input before the experiment: $i_0 = 400\,\mathrm{g\,m^{-2}\,yr^{-1}}$
Added label at $t = 0$: $Y_{\mathrm{label}} = 3Y_0$

Independent
Initial apparent decomposition rates:

- $k_{\mathrm{Y,app}} = k_{\mathrm{Y}} = 1\,\mathrm{yr^{-1}}$
- $k_{\mathrm{O,app}} = k_{\mathrm{O}} = 1\,(40\mathrm{yr})^{-1}$

Microbial efficiency: $\epsilon_{\mathrm{F}} = 0.4$ Initial pools then result from steady state:

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

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 $l_0 = 0.05$.

Dividing the apparent decomposition rates by l_0 then gives the decomposition rates k_{Y} and k_{O}

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

Maintenance rate: $s_{\mathrm{A}} = l_0(\epsilon_{\mathrm{F}} k_{\mathrm{Y}} Y_0 + (\epsilon_{\mathrm{F}} - 1)k_{\mathrm{O}} O_0)/A_0$

BGD
9, 17167–17201, 2012

Microbial turnover rate: $t_A = I_0 k_O O_0 / A_0$

Affinity: $m_a = A_0(k_Y Y_0 - i_0)/i_0$

B2 FaceAct

Input increases from steady state values of $i_0 = 400\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ rapidly ($e_{Fold} = 0.5$ yr) levelling out at $r = 25\,\%$ above i_0.

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

Parameters for ICBM, MicExplicit, and MicSteady are the same as with the LabPriming scenario, unless initial microbial limitation was set to: $I_0 = 0.8$

The LimUptake and the LimFresh model variant neglect maintenance respiration. In order to match the same initial total stocks, the growth respiration had to compensate for the neglected maintenance. Hence the microbial efficiency was decreased by a factor of 0.7143.

The additional lumped limitation parameters can be calculated from initial steady state assumption:

- $a_A = (1 - I_0)\epsilon_F(k_Y Y_0 + k_O O_0)$
- $a_Y = (1 - I_0) Y_0$

B3 FaceLim

Same as FaceAct, unless initial microbial limitation was set to: $I_0 = 0.2$

BGD
9, 17167–17201, 2012

B4 DeadRoot

Input decreases from steady state values of $i_0 = 400\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ slowly ($e_{\mathrm{Fold}} = 10$ yr) to a minimum value of $i_{\mathrm{min}} = i_0/50$.

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

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

Acknowledgements. This work was supported by the ERC starting grant QUASOM (ERC-2007-StG-208516). We thank Sönke Zähle for valuable comments on the manuscript.

The service charges for this open access publication
have been covered by the Max Planck Society.

References

Ågren, G. and Bosatta, E.: Theoretical Ecosystem Ecology – Understanding Element Cycles, Cambridge University Press, Cambridge, 1996. 17169

Allison, S., Wallenstein, M., and Bradford, M.: Soil-carbon response to warming dependent on microbial physiology, Nat. Geosci., 3, 336–340, 2010. 17168

Anderson, T.-H. and Domsch, K.: Ratios of microbial biomass carbon to total organic carbon in arable soils, Soil Biol. Biochem., 21, 471–479, doi:10.1016/0038-0717(89)90117-X, 1989. 17180

Andrén, O. and Kätterer, T.: ICBM: The introductory carbon balance model for exploration of soil carbon balances, Ecol. Appl., 7, 1226–1236, 1997. 17173

Barré, P., Eglin, T., Christensen, B. T., Ciais, P., Houot, S., Kätterer, T., van Oort, F., Peylin, P., Poulton, P. R., Romanenkov, V., and Chenu, C.: Quantifying and isolating stable soil organic carbon using long-term bare fallow experiments, Biogeosciences, 7, 3839–3850, doi:10.5194/bg-7-3839-2010, 2010. 17178

BGD
9, 17167–17201, 2012

Beeftink, H. H., Vanderheijden, R. T. J. M., and Heijnen, J. J.: Maintenance requirements – energy supply from simultaneous endogenous respiration and substrate consumption, Fems Microbiol. Ecol., 73, 203–209, 1990. 17178

Blagodatskaya, E. and Kuzyakov, Y.: Mechanisms of real and apparent priming effects and their dependence on soil microbial biomass and community structure: critical review, Biol. Fert. Soils, 45, 115–131, doi:10.1007/s00374-008-0334-y, 2008. 17178, 17180

Blagodatsky, S. A. and Richter, O.: Microbial growth in soil and nitrogen turnover: a theoretical model considering the activity state of microorganisms, Soil Biol. Biochem., 30, 1743–1755, 1998. 17178

Blagodatsky, S. A., Heinemeyer, O., and Richter, J.: Estimating the active and total soil microbial biomass by kinetic respiration analysis, Biol. Fert. Soils, 32, 73–81, 2000. 17180

Blagodatsky, S., Blagodatskaya, E., Yuyukina, T., and Kuzyakov, Y.: Model of apparent and real priming effects: linking microbial activity with soil organic matter decomposition, Soil Biol. Biochem., 42, 1275–1283, doi:10.1016/j.soilbio.2010.04.005, 2010. 17169

Braakhekke, M. C., Wutzler, T., Beer, C., Kattge, J., Schrumpf, M., Schöning, I., Hoosbeek, M. R., Kruijt, B., Kabat, P., and Reichstein, M.: Modeling the vertical soil organic matter profile using Bayesian parameter estimation, Biogeosciences Discuss., 9, 11239–11292, doi:10.5194/bgd-9-11239-2012, 2012. 17181

Cardon, Z. G., Hungate, B. A., Cambardella, C. A., Chapin III, F. S., Field, C. B., Holland, E. A., and Mooney, H. A.: Contrasting effects of elevated CO_2 on old and new soil carbon pools, Soil Biol. Biochem., 33, 365–373, 2001. 17179

Carney, K. M., Hungate, B. A., Drake, B. G., and Megonigal, J. P.: Altered soil microbial community at elevated CO_2 leads to loss of soil carbon, P. Natl. Acad. Sci. USA, 104, 4990–4995, doi:10.1073/pnas.0610045104, 2007. 17179

Davidson, E. A., Samanta, S., Caramori, S. S., and Savage, K. E.: The Dual Arrhenius and Michaelis-Menten (DAMM) kinetics model for decomposition of soil organic matter at hourly to seasonal time scales, Glob. Change Biol., 18, 371–384, doi:10.1111/j.1365-2486.2011.02546.x, 2012. 17181

Drake, J. E., Gallet-Budynek, A., Hofmockel, K. S., Bernhardt, E. S., Billings, S. A., Jackson, R. B., Johnsen, K. S., Lichter, J., McCarthy, H. R., McCormack, M. L., Moore, D. J. P., Oren, R., Palmroth, S., Phillips, R. P., Pippen, J. S., Pritchard, S. G., Treseder, K. K., Schlesinger, W. H., DeLucia, E. H., and Finzi, A. C.: Increases in the flux of carbon belowground stimulate nitrogen uptake and sustain the long-term enhancement of

BGD
9, 17167–17201, 2012

forest productivity under elevated CO_2, Ecol. Lett., 14, 349–357, doi:10.1111/j.1461-0248.2011.01593.x, 2011. 17179
Fang, C., Smith, P., Smith, J. U., and Moncrieff, J. B.: Incorporating microorganisms as decomposers into models to simulate soil organic matter decomposition, Geoderma, 129, 139–146, 2005. 17169
Fontaine, S. and Barot, S.: Size and functional diversity of microbe populations control plant persistence and long-term soil carbon accumulation, Ecol. Lett., 8, 1075–1087, 2005. 17169, 17178
Fontaine, S., Mariotti, A., and Abbadie, L.: The priming effect of organic matter: a question of microbial competition?, Soil Biol. Biochem., 35, 837–843, 2003. 17180, 17181
Fontaine, S., Barot, S., Barré, P., Bdioui, N., Mary, B., and Rumpel, C.: Stability of organic carbon in deep soil layers controlled by fresh carbon supply, Nature, 450, 277–281, 2007. 17168, 17178, 17179
Gottschalk, P., Bellarby, J., Chenu, C., Foereid, B., Smith, P., Wattenbach, M., Zingore, S., and Smith, J.: Simulation of soil organic carbon response at forest cultivation sequences using 13C measurements, Org. Geochem., 41, 41–54, 2010. 17179
Heath, J., Ayres, E., Possell, M., Bardgett, R. D., Black, H. I. J., Grant, H., Ineson, P., and Kerstiens, G.: Rising atmospheric CO_2 reduces sequestration of root-derived soil carbon, Science, 309, 1711–1713, 2005. 17179
Hilborn, R. and Mangel, M.: The Ecological Detective. Confronting Models with Data, Princeton Univesity Press, Princeton, NJ, 1997. 17169
Jenkinson, D. S. and Coleman, K.: The turnover of organic carbon in subsoils. Part 2. Modelling carbon turnover, Eur. J. Soil Sci., 59, 400–413, doi:10.1111/j.1365-2389.2008.01026.x, 2008. 17169
Jobbagy, E. G. and Jackson, R. B.: The vertical distribution of soil organic carbon and its relation to climate and vegetation, Ecol. Appl., 10, 423–436, 2000. 17168
Kuzyakov, Y., Friedel, J. K., and Stahr, K.: Review of mechanisms and quantification of priming effects, Soil Biol. Biochem., 32, 1485–1498, 2000. 17180
Liski, J., Palosuo, T., Peltoniemi, M., and Sievanen, R.: Carbon and decomposition model Yasso for forest soils, Ecol. Model., 189, 168–182, 2005. 17169
Manzoni, S. and Porporato, A.: Soil carbon and nitrogen mineralization: theory and models across scales, Soil Biol. Biochem., 41, 1355–1379, doi:10.1016/j.soilbio.2009.02.031, 2009. 17169, 17178

BGD
9, 17167–17201, 2012

Monod, J.: The growth of bacterial cultures, Annu. Rev. Microbiol., 3, 371–394, 1949. 17170
Moorhead, D. L. and Sinsabaugh, R. L.: A theoretical model of litter decay and microbial interaction, Ecol. Monogr., 76, 151–174, 2006. 17169
Neill, C. and Gignoux, J.: Soil organic matter decomposition driven by microbial growth: a simple model for a complex network of interactions, Soil Biol. Biochem., 38, 803–811, 2006. 17169
Norby, R. J., DeLucia, E. H., Gielen, B., Calfapietra, C., Giardina, C. P., King, J. S., Ledford, J., McCarthy, H. R., Moore, D. J. P., Ceulemans, R., Angelis, P. D., Finzi, A. C., Karnosky, D. F., Kubiske, M. E., Lukac, M., Pregitzer, K. S., Scarascia-Mugnozza, G. E., Schlesinger, W. H., and Oren, R.: Forest response to elevated CO_2 is conserved across a broad range of productivity, P. Natl. Acad. Sci. USA, 102, 18052–18056, doi:10.1073/pnas.0509478102, 2005. 17175
Norby, R. J., Warren, J. M., Iversen, C. M., Medlyn, B. E., and McMurtrie, R. E.: CO_2 enhancement of forest productivity constrained by limited nitrogen availability, P. Natl. Acad. Sci. USA, 107, 19368–19373, doi:10.1073/pnas.1006463107, 2010. 17179
Panikov, N. S.: Microbial Growth Kinetics, Chapman Hall, London, 1995. 17178, 17180
Panikov, N. S. and Sizova, M. V.: A kinetic method for estimating the biomass of microbial functional groups in soil, J. Microbiol. Meth., 24, 219–230, 1996. 17180
Parton, W. J., Stewart, J. W. B., and Cole, C. V.: Dynamics of C, N, P and S in grassland soils – a model, Biogeochemistry, 5, 109–131, 1988. 17169
Phillips, R. P., Finzi, A. C., and Bernhardt, E. S.: Enhanced root exudation induces microbial feedbacks to N cycling in a pine forest under long-term CO_2 fumigation, Ecol. Lett., 14, 187–194, doi:10.1111/j.1461-0248.2010.01570.x, 2011. 17179
Pirt, S.: The maintenance energy of bacteria in growing cultures, P. Roy. Soc. Lond. B Bio., 163, 224–231, 1965. 17178
Poll, C., Pagel, H., Devers-Lamrani, M., Martin-Laurent, F., Ingwersen, J., Streck, T., and Kandeler, E.: Regulation of bacterial and fungal MCPA degradation at the soil-litter interface, Soil Biol. Biochem., 42, 1879–1887, doi:10.1016/j.soilbio.2010.07.013, 2010. 17169
Potter, C. S., Randerson, J. T., Field, C. B., Matson, P. A., Vitousek, P. M., Mooney, H. A., and Klooster, S. A.: Terrestrial ecosystem production: a process model based on global satellite and surface data, Global Biogeochem. Cy., 7, 811–841, 1993. 17169
Raynaud, X., Lata, J. C., and Leadley, P. W.: Soil microbial loop and nutrient uptake by plants: a test using a coupled C : N model of plant-microbial interactions, Plant Soil, 287, 95–116, doi:10.1007/s11104-006-9003-9, 2006. 17178

BGD
9, 17167–17201, 2012

Schmidt, M. W. I., Torn, M. S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I. A., Kleber, M., Kogel-Knabner, I., Lehmann, J., Manning, D. A. C., Nannipieri, P., Rasse, D. P., Weiner, S., and Trumbore, S. E.: Persistence of soil organic matter as an ecosystem property, Nature, 478, 49–56, doi:10.1038/nature10386, 2011. 17179

Segel, L. A. and Slemrod, M.: The quasi-steady-state assumption: a case study in perturbation, SIAM Rev., 31, 446–477, 1989. 17171, 17177

Smith, P., Smith, J., and Powlson, D.: Soil organic matter network (SOMNET): 1996 model and experimental metadata, 1996. 17182

Todd-Brown, K. E. O., Hopkins, F. M., Kivlin, S. N., Talbot, J. M., and Allison, S. D.: A framework for representing microbial decomposition in coupled climate models, Biogeochemistry, 109, 19–33, doi:10.1007/s10533-011-9635-6, 2012. 17168, 17180

Treseder, K., Balser, T., Bradford, M., Brodie, E., Dubinsky, E., Eviner, V., Hofmockel, K., Lennon, J., Levine, U., MacGregor, B., Pett-Ridge, J., and Waldrop, M.: Integrating microbial ecology into ecosystem models: challenges and priorities, Biogeochemistry, 109, 7–18, doi:10.1007/s10533-011-9636-5, 2011. 17168, 17180

Trueman, R. J. and Gonzalez-Meler, M. A.: Accelerated belowground C cycling in a managed agriforest ecosystem exposed to elevated carbon dioxide concentrations, Glob. Change Biol., 11, 1258–1271, 2005. 17179

van Bodegom, P.: Microbial maintenance: a critical review on its quantification, Microb. Ecol., 53, 513–523, 2007. 17178

Wutzler, T. and Reichstein, M.: Colimitation of decomposition by substrate and decomposers – a comparison of model formulations, Biogeosciences, 5, 749–759, doi:10.5194/bg-5-749-2008, 2008. 17169, 17170

Wutzler, T., Blagodatsky, S., Blagodatskaya, E., and Kuzyakov, Y.: Soil microbial biomass and its activity estimated by kinetic respiration analysis – statistical guidelines, Soil Biol. Biochem., 45, 102–112, doi:10.1016/j.soilbio.2011.10.004, 2012. 17180

BGD
9, 17167–17201, 2012

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

Parameter	Unit	Description	MicExplicit	MicSteady	LimUptake	LimFresh	Independent
k_Y	yr^{-1}	decomposition rate Young pool	+	+	+	+	+
k_O	yr^{-1}	decomposition rate Old pool	+	+	+	+	+
e_F	0...1	microbial efficiency	+	+	+	+	+
t_A	yr^{-1}	turnover rate of active microbial biomass	+	+			
s_A	yr^{-1}	maintenance rate	+	+			
m_A	$gC\,m^{-2}$	affinity, i.e. half saturation	+	+			
a_A	$gC\,m^{-2}\,yr^{-1}$	minimum uptake			+		
a_Y	$gC\,m^{-2}$	minimum high quality substrate				+	

BGD
9, 17167–17201, 2012

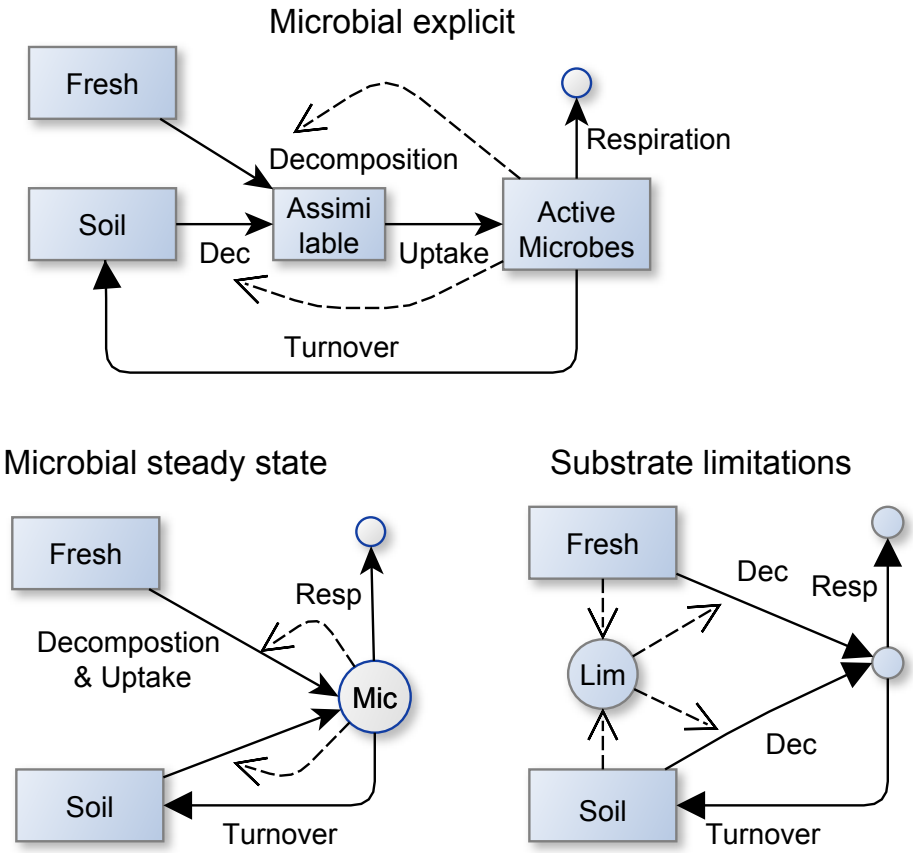

Fig. 1. Basic strategies of implementing substrate interactions. Solid arrows represent carbon fluxes, dashed arrows highlight further controls, boxes represent state variables and circles represent values that are derived from state variables.

BGD
9, 17167–17201, 2012

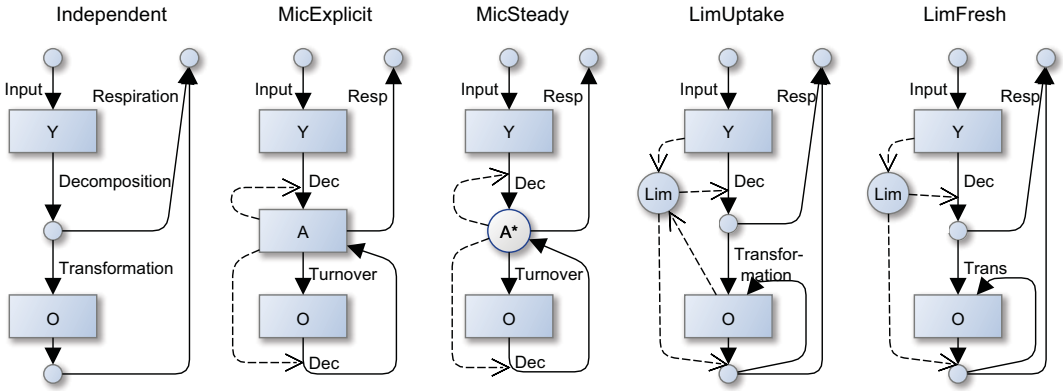

Fig. 2. Structure of the ICBM model variants. Solid arrows denote carbon flows, dashed arrows logical dependencies.

BGD
9, 17167–17201, 2012

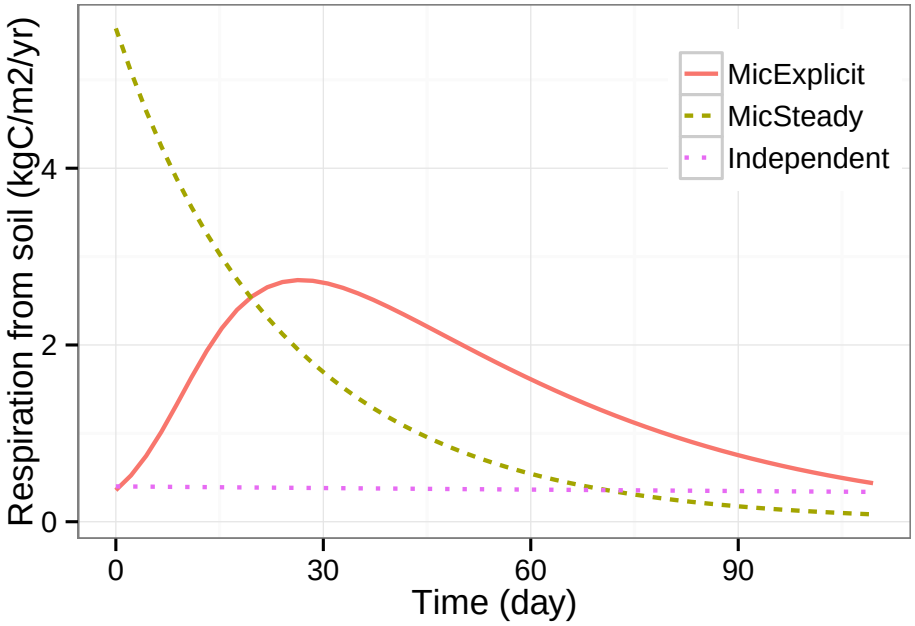

Fig. 3. Time series of respiration of autochthonous SOM in the LabPriming scenario.

BGD
9, 17167–17201, 2012

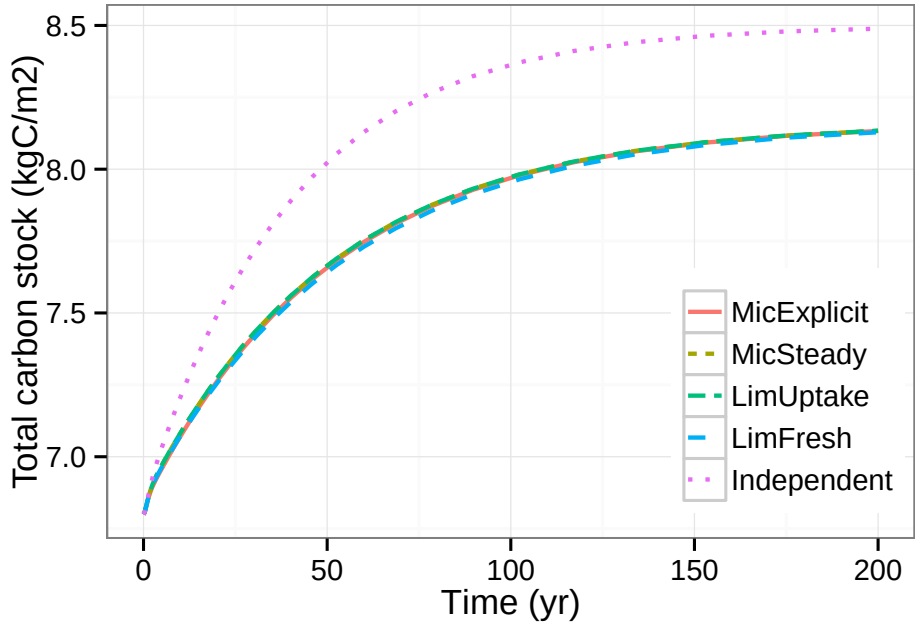

Fig. 4. Time series of total carbon stocks in the FaceAct scenario.

BGD
9, 17167–17201, 2012

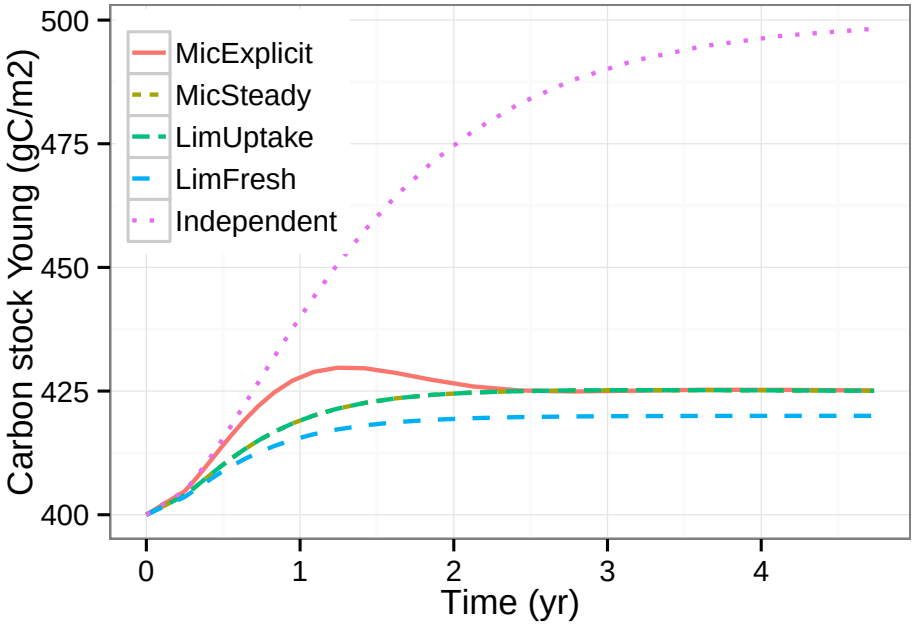

Fig. 5. Time series of carbon in the high-quality pool in the FaceLim scenario.

BGD
9, 17167–17201, 2012

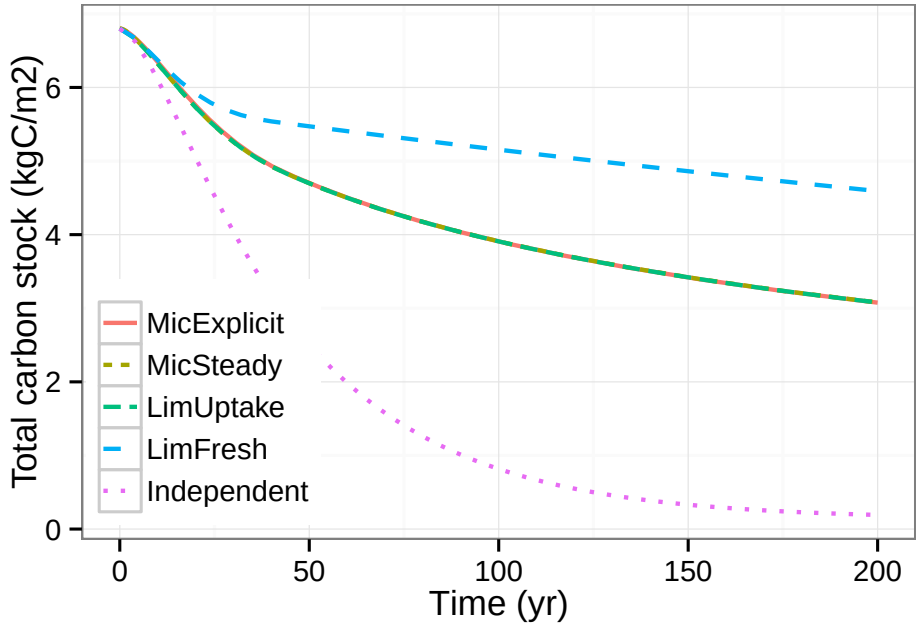

Fig. 6. Time series of total carbon stocks in the DeadRoot scenario.

BGD
9, 17167–17201, 2012

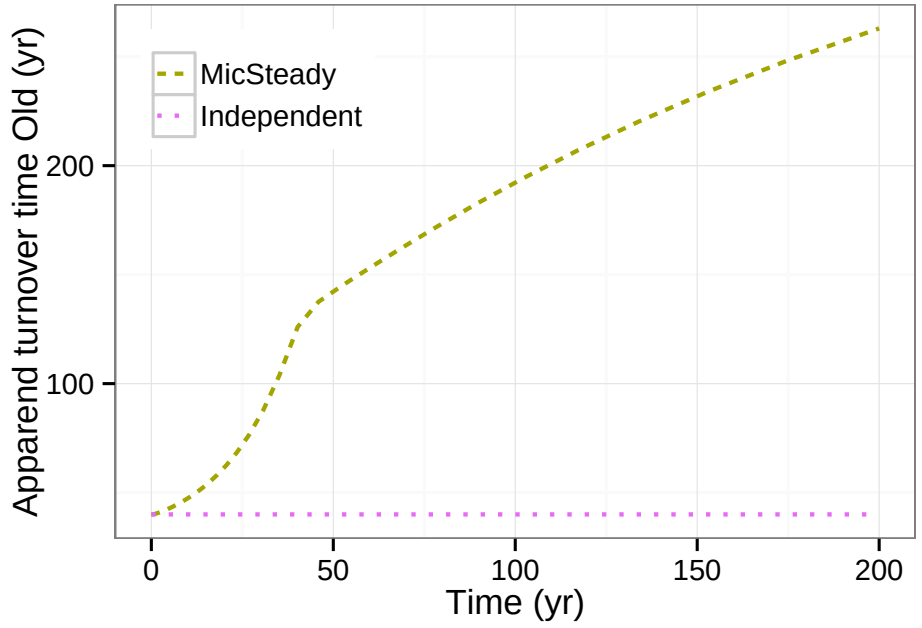

Fig. 7. Increase of apparent turnover time $1/k_{\mathrm{app,\,Old}} = 1/(I\,k_{\mathrm{Old}})$ in the DeadRoot scenario.

BGD
9, 17167–17201, 2012