Is there a theoretical limit to soil carbon storage in old-growth forests? A model analysis with contrasting approaches

Markus Reichstein, Sébastien Fontaine

Markus Reichstein, Sébastien Fontaine. Is there a theoretical limit to soil carbon storage in old-growth forests? A model analysis with contrasting approaches. Old-Growth Forests : Function, Fate and Value, 207, Springer, 2009, Ecological Studies, 978-3-540-92705-1 978-3-540-92706-8. 10.1007/978-3-540-92706-8_12 . hal-02824210

Chapter 12
Is There a Theoretical Limit to Soil Carbon Storage in Old-Growth Forests? A Model Analysis with Contrasting Approaches

Markus Reichstein, Göran Ågren, and Sebastién Fontaine

12.1 Introduction

Apart from the intrinsic worth that nature and forests have due merely to their existence, old-growth forests have always provided a number of additional values through their function as regulators of the water cycle, repositories of genetic and structural biodiversity and recreational areas [see e.g. Chaps. 2 (Wirth et al.), 16 (Armesto et al.), and 19 (Frank et al.), this volume]. In the context of climate change mitigation, carbon sequestration has become another highly valued function of natural and managed ecosystems. In this context, the carbon sequestration potential of old-growth forests has often been doubted and contrasted with the high sequestration potential of young and short-rotation forests, although there can be substantial carbon losses from forest soils following clear-cutting (cf. Chap. 21 by Wirth, this volume).

The question of long-term carbon uptake by old-growth forests has lead to much scientific debate between the modelling and experimental communities in the past. Classical soil carbon turnover models, favoured by certain factions of the modelling community, where soil carbon is distributed among different pools, and decays according to first-order kinetics with pool-specific turnover constants, logically lead to steady state situations. Here, the total input equals the total efflux of carbon and there cannot be a long-term uptake of carbon by ecosystems. However, this theoretical deduction from first-order kinetic pool models seems to contradict a number of observations where long-term carbon uptake has been perceived or at least cannot be excluded (Schlesinger 1990; and see Chap. 11 by Gleixner et al., this volume).

This mostly theoretical chapter will address this apparent contradiction from a more conceptual modelling point of view. A number of modelling approaches to soil carbon dynamics will be reviewed and discussed with respect to their prediction of long-term carbon uptake dynamics. These modelling approaches can be classified into three broad categories: classical first-order decay models with fixed decay rate constants; quality-continuum concepts where it is assumed that, during decay, the quality and decomposability of soil organic matter decreases gradually; and

C. Wirth et al. (eds.), *Old-Growth Forests*, Ecological Studies 207,
DOI: 10.1007/978-3-540-92706-8_12, © Springer-Verlag Berlin Heidelberg, 2009

microbe-centred models where decay depends on the abundance and activity of microbes, which themselves depend on substrate availability (and environmental conditions).

It will be evident that the above-stated modellers' view is strongly contingent on first-order reaction kinetics paradigms, and that there exist both old and recent alternative model formulations predicting that, under certain conditions, soil carbon pools never reach a steady state.

12.2 Observations of Old-Growth Forest Carbon Balance

The carbon balance of old-growth forests is directly accessible via repeated biometric measurements of pool sizes (and component fluxes), through measurements of ecosystem-atmosphere CO_2 exchange (assuming that non-CO_2 fluxes and carbon losses to the hydrosphere are negligible), or indirectly via pool changes along chronosequences (assuming space-for-time substitution is valid). Recently, Pregitzer and Euskirchen (2004) have reviewed such studies, coming to the conclusion that there is a clearly age-dependent net ecosystem productivity in forests. Micrometeorological measurements often indicate a continuation of a strong sink function of forest ecosystems over centuries, while biometric measurements reveal lower net ecosystem carbon uptake. Both methodologies have their specific systematic errors, as discussed elsewhere (Belelli-Marchesini et al. 2007; Luyssaert et al. 2007), but provide strong indications that long-term carbon uptake by old-growth forests is possible [see e.g. Chaps. 5 (Wirth and Lichstein), 7 (Knohl et al.), 14 (Lichstein et al.), 15 (Schulze et al.), and 21 (Wirth), this volume]. In another convincing example, Wardle et al. (2003) show that an increase in carbon stocks in humus may continue for millennia; a sequestration rate of at least 5 – 40 g m^{-2} $year^{-1}$ was inferred from a chronosequence study with natural island forest sites that have had very different frequencies of fire disturbance depending on island size (see Chap. 9 by Wardle, this volume). Other studies and reviews have also revealed long-term carbon sequestration by soils (Syers et al. 1970; Schlesinger 1990). There are, however, at least two reasons to question if it is possible at all to experimentally determine the existence of a limit to carbon storage. Firstly, there is the question of the time required to reach a potential steady state. Ågren et al. (2007) show that it is likely that a steady state for soil carbon requires several millennia of constant litter input, a period well exceeding the time since the last glaciation in many areas. Secondly, anthropogenic disturbances during the last century may have disrupted previous steady states; current levels of nitrogen deposition in particular may have increased forest growth and induced a transient in forest carbon storage (see also Sect. 18.4 in Chap. 18 by Grace and Meir, this volume).

12.3 Is There a Theoretical Limit to Soil Carbon Storage?

12.3.1 Classical Carbon Pool Models

The classical paradigm of soil organic carbon modelling builds upon so-called first-order reaction kinetics, where the absolute rate of decay is proportional to the pool size (Jenny 1941):

$$\frac{dC}{dt} = -k \cdot C(t) \tag{12.1}$$

Usually, soil organic matter is then divided into several conceptual kinetically defined pools with individual decay rate constants *k*, and constant coefficients that determine the transfer between different pools. The simplest useful model that exhibits these pool-specific rate constants and transfer coefficients is the introductory carbon balance model proposed by Hénin and Dupuis (1945) or Andrén and Kätterer (1997) as depicted in Fig. 12.1. More complex models differ mostly in the number of carbon pools (Parton et al. 1988; Jenkinson et al. 1991; Hunt et al. 1996; Parton et al. 1998; Liski et al. 1999) and obey the general mathematical formulation as linear systems:

$$\frac{dC_i}{dt} = I_i - k_i C_i + \sum_j k_j h_{ij} C_j$$

or

$$\frac{d\mathbf{C}}{dt} = \begin{pmatrix} I_1 \\ \cdot \\ \cdot \\ \cdot \\ I_n \end{pmatrix} - \begin{pmatrix} k_1 C_1 \\ \cdot \\ \cdot \\ \cdot \\ k_n C_n \end{pmatrix} + \begin{pmatrix} 0 & h_{12} & \cdot & \cdot & h_{1n} \\ h_{21} & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ h_{n1} & h_{n2} & \cdot & \cdot & 0 \end{pmatrix} \cdot \begin{pmatrix} k_1 C_1 \\ \cdot \\ \cdot \\ \cdot \\ k_n C_n \end{pmatrix} = \mathbf{I} - \mathbf{KC} \tag{12.2}$$

where I_i is the input from primary production into each pool, k_i is the decay rate constant, and h_{ij} is the transfer coefficient from pool *i* into pool *j*. Where more pools are introduced, the larger the number of potential parameters (growing with the square of pools) and, consequently, the more flexibly the model can simulate carbon trajectories from long-term experiments. However, regardless of model complexity, all models relying on first-order kinetics predict a limit to carbon storage in the soil, i.e. given a quasi-constant carbon input to the soil, a dynamic equilibrium (steady-state) will be asymptotically reached with the equilibrium pool sizes of each being equal to $K^{-1}I$ (symbols as in Eq. 12.2). If input ceases, all pools will decrease to zero with infinite time. The length of time required for the asymptotic approach to steady state clearly depends on the smallest decay constant (the smallest real part of

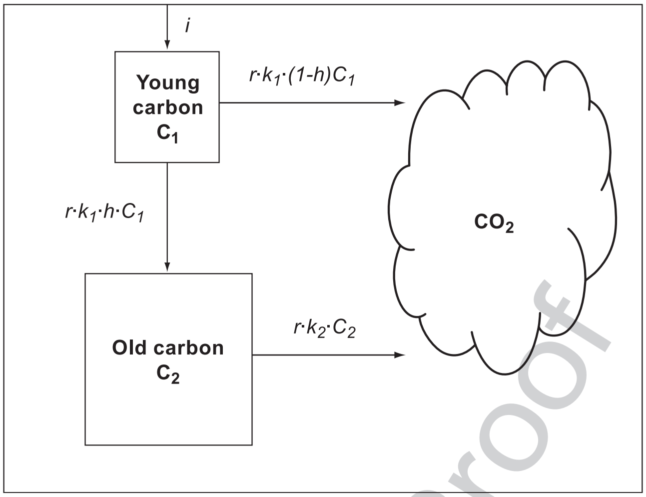


Fig. 12.1 Flow representation of the introductory carbon balance model (ICBM)

eigenvalues to matrix *K*). Hence, with sufficiently small decay rate constants, long-term sequestration of carbon in the soil can be modelled. Nevertheless, a theoretical limit to carbon sequestration remains a feature of this class of models. Climatic variability of the parameters around some mean value does not change this conclusion but complicates the calculation of the now quasi-steady state. One important assumption with this model is the constant rate of litter input. In a closed system with a limited amount of other essential elements (nutrients), increasing sequestration of carbon in soil pools would also imply sequestration of nutrients in the soil. This leaves less nutrients for vegetation, resulting in decreased litter production. With a decreasing nutrient:carbon ratio in the soil, soil carbon sequestration could go on forever.

12.3.2 Alternative Model Concepts of Soil Carbon Dynamics

The models following the classical paradigm as discussed above have two fundamental properties in common: (1) the intrinsic decay rate constants are constant in time, i.e. k_i varies at most around some constant mean as a result of varying environmental conditions such as soil temperature and moisture – in other words the properties of a pool are constant in time; (2) the decomposition of one carbon pool depends only on the state of the pool itself (i.e. the system is linear), not on other pools or microbial populations that are in turn influenced by other pools or nutrients. Relaxing either of these two assumptions leads to models where there is no theoretical limit to carbon sequestration, as discussed in the following sections.

12.3.2.1 Non-Constant Intrinsic Decay Rates

Consider an amount of carbon entering the soil at some point in time, and that the decay rate of this carbon cohort decreases over time (e.g. as a result of chemical transformation or bio-physical stabilisation). For simplicity, we assume that the half life, τ, of this cohort increases linearly over time, i.e. half life $\tau = \tau_0 + \beta t$. The dynamics of a single pool that does not receive any input would then be described by the following equations, where k is a function of time t.

$$C(t) = C_0 \cdot e^{-k(t) \cdot t}, \;\; k(t) = \frac{\ln(2)}{\tau_0 + \beta \cdot t} \qquad 12.3$$

In contrast to the single pool model, here decomposition slows over time. Although it does not become zero, complete decomposition of the substrate will never be reached, even given infinite time, since the cohort will reach an asymptotic size greater than zero:

$$C(t) \overset{t \to \infty}{\to} C_0 \cdot e^{\frac{\ln(2)}{\beta}} > 0 \qquad 12.4$$

Equation 12.4 shows that this change to a dynamic k leads to a very different dynamic, where carbon does not decay completely but stabilises at a certain amount. It is evident that, if new carbon is continually added to the system, this would lead to an infinite accumulation of carbon. This very simple theoretical ‘model’ thus shows that a relaxation of the first-order kinetic model can allow long-term carbon sequestration. Another formulation, which also leaves an indecomposable residue, is the asymptotic model favoured by Berg (e.g. Berg and McClaugherthy 2003).

Conceptually, one could regard the models above as very special cases of the “continuous-quality” model (Bosatta and Ågren 1991; Ågren and Bosatta 1996; Ågren et al. 1996), which postulates the existence of litter cohorts with defined quality q, where biomass quality diminishes by a function of q during each cycle. Both the microbial efficiency$e$ and the growth rate u then depend on q, and the carbon dynamics of a homogeneous substrate is described as:

$$\frac{dC(t)}{dt} = -f_C \cdot \frac{1 - e(q)}{e(q)} \cdot u(q) \cdot C(t) \qquad 12.5$$

with f_C being the fraction of carbon in microbes. The expression on the right hand side of this equation is related to first-order kinetics; however, the rate constants depend on q, and q changes (decreases) over time. Depending on how fast $e(q)$ goes to zero, a single cohort may disappear completely or leave an indecomposable residue. Soil organic matter then consists of the residues of all litter cohorts that have entered that soil. If each litter cohort leaves an indecomposable residue, there will be an infinite build-up of soil organic matter if the litter input can be sustained. However, even if every litter cohort eventually disappears completely, there will be a finite or infinite build-up of soil organic matter depending upon how rapidly $u(q)$ approaches zero with q relative to the behaviour of $e(q)$, and how rapidly the quality of a litter cohort decreases. For a more detailed discussion, the reader is referred to the literature cited above.

12.3.2.2 Rate Constant Dependent on Factors other than Pool Size

The decomposition models discussed above assume that the decay of a pool depends only on its own properties (first-order reaction kinetics). However, in (bio-)chemistry other reaction kinetics are more common, since the likelihood of multiple reactants coming together for a reaction often depends on the concentration of several reactants. Moreover, in biological systems, hence also the soil, reactions are catalysed by enzymes, so that reaction velocities may also depend on the activity of these. Fontaine and Barot (2005) turned the first-order reaction kinetics model of passively decaying soil organic matter (C_s) upside down by hypothesising that the decay of soil organic matter depends only on the microbial pool size (C_mic). The concept has been extended to differentiate between r- and K-strategists and interactions with the nitrogen cycle, but already their simplest formulation (Fig. 12.2) yields to a soil carbon pool never reaching steady state. The system can be described by the following two coupled differential equations (symbols as in Fig. 12.3):

$$\begin{aligned} \frac{dC_s}{dt} &= (s-a)\cdot C_{mic} \\ \frac{dC_{mic}}{dt} &= i + (a-s-r)\cdot C_{mic} \end{aligned} \tag{12.6}$$

For time going to infinity the following equations can be derived:

$$\begin{aligned} \frac{dC_s}{dt} &= \frac{i\cdot(s-a)}{-a+s+r} \\ C_{mic,ss} &= \frac{i}{-a+s+r} \end{aligned} \tag{12.7}$$

Hence, while the microbial pool reaches a steady state, the soil carbon pool continues to increase or decrease linearly with a rate related to carbon input, microbial efficiency and mortality rates. A possibly more realistic representation might be to include a limitation of the carbon decay by microbes and the carbon pool itself. For instance, a generalisation of the introductory carbon balance model (Fig. 12.1) would be the following two equations:

$$\begin{aligned} \frac{dC_1}{dt} &= I - k_1\cdot C_1 \\ \frac{dC_2}{dt} &= h\cdot k_1\cdot C_1 - \left[\left(\frac{C_1}{C_2}\right)^{\alpha}\cdot k_2\right]\cdot C_2 \end{aligned} \tag{12.8}$$

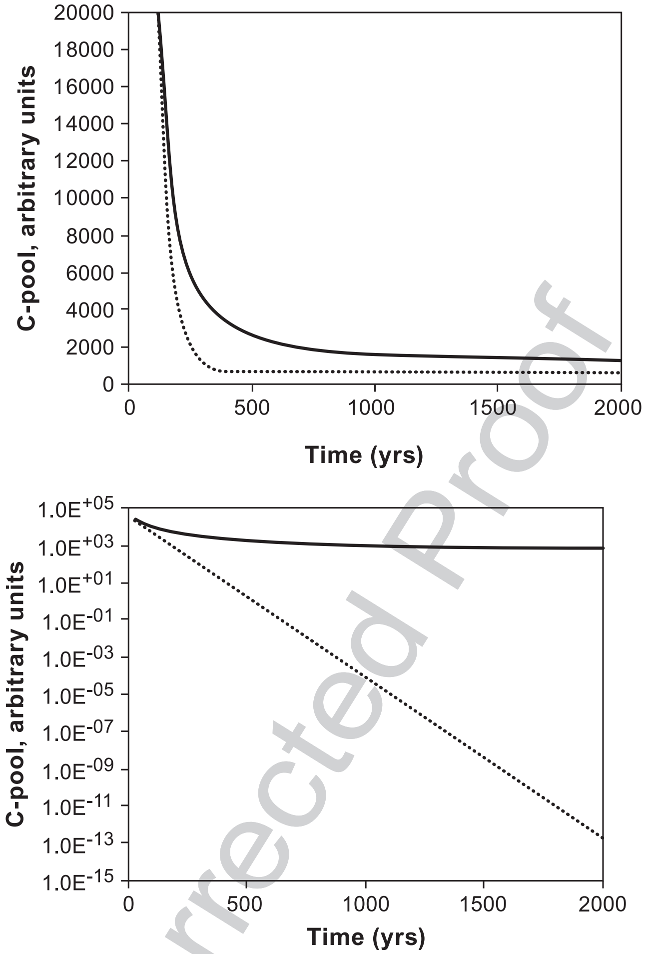
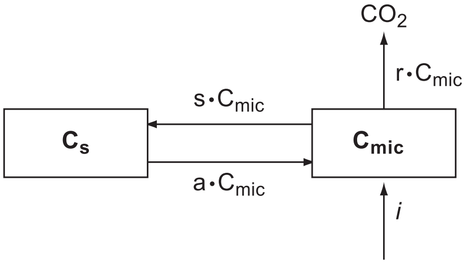


Fig. 12.2 Single pool vs single cohort decomposition dynamics (without input to the pool/cohort). *Solid line* According to first order reaction kinetics with $k = 0.02$ year^{-1} (i.e. a half time of 35 years), *dotted line* according to Eq. 12.5 with the same initial half time $\alpha = 0$ and $\alpha = 0.15$. *Upper panel* Linear *y*-axis, *lower panel* logarithmic

Fig. 12.3 Decomposition model, where the decay of soil carbon (C_s) does not depend on its own pool size, but on the microbial pool (C_{mic}), which itself depends mainly on the input of fresh material (*i*). *r*, *s*, *a* Rate constants that describe utilisation of substrate by microbes and their mortality. After Fontaine and Barot (2005)



with the only difference being that the decay constant of the slow pool (C_2) is now dependent on the ratio of fresh (supports biomass) and slow pool sizes, parameterised with the exponent α.

Over longer time periods ($t >> 1/k_1$), the fast pool can be considered as being in steady state (i.e. $C_{1,ss} = I/k_1$), the dynamics of the slow pool can be described by

$$\frac{dC_2}{dt} = h \cdot I - \left[\left(\frac{I/k_1}{C_2}\right)^{\alpha} \cdot k_2\right] \cdot C_2 = h \cdot I - \left({}^{I}\!/_{k_1}\right)^{\alpha} \cdot k_2 \cdot {C_2}^{1-\alpha} \qquad 12.9$$

with the long-term dynamics depending on the parameter α. With $\alpha \neq 1$ the system is behaving simply as a classical first-order kinetic pool model, asymptotically reaching a steady state, while with $\alpha = 1$ the dynamics becomes analogous to those presented by Fontaine and Barot (2005), where the decay rate is independent of C_2 and the pool size increases linearly over time, never reaching a steady state.

Hence, whether or not a steady state is reached can be built into the model formulation a priori, but will in certain cases depend on specific parameter values. The classical pool models are such that steady states will always be reached, whereas Berg's asymptotic model always produces a non-steady state. Both the generalisation of the ICBM suggested above and the Fontaine-Barot model allow for finite and infinite soil organic matter stores. However, both share the unsatisfactory property of being structurally unstable in the sense that it is only for one single parameter value that the generalisation of the ICBM model leads to anything other than finite soil organic matter stores and the Fontaine-Barot model lacks steady state (there will either be an infinite amount of soil organic matter or none at all). Of the models discussed here, the continuous-quality model is the most general in that it allows all possibilities and is stable over large ranges of parameter values. One challenge is to discriminate the models with observed data as indicated in Fig. 12.4. The single-pool first order model can be excluded, as has long been known (Jenny 1941; Meentemeyer 1978). However, the two alternative models and the different parameterisations of the generalised ICBM model (gICBM) can barely be distinguished over the first 300 years in time. In fact, the gICBM model with $\alpha = 1$, which is analogous to the simplest Fontaine and Barot model, is almost indistinguishable over the whole time series (data not shown).

12.3.3 *Complicating Factors not Considered*

Even simple model formulations, which all bear some plausibility and have been applied in various studies, yield different predictions of whether long-term carbon uptake in forest soils is possible or not. Furthermore, there are certainly a number of additional factors that easily introduce further interactions that may result in additional non-steady state trajectories. Although beyond the scope of this theoretical chapter, we will briefly mention some of these, including references to the literature:

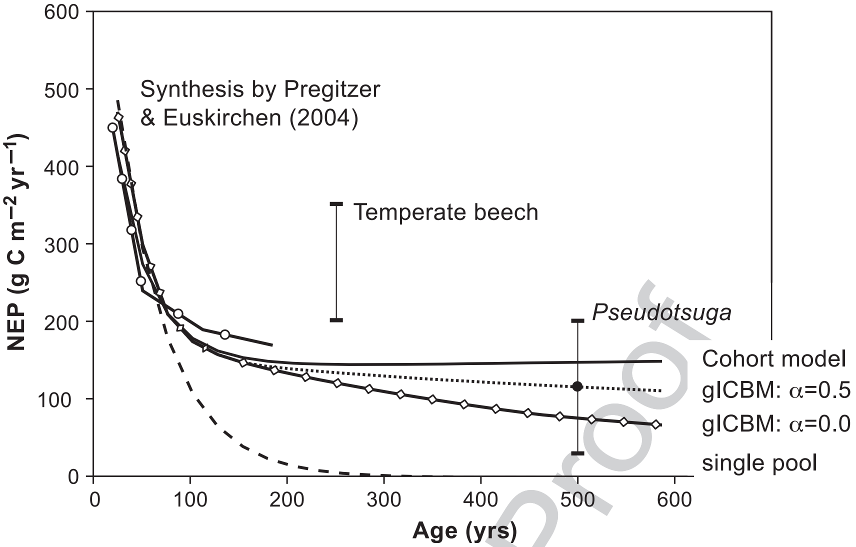


Fig. 12.4 Trajectory of net ecosystem productivity (NEP) as predicted by different types of models with some observed values as in Fig. 12.2. *Dashed line* One pool first-order kinetics model, *solid lines* results from the generalised ICBM model (gICBM) with varying α (cf. Fig. 12.2 and text) and the cohort model. The *line/open circles* contains averaged data from Pregitzer and Euskirchen (2004), and is augmented by two example studies from Knohl et al. (2003) (temperate beech) and Paw U et al. (2002)/Harmon et al. (2004) (*Pseudotsuga*) for illustrative purposes

- Interactions with the nitrogen cycle might lead to retardation of decomposition through either a limitation or excess of nitrogen (e.g. Berg and Matzner 1997; Magill and Aber 1998; Zak et al. 2006).
- Several carbon stabilisation mechanisms via interactions with the mineral soil matrix have been discussed (e.g. Torn et al. 1997; von Lutzow et al. 2006). It is not clear to what extent such interactions are included in model parameters.
- Transport of carbon into deeper layers where unfavourable conditions for decomposition prevail (e.g. energy or oxygen limitation). A particular example is that of peatlands, where the addition of new litter can push the underlying soil organic matter below the water table thus drastically altering environmental conditions (e.g. Frolking et al. 2001).
- Fires can produce very stable carbon compounds (e.g. charcoal) (Czimczik et al. 2003; Gonzalez-Perez et al. 2004).

12.4 Perspectives for a New Generation of Models

It is probably impossible to determine experimentally whether soils have a non-limited capacity to store carbon, not only because it can take several thousands of years to reach a potential steady-state but also because anthropogenic disturbances and climatic changes may have disrupted previous steady states. Moreover, as discussed in Sect. 12.1.3.2, it is not possible to discriminate the different models on the basis of long-term observations of organic stocks. Indeed, such observations are sparse and the variability of measurements precludes testing of the different models. However, these limitations will not prevent us from evaluating the storage capacity of the ecosystems, but such evaluation requires understanding and modelling of the mechanisms controlling long-term carbon accumulation in soils, and testing of these models at the mechanism scale. In the following, we present two tracks of research and experiments that could substantially improve the quality of predictions of future models.

12.4.1 Models Connecting the Decay Rate of Soil Carbon to the Size, Activity and Functional Diversity of Microbe Populations

The use of the classical first-order reaction kinetic, which assumes that the decay rate is limited by the size of the carbon pool, is relevant when describing the decomposition of energy-rich litter compounds. Indeed, these compounds induce a rapid growth of microbes and the reaction velocity is quickly limited by the amount of remaining substrate (Swift et al. 1979). However, this limitation does not apply to the recalcitrant fraction of soil organic matter (Schimel and Weintraub 2003; Fontaine and Barot 2005). In contrast, the decay rate of recalcitrant carbon seems limited by the size of the microbe population since less than 5% soil carbon compounds are colonised by soil microbes, and the increase in microbe populations induced by the supply of fresh carbon accelerates the decomposition of soil carbon (Paul and Clark 1989; Kuzyakov et al. 2000). Some recent theoretical work has shown that including microbial dynamics and functional diversity in models profoundly changes predictions and allows some important empirical results, such as the long-term accumulation of carbon in ecosystems, to be explained (Fontaine and Barot 2005; Wutzler and Reichstein 2007). These results should stimulate the building of a new generation of models connecting microbial ecology to biogeochemical cycles, and lead these two fields to combine their scientific knowledge. A first step towards such models is to find an equation where the decay rate of recalcitrant carbon is controlled by the size of active microbe populations. Several equations are possible, such as this adapted version of the Michaelis–Menten equation:

$$\frac{dC_s}{dt} = \frac{a \, . \, C_{mic} \, . \, C_s}{K + C_s} \qquad 12.10$$

which assumes that the decay rate of soil carbon can increase infinitely as microbial biomass (C_{mic}) increases, and the ratio-dependent equation (Arditi and Saiah 1992),

$$\frac{dC_s}{dt} = \frac{a}{\frac{K}{C_s} + \frac{1}{C_{mic}}} \qquad 12.11$$

which considers that the size of the soil carbon pool (C_s) and the size of microbial biomass (C_{mic}) limit the decay rate. In these equations, *a* is the consumption rate of recalcitrant carbon by the decomposers, and *K* is a constant. The type of equation and the value of parameters greatly influence the predictions of models (Arditi and Saiah 1992; Schimel and Weintraub 2003). However, it is now possible to manipulate the size of the microbial biomass and to measure the decay rate of recalcitrant old soil organic matter thanks to a recent method based on the supply of dual-labelled (^{13}C and ^{14}C) cellulose (Fontaine et al. 2007). Moreover, the size of the soil organic matter pool can be manipulated by diluting soil with sand. This means that it becomes feasible to determine how the size of soil carbon pool and that of microbe populations co-limit soil carbon decay rate and to discriminate between different equations. Determining the value of parameters requires that populations of soil organic matter decomposers be identified among all other populations stimulated by the addition of cellulose. Again, the recent development of molecular methods such as the sequencing of microbial DNA and the possible separation of ^{13}C- and ^{12}C-DNA makes such identification possible (Radajewski et al. 2000; Bernard et al. 2007). Therefore, we suggest that microbiologists and geochemists should set up joint experiments under controlled conditions in order to build a more realistic and microbe-oriented mathematical description of recalcitrant soil carbon decomposition.

12.4.2 Determining the Mechanisms Stabilising Recalcitrant Soil Carbon

Although little is known about the stability of soil carbon compounds, a central question is whether the stabilisation of soil carbon necessarily involves a chemical or physical linkage with soil minerals. If soil carbon persists only when it is bound to soil minerals, and these exist in forms that microbes cannot access, then the storing capacity of soils is limited. Indeed, the amount of carbon that minerals can fix depends on the specific area of these minerals (Eusterhues et al. 2005), which determines the number of binding sites available and the cationic exchange capacity of the minerals (Wattel-Koekkoek and Buurman 2004), which in turn determines the strength with which carbon is retained. More globally, theory predicts that the storing capacity of many soils worldwide has reached its maximum. Moreover, this capacity is likely to decrease due to a decreasing capacity of minerals to fix carbon induced by the weathering of minerals (Torn et al. 1997).

Other theories and experiments, however, suggest that the stability of soil carbon also results from biochemically recalcitrant compounds (Ågren and Bosatta 1996;

Stout et al. 1981; Blondeau 1988; Fontaine et al. 2007). These compounds may persist in soils because the acquisition of energy from such substrates cannot sustain microbial activity. Under such circumstances, theory predicts that soils have no limited capacity to accumulate soil carbon (Fontaine and Barot 2005; Wutzler and Reichstein 2007).

We conclude that the storing capacity of soils depends greatly on the mechanisms involved in the stabilisation of organic carbon and that these mechanisms should be explicitly described in future models. Further research is needed to determine whether a linkage between organic carbon and minerals is necessary to stabilise carbon over a long-term timescale. It would be particularly interesting to measure the turnover of free recalcitrant soil carbon using ^{14}C methods and to determine which factors limit this turnover. Moreover, the ^{14}C dating of soil carbon pools indicates that, irrespective of the mechanism of carbon stabilisation (mineral stabilisation vs biochemical stabilisation), the decomposition of organic carbon is slowed but not stopped in surface layers. This result can be explained by the fact that some microbe populations are able to degrade recalcitrant compounds with their enzymes because they use fresh carbon (litter, exudates) as a energy source (Fontaine et al. 2007). Future theoretical and experimental studies are needed to understand the benefit for microbes of decomposing these recalcitrant compounds, and the factors that could modulate the use of such substrates by the soil microbial community. This means that understanding the capacity of soils to store carbon finally requires an understanding of microbial ecology and biology.

12.5 Conclusion

As shown here, several possible formulations of soil carbon dynamics allow situations where a steady state of soil carbon is never reached. Hence, from a theoretical point of view, there is no justification for excluding the possibility of long-term old-growth forest carbon uptake as has sometimes been suggested from the classical pool model perspective. Rather, we need initiatives and experimental designs that can distinguish between – and potentially exclude – the modelling paradigms that currently co-exist. Since there are already indications that classical first-order kinetic carbon models have severe limitations (because they do not adequately describe the role of soil biota and the interaction between microbes, soil organic matter and soil minerals), the results and predictions from these models – at least in forests – should be approached carefully, with critical assessment of the limitations, and they should not be used for long-term extrapolation. Nevertheless, their merit for assessments and short-term predictions is undoubted (e.g. Kätterer and Andrén 1999; Falloon et al. 2000). There is also a clear need to start to examine the fundamentals of how decomposers attack soil organic matter and to what extent decomposer biomass is dependent upon total soil organic matter or only a fraction of it. The Fontaine-Barot model (Fontaine and Barot 2005) is one example of a model that takes a different perspective. The models by Weintraub and Schimel (2003) and Neill and Gignoux (2006) are two other alternatives, as discussed together with other models in Wutzler and Reichstein (2007).

From a scientific-theory perspective the example of soil carbon storage in old-growth forests reminds us that models should never be confounded with the truth and that they must be critically examined and tested again and again. Otherwise models can turn into fairy tales.

References

Ågren GI, Bosatta E (1996) Quality: a bridge between theory and experiment in soil organic matter studies. Oikos 76:522–528

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

Ågren GI, Johnson DW, Kirschbaum M, Bosatta E (1996) Ecosystem physiology – soil organic matter. In: Melillo JM, Hall DO, Ågren GI (eds) Scope 56. Global change: effects on coniferous forests and grasslands. Scope, pp 207–228

Ågren GI, Hyvönen R, Nilsson T (2007) Are Swedish forest soils sinks or sources for CO_2 – model analyses based on forest inventory data. Biogeochemistry 82:217–227

Arditi R, Saiah H (1992) Empirical evidence of the role of heterogeneity in ratio-dependent consumption. Ecology 73:1544–1551

Belelli-Marchesini L, Papale D, Reichstein M, Vuichard N, Tchebakova N, Valentini R (2007) Carbon balance assessment of a natural steppe of southern Siberia by multiple constraint approach. Biogeosciences 4:165–208

Berg B, Matzner E (1997) Effect of N deposition on decomposition of plant litter and soil organic matter in forest systems. Environ Rev 5:1–25

Berg B, McClaugherty C (2003) Plant litter – decomposition, humus formation, carbon sequestration. Springer, Berlin

Bernard L, Mougel C, Maron PA, Nowak V, Lévêque J, Henault C, Haichar FZ, Berge O, Marol C, Balesdent J, Gibiat F, Lemanceau P, Ranjard L (2007) Dynamics and identification of soil microbial populations actively assimilating carbon from ^{13}C-labelled wheat residue as estimated by DNA- and RNA-SIP techniques. Environ Microbiol 9:752–764

Blondeau R (1988) Biodegradation of natural and synthetic humic acids by the white rot fungus *Phanerochaete chrysosporium*. Appl Environ Microbiol 55:1282–1285

Bosatta E, Ågren GI (1991) Dynamics of carbon and nitrogen in the soil: a generic theory. Am Nat 138:227–245

Czimczik CI, Preston CM, Schmidt MWI, Schulze ED (2003) How surface fire in Siberian Scots pine forests affects soil organic carbon in the forest floor: stocks, molecular structure, and conversion to black carbon (charcoal). Global Biogeochem Cycles 17: 20.1–20.14

Eusterhues K, Rumpel C, Kögel-Knabner I (2005) Organo-mineral associations in sandy acid forest soils: importance of specific surface area, iron oxides and micropores. Eur J Soil Sci 56:753–763

Falloon P, Smith P, Coleman K, Marshall S (2000) How important is inert organic matter for predictive soil carbon modelling using the Rothamsted carbon model? Soil Biol Biochem 32:433–436

Fontaine S, Barot S (2005) Size and functional diversity of microbe populations control plant persistence and long-term soil carbon accumulation. Ecol Lett 8:1075–1087

Fontaine S, Barot S, Barré P, Bdioui N, Mary B, Rumpel C (2007) Stability of organic carbon in deep soil layers controlled by fresh carbon supply. Nature 450:277–280

Frolking S, Roulet NT, Moore TR, Richard PJH, Lavoie M, Muller SD (2001) Modeling northern peatland decomposition and peat accumulation. Ecosystems 4:479–498

Gonzalez-Perez JA, Gonzalez-Vila FJ, Almendros G, Knicker H (2004) The effect of fire on soil organic matter – a review. Environ Int 30:855–870

Harmon ME, Bible K, Ryan MJ, Shaw D, Chen H, Klopatek J, Li X (2004) Production, respiration, and overall carbon balance in an old-growth Pseudotsuga/Tsuga forest ecosystem. Ecosystems 7:498–512

Hénin S, Dupuis M (1945) Essai de bilan de la matière organique du sol. Ann Agron 11:17–29

Hunt ER, Piper SC, Nemani R, Keeling CD, Otto RD, Running SW (1996) Global net carbon exchange and intra-annual atmospheric CO_2 concentrations predicted by an ecosystem process model and three-dimensional atmospheric transport model. Global Biogeochem Cycles 10:431–456

Jenkinson DS, Adams DE, Wild A (1991) Model estimates of CO_2 emissions from soil in response to global warming. Nature 351:304–306

Jenny H (1941) Factors of soil formation. A system of quantitative pedology. McGraw-Hill, New York

Kätterer T, Andrén O (1999) Long-term agricultural field experiments in Northern Europe: analysis of the influence of management on soil carbon stocks using the ICBM model (vol 72, p 165, 1999). Agric Ecosyst Environ 75(1–2):145–146

Knohl A, Schulze E-D, Kolle O, Buchmann N (2003) Large carbon uptake by an unmanaged 250-year-old deciduous forest in Central Germany. Agric For Meteorol 118:151–167

Kuzyakov Y, Friedel JK, Stahr K (2000) Review of mechanisms and quantification of priming effects. Soil Biol Biochem 32:1485–1498

Liski J, Ilvesniemi H, Mäkelä A, Westman KJ (1999) CO_2 emissions from soil in response to climatic warming are overestimated – the decomposition of old soil organic matter is tolerant of temperature. Ambio 28:171–174

Luyssaert S, Inglima I, Jung M, Richardson AD, Reichstein M, Papale D, Piao SL, Schulze ED, Wingate L, Matteucci G, Aragao L, Aubinet M, Beers C, Bernhofer C, Black KG, Bonal D, Bonnefond J-M, Chambers J, Ciais P, Cook B, Davis KJ, Dolman AJ, Gielen B, Goulden M, Grace J, Granier A, Grelle A, Griffis T, Grünwald T, Guidolotti G, Hanson PJ, Harding R, Hollinger DY, Hutyra LR, Kolari P, Kruijt B, Kutsch W, Lagergren F, Laurila T, Law BE, Le Maire G, Lindroth A, Loustau D, Malhi Y, Mateus J, Migliavacca M, Misson L, Montagnani L, Moncrieff J, Moors E, Munger JW, Nikinmaa E, Ollinger SV, Pita G, Rebmann C, Roupsard O, Saigusa N, Sanz MJ, Seufert G, Sierra C, Smith M-L, Tang J, Valentini R, Vesala T, Janssens IA (2007) CO_2 balance of boreal, temperate, and tropical forests derived from a global database. Glob Change Biol 13:2509–2537

Magill AH, Aber JD (1998) Long-term effects of experimental nitrogen additions on foliar litter decay and humus formation in forest ecosystems. Plant Soil 203:301–311

Meentemeyer V (1978) Macroclimate and lignin control of litter decomposition rates. Ecology 59:465–472

Neill C, Gignoux J (2006) Soil organic matter decomposition driven by microbial growth: a simple model for a complex network of interactions. Soil Biol Biochem 38:803–811

Parton WJ, Stewart JWB, Cole CV (1988) Dynamics of C, N, P and S in grassland soils: a model. Biogeochemistry 5:109–131

Parton WJ, Hartman M, Ojima D, Schimel D (1998) Daycent and its land surface submodel: description and testing. Global Planetary Change 19:35–48

Paul EA, Clark FE (1989) Soil microbiology and biochemistry. Academic, San Diego

Paw U KT, Falk M, Suchanek TH, Ustin SL, Chen JQ, Park YS, Winner WE, Thomas SC, Hsiao TC, Shaw RH, King TS, Pyles RD, Schroeder M, Matista AA (2004) Carbon dioxide exchange between an old-growth forest and the atmosphere. Ecosystems 7:513–524

Pregitzer KS, Euskirchen ES (2004) Carbon cycling and storage in world forests: biome patterns related to forest age. Glob Change Biol 10:2052–2077

Radajewski S, Ineson P, Parekh NR, Murell JC (2000) Stale-isotope probing as a tool in microbial ecology. Nature 403:646–649

Schimel JP, Weintraub MN (2003) The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: a theoretical model. Soil Biol Biochem 35:549–563

Schlesinger WH (1990) Evidence from chronosequence studies for a low carbon storage potential of soils. Nature 348:232–234

Stout JD, Goh KM, Rafter TA (1981) Chemistry and turnover of naturally occurring resistant organic compounds in soil. In: Paul EA, Ladd JN (eds) Soil biochemistry. New York, pp 1–73

Swift MJ, Heal OW, Anderson JM (1979) Decomposition in terrestrial ecosystems, Blackwell, Oxford

Syers JK, Adams JA, Walker TW (1970) Accumulation of organic matter in a chronosequence of soils developed on wind-blown sand in New Zealand. J. Soil Sci 21:146–153

Torn MS, Trumbore SE, Chadwick OA, Vitousek PM, Hendricks DM (1997) Mineral control of soil organic carbon storage and turnover. Nature 389:170–173

Von Lutzow M, Kögel-Knabner I, Ekschmitt K, Matzner E, Guggenberger G, Marschner, Flessa http://www.ingentaconnect.com/content/bsc/ejss/2006/00000057/00000004/art00002;jsessionid=38qe7u815i43h.alice?format=print - aff_6 (2006) Stabilisation of organic matter in temperate soils: mechanisms and their relevance under different soil conditions – a review. Eur J Soil Sci 57:426–445

Wardle DA, Hornberg G, Zackrisson O, Kalela-Brundin M, Coomes DA (2003) Long-term effects of wildfire on ecosystem properties across an island area gradient. Science 300:972–975

Wattel-Koekkoek EJW, Buurman P (2004) Mean residence time of kaolinite and smectite-bound organic matter in Mozambiquan soils. Soil Sci Soc Am J 68:154–161

Weintraub MN, Schimel JP (2003) Interactions between carbon and nitrogen mineralisation and soil organic matter chemistry in arctic tundra soils. Ecosystems 6:129–143

Wutzler T, Reichstein M (2007) Soils apart from equilibrium – consequences for soil carbon balance modelling. Biogeoscience 4:125–136

Zak DR, Holmes WE, Tomlinson MJ, Pregitzer KS, Burton AJ (2006) Microbial cycling of C and N in northern hardwood forests receiving chronic atmospheric NO_3-deposition. Ecosystems 9:242–253