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

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

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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

36 microbe-centred models where decay depends on the abundance and activity of
37 microbes, which themselves depend on substrate availability (and environmental
38 conditions).
39   It will be evident that the above-stated modellers' view is strongly contingent on
40 first-order reaction kinetics paradigms, and that there exist both old and recent
41 alternative model formulations predicting that, under certain conditions, soil carbon
42 pools never reach a steady state.

12.2   Observations of Old-Growth Forest Carbon Balance

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

12.3 Is There a Theoretical Limit to Soil Carbon Storage? 73

12.3.1 Classical Carbon Pool Models 74

The classical paradigm of soil organic carbon modelling builds upon so-called first- 75
order reaction kinetics, where the absolute rate of decay is proportional to the pool 76
size (Jenny 1941): 77

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

Usually, soil organic matter is then divided into several conceptual kinetically 78
defined pools with individual decay rate constants k, and constant coefficients 79
that determine the transfer between different pools. The simplest useful model 80
that exhibits these pool-specific rate constants and transfer coefficients is the 81
introductory carbon balance model proposed by Hénin and Dupuis (1945) or 82
Andrén and Kätterer (1997) as depicted in Fig. 12.1. More complex models differ 83
mostly in the number of carbon pools (Parton et al. 1988; Jenkinson et al. 1991; 84
Hunt et al. 1996; Parton et al. 1998; Liski et al. 1999) and obey the general 85
mathematical formulation as linear systems: 86

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

or

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

$$12.2$$

where I_i is the input from primary production into each pool, k_i is the decay rate 87
constant, and h_{ij} is the transfer coefficient from pool i into pool j. Where more pools 88
are introduced, the larger the number of potential parameters (growing with the 89
square of pools) and, consequently, the more flexibly the model can simulate carbon 90
trajectories from long-term experiments. However, regardless of model complexity, 91
all models relying on first-order kinetics predict a limit to carbon storage in the soil, 92
i.e. given a quasi-constant carbon input to the soil, a dynamic equilibrium (steady- 93
state) will be asymptotically reached with the equilibrium pool sizes of each being 94
equal to $K^{-1}I$ (symbols as in Eq. 12.2). If input ceases, all pools will decrease to 95
zero with infinite time. The length of time required for the asymptotic approach to 96
steady state clearly depends on the smallest decay constant (the smallest real part of 97
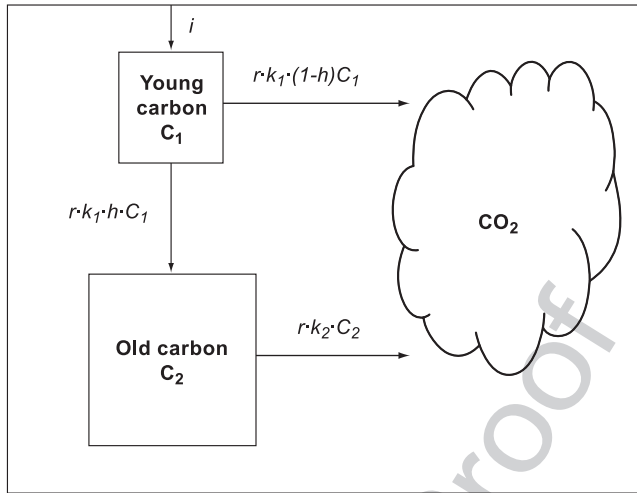
Fig. 12.1 Flow representation of the introductory carbon balance model (ICBM)

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

12.3.2 Alternative Model Concepts of Soil Carbon Dynamics

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

12.3.2.1 Non-Constant Intrinsic Decay Rates 119

Consider an amount of carbon entering the soil at some point in time, and that the 120
decay rate of this carbon cohort decreases over time (e.g. as a result of chemical 121
transformation or bio-physical stabilisation). For simplicity, we assume that the half 122
life, τ, of this cohort increases linearly over time, i.e. half life $\tau = \tau_0 + \beta t$. The 123
dynamics of a single pool that does not receive any input would then be described 124
by the following equations, where k is a function of time t. 125

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

In contrast to the single pool model, here decomposition slows over time. Although 126
it does not become zero, complete decomposition of the substrate will never be 127
reached, even given infinite time, since the cohort will reach an asymptotic size 128
greater than zero: 129

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

Equation 12.4 shows that this change to a dynamic k leads to a very different 130
dynamic, where carbon does not decay completely but stabilises at a certain amount. 131
It is evident that, if new carbon is continually added to the system, this would lead to 132
an infinite accumulation of carbon. This very simple theoretical 'model' thus shows 133
that a relaxation of the first-order kinetic model can allow long-term carbon seques- 134
tration. Another formulation, which also leaves an indecomposable residue, is the 135
asymptotic model favoured by Berg (e.g. Berg and McClaugherthy 2003). 136

   Conceptually, one could regard the models above as very special cases of the 137
"continuous-quality" model (Bosatta and Ågren 1991; Ågren and Bosatta 1996; 138
Ågren et al. 1996), which postulates the existence of litter cohorts with defined 139
quality q, where biomass quality diminishes by a function of q during each cycle. 140
Both the microbial efficiency e and the growth rate u then depend on q, and the 141
carbon dynamics of a homogeneous substrate is described as: 142

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

with f_C being the fraction of carbon in microbes. The expression on the right hand 143
side of this equation is related to first-order kinetics; however, the rate constants 144
depend on q, and q changes (decreases) over time. Depending on how fast $e(q)$ goes 145
to zero, a single cohort may disappear completely or leave an indecomposable 146
residue. Soil organic matter then consists of the residues of all litter cohorts that 147
have entered that soil. If each litter cohort leaves an indecomposable residue, there 148
will be an infinite build-up of soil organic matter if the litter input can be sustained. 149
However, even if every litter cohort eventually disappears completely, there will be 150

151 a finite or infinite build-up of soil organic matter depending upon how rapidly $u(q)$
152 approaches zero with q relative to the behaviour of $e(q)$, and how rapidly the quality
153 of a litter cohort decreases. For a more detailed discussion, the reader is referred to
154 the literature cited above.

12.3.2.2 Rate Constant Dependent on Factors other than Pool Size

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

$$\frac{dC_s}{dt} = (s - a) \cdot C_{mic}$$
$$\frac{dC_{mic}}{dt} = i + (a - s - r) \cdot C_{mic}$$

12.6

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

$$\frac{dC_s}{dt} = \frac{i \cdot (s - a)}{-a + s + r}$$
$$C_{mic,ss} = \frac{i}{-a + s + r}$$

12.7

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

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

12.8

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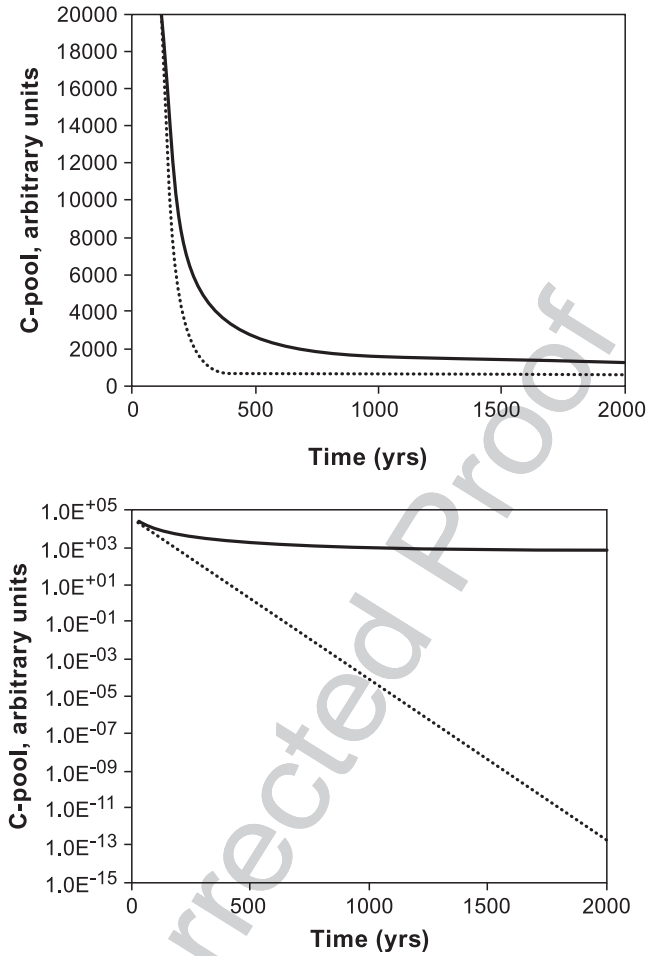

Fig. 12.2 Single pool vs single cohort decomposition dynamics (without input to the pool/cohort). *Solid line* According to first order reaction kinetics with $k = 0.02$ year^{-1} (i.e. a half time of 35 years), *dotted line* according to Eq. 12.5 with the same initial half time $\alpha = 0$ and $\alpha = 0.15$. *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)
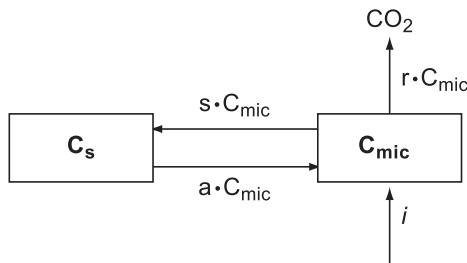
176 with the only difference being that the decay constant of the slow pool (C_2) is now
177 dependent on the ratio of fresh (supports biomass) and slow pool sizes, parame-
178 terised with the exponent α.

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

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

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

186   Hence, whether or not a steady state is reached can be built into the model
187 formulation a priori, but will in certain cases depend on specific parameter values.
188 The classical pool models are such that steady states will always be reached,
189 whereas Berg's asymptotic model always produces a non-steady state. Both the
190 generalisation of the ICBM suggested above and the Fontaine-Barot model allow
191 for finite and infinite soil organic matter stores. However, both share the unsatisfac-
192 tory property of being structurally unstable in the sense that it is only for one single
193 parameter value that the generalisation of the ICBM model leads to anything other
194 than finite soil organic matter stores and the Fontaine-Barot model lacks steady
195 state (there will either be an infinite amount of soil organic matter or none at all). Of
196 the models discussed here, the continuous-quality model is the most general in that
197 it allows all possibilities and is stable over large ranges of parameter values. One
198 challenge is to discriminate the models with observed data as indicated in Fig. 12.4.
199 The single-pool first order model can be excluded, as has long been known (Jenny
200 1941; Meentemeyer 1978). However, the two alternative models and the different
201 parameterisations of the generalised ICBM model (gICBM) can barely be distin-
202 guished over the first 300 years in time. In fact, the gICBM model with $\alpha = 1$, which
203 is analogous to the simplest Fontaine and Barot model, is almost indistinguishable
204 over the whole time series (data not shown).

12.3.3 *Complicating Factors not Considered*

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

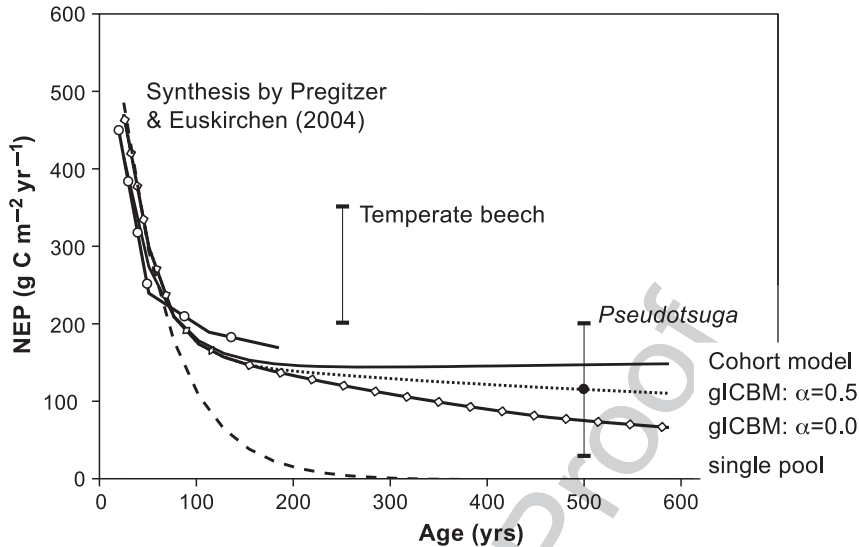12 Is There a Theoretical Limit to Soil Carbon Storage in Old-Growth Forests

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   213
  through either a limitation or excess of nitrogen (e.g. Berg and Matzner 1997;   214
  Magill and Aber 1998; Zak et al. 2006).   215
- Several carbon stabilisation mechanisms via interactions with the mineral soil   216
  matrix have been discussed (e.g. Torn et al. 1997; von Lutzow et al. 2006). It is   217
  not clear to what extent such interactions are included in model parameters.   218
- Transport of carbon into deeper layers where unfavourable conditions for de-   219
  composition prevail (e.g. energy or oxygen limitation). A particular example is   220
  that of peatlands, where the addition of new litter can push the underlying soil   221
  organic matter below the water table thus drastically altering environmental   222
  conditions (e.g. Frolking et al. 2001).   223
- Fires can produce very stable carbon compounds (e.g. charcoal) (Czimczik et al.   224
  2003; Gonzalez-Perez et al. 2004).   225

12.4   Perspectives for a New Generation of Models   226

It is probably impossible to determine experimentally whether soils have a non-   227
limited capacity to store carbon, not only because it can take several thousands of   228
years to reach a potential steady-state but also because anthropogenic disturbances   229

230 and climatic changes may have disrupted previous steady states. Moreover, as
231 discussed in Sect. 12.1.3.2, it is not possible to discriminate the different models
232 on the basis of long-term observations of organic stocks. Indeed, such observations
233 are sparse and the variability of measurements precludes testing of the different
234 models. However, these limitations will not prevent us from evaluating the storage
235 capacity of the ecosystems, but such evaluation requires understanding and model-
236 ling of the mechanisms controlling long-term carbon accumulation in soils, and
237 testing of these models at the mechanism scale. In the following, we present two
238 tracks of research and experiments that could substantially improve the quality of
239 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

243 The use of the classical first-order reaction kinetic, which assumes that the decay
244 rate is limited by the size of the carbon pool, is relevant when describing the
245 decomposition of energy-rich litter compounds. Indeed, these compounds induce
246 a rapid growth of microbes and the reaction velocity is quickly limited by the
247 amount of remaining substrate (Swift et al. 1979). However, this limitation does not
248 apply to the recalcitrant fraction of soil organic matter (Schimel and Weintraub
249 2003; Fontaine and Barot 2005). In contrast, the decay rate of recalcitrant carbon
250 seems limited by the size of the microbe population since less than 5% soil carbon
251 compounds are colonised by soil microbes, and the increase in microbe populations
252 induced by the supply of fresh carbon accelerates the decomposition of soil carbon
253 (Paul and Clark 1989; Kuzyakov et al. 2000). Some recent theoretical work has
254 shown that including microbial dynamics and functional diversity in models pro-
255 foundly changes predictions and allows some important empirical results, such as
256 the long-term accumulation of carbon in ecosystems, to be explained (Fontaine and
257 Barot 2005; Wutzler and Reichstein 2007). These results should stimulate the
258 building of a new generation of models connecting microbial ecology to biogeo-
259 chemical cycles, and lead these two fields to combine their scientific knowledge. A
260 first step towards such models is to find an equation where the decay rate of
261 recalcitrant carbon is controlled by the size of active microbe populations. Several
262 equations are possible, such as this adapted version of the Michaelis–Menten
263 equation:

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

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

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

which considers that the size of the soil carbon pool (C_s) and the size of microbial 266
biomass (C_{mic}) limit the decay rate. In these equations, a is the consumption rate of 267
recalcitrant carbon by the decomposers, and K is a constant. The type of equation 268
and the value of parameters greatly influence the predictions of models (Arditi and 269
Saiah 1992; Schimel and Weintraub 2003). However, it is now possible to manipu- 270
late the size of the microbial biomass and to measure the decay rate of recalcitrant 271
old soil organic matter thanks to a recent method based on the supply of dual- 272
labelled (^{13}C and ^{14}C) cellulose (Fontaine et al. 2007). Moreover, the size of the soil 273
organic matter pool can be manipulated by diluting soil with sand. This means that 274
it becomes feasible to determine how the size of soil carbon pool and that of 275
microbe populations co-limit soil carbon decay rate and to discriminate between 276
different equations. Determining the value of parameters requires that populations 277
of soil organic matter decomposers be identified among all other populations 278
stimulated by the addition of cellulose. Again, the recent development of molecular 279
methods such as the sequencing of microbial DNA and the possible separation of 280
^{13}C- and ^{12}C-DNA makes such identification possible (Radajewski et al. 2000; 281
Bernard et al. 2007). Therefore, we suggest that microbiologists and geochemists 282
should set up joint experiments under controlled conditions in order to build a more 283
realistic and microbe-oriented mathematical description of recalcitrant soil carbon 284
decomposition. 285

12.4.2   Determining the Mechanisms Stabilising Recalcitrant 286
  Soil Carbon 287

Although little is known about the stability of soil carbon compounds, a central 288
question is whether the stabilisation of soil carbon necessarily involves a chemical 289
or physical linkage with soil minerals. If soil carbon persists only when it is bound 290
to soil minerals, and these exist in forms that microbes cannot access, then the 291
storing capacity of soils is limited. Indeed, the amount of carbon that minerals can 292
fix depends on the specific area of these minerals (Eusterhues et al. 2005), which 293
determines the number of binding sites available and the cationic exchange capacity 294
of the minerals (Wattel-Koekkoek and Buurman 2004), which in turn determines 295
the strength with which carbon is retained. More globally, theory predicts that the 296
storing capacity of many soils worldwide has reached its maximum. Moreover, this 297
capacity is likely to decrease due to a decreasing capacity of minerals to fix carbon 298
induced by the weathering of minerals (Torn et al. 1997). 299
 Other theories and experiments, however, suggest that the stability of soil carbon 300
also results from biochemically recalcitrant compounds (Ågren and Bosatta 1996; 301

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

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

324   12.5   Conclusion

325 As shown here, several possible formulations of soil carbon dynamics allow situa-
326 tions where a steady state of soil carbon is never reached. Hence, from a theoretical
327 point of view, there is no justification for excluding the possibility of long-term old-
328 growth forest carbon uptake as has sometimes been suggested from the classical
329 pool model perspective. Rather, we need initiatives and experimental designs that
330 can distinguish between – and potentially exclude – the modelling paradigms that
331 currently co-exist. Since there are already indications that classical first-order
332 kinetic carbon models have severe limitations (because they do not adequately
333 describe the role of soil biota and the interaction between microbes, soil organic
334 matter and soil minerals), the results and predictions from these models – at least in
335 forests – should be approached carefully, with critical assessment of the limitations,
336 and they should not be used for long-term extrapolation. Nevertheless, their merit
337 for assessments and short-term predictions is undoubted (e.g. Kätterer and Andrén
338 1999; Falloon et al. 2000). There is also a clear need to start to examine the
339 fundamentals of how decomposers attack soil organic matter and to what extent
340 decomposer biomass is dependent upon total soil organic matter or only a fraction
341 of it. The Fontaine-Barot model (Fontaine and Barot 2005) is one example of a

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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.

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