

# Chapter 18

## Processes of Soil Carbon Dynamics and Ecosystem Carbon Cycling in a Changing World

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**Abstract** Climate change is evident and increases of carbon dioxide concentration (CO<sub>2</sub>), temperature and extreme weather events are predicted. To predict the effects of such changes on carbon (C) cycling, the processes and mechanisms determining the magnitude of C storage and fluxes must be well understood. The biggest challenge is nowadays to quantify belowground components of the C-cycle. Soil respiration accounts for ~70% of total annual ecosystem respiration. However, the CO<sub>2</sub> flux from soil originates from several sources, such as root respiration, rhizomicrobial respiration, mineralization of litter and mineralization of soil organic matter (SOM). Increasing atmospheric CO<sub>2</sub> concentrations will generally increase plant growth, thus C-input to soil. This higher C-input will be accompanied by higher SOM mineralization due to warming. However, mineralization of more stable pools

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may be affected more by warming compared to mineralization of labile pools. The importance of cropland management is demonstrated in a model scenario. Crop residue incorporation increased C-storage in the soil markedly. However, under the assumption of a higher temperature sensitivity of mineralization of stable C-pools the net-sink of C under recommended management practice is severely reduced. Precise predictions are hampered due to the lack of quantitative, mechanistic knowledge. It is discussed that a more interdisciplinary scientific approach will increase the speed in generating urgently needed understanding of belowground processes of C-cycling.

**Keywords** Climate change • Respiration • Temperature sensitivity • CO<sub>2</sub> fertilization • Soil organic matter • Ecosystem C cycling • Autotrophic organisms • Soil respiration • Litter decomposition • Priming effect • Rhizosphere respiration • Rhizodeposition • Mean residence time • Soil fauna • Root litter • Stabilization of soil organic carbon • Biochemical recalcitrance • Spatial inaccessibility • Organomineral associations • Soil organic matter fractions • Spectroscopic methods • Thermal stability • Depolymerization • FACE experiments • Temperature sensitivity (Q<sub>10</sub>) • Van't Hoff equation • Rate constant • Arrhenius equation • Extreme weather events • Substrate • Roth C model • SOC dynamics • Residues incorporation • CO<sub>2</sub> fertilization effect

## Abbreviations

AGBDM	Aboveground biomass dry matter
AUR	Acid insoluble residue
BIO	Microbial biomass, model pool in RothC
C	Carbon
CH <sub>4</sub>	Methane
CI	Confidence interval
CO <sub>2</sub>	Carbon dioxide
CO <sub>2</sub> -fert	Max-CC and CO <sub>2</sub> fertilization of crops, climate scenario for the modeling example
CON	Control treatment in the Puch experiment

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DJF	December, January, February
DPM	Decomposable plant material, model pool in RothC
ETP	Evapotranspiration
FACE	Free air carbon dioxide enrichment
GHG	Greenhouse gas
GPP	Gross primary production
HUM	Humified organic matter, model pool in RothC
IOM	Inert organic matter, model pool in RothC
IOSDV	“Internationale organische Stickstoff-Dauerdüngungsversuche” (German) International organic long-term nitrogen fertilization experiment
JJA	June, July, August
MAM	March, April, May
MAP	Mean annual precipitation
MAT	mean annual temperature
Max-CC	Maximal climate change, climate scenario for the modelling example
MRT	Mean residence time
N	Nitrogen
NECB	Net ecosystem carbon balance
NEP	Net ecosystem production
No-CC	No climate change climate, scenario for the modelling example
NPP	Net primary production
OM	Organic matter
ppm	Parts per million
$R_A$	Respiration by autotrophic organisms
$R_E$	Ecosystem respiration
RES	Residue incorporation treatment in the Puch experiment
$R_H$	Respiration by heterotrophic organisms
RMSE	Root mean square error
RPM	Resistant plant material model pool in RothC
SOC	Soil organic carbon
SOM	soil organic matter
SON	September October, November

## 18.1 Introduction

It is evident that atmospheric carbon dioxide ( $\text{CO}_2$ ) concentrations rose drastically from 280 ppm during the preindustrial era to about 390 ppm in 2010 (Conway and Tans 2011). Similar drastic increases of other greenhouse gases (GHGs) are also evident. The resulting increase in temperature due to radiative forcing was in the range of 0.10–0.16°C per decade (1956–2005), which is likely the strongest warming since the last 1,300 years (Solomon et al. 2007). Future projections of  $\text{CO}_2$  concentration increase and warming until 2100 depends on underlying emission scenarios. The atmospheric concentration of  $\text{CO}_2$  is projected to increase to up to

1,000 ppm, and global surface warming is estimated to increase by 1.1–4.0°C, with higher values over land compared to oceans. Moreover, extreme weather events such as heat waves, droughts and heavy precipitation are likely to increase in most regions (Solomon et al. 2007).

Uncertainties in climate change modeling for a given emission scenario result mainly from unknown feedback effects between warming and the carbon (C) cycle (Friedlingstein et al. 2006). On one hand, CO<sub>2</sub> fertilization of plants results in higher uptake of CO<sub>2</sub> (negative feedback), thereby more biomass and increased storage of soil organic carbon (SOC) (Heimann and Reichstein 2008). On the other hand, increasing temperature induced by rising GHG concentrations accelerates mineralization of SOC, which in turn results in higher atmospheric CO<sub>2</sub> concentrations (positive feedback). Moreover, drying and rewetting as well as freezing and thawing cycles of the soil may increase or decrease in frequency or severity, with uncertain effects on the global C cycle.

The ecosystem C-cycle begins with C-assimilation by autotrophic organisms, which are the higher plants in most terrestrial ecosystems. The rate of CO<sub>2</sub> uptake depends mainly on light energy (photosynthetically active radiation) and ambient CO<sub>2</sub> concentration, but also on water availability, temperature, nutritional status and plant species. The sum of assimilated C in an ecosystem, typically expressed on annual basis per square meter, is the gross primary production (GPP). A fraction of the assimilated C is used for growth or reserve, in other words for buildup of the biomass, which is the net primary production (NPP). Another fraction is respired by plants to meet energy demands for growth and maintenance. This CO<sub>2</sub> flux is known as respiration by autotrophs (R<sub>A</sub>). Cannel and Thornley (2000) reported that the portion of NPP as GPP normally ranges between 0.4 and 0.6, especially when observed over time scales of several weeks or longer.

In natural ecosystems, most of annual NPP enters the decomposition cycle as leaf litter, root litter, rhizodeposition (exudates, exfoliates) or, woody debris. Most of the decomposition process takes place on or in the soil. The C cycle is closed by mineralization of organic C to CO<sub>2</sub> by microorganisms. This part of the CO<sub>2</sub> flux is termed respiration by heterotrophic organisms (R<sub>H</sub>). Thus, the CO<sub>2</sub> flux from the ecosystem back into the atmosphere is the sum of R<sub>A</sub> and R<sub>H</sub>, and is termed ecosystem respiration (R<sub>E</sub>).

A first step to determine if a particular ecosystem gains (“CO<sub>2</sub>-sink”) or loses (“CO<sub>2</sub>-source”) C over time is the balance, or imbalance, between NPP and R<sub>H</sub> (equals the balance between GPP and R<sub>E</sub>). Chapin et al. (2006) defined this balance as the net ecosystem production (NEP). Valentini et al. (2000) showed for 15 forest ecosystems (latitudes ranging from 41°N to 64°N) that GPP is similar across all locations. Thus, NEP is primarily determined by respiration and we will focus on this topic below. Clearly, the C-balance is also determined by gains and losses not induced by photosynthesis or respiration. This includes e.g. leaching, fire, harvested products, methane (CH<sub>4</sub>) flux, erosion, herbivory and organic fertilization. For net changes of C in ecosystem the term net ecosystem C balance (NECB) has been proposed.

Measuring *net* C-fluxes in ecosystems is relatively straightforward (although expensive) by using eddy-flux towers and automated chambers for measuring soil respiration, and supplementing the data with independent biomass and SOC measurements (Baldocchi 2003). However, predicting the effects of environmental changes on fluxes and pools of C, necessitate understanding of how the components of the *gross* fluxes affect the pools. The biggest challenge in understanding components of C-fluxes is to quantify the belowground processes (Schulze et al. 2009). Therefore, the focus of this chapter is to provide an overview on the sources of soil respiration, mechanisms of litter decomposition and processes of C stabilization by the soil matrix. Finally, a model is also used as an example to illustrate how changes in temperature and CO<sub>2</sub> concentration may influence the SOC dynamics.

## 18.2 Mechanisms and Processes of Belowground Carbon Cycling

Soil respiration accounts for the second largest CO<sub>2</sub> flux after GPP, and amounts for ~70% of total annual R<sub>E</sub> (Yuste et al. 2005). Although soil respiration contributes considerably to annual CO<sub>2</sub> emissions there is a lack of knowledge with regards to the abiotic and biotic impacts on respiratory activity of soils and the true sources of soil derived CO<sub>2</sub> (Kuzyakov 2006; Trumbore 2006).

Soil respiration is highly variable temporarily, but can be measured on very fine time scales by using automated chambers. However, measured fluxes represent a mixture of R<sub>H</sub> and R<sub>A</sub> with the portions of the sources varying among seasons, depending on plant state, substrate supply to heterotrophs as well as temperature and moisture regimes (Ryan and Law 2005). Thus, the biggest challenge in understanding components and fluxes affecting the NECB is quantification of the different sources of soil respiration.

Flux of CO<sub>2</sub> from the soil into the atmosphere originates from different sources. On a basic functional level, respiration is divided into respiration by autotrophs and by heterotrophs. Dominant autotrophic organisms in terrestrial ecosystems are plants. Heterotrophic organisms include various animals and microorganisms. However, contribution of animals is in general of minor importance, only representing a few percent of total respiration by heterotrophs. In general, mean annual R<sub>H</sub> accounts for 54% of soil respiration (Hanson et al. 2000).

Quantification of different sources of soil respiration is important, but remains to be a work in progress (see Box 18.1 for methods). Kuzyakov (2006) identified basically three main compartments as a source of soil respiration: (i) the rhizosphere, (ii) plant residue or litter and (iii) soil organic matter (SOM). While the respiration from litter and SOM is mainly driven by heterotrophic organisms, that from the rhizosphere is driven by C-allocation of plants to roots (Kuzyakov and Gavrichkova 2010).

### **Box 18.1** Overview on Methods for Partitioning of Soil Respiration

For detailed descriptions readers are referred to reviews by e.g. Hanson et al. (2000) and Kuzyakov (2006). For *component integration* all compartments of interest have to be separated by e.g. sieving and handpicking. Commonly, roots, litter and soil is divided by this method. The components are then measured for their specific flux rate, and their contribution to total soil respiration is calculated by the mass balance. Clearly, this method is accompanied by high disturbance of the system, which may lead to a shift in the proportion of contribution of components to total CO<sub>2</sub> flux. This method provides only relative values.

*Root exclusion* techniques include basically root removal, root trenching and gap analysis. All techniques have to deal with the problem to alter microclimatic conditions and nutrient budgets within the soil and as well as with decaying roots, which contribute to respiration

*Isotope tracers* are used for partitioning of CO<sub>2</sub> fluxes from soil without strong disturbance of the system. The principle of all isotopic approaches for CO<sub>2</sub> partitioning is based on differences in C isotopic signature of various SOM pools and living or dead roots. Both, the radioactive <sup>14</sup>C and stable <sup>13</sup>C isotopes as well as their combination are used successfully for partitioning CO<sub>2</sub> fluxes. The differences in isotopic signature of SOM pools may originate from natural processes (radioactive decay of <sup>14</sup>C; natural changes of vegetation) or can be artificially induced. The natural processes usually change the isotopic signature too slowly and therefore, were seldom used (Kuzyakov 2011). The artificially induced changes of SOM pools and root-derived CO<sub>2</sub> were used in the most CO<sub>2</sub> partitioning studies up to now and can be grouped into the following approaches: Continuous or pulse labeling of plants in <sup>13</sup>CO<sub>2</sub> or <sup>14</sup>CO<sub>2</sub> enriched or depleted atmosphere (Werth and Kuzyakov 2008), <sup>13</sup>C natural abundance (Heitkamp et al. 2012a; Rochette et al. 1999), and bomb <sup>14</sup>C approach (Wang and Hsieh 2002). The isotopic methods are precise and less invasive, but are expensive and provide usually results for small areas, only.

### **18.2.1 Rhizosphere Respiration**

The rhizosphere is the soil directly influenced by the root and often comprises of only a few millimeter distance to the root. The rhizosphere is different from surrounding soil by the presence of rhizosphere organisms (e.g. mycorrhiza), and the strong influence of rhizodeposition (Jones et al. 2004; Kuzyakov 2006). The rhizosphere respiration consists of heterotrophic (rhizomicrobial respiration) and autotrophic (root respiration) components. However, with current methodology, these components are hardly distinguishable. Mycorrhizal fungi, for example, are

located inside and outside the roots, and directly utilize C from plant metabolites. Therefore, even isotopic labeling fails to identify the source of respiration (Kuzyakov and Larionova 2005). Rhizomicrobial and root respiration are often lumped together as rhizosphere respiration due to methodological problems in separating the CO<sub>2</sub> fluxes (Chapin et al. 2006).

Rhizodeposition is the release of organic compounds from living roots into the surrounding soil, the rhizosphere. Rhizodeposition occurs in the intercellular space of roots (endorhizosphere), on the root surface (rhizoplane) and outside the root (ectorhizosphere). Released compounds, such as starch, glucose, carboxylic acids and amino acids, are often low in molecular weight and are easily degradable by microorganisms (Fischer et al. 2007; Jones et al. 2004; Schenck zu Schweinsberg-Mickan et al. 2010). Microorganisms in the rhizosphere take up C and N from exudates and exfoliates of roots quickly within a few millimeter distance to roots (Schenck zu Schweinsberg-Mickan et al. 2010) and turnover times are within hours up to weeks (Kuzyakov 2006). The root exudates are mainly produced during daylight through stimulation of photosynthetic plant activity. Dilkes et al. (2004) showed by <sup>14</sup>C labeling that rhizodeposition of wheat (*Triticum aestivum* L.) was the highest 3 h after C-uptake. On average, few hours are necessary for grasses and herbs and about 4 days for mature trees for the release of rhizodeposits from roots after CO<sub>2</sub> assimilation in leaves (Kuzyakov and Gavrichkova 2010).

Due to their low mean residence time (MRT), rhizodeposition does not contribute significantly to C storage in soil. However, contribution to respiration during daylight hours might be substantial (Kuzyakov 2006). Furthermore, the labile nature of rhizodeposits can influence activity and enzyme production of microorganisms and, therefore, accelerate or retard mineralization from SOM or litter (i.e. priming effect, Kuzyakov et al. 2000). Priming can significantly alter mineralization kinetics. For example, Seiffert et al. (2011) showed under laboratory conditions that after addition of glucose microorganisms incorporated and mineralized black slate, a low grade metamorphic rock formed from shale. Therefore, increased rhizodeposition can induce mineralization of the stabilized SOC pool (Fontaine et al. 2007).

### 18.2.2 Decomposition of Litter

In a broad sense, litter includes all solid debris such as leaves, roots, stems, stalks and wood (Zhang et al. 2008). However, most research has been conducted on leaf litter decomposition in forest ecosystems (Prescott 2010), and crop residues (Abiven et al. 2005; Jensen et al. 2005).

Litter decomposition includes chemical alteration of litter, assimilation by decomposers and mineralization to CO<sub>2</sub>. Mass loss from the so termed litter bags (Box 18.2) without quantification of CO<sub>2</sub> flux is the common approach to measure litter decomposition under field conditions. Exposure of litter bags in the field includes losses by leaching and export by fauna. Therefore, rates of mass loss are higher than decomposition or mineralization rates but not *vice versa*. Besides these

methodological shortcomings, the mass loss is closely related to C-mineralization, justifying to use “mass loss” as a proxy for “C-loss” and “C-mineralization” (Cotrufo et al. 2010).

In most modeling approaches it is accepted that for one litter type under constant conditions, mass loss or C-mineralization follows decay by the first order kinetics. Therefore mass loss can be described by Eq. 18.1:

$$Y(t) = \sum_{i=1}^n Y_i \times e^{-k_i t} \quad (18.1)$$

Where,  $Y(t)$  is the mass remaining at time  $t$ ,  $Y_i$  is the initial mass of compartment  $i$ ,  $k_i$  is the decay constant of compartment  $i$ . A model with one compartment ( $n=1$ ) is often successfully used in litter decomposition studies (Zhang et al. 2008), but two compartment models are also used to account for different decomposition stages (Gholz et al. 2000). The reciprocal value of the decay constant is termed MRT. After the time span of the MRT, approximately 2/3 of the initial mass is lost. In a global meta-analysis including 70 studies at 110 sites, MRT for litter of different biomes ranged from 0.2 to 10 years with a median of 3.3 years (Zhang et al. 2008). The wide range of MRTs is a result of climate, litter quality and decomposer community (Swift et al. 1979).

*Climate* influences the decomposition rate through the effects of soil temperature and moisture regimes (Swift et al. 1979). This influence is not always straightforward, but thresholds exist. For example if mean annual temperature (MAT) is lower than 10°C, the rate of decomposition is slow regardless of litter type. The same is true for the moisture contents below 30% and above 80% (Prescott 2010). Therefore, in studies at sites in Canada, MAT was the principal control of decomposition dynamics, whereas in tropical studies, moisture is relatively more important (Powers et al. 2009; Trofymow et al. 2002). One limiting factor can hence determine the decomposition kinetics: in the tropics temperature is high throughout and decomposition is governed by moisture conditions. Zhang et al. (2008) reported in their meta-analysis that MAT and mean annual precipitation (MAP) only explained 30% of variation in k-values. However, climate and litter quality are closely linked by the common vegetation in bioclimatic zones differing in the chemical decomposition of litter.

The chemical composition is often referred to as *litter quality*. Litter decomposition rates are often correlated with litter fractions obtained by stepwise chemical digestion, operationally defined as cellulose, hemicellulose or acid insoluble residue (AUR, often referred to as “lignin”), and N-content or other nutrients (Berg and McClaugherty 2003; Swift et al. 1979). Prescott (2010) pointed out that a good correlation between litter quality and decomposition is likely over a range of intermediate values. If, e.g. the ratio of AUR-to-N is below 10 or above 40, other factors are likely to control the rate of decomposition and no significant correlation can be found between AUR-to-N ratio and MRT.

Using a global dataset, Zhang et al. (2008) observed that AUR-to-N, N-content and C-to-N ratio explained 73% of variation in decomposition rate constants, making litter quality the most influential factor in decomposition. However, global analyses



**Table 18.1** Average mean residence time (MRT, in years) of above (Zhang et al. 2008) and belowground litter (Silver and Miya 2001) of broad life form categories

	Broadleaf	Conifer	Graminoid
Leaves or needles	1.3 (115)	2.9 (55)	0.9 (15)
Fine roots (< 2 mm)	2.2 (43)	5.9 (10)	0.7 (35)

Mean values across a broad range of biomes

Figures in brackets are the numbers of values (n)

### **Box 18.2** Methods for Measuring Litter Decomposition (Cotrufo et al. 2010)

*Litter bag* approach: Litter is placed in synthetic bags with varying mesh sizes either to include or exclude fauna of various sizes. The litter bags are then exposed in the field, either on the ground or buried in soil. Mass or nutrient loss is regularly determined by weighing harvested bags.

*Litter input and standing litter* can be measured and annual decomposition can be calculated by dividing input by standing mass. This approach provides estimates of MRT on annual basis. Furthermore, the calculated MRT integrates input and standing litter from all species present. This approach is only possible in ecosystems where MRT of litter is longer than 1 year.

*Laboratory incubation* studies with analysis of CO<sub>2</sub> dynamics are especially useful to compare one particular property or process under controlled conditions. This approach renders interpretation more straightforward than field studies. However, extrapolation to field conditions is difficult.

*Isotope tracers* can be used instead of, or in addition to, measuring the isotopic signal in respired CO<sub>2</sub> (Box 18.1). The exposed material is sampled and directly analyzed.

are subject to intercorrelation: the vegetation type is clearly influenced by climate and soil conditions. For example, the lowest decomposition rates have been reported for Tundra ecosystems where decomposition is slow due to low temperatures, frozen soil and often waterlogged conditions. Furthermore, common Tundra vegetation is inherently resistant to decomposition. It is important to recognize that a change in vegetation (i.e. litter quality) due to climate change may affect decomposition rates of litter (Table 18.1) perhaps as strong as increasing temperature (see also Sect. 18.3.2).

A still unresolved issue is the influence of *fauna* on litter decomposition. Whereas past studies have reported mostly the positive influence on decomposition rate, recent studies report mostly neutral or even slowing effects (Prescott 2010). This trend might be due to methodological issues. Moreover, fauna can alter litter composition and increase contact with soil particles by bioturbation. This in turn can lead to chemical or physical stabilization of litter, but can also increase initial decomposition due to favorable moisture conditions and higher nutrient availability

(Jacobs et al. 2011; Potthoff et al. 2005). Knowledge on litter decomposition, mostly in forest ecosystems, was greatly enhanced by cross-site studies. Wall et al. (2008) concluded that invertebrate fauna increased decomposition under temperate and tropical climates. In case of temperature or moisture limited decomposition rates, faunal effects became neutral. However, the standardized methodology across 30 sites did not allow mixing with soil particles. Therefore, the magnitude and rate of measured decomposition rates may differ from the true rates. Nevertheless, inclusion of fauna in decomposition models is an important and a challenging task.

*Root litter* has often higher MRTs as compared to leaf or needle litter (Table 18.1). It has been hypothesized that most of SOC is root derived (Rasse et al. 2005). A part of the higher MRT of roots can be explained by the quality. Roots often contain higher amounts of recalcitrant compounds, such as lignin, suberin, lignin and tannin. However, it is likely that physical or chemical protection by the soil matrix contributes to the higher MRT of roots. These mechanisms are discussed in Sect. 18.2.3.

The short overview presented above indicates that climate change may affect litter decomposition by increasing temperature, especially when rising above the threshold and by altering the duration of very wet or dry phases. Large effects may also result from changes in the vegetation pattern (i.e. in litter chemistry) and accompanying changes in faunal and microbial communities. Decomposition dynamics can even change without completely changing the vegetation. Jacob et al. (2010) showed that beech (*Fagus sylvatica* L.) leaf litter decomposed slower in the presence of litter from other tree species. Therefore, occurrence or absence of a few species can influence significantly the C-cycle. Nevertheless, even highly decomposed litter is not intrinsically stable, as has been shown by Harmon et al. (2009): even after 10 years of decomposition in litter bags the decay rate was an order of magnitude higher compared to that of SOC in mineral soil. This trend shows that studies of soil respiration, litter decomposition and stabilization of C in mineral soil should be linked more closely for better insight in the belowground C cycle (Fierer et al. 2009; Kuzyakov 2011; Ryan and Law 2005).

### 18.2.3 Stabilization of Soil Organic Carbon

The stabilization of SOC is defined as all mechanisms that protect it against decomposition and, thus, slow down mineralization (Baldoock and Skjemstad 2000; von Lützow et al. 2006). Destabilization is defined as the reverse of stabilization, increases the susceptibility of SOC to decomposition (Sollins et al. 1996), and is, thus, one of the mechanisms regulating CO<sub>2</sub> emission from soils. Therefore, stabilization and destabilization are closely related to each other and a detailed knowledge of the mechanisms regulating them is required to better predict CO<sub>2</sub> efflux from soil (Schmidt et al. 2011; Trumbore 2006).

Over decades, several studies have been conducted to describe and to distinguish different mechanisms of SOC stabilization. The traditional theory of SOC stabilization is based on the understanding that dead organic matter once entered the soil is

either mineralized or humified by the soil microorganisms. These biologically produced “humic substances” were assumed to be resistant to mineralization due to their biochemical structure (MacCarthy 2001). However, evidence against this hypothesis emerged (Burdon 2001; MacCarthy 2001; von Lützow et al. 2006). More recent studies take into account that C can be stabilized in the soil being biochemically relatively unaltered: SOC is in general a mixture of plant and microbial derived compounds (Burdon 2001). The current conceptual model of SOC stabilization is mainly based on Sollins et al. (1996), and has been synthesized by von Lützow et al. (2006) who provided an excellent and detailed description. For temperate zones, basically three main stabilization mechanisms are identified: (i) biochemical recalcitrance, (ii) spatial inaccessibility and (iii) organo-mineral association. Baldock et al. (2004) proposed that the capacity of the decomposer community must also be considered as a fourth mechanism which leads, when capacity is limited, to slow mineralization. It should be noted however, that not any of these stabilization mechanisms explains the origin and production of the humic substances which are ubiquitous in soil.

All stabilization mechanisms can occur simultaneously (spatially and temporally), they may affect each other, and co-limitation is possible (Heimann and Reichstein 2008; Wutzler and Reichstein 2008). The relevance of the respective stabilization mechanism differs among environmental, geographical, and land-use characteristics (von Lützow et al. 2006). Thus, a general classification and evaluation of the stabilization mechanisms is difficult. The scientific community is challenged to bridge between conceptual models and ecosystem-specific processes (Heimann and Reichstein 2008; Schmidt et al. 2011). Moreover, there is currently not method which is capable to isolate equivalents of the conceptual model pools (Box 18.3). However, the conceptual model of stabilization (Sollins et al. 1996; von Lützow et al. 2006) is the main basis of the recent understanding of SOC dynamics and, thus, is presented herein.

### **Box 18.3** Methods for Isolating Soil Organic Matter Fractions

*Physical fractionation* procedures separate the SOC due to physical properties, according to particle size, aggregate size, or density (light, heavy, free, and occluded organic particles). Thereafter, the mass of the fraction and the respective C concentrations are measured (Christensen 2001). Density fractionation is particularly useful because fractions influenced by the main stabilization mechanisms can be separated (Golchin et al. 1994).

*Chemical fractionation* means to extract (e.g. hot water, 6 M HCl, H<sub>2</sub>O<sub>2</sub>, NaOCl, Na<sub>2</sub>S<sub>2</sub>O<sub>8</sub>) more labile fractions of total SOC (Balesdent 1996; Helfrich et al. 2006). The SOC is quantified before and after the procedure. Chemical treatments are not completely standardized and may differ in terms of concentration, duration, and external energy added making comparisons difficult.

*Biological fractionation* is applied to determine the CO<sub>2</sub> evolved during incubation of soil samples. The CO<sub>2</sub> emitted in a certain time is assumed to represent a SOC fraction with a respective turnover time. Pool sizes and cor-

(continued)

**Box 18.3** (continued)

responding turnover times can be analyzed by curve fitting (e.g., Eq. 18.1, Paul et al. 2006). Because only labile SOC is mineralized in incubation studies, this approach is best supplemented by another fractionation approach (Haile-Mariam et al. 2008; Heitkamp et al. 2009).

*Thermal stability* of OM can be used as a measure for resistance to mineralization. By thermogravimetry mass loss of a sample over a range of temperature (typically 20–550°C for release of organic matter) is measured. The higher the energy needed to induce a reaction (i.e. oxidation of organic C to CO<sub>2</sub>), the more stable (recalcitrant) the fraction (Rovira et al. 2008). At least two peaks, representing SOC of different stability, can be identified by thermogravimetry (Siewert 2004). However, by measuring directly the CO<sub>2</sub> release during heating it is possible to identify up to four clear peaks (H. F. Jungkunst, unpublished data).

*Spectroscopic methods*, e.g. infrared-spectroscopy or nuclear magnetic resonance spectroscopy deliver information of the chemical composition of SOC in a sample (Ellerbrock et al. 1999; Golchin et al. 1995). However, information is only useful when the turnover time of a respective substance or functional group is known.

Analytical techniques using C isotopes are a very helpful tool for determination of turnover times or the age of SOC fractions (Balesdent 1996; Wang and Hsieh 2002). Isotopic measurements are the only way to assign respiration to certain SOC fractions (Kuzyakov 2011).

*Biochemically recalcitrant* substances have a molecular structure which leads to a selective discrimination by the soil microorganisms. Such substances are: (i) not “attractive” to microorganisms since the net gain in energy by depolymerization is low (Fontaine et al. 2004; Wutzler and Reichstein 2008) and/or (ii) cannot be hydrolyzed by common enzymes (von Lützow et al. 2006). Biochemical recalcitrance is mainly caused by a complex macromolecular structure as aromatic and aliphatic compound, e.g., waxes, lipids, chitin (Derenne and Largeau 2001), while compounds of a low-molecular weight, e.g., sugars, amino acids, are more easily degradable (Sollins et al. 1996). However, in various experiments e.g., sugars with longer MRT than the SOC has on average were observed (Schmidt et al. 2011; Thevenot et al. 2010). Overall, no matter if plant or microbial derived, biochemical recalcitrance of certain SOC compounds leads to a selective preservation compared to easily degradable material (von Lützow et al. 2006). Recalcitrance is relevant to stabilization in the time frame of up to a few decades. An exception is so called “black carbon”, which might be stable over millennial time frames (Hammes et al. 2007; Kuzyakov et al. 2009).

*Spatial inaccessibility* may be the result of occlusion of organic particles (particulate organic matter) within aggregates (Balesdent et al. 2000; Oades 1984).

Aggregate formation is induced by biotic activity: Organic and mineral particles are glued together either in the intestinal tract of soil fauna or by excreted metabolites of microorganisms as well as by root exudates (Elliott 1986; Oades 1984, 1993). Moreover, fungal hyphae are a major agent in formation of macroaggregates (>250  $\mu\text{m}$ , Tisdall and Oades 1982). Since microbial activity drives aggregate formation, the latter also depends on litter quality (Martens 2000). Aggregates play a substantial role in the stabilization of SOC, for the formation and stability of the soil structure, and, thus, for fertility of cropland soil (Abiven et al. 2009; Trumbore and Czimczik 2008). The formation of water-repellent surfaces (hydrophobicity) is also a type of spatial inaccessibility of SOC to microorganisms (Lamparter et al. 2009; Piccolo et al. 1999).

Chemical reactions of SOM with the mineral surface have been considered to be strong and durable forms of stabilization since the oldest SOC is found often in *organo-mineral associations* (Eusterhues et al. 2003; von Lützow et al. 2006). Due to their variable or permanent negative charge of the surface, mainly clay particles, silicates, and oxides act as mineral sorbents (Sollins et al. 1996; Wiseman and Puttmann 2005). Positively and negatively charged organic groups can bond to the sorbent by ligand exchange and/or polyvalent cation bridges. The complexation and/or precipitation of SOM with metal ions, mainly  $\text{Ca}^{2+}$ ,  $\text{Al}^{3+}$ , and  $\text{Fe}^{3+}$ , is a further process of inaccessibility (Kiem and Kögel-Knabner 2002; von Lützow et al. 2006). Further, bonding mechanisms are water bridging and van der Waals forces which are relatively weak (von Lützow et al. 2006). There is evidence that, depending on texture and environmental conditions, the capacity for organo-mineral associations in soils is limited (Baldoock and Skjemstad 2000; Wiseman and Puttmann 2005).

Destabilization is the process of reversing physical or chemical protection of SOC, rendering SOC to microbial attack, i.e. mineralization. External factors, as ecosystem properties and soil management, are the major agents controlling timing and kinetics of SOC destabilization (Schmidt et al. 2011; von Lützow et al. 2006). Thus, the determination and evaluation of destabilization mechanisms is complicated and needs more detailed research (Trumbore and Czimczik 2008). Kuzyakov (2011) observed that it is crucial to directly link SOC fractions to  $\text{CO}_2$  fluxes in future experiments. Thus, physico-chemical factors that control destabilization are briefly discussed herein.

Depolymerization, dissolution, and desorption are the reactions which reduce biochemical recalcitrance and organo-mineral associations. Organo-mineral associations may disintegrate due to changes in the pH, the redox potential and cation concentration (Sollins et al. 1996). Macroaggregates may disrupt when they are exposed to physical stress, as dry-wetting and thaw-freeze cycles and cropland soil management (Denef et al. 2002; Navarro-García et al. 2012). The input of easily degradable organic matter (OM) can initiate the decomposition of recalcitrant compounds (priming effect) (Kuzyakov et al. 2000; Trumbore 2006). Further, all factors that are able to enhance microbial activity (climate, availability of easily degradable compounds, availability of N) increase the susceptibility of SOM to mineralization.

## 18.3 Potential Alterations of the Carbon Cycle in a Changing World

In the next sections, an overview of the possible effects of climate change on the C-cycle is presented, with emphasis on those processes in soil which are the least understood. Firstly, the effect of elevated CO<sub>2</sub> concentrations on NPP and below-ground processes is reviewed. Next, uncertainties of how warming can effect C-mineralization are discussed, and finally the effects of extreme weather events, (i.e. rewetting and thawing) on C cycling are presented.

### 18.3.1 Elevated Atmospheric Carbon Dioxide Concentration

A reduction of the increase of atmospheric CO<sub>2</sub> concentrations is expected due to the CO<sub>2</sub>-fertilization of plants (i.e. negative feedback, Friedlingstein et al. 2006; Heimann and Reichstein 2008). It has been shown that the light saturated uptake of CO<sub>2</sub> increases (in C3 plants) with increasing CO<sub>2</sub> concentration (Leakey et al. 2009).

Much effort is going on to test the effects of elevated CO<sub>2</sub> concentrations on the C-cycle. Globally, 36 free air CO<sub>2</sub> enrichment (FACE) experiments have been conducted, and some are still running. A list is available online ([http://public.ornl.gov/face/global\\_face.shtml](http://public.ornl.gov/face/global_face.shtml)). FACE plots are surrounded by pipes injecting a CO<sub>2</sub> stream into the air. Concentrations of CO<sub>2</sub> of up to 600 ppm are tested by this method in forest, grassland, cropland and desert ecosystems (Ainsworth and Long 2005). Albeit restricted plot size (up to 30 m diameter), this method provides the possibility to test the effect of elevated CO<sub>2</sub> concentration under field conditions. However, no forest experiments were conducted in boreal and tropical regions, and no FACE experiment fumigates mature forests (Hickler et al. 2008). Furthermore, many forest FACE are only running until 2011 (Ledford 2008).

Effects of changing climate and increasing CO<sub>2</sub> concentration on NPP are of high importance. Ainsworth and Long (2005) showed, by summarizing data from FACE experiments, that biomass and yield of plant species with C4 photosynthetic pathway are largely unaffected by CO<sub>2</sub> concentration. However, most C3 crops and juvenile trees showed increased aboveground biomass and crop yields (Table 18.2). FACE experiments have been extremely valuable, but they are implemented only at a very limited number of sites and for only a few plant species. De Graaff et al. (2006) summarized data from FACE in a meta-analysis and concluded that below-ground biomass may even increase by 34%. Thus, increased biomass production may increase C-input into soil, enhancing the SOC storage and mitigate the increased mineralization caused by warming. However, this may only be true if other nutrients will not limit plant growth (de Graaff et al. 2006).

Considering only the increases in C-input in the ecosystem is only one issue with respect to global change. For the C balance studies, the amount of C retained in the ecosystem is crucial. Specifically, if mineralization also increases with C-input the C balance may be unaffected. It has been documented that microbial growth rates in

**Table 18.2** Aboveground dry matter and crop yield changes as affected by increased CO<sub>2</sub> concentration (ca. 500–600 ppm) at FACE experiments

	No. of species	No. of sites	Change (%)		
			Mean	Lower CI	Upper CI
ABGDM	34	6	17.0	14.5	19.6
Tree	7	2	28.0	6.4	54.1
C4 crop	1	1	6.7	-2.2	16.6
C3 grass	8	3	10.5	6.5	14.8
Legume	6	3	20.3	13.7	27.3
Crop yield	6	3	17.3	10.2	24.9
Cotton	–	1	42.2	23.7	63.6
Wheat	–	1	14.4	-1.6	33.1
Rice	–	1	10.4	-4.4	30.2
Beet	–	1	12.5	n.d.	n.d.

Data compiled from Ainsworth and Long (2005) and Manderscheid et al. (2010)

ABGDM Aboveground dry matter, CI 95% confidence interval, n.d. not determined

soil increase linearly with increasing atmospheric CO<sub>2</sub> concentration (Blagodatskaya et al. 2010). Bacterial respiration, but not that of saprotrophic fungi is enhanced under elevated CO<sub>2</sub> (Anderson and Heinemeyer 2011). This indicates the preferential increase of fast growing microorganisms (r-strategists), probably due to more rhizodeposition. Increased microbial growth on labile substrates can induce priming effects on SOC mineralization (Kuzakov et al. 2000) and encounter the increased C-input of plants caused by CO<sub>2</sub>-fertilization. On the other hand, Rillig and Allen (1999) showed an increase of glomalin produced by arbuscular mycorrhizal fungi after 3 years of elevated CO<sub>2</sub>. Glomalin is a recalcitrant organic glycoprotein which is preferentially fixed in macroaggregates and, therefore, protected against microbial breakdown (Rillig and Allen 1999). However, direct quantification of glomalin is not possible up to now, all available methods having specific drawbacks (Rosier et al. 2006). Nevertheless, glomalin seems to have a relatively long MRT (few decades) and can, therefore, account for a significant C-pool in ecosystems (Treseder and Allen 2000; Treseder and Turner 2007). Whether priming or production of glomalin affects SOC storage in the long-term is unknown, and is likely to be ecosystem specific.

In fertilized agroecosystems the effect of priming may be less compared to N-limited systems such as forests. Anderson et al. (2011) showed that SOC stocks under cropland use increased by 10% in 6 years under elevated CO<sub>2</sub> (550 ppm) relative to ambient CO<sub>2</sub> concentration. In a warm temperate forest (Duke FACE) Drake et al. (2011) showed that C-fluxes increased under elevated CO<sub>2</sub> (ambient plus 200 ppm). This trend also increased the N-turnover, presumably increasing N mineralization from SOM. As a consequence, tree biomass increased (2003–2007), but SOC stocks remained unaffected. Thus, N or other nutrients may become a limiting factor for biomass increase in non-fertilized ecosystems (de Graaff et al. 2006). Thus, CO<sub>2</sub> fertilization may enhance the ecosystem C-sink, but only to a minor extent, which could also be offset by warming.



### 18.3.2 Increase in Temperature

Microbial decomposition is, as are all chemical or biochemical reactions, temperature dependent. Therefore, it implies that rising temperature can induce a positive feedback: C-mineralization will increase with temperature and the higher release of CO<sub>2</sub> will cause additional warming. Therefore, it is important to quantify the effect of temperature on respiration for improved predictions of effects on SOC storage.

Temperature sensitivity is often expressed as Q<sub>10</sub> values by the van't Hoff equation (Eq. 18.2):

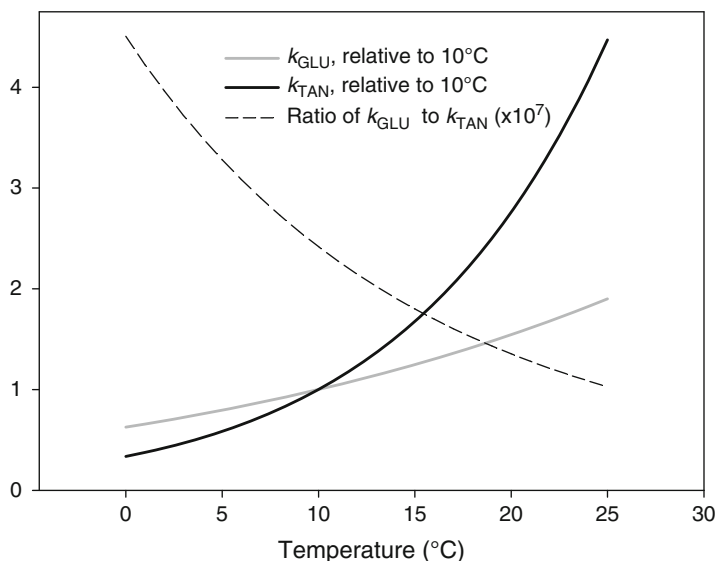
$$Q_{10} = (k_2 / k_1)^{10/(T_2 - T_1)} \quad (18.2)$$

Where,  $k_2$  and  $k_1$  are rate constants of a certain process and  $T_2$  and  $T_1$  the corresponding temperatures. An often assumed Q<sub>10</sub> of 2 means that respiration would increase twofold by raising the temperature from 10°C to 20°C. While this empirical relationship has been often used (Davidson and Janssens 2006; Vicca et al. 2009; von Lützow and Kögel-Knabner 2009), the theoretical basis is determined by thermodynamical laws. Arrhenius formulated an equation which relates the reaction rate constant ( $k$ ) of a certain compound to its bio-chemical stability, i.e. activation energy ( $E_a$ ). This relationship is presented in Eq. 18.3:

$$k = \alpha \times e^{(-E_a/RT)} \quad (18.3)$$

where,  $\alpha$  is a pre-exponential factor,  $R$  the gas constant (8.324 J K<sup>-1</sup> mol<sup>-1</sup>) and  $T$  temperature (K). There are two important implications of the Arrhenius equation for the temperature sensitivity of C-mineralization. Firstly, the relation shows that Q<sub>10</sub> values decrease with increase in temperature for a certain compound. That is, Q<sub>10</sub> values are not constant even for pure substances over a range of different temperatures. Secondly, substances with higher activation energies (i.e., less reactive and more recalcitrant) exhibit higher sensitivity to changing temperatures (Fig. 18.1). This theoretical basis gives rise to the assumption that more stable (i.e. presumably more decomposed) SOC fractions are affected relatively more by increasing temperatures than labile fractions (Knorr et al. 2005). Figure 18.1 shows an example adapted from Davidson and Janssens (2006) for reaction of glucose ( $E_a \approx 30$  kJ mol<sup>-1</sup>) and tannin ( $E_a \approx 70$  kJ mol<sup>-1</sup>) relative to 10°C. The relative effect of temperature on  $k$  of tannin is much higher. However, the absolute change in reaction speed of glucose in relation to tannin ( $k_{\text{GLU}}/k_{\text{TAN}}$ ) is negligible, given the order of magnitude presented in Fig. 18.1. On the other hand, labile pools or fractions normally form a minor part of the SOC stocks. Therefore, despite slow turnover, mineralization of stable pools can contribute significantly to CO<sub>2</sub> efflux from SOC to the atmosphere (Flessa et al. 2000). Concerns that stable SOC pools/fractions are more sensitive to warming (Knorr et al. 2005) may only be true if stability is induced by recalcitrance (see Sect. 18.2.3, Schmidt et al. 2011). Moreover, the Arrhenius equation is only





**Fig. 18.1** Relative effect of temperature on reaction rate constant ( $k$ ) of glucose and tannin and the ratio of the absolute rate constants. The reaction rate at 10°C is accepted as 1

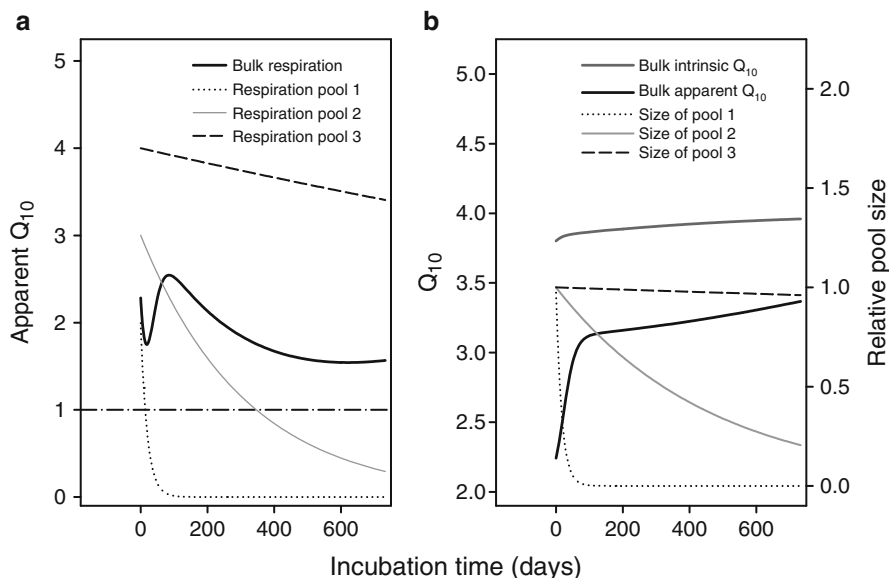
valid under the assumption of unlimited substrate availability. Theoretically, the Arrhenius equation can be combined with Michaelis-Menten kinetics (i.e. describing reaction rates affected by substrate limitation) but such attempts are difficult in a complex media such as soil. Therefore, empirical observation and phenomenological description seem to be the only ways to determine temperature sensitivity of SOC, as well as of its fractions (Kirschbaum 2006).

The determination of  $Q_{10}$  values seem to be straightforward. Measuring respiration rates during laboratory or field studies and application of Eq. 18.2 should be easy. However, a wide range of  $Q_{10}$  values (1.4–6.9) have been reported (von Lützw and Kögel-Knabner 2009). Several methodological problems arise in determining  $Q_{10}$  values under field conditions. First of all, soil respiration consists of several components, which are not easy to distinguish (see Sect. 18.2.1). Moreover, increasing temperature is often accompanied with decreasing soil moisture. Therefore, respiration may not, or less, increase with temperature because moisture is limiting. This bias the determination of  $Q_{10}$  towards underestimation. Water logged conditions, freezing-thawing or drying-rewetting cycles and different substrate supply also hamper determination of temperature sensitivity under field conditions. For this reason, Kirschbaum (1995, 2006) recommended laboratory incubations under controlled conditions as the best method to determine temperature sensitivity of SOC mineralization (Box 18.4).

### Box 18.4 Methodological Considerations for Determination of $Q_{10}$ Values During Laboratory Incubations

A common way for determination of  $Q_{10}$  values is incubation of a soil sample at different temperatures under otherwise equal conditions (i.e. optimal moisture content) and measuring respiration rate at different times. Using such “parallel incubations”, result in “apparent”  $Q_{10}$  values which are strongly biased by the substrate supply. Figure 18.2a illustrates a simplified example with pool sizes and turnover times taken from Heitkamp et al. (2009). Bulk respiration is modeled as contributions from pool 1 (0.4 Mg C ha<sup>-1</sup>; k=0.059), pool 2 (3.2 Mg C ha<sup>-1</sup> k=0.002) and pool 3 (16.8 Mg C ha<sup>-1</sup>; k=0.0001). The  $Q_{10}$  values of 2, 3 and 4 are assigned to pools 1, 2 and 3, respectively. Figure 18.2a shows that apparent  $Q_{10}$  values of all pools decrease with time and even fall below 1. That is the case when pool 1 is exhausted at higher temperature, but still contributes to respiration at lower temperature. A false conclusion from this pattern is that stable pools (i.e., contributing to respiration at later incubation time) are less sensitive to temperature than labile pools (i.e., contributing to respiration at early stages). Reichstein et al. (2000) tried to overcome this problem by determining pool sizes and decay constants at each temperature. Then, the pool sizes were held constant, and the  $Q_{10}$  values were determined for the decay constant. This approach indeed overcomes the problems with substrate depletion, but the non-linear curve fitting approach for determining pool size and decay constant is itself not straightforward and results depend on incubation conditions (Böttcher 2004; Heitkamp et al. 2009; Sierra 1990). By applying the approach to specific compounds sampled during incubation, Feng and Simpson (2008) showed, in accordance with the Arrhenius equation, that lignin monomers exhibited higher temperature sensitivity than n-alkanoic compounds. Nevertheless, a  $Q_{10}$  could not be calculated for almost 50% of the dataset due to poor model fits.

Another solution is to incubate all samples at the same temperature and exposing the sample only for short period to different temperatures (Leifeld and Fuhrer 2005). This approach avoids *different* substrate supply at different temperature for the *same* pool. Nevertheless, pool sizes change with time (Fig. 18.2b) simultaneously affecting bulk apparent  $Q_{10}$  values (i.e. apparent  $Q_{10}$  of respired C). In the present example, the bulk intrinsic  $Q_{10}$  (i.e.,  $Q_{10}$  value inherent to a compound due to its chemical properties) value is largely determined by pool 3, due to its large size. Therefore, bulk apparent  $Q_{10}$  values increase towards the bulk intrinsic  $Q_{10}$  value with time, but do not coincide during the short incubation time because respiration is largely determined by pool 2. The bulk intrinsic  $Q_{10}$  increases with incubation time due to depletion of more labile substrates with lower  $Q_{10}$  values. If there would be any possibility to measure contribution of pools directly, the “rotating incubation” method would be straightforward and yield intrinsic  $Q_{10}$  values for each pool at any time. Attempts using <sup>13</sup>C natural abundance after C3/C4 vegetation changes indeed indicate that “old” SOC is more sensitive to temperature compared to “young” SOC (Vanhala et al. 2007; Waldrop and Firestone 2004).



**Fig. 18.2** Theoretical effect of incubation time on  $Q_{10}$  values calculated by respiration from different pools by parallel incubation (a) and relation between remaining pool size and calculated intrinsic and apparent  $Q_{10}$  value of bulk respiration with rotating incubation (b). Parallel incubation means incubation of samples at different temperatures throughout, whereas rotating incubation is incubation at one temperature and exposure to different temperature only for short time frames

Current knowledge indicates that recalcitrance does not lead to stabilization of SOC on millennial time scales (Kögel-Knabner et al. 2008). If stabilization of C in soil is a consequence of chemical protection against decomposition, the Arrhenius equation might not be relevant for temperature sensitivity of stabilized SOC. However, Craine et al. (2010) showed that physical or chemical stabilization may happen without altering temperature sensitivity. For example, mineralization data of soil and litter samples differed in their respiration rate by an order of magnitude ( $30$  and  $420 \mu\text{g C (g C h)}^{-1}$ , respectively), but not in their activation energies ( $59 \text{ kJ mol}^{-1}$ ). Thus, physical and chemical stabilization mechanisms seem to be less sensitive to temperature compared to biochemical stabilization (i.e. recalcitrance). In contrast, Gillabel et al. (2010) compared temperature sensitivity of topsoil and subsoil samples. In subsoil, the amount of chemically stabilized SOC is assumed to be relatively higher compared to topsoil (Rumpel and Kögel-Knabner 2011). Gillabel et al. (2010) observed that respiration from topsoil samples was in accordance with the Arrhenius equation, whereas subsoil respiration was not sensitive at all to temperature. It was hypothesized that chemical protection induced these trends. The Arrhenius equation only applies to conditions of unlimited substrate availability. Due to low substrate availability in subsoil, the effect of temperature might be cancelled out by processes described by Michaelis-Menten kinetics in the subsoil (von Lützow and Kögel-Knabner 2009). Therefore, the apparent temperature sensitivity is determined by substrate availability (i.e., abundance and availability of substrate

and stabilization mechanism), whereas the intrinsic sensitivity (see Box 18.4) is determined by the chemistry of the compound. Future research is needed to distinguish between the effects of these different processes (Conant et al. 2011).

### 18.3.3 *Frequency of Extreme Weather Events*

Besides increasing temperature and changes in precipitation increases in extreme weather events are also predicted in a future climate (Christensen et al. 2007). Thus, increasing numbers of drying and wetting and/or freezing and thawing events are likely in most ecosystems.

A flush of CO<sub>2</sub> efflux occurs upon rewetting of a soil. This is termed the “Birch effect”. Birch (1958) speculated that the CO<sub>2</sub> flush is derived from “solid organic material” and regulated by microbial state before and during rewetting. Death of microbial cells due to drying and subsequent re-utilization as substrate after rewetting is another explanation (Kieft et al. 1987). Whereas microbial death and re-utilization of cell debris after rewetting remain a common explanation, Fierer and Schimel (2003) reported that the CO<sub>2</sub> release can additionally be explained by accumulation of labile substrate and possibly also of enzymes. Disruption of aggregates, thus exposure of physical protected SOC to mineralization, may be in part responsible for increased respiration (Navarro-García et al. 2012). However, drying and rewetting can also increase aggregate stability in the long-term (Denef et al. 2002). Aggregate size and stability (i.e., soil structure) also determine gas diffusion. Therefore, oxygen supply and thus microbial activity can be influenced by changes in soil structure (Jäger et al. 2011).

After several cycles, the CO<sub>2</sub> flush after rewetting is reduced, indicating depletion of substrate affected by rewetting (Fierer and Schimel 2002). Moreover, the short flush may contribute only a small portion to annual emissions. Muhr et al. (2008) reported even decreased cumulative CO<sub>2</sub> emissions from soil samples with drying and rewetting cycles compared to continuously moist samples. If cumulative respiration is reduced depends on the duration of the dry phase, where microbial activity is limited by soil moisture. Furthermore, microbial respiration can be reduced after the rewetting flush (Fierer and Schimel 2002), probably because of substrate depletion and acclimation of the microbial community (Lundquist et al. 1999). Whereas fungal growth was not affected by drying and rewetting cycles, bacterial growth decreased after exposure to several cycles (Bapiri et al. 2010). An increase of fungal population may shift the specific respiration (i.e. respiration per unit microbial biomass) to lower values, since saprotrophic fungi are more effective in substrate utilization than bacteria (Joergensen and Wichern 2008). Physical, chemical and biological interactions apparently govern the net-effects of drying and rewetting on SOC mineralization (Kim et al. 2011). In the long term, the duration of dry phases (Bottner et al. 2000) and the number of cycles may determine the net effect on annual C-mineralization.

Similar to drying and rewetting cycles, a flush of CO<sub>2</sub> is also observed after thawing of a frozen soil (Kim et al. 2011; Matzner and Borken 2008). The flush is ascribed to

microbial death and subsequent utilization of cell debris. Also, diffusion barriers might be involved. Specifically, microbial activity continues at unfrozen microsites and/or in subsoil. After thawing, gas can diffuse out of the soil (Teepe et al. 2001). Aggregate stability is often reduced after thawing, depending on the water content before the freezing event (Dagesse 2011). Reduced physical protection can, therefore, contribute to the CO<sub>2</sub> flush after thawing. Further, biology and chemistry of soil also changes after freezing and thawing. Schmitt et al. (2008) reported a decrease in fungal biomass, whereas bacteria were largely unaffected by freezing and thawing cycles. Besides the observed flush after thawing, the net-effect on soil respiration is not entirely clear. Matzner and Borken (2008) reported in their review that cropland soils seem to lose slightly more (<5%) C by respiration after freeze-and-thaw cycles compared to unfrozen soil. The opposite has been reported for natural vegetation. Comparison of studies is further complicated by methodological issues, such as freezing or thawing temperature, sampling time and experimental duration (Hugh 2007).

For both events, the net effect likely depends on the frequency of cycles, but seem to be small on annual basis (Fierer and Schimel 2002; Matzner and Borken 2008). However, the lack of understanding the processes involved hampers a general conclusion. Most knowledge is based on laboratory studies, which is also a consequence of methodological issues in measuring soil respiration in the field. Studies involving subsequent events of dry-and-rewet and freeze-and-thaw (e.g., effects of subsequent freezing and thawing during winter and subsequent drying and rewetting in spring) seem to be entirely missing, but are most important to elucidate effects of climate change on SOC mineralization.

## 18.4 Cropland Management, Elevated Carbon Dioxide, and Temperature Increase: A Model Scenario

The following section of this chapter exemplifies effects of CO<sub>2</sub>-fertilization and warming on SOC stocks for two cropland management options with a modeling scenario. However, a model can hardly take into account all factors affecting predictions of SOC dynamics over the next 100 years. There will be changes in management, fertilization techniques, and plant cultivars. Further, climate change is not simply increasing temperature and precipitation but also cause increases in extreme weather conditions, which may lead to hardly predictable socio-economic and agro-ecological changes. Therefore, the model was applied as a tool to separate the possible quantitative influence of selected variables within a certain scenario on SOC dynamics. This approach is useful to identify the magnitude of some factors related to climate change.

The Rothamsted Carbon Model 26.3 (RothC) is chosen as a tool because it is useful in simulating SOC dynamics (Smith et al. 1997). Furthermore, RothC works well at the chosen site (Heitkamp et al. 2012b) and the model can easily be re-parameterized (Gu et al. 2004; Heitkamp et al. 2012b).

### 18.4.1 Site Conditions and Model Setup

By using regional projections of changing temperature and precipitation, the effects of climate change and residue management on SOC dynamics at a cropland site at Puch, Germany were modeled. The long-term (1960–1990) MAT of the site is 7.9°C and MAP is 922 mm. The soil is a Luvisol which developed on loess deposits, thus silt is the dominating particle size class (9% sand, 73% silt and 18% clay). The fertilization experiment was set up within the network of the “Internationale Organische Stickstoff Dauerduengungsversuche” (IOSDV) in 1983. Crop rotation consisted of sugar beet (*Beta vulgaris* L.), winter wheat and winter barley (*Hordeum vulgare* L.). This analysis was based on two out of several treatments: (i) removal of straw and beet leaves (CON) and (ii) incorporation of straw and beet leaves (RES). All treatments were under conventional tillage. The SOC content was measured episodically, in 1983 in samples composited among plots with different N-rates; in 1986, 1989 and 2003 bulked among field replicates, and in 1994 and 2004 for individual plots (n=3). Ploughing depth was 25 cm and bulk density was assumed to be 1.5 g cm<sup>-3</sup> for conversion of SOC concentration into stocks. Nitrogen was applied at a rate (kg N ha<sup>-1</sup>) of 100 to beet, 80 to wheat and 60 to barley until 1998 and was raised by 20 for cereals thereafter. Straw for incorporation was weighed until 1998, thereafter a harvest index of 0.5 was applied. Beet leaves were weighed throughout until 2004. Residue input by stubbles, roots and rhizodeposition was estimated by linear regression of yield (grain and beet) and C-input as shown by Eq. 18.4:

$$I = (Y \times F + K) \times R \quad (18.4)$$

Where,  $I$  is the C-input (Mg ha<sup>-1</sup>),  $Y$  is crop yield (fresh mass for beet, incl. 13% water in grain; Mg ha<sup>-1</sup>),  $F$  (Mg C (Mg Y)<sup>-1</sup>) and  $K$  (Mg C ha<sup>-1</sup>) are crop-specific constants and  $R$  is a multiplier to account for rhizodeposition (Franko 1997; Ludwig et al. 2007). Crop yields were published (Hege and Offenberger 2006),  $F$  was set to 0.008 (winter cereals) or 0.0008 (sugar beet),  $K$  was set to 0.4 (winter cereals) or 0.16 (sugar beet), and  $R$  was set to 1.5 or 1.2 (winter cereals and sugar beet), respectively. The constants are published in Franko (1997) and for rhizodeposition see Domanski et al. (2001) and Ludwig et al. (2007).

The RothC model was used for modeling SOC dynamics (Coleman and Jenkinson 1999). The model consists of five pools with different turnover, is easy to calibrate and was proven useful for simulating SOC dynamics (Ludwig et al. 2007; Smith et al. 1997). Every pool has a specific decay constant which is modified by temperature, moisture, and plant cover. Partitioning between mineralization and humification is influenced by clay content (Coleman and Jenkinson 1999). The original temperature function of RothC was replaced by Eq. 18.2 to evaluate the effect of different temperature sensitivity of pools (Gu et al. 2004). The replaced function with the commonly assumed  $Q_{10}$  of 2 (Davidson and Janssens 2006) was tested against the original model and only minor differences occurred. In Model A, Eq. 18.2 was used with  $Q_{10}=2$  for all pools. As stated above, more stable pools might have a higher sensitivity to temperature changes. Therefore, for Model B, a  $Q_{10}$  of 2 was

**Table 18.3** Maximal projected increases in temperature and precipitation (Christensen et al. 2007) and potential evapotranspiration (Baguis et al. 2010) until the period of 2080–2099 for Northern Europe

	Temperature (°C)	Precipitation (%)	ETP (%)
DJF	8.2	25	40
MAM	5.3	21	20
JJA	5.4	16	33
SON	5.4	13	30

*DJF* December, January, February, *MAM* March, April, May, *JJA* June, July, August; *SON* September, October, November, *ETP* evapotranspiration

used for DPM and BIO (Davidson and Janssens 2006), a  $Q_{10}$  of 3 for RPM (Wetterstedt et al. 2010) and a  $Q_{10}$  of 4 for the HUM pool (Leifeld and Fuhrer 2005). The model was initialized with an equilibrium run to 1983. For this purpose, C-input and size of inert organic matter (IOM) pool were adjusted. From 1984 to 2004, the model was run with available weather data and C-input was measured or calculated independently (Eq. 18.4). From 2004 to 2099 different climate change scenarios were assumed (Table 18.3).

As a reference scenario (No-CC), monthly temperature, precipitation, and actual evapotranspiration were assumed to be constant at the mean value of the period 1983–2004. This period is close to that (1980–1999) used for modeling of regional climate change projections for 2080–2099 by the IPCC (Christensen et al. 2007). The input of C was calculated as mean value between 1984 and 2004. Assuming a scenario without changing temperature and precipitation was necessary because SOC stocks were not in equilibrium in 2004 and management effects must be separated from climate change effects.

The second scenario (Max-CC) represents a regional climate scenario with maximum assumed temperature increase and precipitation changes for Northern Europe (Christensen et al. 2007). All increases are supposed to be linear and are originally projected from the period of 1980–1999 to the period of 2080–2099 (Table 18.3).

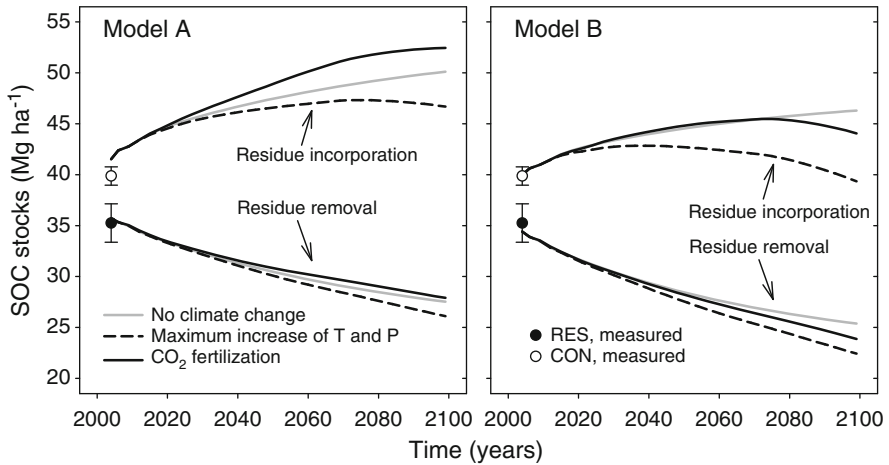
The third scenario is the same as the second (Max-CC), but with consideration of CO<sub>2</sub> fertilization effects on crop growth. A linear increase in growth of up to 16% was assumed until 2050 (Leakey et al. 2009). From 2050 to 2100, an additional increase of 8% was assumed. Therefore the total increase was in the range reported from FACE (de Graaff et al. 2006).

Modeling of all scenarios was done in monthly resolution. For presentation of data the modeled SOC stocks were averaged over a crop rotation period of 3 years.

### 18.4.2 Effect of Residue Incorporation

During the observed period from 1983 to 2004, SOC stocks showed marked changes. For instance, SOC stocks (Mg ha<sup>-1</sup> ± standard error) of CON were 35.3 ± 3.3 and stocks of RES were 39.9 ± 1.6. Model fits were satisfactory with root mean square





**Fig. 18.3** Modeled SOC dynamics for residue removal (*CON*) and incorporation (*RES*) for the different climate change scenarios in Puch, Germany. In *model A* the same temperature sensitivity for mineralization is assumed for all model pools. In *model B*, temperature sensitivity increases with the MRT of pools (see Table 18.4). Measured stocks in 2004 are means with standard errors

errors (RMSE) between 5.0 and 7.8, and with the mean differences between observed and predicted values ( $-1.6$  to  $1.8$ ) well in the range of the standard errors (Smith et al. 1997).

With both model parameterizations, the increasing gap in predicted SOC storage between cropland management with residue incorporation and with residue export (Fig. 18.3) became obvious. The SOC stocks in the *RES* treatment were about twice as large as those in *CON* treatments (Table 18.4) at the end of the modeled period. In the *CON* treatment modeled SOC stocks ranged from 26.1 to 27.9 Mg ha<sup>-1</sup>, losing between 7.8 and 9.6 Mg C ha<sup>-1</sup>. The estimated SOC stocks were low, but considering the low C-input (Table 18.4) this is in a realistic range. For example, Rühlmann (1999) summarized SOC stocks for long-term bare fallow experiments. According to the empirical equation used by Rühlmann (1999), the SOC stock under bare fallow (i.e., no C-input) at the Puch site is estimated to be 17 Mg ha<sup>-1</sup>. The modeled data indicate that SOC stocks of both treatments will not attain equilibrium until 2100, which contradicts observations of West and Post (2002), who estimated that a new equilibrium due to enhanced crop rotation will be reached after 40–60 years. One explanation may be the large difference in C-input between treatments at the Puch site (Table 18.4).

### 18.4.3 Effect of Climate Change Scenarios

Evaluation of climate change effects was done in comparison to a scenario where no climate change will be present. This was done by creating a scenario which used the



**Table 18.4** Model results for the period 2005–2100 for different climate change scenarios and model parameterization

Scenario	C-input	Model A			Model B		
		SOC	$\Delta$ SOC	CC-effect	SOC	$\Delta$ SOC	CC-effect
CON							
No CC	106	27.5	-8.2	-	25.4	-9.0	-
Max CC	106	26.1	-9.6	-1.4	22.4	-12.0	-3.0
CO <sub>2</sub> fert	121	27.9	-7.8	+0.4	23.9	-10.5	-1.5
RES							
No CC	340	50.1	8.6	-	46.3	6.3	-
Max CC	340	46.7	5.2	-3.4	39.3	-0.6	-7.0
CO <sub>2</sub> fert	387	52.5	10.9	+2.3	44.1	4.1	-2.2

Given SOC stocks are modeled for the year 2100, whereas  $\Delta$  SOC is the difference of the measured stocks in 2004 and the modeled stocks in 2100. Stocks of SOC at the start of the experiment in 1983 were 40.5 Mg ha<sup>-1</sup>. All figures in Mg ha<sup>-1</sup>

*CON* crop residue removed, *RES* crop residue incorporated, *No CC* scenario with average temperature and precipitation, no climate change, *Max CC* maximal climate change, scenario described in Table 18.3, *CO<sub>2</sub> fert* Max CC but with CO<sub>2</sub> fertilization of plants, *Model A* Q<sub>10</sub>=2 for all pools, *Model B* Q<sub>10</sub>=2 for DPM and BIO, Q<sub>10</sub>=3 for RPM and Q<sub>10</sub>=4 for HUM

monthly mean values of the Puch site during the experimental period 1984–2004. However, during that period an increase of MAP by 0.07°C year<sup>-1</sup> was reported by Hege and Offenberger (2006). Therefore, choosing that period as baseline is somewhat arbitrary because temperature already increased. However, this approach coincides with that used in the IPCC for regional climate scenarios (Christensen et al. 2007).

The data predicted by model A (Q<sub>10</sub>=2 for all pools) showed only small effects of climate change scenarios on SOC stocks in the CON treatments. Loss of SOC in case of the Max-CC scenario was predicted to be 1.4 Mg C ha<sup>-1</sup>. That difference was cancelled out under the assumption of CO<sub>2</sub>-fertilization (Fig. 18.3, Table 18.4). The predicted differences were in a range hardly detectable under field conditions, given the effects of soil heterogeneity (Ellert et al. 2008; Heinze et al. 2010; Heitkamp et al. 2011). Predicted outcomes were different for the RES treatment. Modeled SOC loss induced by climate change (Max-CC) until the year 2100 was 3.4 Mg C ha<sup>-1</sup>. Remarkably, there is a tipping point around the year 2075 (at 47.3 Mg C ha<sup>-1</sup>) after which SOC stocks in the RES treatment are predicted to decrease. Inclusion of CO<sub>2</sub> fertilization in the scenario even increased the C-sink in the soil by 2.3 Mg C ha<sup>-1</sup>, as compared to No-CC.

A different sensitivity of pools to temperature was incorporated in model B, changing the outcome of predictions markedly. Effect of warming (Max-CC) was predicted to be strong on SOC stocks of the RES treatment (Table 18.4). The tipping point from sink to source was predicted for the year 2039, turning the soil of the RES treatment for that scenario over the almost 100 years into a source of CO<sub>2</sub>. Assuming CO<sub>2</sub> fertilization occurs led to almost identical predictions in SOC stocks of No-CC and CO<sub>2</sub>-Fert scenarios until 2075. Therefore, the predicted source-sink tipping point was procrastinated by 36 years, as compared to the Max-CC scenario.

It has to be pointed out that model B predicted in general higher mineralization as compared to model A.

For the chosen scenarios changes of  $+2.3$  to  $-7.0$  Mg C ha<sup>-1</sup>, were predicted to be induced by climate change from 2005 until 2100 for the Puch site. Therefore, the feedback between climate change and SOC balance is likely positive, as is also assumed in several global feedback simulations (Friedlingstein et al. 2006). However, when comparing the predicted (2005–2100) effects of climate change ( $+2.3$  to  $-7.0$  Mg C ha<sup>-1</sup>) and residue incorporation or export ( $+12.6$  and  $-12.8$  Mg C ha<sup>-1</sup>, respectively) it becomes obvious that appropriate management of cropland soils is of outstanding importance for reducing CO<sub>2</sub> emissions from these agroecosystems. Nevertheless, SOC accumulation by recommended management practices may be severely reduced by warming. This effect will be stronger if sensitivity of mineralization differs between pools of different stability.

## 18.5 Conclusions and Outlook

Soils are of major importance for C storage and vice versa. CO<sub>2</sub> can accumulate in soil as OM which is beneficial in terms of reduction of atmospheric CO<sub>2</sub> concentrations and improving soil fertility. Despite their outstanding importance for the C cycle, soils are still treated as a “black box” in most models. To predict feedbacks between soil, biosphere and atmosphere, progress is needed to shed light into this black box, i.e., to apply strategies for reducing SOC loss or re-accumulating SOC, quantitative predictions on the outcome of diverse strategies must be possible. There is no doubt that soils have the potential to reduce atmospheric CO<sub>2</sub> concentrations. However, many uncertainties in our understanding of C-cycling in soils hamper quantitative predictions of the sink potential and feedbacks between climate change and SOC dynamics. It must be certain that soil management does not turn soils into a net-source of CO<sub>2</sub>. Therefore, research on this topic must continue, and increase, but it is clear that the mitigation potential of soil is not well enough understood to rely on it: reducing anthropogenic GHG emissions is essential to mitigate climate change.

The mechanistic understanding of processes and mechanisms on C-cycling in soils has vastly improved, but many uncertainties still remain. The analysis presented show that the temperature sensitivity of different SOC pools significantly affects the outcome of model predictions of SOC dynamics. Still, there is no consensus on a general applicable sensitivity of mineralization of SOC. In fact, today there is a lack of methodological tools to determine temperature effects, and there exists a strong need for new and well designed experiments (Conant et al. 2011). With no reliable quantitative model to assess the temperature response of SOC mineralization, it is difficult to predict the outcome of complex processes such as drying-and-rewetting or freezing-and-thawing. Such events are likely to increase in frequency in the future, and it is essential to improve the mechanistic knowledge of these processes. Even increased productivity of plants by CO<sub>2</sub> fertilization can potentially destabilize SOC by priming effects (Fontaine et al. 2007). Knowledge is

generated in many different disciplines which are often only weakly linked in terms of exchanging results. This limits the progress at a time where fast action is required. However, the speed of progress may be advanced by the following considerations.

### ***18.5.1 Connect Research Communities***

Knowledge on C cycling was and is generated by many different disciplines. Atmospheric science, soil science, plant ecology, forestry, geography and many more disciplines are working on the topic. When reading the different subchapters, it becomes obvious that there is different terminology, even in related topics: studies in “litter decomposition” and “SOC stabilization” evolved largely independent from each other. Disconnect between “general ecology” and “soil ecology” was demonstrated recently by tracking citation between specialized journals (Barot et al. 2007). Knowledge transfer between the disciplines is slow, but is beginning to emerge (Prescott 2010; Schmidt et al. 2011). By exchanging results, concepts and ideas, scientific knowledge should increase faster and more effectively.

### ***18.5.2 Connect Empirical Result with Models***

Advances in mechanistic understanding of SOC stabilization are only poorly incorporated into quantitative models. To date, only one model exists which can simulate C-dynamics by inclusion of aggregate turnover (Yoo et al. 2011). Soil scientists use models only sparingly (Barot et al. 2007). Yet, the concepts must be quantified and validated. By using models as a tool to quantitatively synthesize various processes and mechanism, it is possible to better predict how changing conditions may influence the C cycle in general (Schmidt et al. 2011).

### ***18.5.3 Connect Specificity and Generality***

Under “specificity” empirical case studies are understood, whereas “generality” refers to the broad application of result and synthesis in theories. Both “specificity” and “generality” are essential to the scientific progress, but more merit should be given for synthesizing existing data. Entering e.g. “litter decomposition” in web of knowledge (7th November 2011) yielded 12,600 results, the first listed study being from 1930 (Melin 1930). Entering all these data into a global database and making it available for the scientific community will likely increase the precision of models describing litter decomposition across biomes. It is not said that that no experimental research will be needed after a global synthesis. Rather by developing a more general and quantitative model upon the vast data already existing it will be possible to identify gaps in knowledge and concentrate research efforts.

### 18.5.4 Using Long-Term Cross-Site Experiments

One reason why specificity seems to dominate research in soil science is the heterogeneous nature of soils. A lot of knowledge is generated under controlled laboratory conditions. However, it is also important to identify or design field studies, where the same treatment is implemented across several sites. Selecting or laying out such cross-site studies for long-term research will add to the knowledge generated in laboratory or single-site field studies, increase scientific output in many disciplines, and create excellent opportunities to test hypothesis and theories (Leuschner et al. 2009).

## References

- Abiven S, Recous S, Reves V et al (2005) Mineralisation of C and N from root, stem and leaf residues in soil and role of their biochemical quality. *Biol Fert Soils* 42:119–128
- Abiven S, Menasseri S, Chenu C (2009) The effects of organic inputs over time on soil aggregate stability – A literature analysis. *Soil Biol Biochem* 41:1–12
- Ainsworth EA, Long SP (2005) What have we learned from 15 years of free-air CO<sub>2</sub> enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO<sub>2</sub>. *New Phytol* 165:351–371
- Anderson T-H, Heinemeyer WH-J (2011) Changes in the fungal-to-bacterial respiratory ratio and microbial biomass in agriculturally managed soils under free-air CO(2) enrichment (FACE): a six-year survey of a field study. *Soil Biol Biochem* 43:895–904
- Baguis P, Roulin E, Willems P et al (2010) Climate change scenarios for precipitation and potential evapotranspiration over central Belgium. *Theor Appl Climatol* 99:273–286
- Baldocchi DD (2003) Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. *Glob Chang Biol* 9:479–492
- Baldock JA, Skjemstad JO (2000) Role of the soil matrix and minerals in protecting natural organic materials against biological attack. *Org Geochem* 31:697–710
- Baldock JA, Masiello CA, Gelinas Y et al (2004) Cycling and composition of organic matter in terrestrial and marine ecosystems. *Mar Chem* 92:39–64
- Balesdent J (1996) The significance of organic separates to carbon dynamics and its modelling in some cultivated soils. *Eur J Soil Sci* 47:485–493
- Balesdent J, Chenu C, Balabane M (2000) Relationship of soil organic matter dynamics to physical protection and tillage. *Soil Till Res* 53:215–230
- Bapiri A, Bååth E, Rousk J (2010) Drying-rewetting cycles affect fungal and bacterial growth differently in an arable soil. *Microb Ecol* 60:419–428
- Barot S, Blouin M, Fontaine S et al (2007) A tale of four stories: soil ecology, theory evolution and the publication system. *PloS One* 2(11):e124810
- Berg B, McClaugherty C (2003) *Plant litter – decomposition, humus formation carbon sequestration*. Springer, Berlin
- Birch HF (1958) The effect of soil drying on humus decomposition and nitrogen availability. *Plant Soil* 10:9–31
- Blagodatskaya E, Blagodatsky S, Dorodnikov M et al (2010) Elevated atmospheric CO<sub>2</sub> increases microbial growth rates in soil: results of three CO<sub>2</sub> enrichment experiments. *Glob Chang Biol* 16:836–848
- Böttcher J (2004) Uncertainties of nonlinearly estimated parameters from incubations of soil organic matter. *J Plant Nut Soil Sci* 167:293–302

- Bottner P, Couteaux MM, Anderson JM et al (2000) Decomposition of C-13-labelled plant material in a European 65–40 degrees latitudinal transect of coniferous forest soils: simulation of climate change by translocation of soils. *Soil Biol Biochem* 32:527–543
- Burdon J (2001) Are the traditional concepts of the structures of humic substances realistic? *Soil Sci* 166:752–769
- Cannell MGR, Thornley JHM (2000) Modelling the components of plant respiration: some guiding principles. *Ann Bot* 85:45–54
- Chapin F, Woodwell G, Randerson J et al (2006) Reconciling carbon-cycle concepts, terminology, and methods. *Ecosystem* 9:1041–1050
- Christensen BT (2001) Physical fractionation of soil and structural and functional complexity in organic matter turnover. *Eur J Soil Sci* 52:345–353
- Christensen JH, Hewitson B, Busuioic A et al (2007) Regional climate projections. In: Solomon S, Qin D, Manning M et al (eds) *Climate change 2007: the physical science basis. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge
- Coleman K, Jenkinson DS (1999) RothC-26.3 a model for the turnover of carbon in soil. IACR, Rothamsted
- Conant RT, Ryan MG, Agren GI et al (2011) Temperature and soil organic matter decomposition rates – synthesis of current knowledge and a way forward. *Glob Chang Biol* 17:3392–3404
- Conway T, Tans P (2011) Trends in atmospheric carbon dioxide. NOAA/ESRL. <http://www.esrl.noaa.gov/gmd/ccgg/trends>. Accessed 27 Nov 2011
- Cotrufu MF, Ngao J, Marzaioli F et al (2010) Inter-comparison of methods for quantifying above-ground leaf litter decomposition rates. *Plant Soil* 334:365–376
- Craine JM, Fierer N, McLauchlan KK (2010) Widespread coupling between the rate and temperature sensitivity of organic matter decay. *Nat Geosci* 3:854–857
- Dagesse D (2011) Effect of freeze-drying on soil aggregate stability. *SSSA J* 75:2111–2121
- Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440:165–173
- de Graaff M-A, van Groenigen K-J, Six J et al (2006) Interactions between plant growth and soil nutrient cycling under elevated CO<sub>2</sub>: a meta-analysis. *Glob Chang Biol* 12:2077–2091
- Denef K, Six J, Merckx R et al (2002) Short-term effects of biological and physical forces on aggregate formation in soils with different clay mineralogy. *Plant Soil* 246:185–200
- Derenne S, Largeau C (2001) A review of some important families of refractory macromolecules: composition, origin, and fate in soils and sediments. *Soil Sci* 166:833–847
- Dilkes NB, Jones DL, Farrar J (2004) Temporal dynamics of carbon partitioning and rhizodeposition in wheat. *Plant Physiol* 134:706–715
- Domanski G, Kuzyakov Y, Siniakina SV et al (2001) Carbon flows in the rhizosphere of ryegrass (*Lolium perenne*). *J Plant Nut Soil Sci* 164:381–387
- Drake JE, Gallet-Budynek A, Hofmockel KS et al (2011) Increases in the flux of carbon below-ground stimulate nitrogen uptake and sustain the long-term enhancement of forest productivity under elevated CO<sub>2</sub>. *Ecol Lett* 14:349–357
- Ellerbrock RH, Hohn A, Gerke HH (1999) Characterization of soil organic matter from a sandy soil in relation to management practice using FT-IR spectroscopy. *Plant Soil* 213:55–61
- Ellert BH, Janzen HH, VandenBygaart AJ et al (2008) Measuring change in soil organic carbon storage. In: Carter MR, Gregorich EG (eds) *Soil sampling and methods of analysis*. Taylor & Francis, Boca Raton
- Elliott ET (1986) Aggregate structure and carbon, nitrogen, and phosphorus in native and cultivated soils. *SSSA J* 50:627–633
- Eusterhues K, Rumpel C, Kleber M et al (2003) Stabilisation of soil organic matter by interactions with minerals as revealed by mineral dissolution and oxidative degradation. *Org Geochem* 34:1591–1600
- Feng XJ, Simpson MJ (2008) Temperature responses of individual soil organic matter components. *J Geophys Res Biogeosci* 113

- Fierer N, Schimel JP (2002) Effects of drying-rewetting frequency on soil carbon and nitrogen transformations. *Soil Biol Biochem* 34:777–787
- Fierer N, Schimel JP (2003) A proposed mechanism for the pulse in carbon dioxide production commonly observed following the rapid rewetting of a dry soil. *SSSA J* 67:798–805
- Fierer N, Grandy AS, Six J et al (2009) Searching for unifying principles in soil ecology. *Soil Biol Biochem* 41:2249–2256
- Fischer H, Meyer A, Fischer K et al (2007) Carbohydrate and amino acid composition of dissolved organic matter leached from soil. *Soil Biol Biochem* 39:2926–2935
- Flessa H, Ludwig B, Heil B et al (2000) The origin of soil organic C, dissolved organic C and respiration in a long-term maize experiment in Halle, Germany, determined by C-13 natural abundance. *J Plant Nut Soil Sci* 163:157–163
- Fontaine S, Bardoux G, Abbadie L et al (2004) Carbon input to soil may decrease soil carbon content. *Ecol Lett* 7:314–320
- Fontaine S, Barot S, Barre P et al (2007) Stability of organic carbon in deep soil layers controlled by fresh carbon supply. *Nature* 450:277–U210
- Franko U (1997) Modellierung des Umsatzes der organischen Bodensubstanz. *Arch Acker Pfl Boden* 41:527–547
- Friedlingstein P, Cox P, Betts R et al (2006) Climate-carbon cycle feedback analysis: results from the C<sup>4</sup>MIP model intercomparison. *J Climate* 19:3337–3353
- Gholz HL, Wedin DA, Smitherman SM et al (2000) Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. *Glob Chang Biol* 6:751–765
- Gillabel J, Cebrian-Lopez B, Six J et al (2010) Experimental evidence for the attenuating effect of SOM protection on temperature sensitivity of SOM decomposition. *Glob Chang Biol* 16:2789–2798
- Golchin A, Oades J, Skjemstad J et al (1994) Study of free and occluded particulate organic matter in soils by solid state <sup>13</sup>C Cp/MAS NMR spectroscopy and scanning electron microscopy. *Aust J Soil Res* 32:285–309
- Golchin A, Oades JM, Skjemstad JO et al (1995) Structural and dynamic properties of soil organic-matter as reflected by C-13 natural-abundance, pyrolysis mass-spectrometry and solid-state C-13 NMR-spectroscopy in density fractions of an Oxisol under forest and pasture. *Aust J Soil Res* 33:59–76
- Gu L, Post WM, King AW (2004) Fast labile carbon turnover obscures sensitivity of heterotrophic respiration from soil to temperature: a model analysis. *Glob Biogeochem Cycle* 18:GB1022
- Haile-Mariam S, Collins HP, Wright S et al (2008) Fractionation and long-term laboratory incubation to measure soil organic matter dynamics. *SSSA J* 72:370–378
- Hammes K, Schmidt MWI, Smernik RJ et al (2007) Comparison of quantification methods to measure fire-derived (black/elemental) carbon in soils and sediments using reference materials from soil, water, sediment and the atmosphere. *Glob Biogeochem Cycle* 21:GB3016
- Hanson PJ, Edwards NT, Garten CT et al (2000) Separating root and soil microbial contributions to soil respiration: a review of methods and observations. *Biogeochem* 48:115–146
- Harmon ME, Silver WL, Fasth B et al (2009) Long-term patterns of mass loss during the decomposition of leaf and fine root litter: an intersite comparison. *Glob Chang Biol* 15:1320–1338
- Hege U, Offenberger K (2006) Effect of differentiated mineral fertilization and organic manuring on yield, product quality and N balances in the International Permanent Organic Nitrogen Fertilization Experiment (IOSDV). *Puch Arch Agron Soil Sci* 52:535–550
- Heimann M, Reichstein M (2008) Terrestrial ecosystem carbon dynamics and climate feedbacks. *Nature* 451:289–292
- Heinze S, Raupp J, Joergensen RG (2010) Effects of fertilizer and spatial heterogeneity in soil pH on microbial biomass indices in a long-term field trial of organic agriculture. *Plant Soil* 328:203–215
- Heitkamp F, Raupp J, Ludwig B (2009) Impact of fertilizer type and rate on carbon and nitrogen pools in a sandy Cambisol. *Plant Soil* 319:259–275
- Heitkamp F, Raupp J, Ludwig B (2011) Effects of fertilizer type and rate on labile soil fractions of a sandy Cambisol – long term and short-term dynamics. *J Plant Nut Soil Sci* 174:121–127

- Heitkamp F, Jäger N, Flessa H et al (2012a) Effect of fertilization on respiration from different sources in a sandy Cambisol of an agricultural long-term experiment. *Arch Agron Soil Sci*. doi:10.1080/03650340.2011.555762
- Heitkamp F, Wendland M, Offenberger K et al (2012b) Implications of input estimation, residue quality and carbon saturation on the predictive power of the Rothamsted Carbon Model. *Geoderma* 170:168–175
- Helfrich M, Ludwig B, Buurman P et al (2006) Effect of land use on the composition of soil organic matter in density and aggregate fractions as revealed by solid-state C-13 NMR spectroscopy. *Geoderma* 136:331–341
- Hickler T, Smith B, Prentice IC et al (2008) CO<sub>2</sub> fertilization in temperate FACE experiments not representative of boreal and tropical forests. *Glob Chang Biol* 14:1531–1542
- Hugh HAL (2007) Soil freeze-thaw cycle experiments: trends, methodological weaknesses and suggested improvements. *Soil Biol Biochem* 39:977–986
- Jacob M, Viedenz K, Polle A et al (2010) Leaf litter decomposition in temperate deciduous forest stands with a decreasing fraction of beech (*Fagus sylvatica*). *Oecologia* 164:1083–1094
- Jacobs A, Helfrich M, Dyckmans J et al (2011) Effects of residue location on soil organic matter turnover: results from an incubation experiment with 15N-maize. *J Plant Nut Soil Sci* 174:634–643
- Jäger N, Stange CF, Ludwig B et al (2011) Emission rates of N<sub>2</sub>O and CO<sub>2</sub> from soils with different organic matter content from three long-term fertilization experiments—a laboratory study. *Biol Fert Soils* 47:483–494
- Jensen LS, Salo T, Palmason F et al (2005) Influence of biochemical quality on C and N mineralisation from a broad variety of plant materials in soil. *Plant Soil* 273:307–326
- Joergensen RG, Wichern F (2008) Quantitative assessment of the fungal contribution to microbial tissue in soil. *Soil Biol Biochem* 40:2977–2991
- Jones DL, Hodge A, Kuzyakov Y (2004) Plant and mycorrhizal regulation of rhizodeposition. *New Phytol* 163:459–480
- Kieft TL, Soroker E, Firestone MK (1987) Microbial biomass response to a rapid increase in water potential when dry soil is wetted. *Soil Biol Biochem* 19:119–126
- Kiem R, Kögel-Knabner I (2002) Refractory organic carbon in particle-size fractions of arable soils II: organic carbon in relation to mineral surface area and iron oxides in fractions <6 µm. *Org Geochem* 33:1699–1713
- Kim D-G, Vargas R, Bond-Lamberty B et al (2011) Effects of soil rewetting and thawing on soil gas fluxes: a review of current literature and suggestions for future research. *Biogeosci Discuss* 8:9847–9899
- Kirschbaum MUF (1995) The temperature dependence of soil organic matter decomposition, and the effect of global warming in soil organic C storage. *Soil Biol Biochem* 27:753–760
- Kirschbaum MUF (2006) The temperature dependence of organic matter decomposition – still a topic of debate. *Soil Biol Biochem* 38:2510–2518
- Knorr W, Prentice IC, House JJ et al (2005) Long-term sensitivity of soil carbon turnover to warming. *Nature* 433:298–301
- Kögel-Knabner I, Guggenberger G, Kleber M et al (2008) Organo-mineral associations in temperate soils: integrating biology, mineralogy, and organic matter chemistry. *J Plant Nut Soil Sci* 171:61–82
- Kuzyakov Y (2006) Sources of CO<sub>2</sub> efflux from soil and review of partitioning methods. *Soil Biol Biochem* 38:425–448
- Kuzyakov Y (2011) How to link soil C pools with CO<sub>2</sub> fluxes? *Biogeosciences* 8:1523–1537
- Kuzyakov Y, Gavrichkova O (2010) Time lag between photosynthesis and carbon dioxide efflux from soil: a review of mechanisms and controls. *Glob Chang Biol* 16:3386–3406
- Kuzyakov Y, Larionova AA (2005) Root and rhizomicrobial respiration: a review of approaches to estimate respiration by autotrophic and heterotrophic organisms in soil. *J Plant Nut Soil Sci* 168:503–520
- Kuzyakov Y, Friedel JK, Stahr K (2000) Review of mechanisms and quantification of priming effects. *Soil Biol Biochem* 32:1485–1498
- Kuzyakov Y, Subbotina I, Chen H et al (2009) Black carbon decomposition and incorporation into soil microbial biomass estimated by 14C labeling. *Soil Biol Biochem* 41:210–219



- Lamparter A, Bachmann J, Goebel M-O et al (2009) Carbon mineralization in soil: Impact of wetting-drying, aggregation and water repellency. *Geoderma* 150:324–333
- Leakey ADB, Ainsworth EA, Bernacchi CJ et al (2009) Elevated CO<sub>2</sub> effects on plant carbon, nitrogen, and water relations: six important lessons from FACE. *J Exp Bot* 60:2859–2876
- Ledford H (2008) Forestry carbon dioxide projects to close down. *Nature* 456:289–289
- Leifeld J, Fuhrer J (2005) The temperature response of CO<sub>2</sub> production from bulk soils and soil fractions is related to soil organic matter quality. *Biogeochemistry* 75:433–453
- Leuschner C, Jungkunst HF, Fleck S (2009) Functional role of forest diversity: pros and cons of synthetic stands and across-site comparisons in established forests. *Basic Appl Ecol* 10:1–9
- Ludwig B, Schulz E, Rethemeyer J et al (2007) Predictive modelling of C dynamics in the long-term fertilization experiment at Bad Lauchstädt with the Rothamsted Carbon model. *Eur J Soil Sci* 58:1155–1163
- Lundquist EJ, Scow KM, Jackson LE et al (1999) Rapid response of soil microbial communities from conventional, low input, and organic farming systems to a wet/dry cycle. *Soil Biol Biochem* 31:1661–1675
- MacCarthy P (2001) The principles of humic substances. *Soil Sci* 166:738–751
- Manderscheid R, Pacholski A, Weigel H-J (2010) Effect of free air carbon dioxide enrichment combined with two nitrogen levels on growth, yield and yield quality of sugar beet: Evidence for a sink limitation of beet growth under elevated CO<sub>2</sub>. *Eur J Agric* 32:228–239
- Martens DA (2000) Plant residue biochemistry regulates soil carbon cycling and carbon sequestration. *Soil Biol Biochem* 32:361–369
- Matzner E, Borken W (2008) Do freeze-thaw events enhance C and N losses from soils of different ecosystems? A review. *Eur J Soil Sci* 59:274–284
- Melin E (1930) Biological decomposition of some types of litter from north American forests. *Ecology* 11:72–101
- Muhr J, Goldberg SD, Borken W et al (2008) Repeated drying-rewetting cycles and their effects on the emission of CO<sub>2</sub>, N<sub>2</sub>O, NO, and CH<sub>4</sub> in a forest soil. *J Plant Nutr Soil Sci* 171:719–728
- Navarro-García F, Casermeiro MÁ, Schimel JP (2012) When structure means conservation: Effect of aggregate structure in controlling microbial responses to rewetting events. *Soil Biol Biochem* 44:1–8
- Oades JM (1984) Soil organic-matter and structural stability – mechanisms and implications for management. *Plant Soil* 76:319–337
- Oades JM (1993) The role of biology in the formation, stabilization and degradation of soil structure. *Geoderma* 56:377–400
- Paul EA, Morris SJ, Conant RT et al (2006) Does the acid hydrolysis-incubation method measure meaningful soil organic carbon pools? *SSSA J* 70:1023–1035
- Piccolo A, Spaccini R, Haberhauer G et al (1999) Increased sequestration of organic carbon in soil by hydrophobic protection. *Naturwissenschaften* 86:496–499
- Potthoff M, Dyckmans J, Flessa H et al (2005) Dynamics of maize (*Zea mays* L.) leaf straw mineralization as affected by the presence of soil and the availability of nitrogen. *Soil Biol Biochem* 37:1259–1266
- Powers JS, Montgomery RA, Adair EC et al (2009) Decomposition in tropical forests: a pan-tropical study of the effects of litter type, litter placement and mesofaunal exclusion across a precipitation gradient. *J Ecol* 97:801–811
- Prescott CE (2010) Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils? *Biogeochemistry* 101:133–149
- Rasse DP, Rumpel C, Dignac MF (2005) Is soil carbon mostly root carbon? Mechanisms for a specific stabilization. *Plant Soil* 269:341–356
- Reichstein M, Bednorz F, Broll G et al (2000) Temperature dependence of carbon mineralisation: conclusions from a long-term incubation of subalpine soil samples. *Soil Biol Biochem* 32:947–958
- Rillig MC, Allen MF (1999) What is the role of arbuscular mycorrhizal fungi in plant-to-ecosystem responses to elevated atmospheric CO<sub>2</sub>? *Mycorrhiza* 9:1–8
- Rochette P, Angers DA, Flanagan LB (1999) Maize residue decomposition measurement using soil surface carbon dioxide fluxes and natural abundance of carbon-13. *SSSA J* 63:1385–1396



- Rosier CL, Hoye AT, Rillig MC (2006) Glomalin-related soil protein: assessment of current detection and quantification tools. *Soil Biol Biochem* 38:2205–2211
- Rovira P, Kurz-Besson C, Couteaux MM et al (2008) Changes in litter properties during decomposition: a study by differential thermogravimetry and scanning calorimetry. *Soil Biol Biochem* 40:172–185
- Rühlmann J (1999) A new approach to estimating the pool of stable organic matter in soil using data from long-term field experiment. *Plant Soil* 213:149–160
- Rumpel C, Koegel-Knabner I (2011) Deep soil organic matter—a key but poorly understood component of terrestrial C cycle. *Plant Soil* 338:143–158
- Ryan MG, Law BE (2005) Interpreting, measuring, and modeling soil respiration. *Biogeochemistry* 73:3–27
- Schenck zu Schweinsberg-Mickan M, Joergensen RG, Mueller T (2010) Fate of <sup>13</sup>C- and <sup>15</sup>N-labelled rhizodeposition of *Lolium perenne* as function of the distance to the root surface. *Soil Biol Biochem* 42:910–918
- Schmidt MWI, Torn MS, Abiven S et al (2011) Persistence of soil organic matter as an ecosystem property. *Nat Geosci* 478:49–56
- Schmitt A, Glaser B, Borken W et al (2008) Repeated freeze-thaw cycles changed organic matter quality in a temperate forest soil. *J Plant Nut Soil Sci* 171:707–718
- Schulze E-D, Luysaert S, Ciais P et al (2009) Importance of methane and nitrous oxide for Europe's terrestrial greenhouse-gas balance. *CarboEuropeTeam* 2:842–850
- Seifert A-G, Trumbore S, Xu X et al (2011) Variable effects of labile carbon on the carbon use of different microbial groups in black slate degradation. *Geochim Cosmochim Acta* 75:2557–2570
- Sierra J (1990) Analysis of soil nitrogen mineralization as estimated by exponential models. *Soil Biol Biochem* 22:1151–1153
- Siewert C (2004) Rapid screening of soil properties using thermogravimetry. *SSSA J* 68:1656–1661
- Silver WL, Miya RK (2001) Global patterns in root decomposition: comparisons of climate and litter quality effects. *Oecologia* 129:407–419
- Smith P, Smith JU, Powlson DS et al (1997) A comparison of the performance of nine soil organic matter models using datasets from seven long-term experiments. *Geoderma* 81:153–225
- Sollins P, Homann P, Caldwell BA (1996) Stabilization and destabilization of soil organic matter: mechanisms and controls. *Geoderma* 74:65–105
- Solomon S, Qin D, Manning DAC et al (2007) Climate change 2007: the physical science basis – contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on climate change. Cambridge University Press, Cambridge
- Swift MJ, Heal OW, Anderson JM (1979) Decomposition in terrestrial ecosystems. Blackwell Scientific Publications, Oxford
- Teepe R, Brumme R, Beese F (2001) Nitrous oxide emissions from soil during freezing and thawing periods. *Soil Biol Biochem* 33:1269–1275
- Thevenot M, Dignac M-F, Rumpel C (2010) Fate of lignins in soils: a review. *Soil Biol Biochem* 42:1200–1211
- Tisdall JM, Oades JM (1982) Organic-matter and water-stable aggregates in soils. *J Soil Sci* 33:141–163
- Treseder KK, Allen MF (2000) Mycorrhizal fungi have a potential role in soil carbon storage under elevated CO<sub>2</sub> and nitrogen deposition. *New Phytol* 147:189–200
- Treseder KK, Turner KM (2007) Glomalin in ecosystems. *Soil Sci Soc Am J* 71:1257–1266
- Trofymow JA, Moore TR, Titus B et al (2002) Rates of litter decomposition over 6 years in Canadian forests: influence of litter quality and climate. *Can J For Res-Revue Canadienne De Recherche Forestiere* 32:789–804
- Trumbore S (2006) Carbon respired by terrestrial ecosystems – recent progress and challenges. *Glob Chang Biol* 12:141–153
- Trumbore SE, Czimczik CI (2008) An uncertain future for soil carbon. *Science* 321:1455–1456
- Valentini R, Matteucci G, Dolman AJ et al (2000) Respiration as the main determinant of carbon balance in European forests. *Nature* 404:861–865

- Vanhala P, Karhu K, Tuomi M et al (2007) Old soil carbon is more temperature sensitive than the young in an agricultural field. *Soil Biol Biochem* 39:2967–2970
- Vicca S, Janssens IA, Flessa H et al (2009) Temperature dependence of greenhouse gas emissions from three hydromorphic soils at different groundwater levels. *Geobiology* 7:465–476
- von Lützow M, Kögel-Knabner I (2009) Temperature sensitivity of soil organic matter decomposition – what do we know? *Biol Fert Soils* 46:1–15
- von Lützow M, Kögel-Knabner I, Ekschmitt K et al (2006) Stabilization of organic matter in temperate soils: mechanisms and their relevance under different soil conditions – a review. *Eur J Soil Sci* 57:426–445
- Waldrop MP, Firestone MK (2004) Altered utilization patterns of young and old soil C by microorganisms caused by temperature shifts and N additions. *Biogeochemistry* 67:235–248
- Wall DH, Bradford MA, St John MG et al (2008) Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. *Glob Chang Biol* 14:2661–2677
- Wang Y, Hsieh Y-P (2002) Uncertainties and novel prospects in the study of the soil carbon dynamics. *Chemosphere* 49:791–804
- Werth M, Kuzyakov Y (2008) Root-derived carbon in soil respiration and microbial biomass determined by  $^{14}\text{C}$  and  $^{13}\text{C}$ . *Soil Biol Biochem* 40:625–637
- West TO, Post WM (2002) Soil organic carbon sequestration rates by tillage and crop rotation: a global data analysis. *SSSA J* 66:1930–1946
- Wetterstedt JAM, Persson T, Agren GI (2010) Temperature sensitivity and substrate quality in soil organic matter decomposition: results of an incubation study with three substrates. *Glob Chang Biol* 16:1806–1819
- Wiseman CLS, Puttmann W (2005) Soil organic carbon and its sorptive preservation in central Germany. *Eur J Soil Sci* 56:65–76
- Wutzler T, Reichstein M (2008) Colimitation of decomposition by substrate and decomposers – a comparison of model formulations. *Biogeosciences* 5:749–759
- Yoo G, Yang XM, Wander MM (2011) Influence of soil aggregation on SOC sequestration: a preliminary model of SOC protection by aggregate dynamics. *Ecol Eng* 37:487–495
- Yuste JC, Nagy M, Janssens IA et al (2005) Soil respiration in a mixed temperate forest and its contribution to total ecosystem respiration. *Tree Physiol* 25:609–619
- Zhang D, Hui D, Luo Y et al (2008) Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. *J Plant Ecol-UK* 1:85–93