

# 1 • Soil carbon relations: an overview

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## 1.1 INTRODUCTION

Soils are localized between base rock, atmosphere and vegetation, and represent a home for numerous organisms and the place of countless biogeochemical transformation and transfer processes. In addition, soils store many substances that are essential to maintain human life and ecosystem processes. Therefore, soils have been a research focus for more than a century and soil science has deep connections to ecology, agriculture and nature conservation.

The most important practical applications of soil science are diagnostics and maintenance of soil fertility and, more recently, definition of the role of soils in the terrestrial carbon balance in the context of increasing atmospheric CO<sub>2</sub> concentration and the resulting greenhouse effect. Carbon stored in soils represents the largest carbon pool in nearly all terrestrial biomes (Bolin *et al.*, 2001) and thus it has a huge potential for either sequestering or releasing carbon into the atmosphere. Consequently, knowledge of the dynamics of soil carbon is essential for a better understanding of the terrestrial carbon balance. However, inter-annual changes in soil carbon stocks are small compared to the total carbon stored in soils, and thus determining any changes in soil carbon stocks by repeated inventories is difficult. On the other hand, flux measurements also bear inaccuracies and uncertainties, confounding attempts to directly measure and model the CO<sub>2</sub> flux from the soil and linking this flux to the underlying processes. There are considerable challenges in monitoring soil fluxes without disturbing the plant–soil carbon flow. Furthermore, we must also deal with considerable spatial and temporal variability inherent to nearly all ecosystems.

The above challenges imply some conceptual and technical consequences in the methodology of soil

carbon studies. It is the intention of this book to summarize the actual state-of-the-art methods on soil carbon stock and flux measurements and modelling approaches. However, the authors intend to provide more than a ‘manual’ for several methods. The goal is a critical review on the potentials and limitations of different concepts and underlying methodological approaches as well as giving guidance on their informational value and their possible integration. The main aim is, firstly, to provide a more integrated methodology on soil carbon stock and flux measurements at different scales and, secondly, to discuss the relevance of such measurements within the terrestrial carbon cycle and climate system.

## 1.2 SOIL CARBON RELATIONS: A BASIC CONCEPT

In terrestrial ecosystems the source of soil organic carbon input is from photosynthesis or net primary productivity. Assimilates can be transferred directly to the roots via the phloem or can be converted to biomass that might be transferred to the soil via litter (Fig. 1.1). The ‘assimilate-fed’ and the ‘litter-fed’ pathways have also been named ‘autotrophic’ and ‘heterotrophic’ components of soil respiration in many studies. For many concepts and methods related to soil carbon dynamics it is a prerequisite to distinguish between these components of soil respiration because they depend on very different mechanisms determining their response to environmental conditions.

The autotrophic component can be further separated into respiration of the roots *sensu stricto* and their mycorrhizal symbionts and the microbiota of the rhizosphere, which depend directly or indirectly on carbohydrate sources from roots or mycorrhiza.

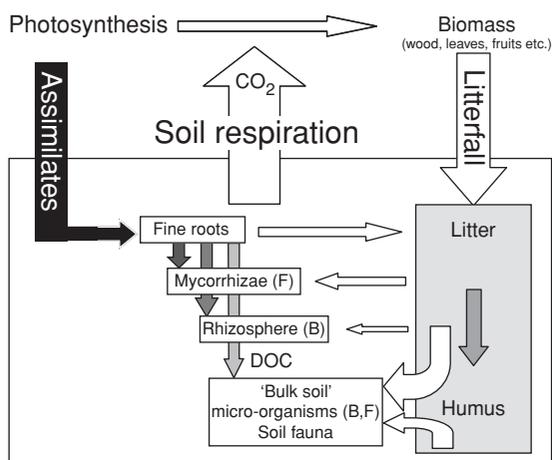


Figure 1.1 Basic concept model of soil carbon dynamics.

In many conceptual (i.e. modelling) approaches three pools of organic matter are distinguished. The easily decomposable active soil organic matter and the more stable slow and passive humic substances, also often called the recalcitrant pool. These pools receive fresh organic matter via litter input but also from microbial turnover and other events such as fire. Litter and the resulting humic substances are decomposed, mainly by the bulk soil micro-organisms that comprise bacteria, fungi and the soil meso- and macro-fauna, resulting in respiration and subsequent soil CO<sub>2</sub> efflux and changes in the chemical composition of soil organic matter (SOM). This biological activity is the driving force for the conversion of litter into stable humus and is also related to bioturbation (e.g. earthworm activity), which causes both aeration and SOM incorporation into clay minerals or deeper soil layers. Importantly, this biological activity, although crucial in determining SOM turnover and soil carbon storage capacity, is not yet adequately included in most modelling frameworks.

The above conceptual framework has at least three weak points: (1) rhizosphere micro-organisms as well as mycorrhizas do not solely depend on root exudates as they also break down soil organic matter, even though most of the energy required for this process is received via fresh root-derived carbon; (2) the fine-root and mycorrhizal compartments are not only respiratory components but also feed into the litter pool themselves; and (3) soil organic matter is a complex mixture of thousands of chemical compounds, each with its own rate

of decomposition depending on the soil microbial and faunal community, their activity and their potential to access compounds adhered to or occluded by mineral surfaces.

Nevertheless, it will be shown later that – despite these limitations – the two-pathway conceptual model is a useful tool for many methods and for their integration.

### 1.3 RESEARCH LINES

Four different lines of research concerning soil carbon relations have been distinguished in the past: a chemical, physical, physiological and an ecological line. This fragmentation had some fatal consequences: in 1961 Domsch remarked that the research on soil respiration had a ‘borderland character’ being located between soil science, hygiene, meteorology, microbiology, agricultural chemistry, ecology, horticulture, forestry, biochemistry and phytopathology. He concluded that this led (and still leads) to the consequence that new information was often isolated in one scientific community and did not spread through the whole facet of disciplines. The result was a number of ‘quaint rediscoveries’ throughout the years that can still be found even in very recent publications.

#### 1.3.1 Soil chemistry

The *chemical line* concentrates on the chemical characterization of soil organic matter and the resulting decomposition rates. Chemical properties and the amount of soil organic matter determine the basic structure and function of an ecosystem.

The chemical properties, often called the ‘quality’ of SOM, play an important role in the regulation of microbial activity. In addition to basic chemical properties such as pH values, element concentrations as well as element ratios (e.g. C/N), ratios of substrate groups (e.g. cellulose to lignin), or between substrate groups and elements (e.g. lignin to N) are usually used to determine organic matter quality (e.g. Vance and Chapin, 2001). Ågren and Bosatta (1996) called the litter quality ‘the bridge between plant and soil’. Numerous techniques that have been developed during the past decades promise deeper insights into the chemistry and dynamics of soil organic matter (Kögel-Knabner *et al.*, 2008).

However, determining changes in the amount of soil organic matter over time is challenging because

it means detecting a small change in a large number. Therefore, most of the studies using this method have been, and indeed should be, conducted at long-term experimental sites (Jenkinson and Johnston, 1977; Körschgens, 1996; Huggins *et al.*, 1998) that are merged in regional or global networks (Smith *et al.*, 1996; Powlson *et al.*, 1998; [www.rothamsted.bbsrc.ac.uk/aen/somnet](http://www.rothamsted.bbsrc.ac.uk/aen/somnet)).

The potential for directly detecting short-term changes through repeated soil sampling was recently examined in several studies (Conant *et al.*, 2003; Conen *et al.*, 2003; Smith, 2004). The minimum time resolution of this approach depends on the spatial heterogeneity of a system in relation to the number of samples and the magnitude of change. Most of the studies conclude that changes in the amount of soil organic matter expected as a result of climate or land-use change cannot be detected statistically significantly within less than a decade.

### 1.3.2 Physical mechanisms

The second line centres on the *physical* mechanisms that drive the mass flow of CO<sub>2</sub> from the soil to its boundary layer with the atmosphere. It is affected by an old dispute about the driving force of this mass flow. From the first systematic measurements, Romell (1922) drew the conclusion that the diffusion along a CO<sub>2</sub> gradient was the main driving force of soil CO<sub>2</sub> efflux. Nevertheless, other authors suggested additional meteorological and hydrological factors that were summarized by Albertsen (1977):

- temperature-induced differences in density and diffusivity between ground air and atmosphere
- barometric pressure changes
- displacement of ground air by the percolation of water (rain, irrigation)
- changes in the groundwater table
- solution and transport of gases in the sewage water
- pressure changes induced by vertical wind.

Although these factors can play a distinct role in certain situations, most authors rate diffusion as the most relevant factor (van Bavel, 1951, 1952). Therefore, many studies have focused on the physical parameters that influence the diffusivity of CO<sub>2</sub> through soils, such as porosity, texture and water content.

Nevertheless, the additional factors and their contribution to driving soil CO<sub>2</sub> efflux have been re-analyzed several times since new and more accurate measuring instruments for pressure and wind speed became available. From several studies it became evident that turbulent transport can indeed play an important role (Kimball and Lemon, 1971; Kutsch, 1996; Fang and Moncrieff, 1999; Moncrieff and Fang, 1999; Kutsch *et al.*, 2001a; Takle *et al.*, 2004; Flechard *et al.*, 2007). However, a systematic study about the influence of wind-induced turbulence on soil CO<sub>2</sub> efflux is still missing.

### 1.3.3 The physiological research line

Beyond flux component analysis as depicted in Fig. 1.1 and discussed above, the basic goal of the physiological research line is to understand the eco-physiological performance of soil biota. Since most of the soil CO<sub>2</sub> originates from respiratory processes by plant roots and soil organisms, the *physiological research line* analyzes how these processes are influenced by climate, structure and activity of the microbial biomass, roots and mycorrhiza, as well as trophic interactions in the soil food web and the physico-chemical properties of the soil. This research comprises soil microbiology, zoology, the physiology of roots and mycorrhizae, and rhizosphere processes.

The physiological work on bulk soil microorganisms is usually done with soil samples in the laboratory. This enables researchers to isolate single processes or factors, e.g. by keeping all other factors constant. The basic information about the reaction of soil biota to short-term changes in temperature and moisture as well as the influence of pH, oxygen and nutrients were obtained as early as the second half of the nineteenth century (Wollny, 1880; van Suchtelen, 1910; Stoklasa and Ernest, 1922). In later studies the properties of the micro-biota in soils were also used as a measure of soil quality or soil integrity when environmental problems had to be evaluated, such as acidification (Bewley and Stotzky, 1983; Lohm *et al.*, 1984; Mai and Fiedler, 1988), pesticides (Chopra and Magu, 1985), heavy metals (Wilke, 1988) or dioxins and polychlorinated biphenyls (PCBs) (Arthur and Frea, 1988).

Another branch of the physiological line specifically analyzes the regulation of 'autotrophic respiration',

going back at least to the third decade of the twentieth century (Eidmann, 1943). Estimates of autotrophic respiration have been reported to comprise between 5% and 90% of total soil respiration, most studies give values between 40% and 70% (Hanson *et al.*, 2000; Bond-Lamberty *et al.*, 2004; Subke *et al.*, 2006). Two groups of approaches have been used to determine the proportion of autotrophic respiration. The first group consists of approaches that work with exclusion or down-regulation of root respiration and comparing soil respiration in areas with and without root activity. In agricultural ecosystems this can be done easily by keeping parts of a crop field bare. In forest ecosystems roots can be excluded by ‘trenching’ small soil areas (Epron *et al.*, 1999) or root activity can be ceased by ‘girdling’ groups of trees (Högberg *et al.*, 2001). Grasslands may be the most difficult systems to apply trenching methods to as the disturbance induced by the use of chamber techniques in the dense canopy is high and the required clipping can considerably change the soil environment.

The other (far less intrusive) group of approaches uses isotopes of the element carbon – either in the form of the radioactive  $^{14}\text{C}$  or the stable  $^{13}\text{C}$ . Isotopic approaches rely on artificial enrichment or natural biochemical fractionation that occurs in the pathway from air to plant and soil, and can apply mixing models for separating source components.

Like all respiration processes autotrophic respiration is influenced by temperature and moisture. However, because it utilizes plant assimilates as substrate, it also depends on net primary productivity and carbon partitioning in the plants and as such might be less temperature dependent than soil microbial respiration. In addition, root respiration *sensu stricto* is affected by root nitrogen concentration (Burton *et al.*, 1998; Bahn *et al.*, 2006). Also species, root diameter and seasonal dynamics play a distinct role. Lambers *et al.* (1991) related root respiration to the three basic functions: growth, maintenance and ion uptake. The latter can account for up to one quarter of root respiration.

More recently, new approaches have drawn attention to the regulation of mycorrhizal respiration (Heinemeyer *et al.*, 2006, 2007; Moyano *et al.*, 2007), since more than one third of the respiratory energy requirement of roots can be due to mycorrhizas (Lambers *et al.*, 1998). These studies, using mesh bags that enable the mycelium to grow into a soil column

but exclude roots, showed that mycorrhizal respiration depends more on the supply of photosynthates than on temperature. However, more data and improved techniques are needed, avoiding artefacts such as soil moisture changes and the need to assess the potential of any changes in heterotrophic respiration due to the exclusion of roots and mycorrhizas (e.g. ‘Gadgil effect’, Gadgil and Gadgil, 1971), and the decomposition of cut root fragments.

In the *ecological* research line the soil carbon relations are understood as a part of the ecosystem matter cycling. Soil organic matter plays an important role in determining the structure and function of ecosystems, e.g. by storage as well as the interaction of carbon and nutrient cycles (Odum, 1969).

#### 1.3.4 The ecological research line

In this context a flux-based approach has become widely adopted, focusing on field measurements of soil  $\text{CO}_2$  efflux. The definition of the term ‘soil respiration’ as  $\text{CO}_2$  evolution from the soil surface, and the beginning of field studies, dates back more than 80 years. It was the Swedish scientist Henrik Lundegårdh (1924, 1927) who started first measurements with a method that we would call ‘static closed chamber’ today. It is remarkable that Lundegårdh’s work on soil respiration was part of his more integrative studies on carbon cycling in agricultural ecosystems that he summarized 1924 in a book called *Der Kreislauf der Kohlensäure in der Natur* (the cycling of carbonic acid in nature). This tells us that field measurements of soil respiration were part of an ecosystem approach from their early beginnings, about a decade before the term ‘ecosystem’ itself was defined by Tansley in 1935. A lot of later studies combined basic and applied aspects: focusing on either the analysis of the major factors driving soil respiration and the accumulation or loss of soil organic matter, or on defining indicators of soil fertility, health, integrity or sustainability (Haber, 1958; Walterscheidt, 1960; Edwards and Sollins, 1973; Singh and Gupta, 1977; Trumbore, 2006).

More recently soil carbon relations became a central part of the research on climate change. Since the 1970s it became more and more evident that anthropogenic emissions of  $\text{CO}_2$  result in an increase of the natural greenhouse effect of atmospheric trace gases and hence to an increase of the earth’s surface temperature

(IPCC, 2001). In view of the large size of global terrestrial soil carbon stocks and a general temperature sensitivity of biological and biochemical processes, there has been increasing recognition of the potential role of soils for the terrestrial carbon cycle in a globally changing environment. In this context, a number of important questions have recently become issues of debate.

- How do temperature and precipitation changes affect the mineralization of soil organic matter? Will soil respiration increase significantly with rising temperatures or will acclimation processes occur?
- How much atmospheric CO<sub>2</sub> can be sequestered for how long in soil organic matter and in which ecosystems? Conversely, which ecosystems might potentially release large amounts of soil carbon?
- Will increased net primary production, due to anthropogenic CO<sub>2</sub> and nitrogen fertilization effects, lead to increased litter production and hence increased soil carbon storage?

The answers to these questions require a deep knowledge on the regulation of soil carbon fluxes and its underlying processes. Soil temperature and soil moisture were often defined as primary factors driving the mineralization of soil organic matter. In most cases they explain a high proportion of (short-term) temporal variations in soil respiration at one distinct site. However, the individual components of the measured soil CO<sub>2</sub> efflux (e.g. root-derived respiration) might respond differently to environmental change (Staddon *et al.*, 2002).

#### 1.4 CURRENT CHALLENGES

As simple as measuring soil CO<sub>2</sub> efflux or determining the soil carbon stocks of a site might appear, this basic research on soil carbon dynamics provides many challenges. In contrast to above-ground carbon relations, the world of soil carbon turnover and decomposition is covered within the 'hidden half' of terrestrial ecosystems. It involves literally thousands of species of soil organisms, ranging from the metre or centimetre to less than micrometre scale.

It is surprising how little we know globally about those biological components that drive turnover rates of litter and organic matter. Many of the decomposer bacteria, for example, are still unknown, but their role is important in aerobic, and even more so in anaerobic, decomposition. We are not yet able to name most of

them at species level or to group them into functional types as is commonly done when modelling plant carbon dynamics at the larger scales. About another important group, the soil fungi, we do not yet fully understand their life cycles, environmental responses or specific role in the carbon cycle. Only recently, the advance of molecular techniques enabled us to realize the level of complexity of processes involved in the decomposition of organic matter, and the combination of these novel molecular techniques with stable isotope probing will hopefully improve our understanding in the near future.

In addition, the activity of below-ground decomposer organisms is influenced by many factors such as the amount and chemical quality of litter and soil organic matter, soil texture and porosity, pH value, input via litterfall and root turnover, root biomass and root activity. Also past and recent disturbances, such as fire or erosion as well as ploughing, agro chemicals or acid deposition, can affect the soil carbon turnover substantially. Therefore, site inter-comparisons even for the same soil type are difficult to interpret.

Moreover, our basic ability to adequately separate autotrophic and heterotrophic flux components (see Fig. 1.1) and their respective responses to environmental changes is still limited. However, the proper link between above- and below-ground carbon flow in the plant-soil carbon flux continuum needs to be established, as can be seen in the continued debate on the existence and role of soil priming, which may alter turnover of older organic matter as a result of fresh plant-derived soil carbon input. Finally, all these novel aspects need to be considered by the modelling community, for which the incorporation of basic soil biology still seems a major obstacle.

In the following description of the main book sections we will try to highlight the most important issues regarding soil carbon fluxes. The book chapters aim not only to outline the most important approaches but also to highlight cutting-edge methodologies and future directions of research.

##### 1.4.1 Experimental design of flux measurements and stock taking: limitations at the plot scale

Soil respiration measurements in the field are one of the most difficult among the ecosystem flux measurements. So far, no single method has been established as

standard but comparisons, which give important indications on their accuracy, have been performed (Janssens *et al.*, 2000; Pumpanen *et al.*, 2004; Butnor *et al.*, 2005). Notably, all methods can affect the object being measured by disturbing the biochemical processes involved in CO<sub>2</sub> production, the physical properties influencing CO<sub>2</sub> movement towards the soil surface or by changing the environmental conditions in the soil. In addition, although collar insertion assures a good chamber-to-soil seal, at the same time it cuts through parts of the surface rooting zone, causing in effect a miniature trenching effect.

Furthermore, it is important to unravel the sources of variability observed in soil CO<sub>2</sub> efflux and to distinguish spatial and temporal variations for both biotic and abiotic factors (e.g. 'hot spots' of decomposition). Whereas biotic variations can occur at micrometre scales, abiotic variability is predominantly at much larger scales (e.g. throughfall patterns). In this context, the relation of high frequency (i.e. capturing diurnal response times and correlations) versus infrequent measurements (capturing spatial resolution) might specifically need to be addressed.

Chapters 2 (Pumpanen *et al.*) and 3 (Subke *et al.*) of this book summarize the challenges in chamber design, experimental setup and scaling up from sparse and infrequent measurements to the level of, for example, catchment, region, or even continental or global scales bearing a considerable degree of uncertainty. The two chapters conclude with a step-wise guide to experimental planning and hypotheses testing with a particular emphasis on including consideration of pre-treatment periods and how to adequately address spatial variability and to up-scale point results within a geographical information systems (GIS) framework. Chapter 3 also includes a specific introduction to addressing sampling strategies and spatial autocorrelation with the use of a simple semivariogram as part of an initial site survey with consideration of budget and manpower constraints. This chapter aims to offer the basis for sound statistical design leading to meaningful data and their adequate interpretation.

International environmental policy programmes (e.g. the United Nations Framework Convention on Climate Change; [http://unfccc.int/kyoto\\_protocol/items/2830.php](http://unfccc.int/kyoto_protocol/items/2830.php)) are increasingly requiring assessment of the soil carbon sink or source potential, and more accurate net soil carbon balance measurements. As such, a full carbon balance often also needs to consider many

rather difficult components such as dissolved organic carbon (DOC) fluxes or effects of fire.

Chapter 4 (Rodeghiero *et al.*) focuses on organic soil carbon stocks and the associated measurement techniques and starts with an overview of global datasets on soil carbon stocks across biomes and a schematic soil carbon cycle also considering hypothetical relationships between soil carbon stocks and environmental change (i.e. temperature, elevated CO<sub>2</sub> and nitrogen). Like flux measurements, the repeated inventory approach to determine soil carbon changes over time has considerable simplifications and uncertainties. Notably, it requires a consistent sampling design and analytical approach between inventories to allow meaningful comparison and detect changes in soil carbon stocks with sufficient precision. In particular, soil sampling procedure, measurements of soil bulk density and conversion factors of soil organic matter (SOM) to soil organic carbon (SOC) are highlighted as a source of significant error in SOC stocks and their estimated changes, in particular in organic soils. Issues of a strict protocol, soil sampling by horizon or depth increments, excavation pits, required sample number and sampling time interval in relation to the minimum detectable difference are all discussed in Chapter 4. The chapter considers and compares all of the major methods of analyzing soil for organic carbon and points out their individual advantages and shortfalls (e.g. SOM conversion factors). Importantly, this chapter also offers a simple flow chart for soil analysis for selecting an appropriate soil carbon analysis.

#### 1.4.2 Litter and soil organic matter: a meaningful separation and characterization of carbon pools

The second section (Chapters 5, Cotrufo *et al.*, and 6, Denef *et al.*) discusses a large number of techniques that have been developed for the characterization of litter and SOM, the non-living organic material within the soil matrix, and cautiously addresses how to interpret the results in a meaningful way, also using stable isotope techniques. This work is intended to gain insight in the stabilization and destabilization mechanisms that underlie SOM dynamics in the short and long term.

Chapter 6 (Denef *et al.*) shows that a suite of techniques combining physical or chemical fractionation, analytical pyrolysis or nuclear magnetic resonance

(NMR) for biochemical characterization, and isotopic analysis techniques for an assessment of dynamics, is necessary for an exhaustive examination of the nature and dynamics of SOM. These developing techniques will hopefully deliver some of the data needed for an increased process understanding of long-term soil carbon storage and the evaluation of the commonly used model parameters of SOM decomposition. However, there are some clear limitations in most studies in understanding long-term carbon storage as the nature of sampling destroys, to some degree, the structures to be investigated.

Soil organic matter fractionation approaches generally provide useful measures of SOM stability (e.g. age and turnover times) and microbial functioning, yet methodologies and protocols need to be developed further. For example, in contrast to the common assumption that clay content is the most important determinant of SOC storage, in many soils, the type of organo-mineral complex appears to be even more important (Koch *et al.*, 1988; Bardgett and Saggar, 1994; Torn *et al.*, 2002). There is a clear mandate for studying the composition and stability of physical SOM fractions in different soil types and environments following recently standardized fractionation procedures.

Litter decomposition is a crucial step in determining SOC accumulation and changes over time. Overall litter chemistry and nutrient levels, climate and soil biology control the processes involved in litter incorporation into SOM and eventually its turnover into CO<sub>2</sub>, H<sub>2</sub>O or CH<sub>4</sub> and other fermentation products (Kögel-Knabner *et al.*, 2008). However, despite a large number of studies, general conclusions are still difficult to draw and, as recently underlined by Prescott *et al.* (2004), ‘many of the well-known facts about litter decomposition need to be revised’. Chapter 5 (Cotrufo *et al.*) outlines the current state of knowledge on litter decomposition processes and identifies avenues of future research. Future research is needed where theoretical and experimental work are designed and executed in coordination, to measure ‘true’ processes and to model measurable pools and fluxes.

Litter quality cannot be described by a universally accepted index and is mainly based on defining known recalcitrant litter fractions (e.g. lignin, tannins, phenolic compounds etc.). There are novel and promising non-destructive techniques (such as mid-infrared (MIR), near-infrared (NIR) and diffuse reflectance

infrared Fourier-transform (DRIFT) spectroscopy), which could make important contributions to rapidly assess litter or SOM quantity and quality and directly relate quality to dynamics and microbial functioning. Although microbes are able to degrade virtually all biological compounds, differences exist between fungal and bacterial communities and their decomposition potential, mostly relating to litter type and soil chemistry.

A good understanding of the feedback and interactions between the characteristics of litter and SOM and the biological activity is still limited. Therefore, the next two sections focus on biotic soil activities, starting with two chapters on methods for partitioning autotrophic versus heterotrophic respiration and two further chapters focusing in more detail on microbial communities and soil food webs, respectively.

#### 1.4.3 Measuring autotrophic versus heterotrophic fluxes: available methods and their meaning

It has been widely acknowledged that we need an increased understanding of how autotrophic and heterotrophic flux components vary over time and with climate. In particular, as root-derived carbon fluxes might lead to additional SOM turnover or ‘soil priming’. The research focus has recently shifted to the role of mycorrhizal fungi in plant–soil carbon supply and implications for SOM turnover.

Chapters 7 (Moyano *et al.*) and 8 (Epron) provide an in-depth overview of the current understanding and the available techniques for partitioning autotrophic and heterotrophic respiration. Chapter 7 describes in detail physiological approaches to assessing the respiration of roots and the mycorrhizosphere, whereas Chapter 8 focuses on gap, trenching, girdling and clipping techniques in order to assess root-derived respiration.

Integrating the results of these different approaches is difficult. One reason is that mycorrhizal fungi are usually included in the autotrophic flux component. Consequently, root respiration *sensu stricto* has been overestimated when derived from girdling or trenching without further partitioning (Pendall *et al.*, 2004). When using lab-based respiration rates of excised (mycorrhizal-deprived) roots, the ignored extra-radical mycelium (ERM) respiration component might explain why scaled-up respiration measurements show low estimates of autotrophic respiration when compared to

girdling (Högberg *et al.*, 2001) or trenching experiments, which include the ERM component (Simard *et al.*, 1997; Högberg *et al.*, 2002). In addition, it is important to note that trenching and girdling changes the presence and activity of biota in soils (Schulze *et al.*, 2005).

A major demand for the field ecologist is to enable continuous and high-frequency measurements of soil or soil-component respiration in order to capture the highly variable contribution of the autotrophic carbon flux components. A combination of mesh collars with isotope tracer studies within the footprint of an eddy covariance system will deliver simultaneous data of canopy photosynthesis and plant carbon allocation to the rhizosphere, and seems a most promising way forward to increase our understanding of the soil CO<sub>2</sub> flux components, the contribution changes over time, their environmental responses and impacts on SOM decomposition.

#### 1.4.4 Soil microbes, soil fauna and trophic interactions: describing communities, their functions and activity

In general, the knowledge about microbial activity in soils under field conditions and its adjustment to changing environmental constraints is small (Vance and Chapin, 2001; Kögel-Knabner *et al.*, 2008). This has methodological reasons, because many microbiological analyses cannot be conducted *in situ* and field measurements of soil respiration are very seldom directly connected with microbiological analyses in the laboratory. In addition, it has been impossible until recently to analyze the species spectra of soil microbial communities, their micro-habitats and their position in the soil carbon cycle (Ekschmitt *et al.*, 2008). Microbial eco-physiology preferred to work with functional groups or with the characterization of whole soil microbial biomass by applying metabolic quotients (Paul and Clark, 1989; Anderson and Domsch, 1990; Ritz *et al.*, 1994; Alef and Nannipieri, 1995). Measurements such as microbial biomass, basal respiration or the metabolic quotient ( $q\text{CO}_2$ ) can reveal valuable information about the capacity of a microbial community to mineralize soil organic matter, but they can never be used directly for estimating carbon fluxes in the field because this capacity is mediated by the variations of environmental factors, such as soil temperature or moisture and

changes in soil chemical properties, but also by temporal changes in root-derived carbon supply, in effect 'fuelling' decomposition.

An exciting new branch of microbiological research has developed very rapidly during the past years. New molecular technologies reveal deeper insights into microbial community dynamics and the way they interact with element cycles for the first time (Nannipieri *et al.*, 2003). It will be interesting to see how these novel approaches can be integrated into quantitative soil carbon studies. In particular, evolving stable-isotope probing (SIP) techniques (Manefield *et al.*, 2002) will enable fast insights in this area. Chapter 9 (Kutsch *et al.*) introduces traditional and novel approaches in soil microbiology.

Trophic interactions and the principal ways by which they influence soil carbon fluxes are a frequently overlooked issue. Above- and below-ground herbivory has various impacts on soil carbon dynamics while soil fauna plays a key role in organic matter decomposition, either directly via the consumption of litter, or indirectly via feeding on saprotrophs or the movement of organic matter. Numerous experiments have shown that the presence of a range of different soil fauna, including collembolas, mites, enchytraeids, isopods and earthworms, typically increase rates of mass loss and carbon mineralization. However, as often as the mediation of decomposition by animals has been shown qualitatively, it is extremely difficult to determine its relative importance because many mechanisms typically occur simultaneously. Notably, Chapter 10 (Ayles *et al.*) gives an introduction to the main trophic interactions in soils and emphasizes important relationships between biodiversity and ecosystem function, particularly in relation to soil carbon cycling.

#### 1.4.5 Temperature sensitivity and acclimation: application and shortfalls of different concepts

The influence of soil temperature on soil respiration or decomposition is a cross-section topic that is related to almost every chapter in this book. It is an actual challenge because our understanding of temperature effects on soil carbon turnover has a huge impact on the prediction of the global carbon cycle under future climate (Cox *et al.*, 2000). Early studies predicted a feedback cycle where increasing CO<sub>2</sub> concentration in the atmosphere caused increasing temperature, which itself led

to higher soil respiration rates and, consequently, an accelerated increase in atmospheric CO<sub>2</sub>. Later studies doubted the realism of such a positive ‘runaway’ feedback cycle for three reasons: (1) physiological acclimation and community adjustment decrease carbon mineralization rates; (2) in the long run the mineralization of soil organic matter is driven by substrate input and should develop a relatively temperature-independent equilibrium; (3) parts of the new input via the litter pathway are stable and, thus, are transferred to the ‘protected’, more stable, soil carbon pools (Liski and Westman, 1997; Liski *et al.*, 1999; Thornley and Cannell, 2001). The third reason could even result in an increase of soil organic matter, when litter production is increased due to higher atmospheric CO<sub>2</sub>.

One crucial question in the current debate in this field is: how does the older and chemically more resistant SOM pool (or recalcitrant SOM) behave under the conditions of climate change? The answer is important to interpret recent findings from soil-warming experiments, which often show a transient response of soil respiration to a temperature increase (McHale *et al.*, 1998; Luo *et al.*, 2001; Melillo *et al.*, 2002; Eliasson *et al.*, 2005). Using another approach, Christensen *et al.* (1996) found that the response of soil respiration to temperature decreases with increasing soil depth. All these findings lead to the hypothesis that the recalcitrant SOM mineralization either adjusts to the temperature or is generally less temperature sensitive. In contrast, an alternative interpretation suggests that the observed, apparent adjustment is in fact the result of a depletion of the labile carbon pools following a transient stimulation of mineralization rates by increasing temperature (Kirschbaum, 2004; Eliasson *et al.*, 2005). This was confirmed by recent laboratory incubations of soil samples indicating that the decomposition of the recalcitrant SOM pool may be as sensitive to temperature as that of the labile one (Fang *et al.*, 2005b). From a model study Knorr *et al.* (2005a) concluded that it is even more temperature sensitive, a conclusion that caused an intense debate (Fang *et al.*, 2005a; Knorr *et al.*, 2005b; Reichstein *et al.*, 2005). Davidson and Janssens (2006) and Davidson *et al.* (2006) have shown theoretically that substrate quality and temporal and spatial differences in substrate availability contribute to the large variability in  $Q_{10}$  observed in nature.  $Q_{10}$  is the factor by which respiration is multiplied when temperature increases by 10 °C (van 't Hoff, 1898).

Davidson *et al.* (2006) suggest including substrate turnover via Michaelis–Menten kinetics into the mathematical description of decomposition and heterotrophic soil respiration. A more recent concept is the  $Q_{10-q}$  in which Contant *et al.* (2008) derived a novel approach that accounts for changes in soil organic matter quality during decomposition as more resistant soil carbon seem to have a higher  $Q_{10}$  than labile compounds.

As interesting and straightforward this debate has been, it is characterized by a complete lack of a biological component. Kutsch and Kappen (1997) and Luo *et al.* (2001) already proposed that the seasonal differences in short-term temperature sensitivity reflect an adjustment of the soil microflora to temperature and moisture history. This can be the result of both: changes in the physiology of particular species and of changes of species composition. Temperature adjustment of the biotic components is discussed in Chapters 7 (Moyano *et al.*) and 9 (Kutsch *et al.*).

The current debate around temperature sensitivity of soil respiration shows that the drivers of soil carbon fluxes are still not completely unravelled. Since there is evidence that soil temperature and moisture as primary factors cannot explain most differences between sites (Raich and Schlesinger, 1992; Giardina and Ryan, 2000; Janssens *et al.*, 2001), it remains a challenge to integrate soil chemical and biological methods because the linkage between the bio-physico-chemical quality of SOM and the temperature response of SOM turnover remains poorly understood, or even elusive, especially as fractionation methods have seldom been directly linked to microbial functioning and resulting SOM dynamics. The combination of stable-isotope probing (SIP) of nucleic acids (DNA and rRNA) with promising non-destructive techniques (such as MIR, NIR and DRIFT spectroscopy) could make important contributions to rapidly assess SOM quantity and quality, and directly relate SOM quality to SOM dynamics and microbial functioning.

#### 1.4.6 Modelling soil carbon dynamics: current and future model validation and structures

Chapters 11 (Reichstein and Janssens) and 12 (Fallon and Smith) give an overview over the current state of modelling soil carbon cycling. Whereas Chapter 11 focuses on carbon fluxes, Chapter 12 considers the

long-term SOM turnover. Ultimately the two are inter-linked but each deserves its own consideration.

Modelling soil respiration in contrast to above-ground processes has certain key challenges:

- what is the functional unit?
- what are the biochemical processes involved?
- what do we know about the key contributing species?

The answers to all of those are clearly ‘very much unknown at present’, mainly as soil is very heterogeneous without a single functional unit. Instead a largely unknown number of organisms and enzymes are decomposing a large variety of chemical substances. Consequently, modelling approaches are mostly substrate orientated (Wallman *et al.*, 2004).

A major drawback of most soil respiration models is that they see the soil as a homogeneous structure, whereas in fact the soil is a horizontally and vertically very heterogeneous system. For example, animal activity concentrates in the most suitable areas and as such the average soil environment might not reflect the overall activity. Also ‘memory effects’ are commonly overlooked as site history might explain soil respiration rates over many decades or even centuries. Chapter 11 outlines several dominant temporal scales of factors and processes influencing soil respiration, and points out several issues with comparing laboratory versus field studies (e.g. disturbance effect and limited root-derived carbon supply). Another major issue is the influence of net primary productivity (NPP) on soil respiration (Nadelhoffer and Raich, 1992; Raich and Tufekciogul, 2000; Janssens *et al.*, 2001). To include NPP into algorithms modelling soil respiration will be a key future challenge and, as shown by Reichstein *et al.* (2003), it is possible and necessary to separate climatic and biological effects on soil respiration. However, other factors, such as soil acidity, oxygen and nutrient availability, have also received inadequate attention although they seem to be crucial in determining long-term carbon accumulation, particularly in peatlands.

Mechanistic models tend to also include specific decomposition rates of assumed SOM fractions, which are then modified based on environmental factors such as temperature and moisture leading to humification and formation of recalcitrant SOM according to Akselsson *et al.* (2005). However, a major shortfall of these models is that crucial biological processes (e.g. priming or

microbial growth dynamics) are not explicitly considered, and no direct link (other than litter fall) from assimilation to below-ground processes is provided. As such the models reflect the state-of-the-art in science as discussed in the former section. Consequently the parameterization is very uncertain and the ‘right number’ might be a result for ‘the wrong reasons’. The chapter finishes with an overview of how to address the problem of different scales and emphasizes that any direct comparisons should only be performed at corresponding levels.

Modelling frameworks of decomposition have similar aims to the above, they are used to better understand processes, extrapolate or interpolate experimental results in time, space and to different environmental conditions or to investigate scenarios that are beyond the realm of experimental work; this resulted in many different SOM modelling approaches. SOMNET contains over 30 current operational multi-compartment, process-based SOM models (<http://www.rothamsted.bbsrc.ac.uk/aen/somnet/>). Chapter 12 focuses on two of the most widely used SOM models, RothC and CENTURY, and provides detailed case studies of model formulation, development and application. However, in so far as these models only model SOM turnover, it does not include root-derived respiration and as such makes comparison to, or model validation with, field flux data impossible (Luckai and Larocque, 2002).

So far, the differences between the central SOM decomposition modules in compartmental SOM models are generally small and may give similar results when driven with equivalent input data (Smith *et al.*, 1997; Falloon and Smith, 2002). Another challenge is that in nature soils grow as cohorts (see McGill, 1996; i.e. new leaf litter fall). This characterizes peatlands, containing the largest global soil carbon stocks, and a major question remains how non-cohort-based models can actually be used to model peatland SOM dynamics. This also includes model descriptions of the soil water balance, which mostly does not allow for water table movement up to the surface but rather allocating surplus water to runoff. However, these still in many ways limited SOM models are increasingly being used by policy makers at the national, regional or global scale, for example in the post-Kyoto Protocol. Consequently, the chapter also provides an overview of related model weaknesses, including root distribution, soil layering,