

---

# Characterizing Organic Carbon Stocks and Flows in Forest Soils

# 2

Samuel P. Price, Mark A. Bradford,  
and Mark S. Ashton

---

## Executive Summary

Forests are expected to store additional carbon as part of the global initiative to offset the buildup of anthropogenic carbon dioxide (CO<sub>2</sub>) in the atmosphere (IPCC 2007). Soil organic carbon (SOC) stored and cycled under forests is a significant portion of the global total carbon stock, but remains poorly understood due to its complexity in mechanisms of storage and inaccessibility at depth. This chapter first reviews our understanding of soil carbon inputs, losses from biotic respiration and the different soil carbon storage pools and mechanisms. Secondly, the paper evaluates methods of measurement and modeling of soil carbon. Thirdly, it summarizes the effects of diverse management histories and disturbance regimes that compound the difficulties in quantifying forest soil carbon pools and fluxes. Alterations of soil carbon cycling by land use change or disturbance may persist for decades or centuries, confounding results of short-term field studies. Such differences must be characterized and sequestration mechanisms elucidated to inform realistic climate change policy directed at carbon management in existing native forests, plantations, and

agroforestry systems, as well as reforestation and afforestation. Such knowledge gains will also provide a theoretical basis for sound, stable investment in sequestration capacity. Lastly, the chapter provides recommendations for further research on those areas of soil carbon where knowledge is either scant or absent. Key findings of this review comprise what we do and do not know about soil organic carbon – inorganic carbon is also an important reservoir, especially in arid soils, but is not considered here.

### What We Do Know About Soil Carbon

Substantial work has been done that provides knowledge on many processes of soil carbon dynamics, such as:

- our understanding of how dissolved organic matter (DOM) additions from litter infiltrate the mineral soil.
- fine roots are the main source of carbon additions to soils, whether through root turnover or via exudates to associated mycorrhizal fungi and the rhizosphere.
- the dynamic between nitrogen deposition and carbon storage in forest soils is different on low-quality, high-lignin litter than on high-quality, low-lignin litter, which provides an explanation for many contradictory studies on the effects of nitrogen deposition.
- roots and mycorrhizal fungi produce about half of total respired CO<sub>2</sub>, with the balance from heterotrophic breakdown of organic matter.

---

S.P. Price • M.A. Bradford • M.S. Ashton (✉)  
Yale University, School of Forestry and Environmental  
Studies, Prospect Street 360, 06511 New Haven, CT, USA  
e-mail: mark.ashton@yale.edu

- bacterial and fungal, as well as overall faunal community composition, are hypothesized to have significant effects ( $\pm$ ) on soil carbon dynamics.
- fossil fuel burning, particulate deposition from forest fires, and wind erosion of agricultural soils is expected to affect microbial breakdown of organic matter and alter forest nutrient cycling.
- organic matter can be stabilized through microbial action, and from these actions by biochemical resistance or by physical protection within soil aggregates or microsites. Stabilization also occurs from poor drainage (water logging), fire and deep charcoal burial, and is dependent on texture and mineralogy of soil.

### What We Do Not Know About Soil Carbon

More research is needed to understand how the processes of soil carbon dynamics, that are now becoming understood, vary across different forest regions and soil depths. New research is needed that characterizes:

- controls on the depth of the organic layer by leaching of dissolved organic carbon (DOC) into the mineral soil.
- rates of fine root turnover among species and biomes.
- patterns of bacterial, fungal and plant respiration and responses to physical and biotic factors and stresses (such as drought, increased temperature).
- dynamics of functionally-distinct soil carbon pools, rather than the most-easily measured and fractionated pools.
- the most accurate methods for quantifying forest soil carbon stocks and fluxes.

The global nature of the carbon cycle requires a globally-distributed and coordinated research program, but thus far research has been largely limited to the developed world, the top 30 cm of the soil profile, temperate biomes, and agricultural soils. Forest soils in tropical moist regions are represented by only a handful of studies, as are examinations of sequestration of carbon at depth but, perhaps most importantly, the dominant reservoir of soil carbon is at high latitudes and the response of this store to climate change is highly uncertain.

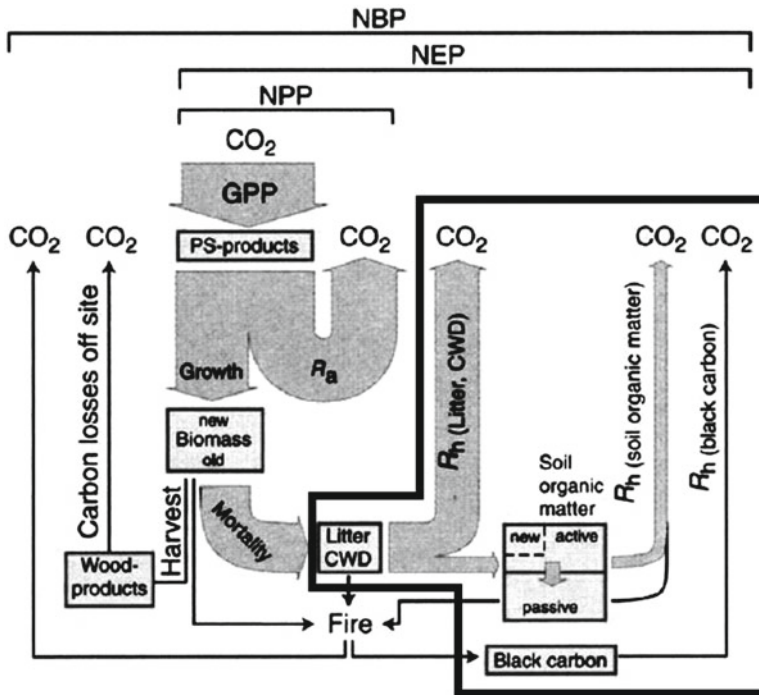
## 1 Introduction

Organic carbon enters the terrestrial biosphere primarily through photosynthesis, and is shunted to the soil system by leaf- and debris-fall, the turnover (cycle of death and new growth) of roots, and by the allocation of plant photosynthate to mycorrhizal fungi and saprotrophic microbes in soil immediately surrounding roots. Plant residues are broken down by bacteria and saprophytic fungi, resulting in a cascade of complex organic carbon compounds that leach deeper into the soil. Carbon that leaves the forest soil system exits via  $\text{CO}_2$  respired by plants, bacteria and fungi (Fig. 2.1), and through leaching of dissolved organic matter (DOM) to groundwater and rivers (not shown in Fig. 2.1).

The divergent respiration pathways differ in rate, substrate preference (e.g. type of litter, root or woody debris), and response to environmental change, complicating our capacity to characterize them. Carbon that remains in soil does so because it is stabilized by its own intrinsic chemical properties, through production of secondary microbial compounds, by physical separation from microbial breakdown, by molecular interactions with metals or other bio-molecules, or by freezing, inundation from flooding or carbonization.

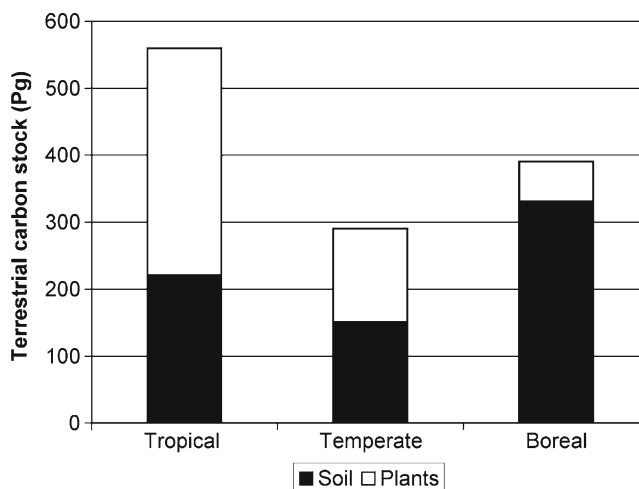
This is an introductory summary of the portion of the carbon cycle that is closely linked and affected by soil forming processes in terrestrial ecosystems, and most importantly, in forests. What is clear is that soil carbon, as a component of the ecosystem, varies enormously across different forest biomes (Fig. 2.2), and across different soil orders (Fig. 2.3).

In general, soil carbon is strongly associated with rainfall distribution and therefore there is more carbon stock in forests than in other terrestrial ecosystems (Fig. 2.4). The nature and condition of forests, by implication, can therefore play a critical role in soil carbon sequestration and storage processes. In this paper the carbon in soils is described in the form of inputs, losses, and as that portion of carbon that remains stable within soil. The paper proceeds with a review of methods of quantifying soil carbon processes and



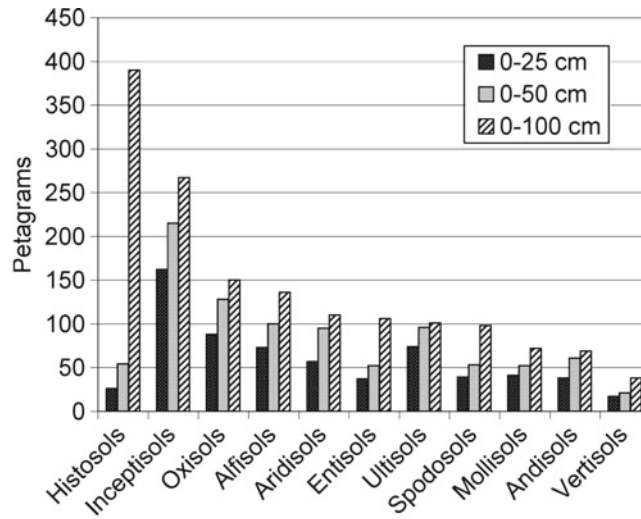
**Fig. 2.1** Forest carbon flux. A conceptual diagram illustrating the limits of the belowground carbon cycle. Arrows represent fluxes and boxes indicate pools; the size of each indicates the relative rate of flux or size of pool. Litter and coarse woody debris on the forest floor are included in the belowground portion of the forest carbon cycle. *NBP* net

biome productivity, *NEP* net ecosystem productivity, *NPP* net primary productivity, *GPP* gross primary productivity, *PS* photosynthesis,  $R_h$  heterotrophic (bacterial) respiration,  $R_a$  autotrophic (plant and associated mycorrhizal fungal) respiration, *CWD* coarse woody debris (Source: Schulze et al. 2000. Reprinted with permission from AAAS)

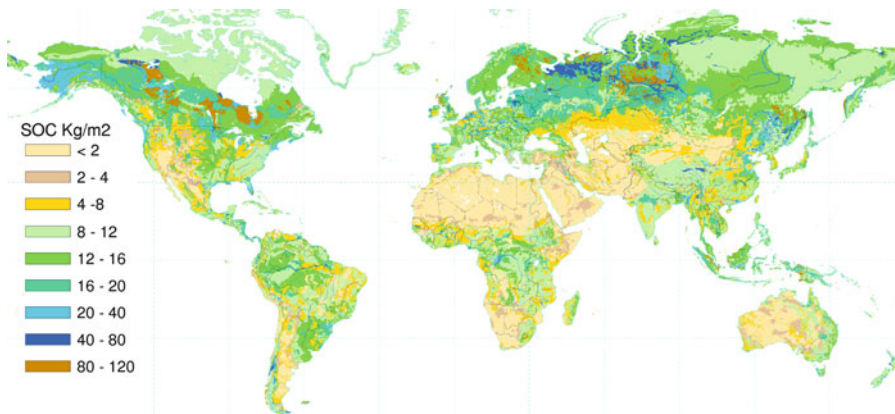


**Fig. 2.2** Distribution of world forest carbon stocks by biome. Tropical forests worldwide contain approximately as much carbon in living plants (340 Pg) as boreal forests contain underground (338 Pg), indicating

broad differences in carbon dynamics between biomes (Source: Data compiled from Vogt et al. 1998; Eswaran et al. 1995; Goodale et al. 2002; Guo and Gifford 2002)



**Fig. 2.3** Soil organic carbon (SOC) stocks worldwide, by soil order. Histosols store the majority of the world’s SOC due to seasonal or continuous inundation, and do so at depths between 50 and 100 cm (Source: Adapted from Eswaran et al. 1995)



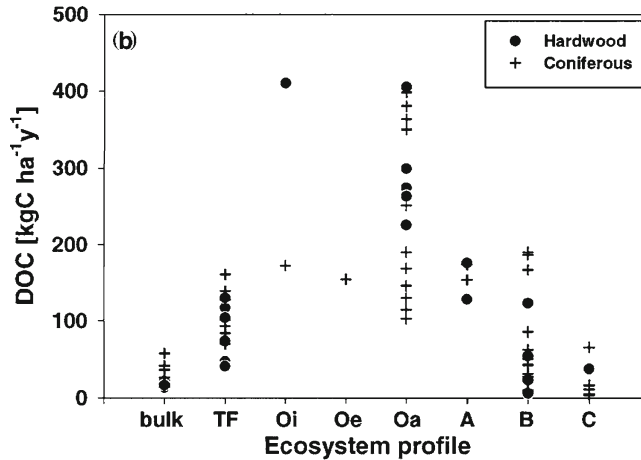
**Fig. 2.4** Density of soil carbon stocks worldwide. Note the swaths of highest density across the boreal regions of North America, Europe and Asia. Across the boreal forest SOC stocks are spatially variable (Source: US Department

of Agriculture, Natural Resources Conservation Service, Soil Survey Division. Washington D.C. <http://soils.usda.gov/use/worldsoils/mapindex/soc.html>. Reprinted with permission)

pools directly with measurements and through modeling. It concludes with a discussion of effects of management on the carbon in forest soils and finally makes recommendations on what further research and knowledge is needed and where.

## 2 Carbon Inputs to Forest Soils

Plants absorb CO<sub>2</sub> and produce sugars under photosynthesis. Photosynthetic products are used to drive cellular respiration and root exudation, or



**Fig. 2.5** Synthesis of 42 studies of DOC from the temperate forest biome showing annual fluxes of DOC through the organic and mineral soil profile. The greatest annual fluxes and greatest variability are for the lowest humified organic layer (Oa – soil organic layer). The figure depicts a lack of studies of DOC flux from Oi and Oe layers. DOC flux decreases with depth in the mineral soil. Note the significant contribution of DOC from throughfall

(TF), a result of microbial breakdown of organic matter in the canopy. There was no significant difference between DOC fluxes under coniferous versus deciduous forest. Bulk precipitation, TF throughfall precipitation, Oi litter layer, Oe fermented layer, Oa humic layer, A, B and C successively deeper mineral soil horizons (Source: From Michalzik et al. 2001. Reprinted with permission)

are stored for consumption, reproduction, and/or allocation to root, shoot and wood growth. When leaves, branches or roots outlast their useful life and cease to provide a net contribution to plant growth, they senesce (i.e. cease to live). Plants thus control the input of carbon to the soil system via above- and below-ground carbon inputs into forest soils from plant litter, coarse woody debris, fine root turnover, and root exudates.

## 2.1 Aboveground Carbon Inputs: Litter and Coarse Woody Debris

Carbon from aboveground sources enters the soil system when it falls to the forest floor in the form of dead leaves, bark, wood and/or herbivore inputs such as greenfall, carcasses and frass. Carbon is lost from surface organic matter as CO<sub>2</sub> by microbial respiration, by mixing and incorporation of surface organic matter into mineral soil horizons by soil fauna, and by leaching of dissolved organic matter (DOM) of which dissolved organic carbon (DOC) is an important constituent.

In a synthesis of 42 studies from temperate forests, Michalzik et al. (2001) reported that

precipitation was strongly positively correlated with the flux rate of DOC from the forest floor into the mineral soil. The concentration of DOC in leachate from the forest floor to the mineral soil was positively correlated with pH, suggesting that more basic conditions favor microbial decomposition and thus DOC production. They also found that the greatest annual fluxes and greatest variability were in the lowest humified organic layer (Oa). There were very few studies of DOC flux from the upper organic layers. DOC flux decreases with depth in the mineral soil. There was a significant contribution of DOC from throughfall (TF), a result of microbial breakdown of organic matter in the canopy and also potentially from sap-sucking herbivores. There was no significant difference between DOC fluxes under coniferous versus deciduous forest (Fig. 2.5). More recent <sup>14</sup>C labeling studies from both Sweden and Tennessee, USA, corroborated these results (Froberg et al. 2007a, b), indicating that most litter-derived DOC is either respired before it reaches the mineral soil or immobilized in the Oe and Oa surface layers of the soil (Fig. 2.5).

In a litter manipulation study at a hardwood forest in Bavaria, Germany the net loss of DOC

from organic horizons was related to depth of those horizons rather than microbial respiration. DOM is continually leaching through the soil profile, such that leachate at any depth will be a combination of new litter-derived DOM and older DOM released from humic or lower layers (Park and Matzner 2003). DOC from older litter showed a higher contribution of carbon from lignin and lower biodegradability relative to fresh litter (Don and Kalbitz 2005; Kalbitz et al. 2006). Conflicting results from laboratory and field studies have been hard to reconcile because of lack of experimental control across studies for hydrology, as well as nitrogen and phosphorus availability (Kalbitz et al. 2000).

Different physical properties of litter affect microbial colonization rates and thus litter breakdown rates (Hyvonen and Agren 2001). Litter, coarse woody debris, and roots of trees show differences in chemistry, rates of mass loss of litter due to decomposition, and nitrogen dynamics by species. It was suggested that increased atmospheric CO<sub>2</sub> might lead to altered degradability of organic matter due to chemical changes in leaf or root chemistry (Hyvonen and Agren 2001). But it appears from free-air CO<sub>2</sub> enrichment (FACE) studies that species-specific differences in organic chemistry (e.g. pine versus birch) outweigh changes due to CO<sub>2</sub> enrichment. For temperate forests at least, changes in species competitive growth advantages due to heightened CO<sub>2</sub> will be the real driver of change in litter decomposition dynamics (King et al. 2001, 2005; Finzi and Schlesinger 2002; Hagedorn and Machwitz 2007). Barring limiting nutrients or water, litterfall (leaf productivity and turnover) for any one species is expected to increase under heightened atmospheric CO<sub>2</sub> without a concomitant change in litter chemistry (Allen et al. 2000).

Recent work suggests an interesting dynamic between nitrogen deposition and carbon storage in forest soils. Specifically, under nitrogen deposition on low-quality, high-lignin litter, decomposition of the organic layer slows, while nitrogen deposition on high-quality, low-lignin litter tends to accelerate decomposition (Knorr et al. 2005a). This dynamic provides an explanation for many contradictory studies on the effects of nitrogen

deposition. A long-term study in Michigan, USA, demonstrated that chronic nitrogen additions increase soil carbon storage through reduced mineralization of surface and soil organic matter (Pregitzer et al. 2008), although a contrasting study indicated increased litter mass loss under high-nitrogen inputs using experimental microcosms (Manning et al. 2008). Furthermore, the progressive nitrogen limitation hypothesis suggests that CO<sub>2</sub> fertilization effects on forest productivity will not be realized if nitrogen is bound to aggrading organic matter pools. Recent work suggests that this hypothesis may be falsified if plants compensate by shunting more carbon belowground, to fuel the breakdown of organic matter by soil microbes (see Phillips et al. 2011).

## 2.2 Belowground Carbon Inputs: Fine Root Turnover and Exudates

Fine roots are the main source of carbon additions to soils, whether through root turnover or via exudates to associated mycorrhizal fungi and the rhizosphere (the soil immediately surrounding the roots). Quantifying fine root turnover *in situ* is important but difficult because of their variable turnover rates. Previous studies had indicated an extremely rapid turnover of fine roots, on the order of months to just a few years (Vogt et al. 1998). More recent studies using radiocarbon dating, however, indicated that fine roots were turning over on a 5–10 year cycle (Trumbore 2006). These opposing observations can be reconciled if the distribution of root ages is assumed to be positively skewed, with many small and ephemeral roots turning over in a matter of weeks, with a long tail of older roots surviving upwards of two decades (Trumbore and Gaudinski 2003). Results underline the need to conceptualize and model root turnover with multiple root pools rather than a single pool with a universally-applied turnover time (see below for a discussion of problems encountered in determining the rate of fine root turnover).

While DOM additions from leaf litter have been extensively researched and reviewed, the fate of DOM additions from root litter has been



investigated rarely. Uselman et al. (2007) found that root litter at the soil surface lost most carbon, with decreasing percentage loss with depth of litter addition, suggesting an important role for deep roots in adding stable carbon to the soil system. A large scale tree girdling experiment in a Scots pine forest in Sweden resulted in a 40% drop in DOC, suggesting that current photosynthate contributes significantly to soil DOC through ectomycorrhizal fungi growing in association with roots (Giesler et al. 2007). This finding contrasts with the popular paradigm that DOC is primarily the product of root decomposition, since DOC should have increased following girdling had decomposition been the primary avenue for DOC production (Hogberg and Hogberg 2002; Giesler et al. 2007). A recent Free Air Carbon Dioxide Enrichment (FACE) experiment documented 62% of carbon entering the SOM pool through mycorrhizal turnover (Godbold et al. 2006), which may explain the close link between recent photosynthesis and DOC additions to soil. In addition to this, there is increasing evidence that roots directly supply low-molecular weight carbon compounds to rhizosphere soils, and that this flux may fuel from 30 to sometimes 100% of heterotrophic soil respiration (Van Hees et al. 2005). In contrast to anticipated increases in this rhizosphere flux, results are inconclusive as to the impact of elevated CO<sub>2</sub> on fine root production and turnover, with some studies indicating modest positive increases in root productivity (Luo et al. 2001b; Wan et al. 2004), while others show little or no increase (Pritchard et al. 2001; King et al. 2005; Pritchard et al. 2008). A recent study also showed that elevated atmospheric CO<sub>2</sub> does not cause changes in fine root chemistry; the concern was that elevated CO<sub>2</sub> would increase recalcitrant compounds that might slow decomposition (King et al. 2005).

---

### 3 Carbon Loss Through Root, Fungal, and Bacterial Respiration

Our increasing ability to measure accurately respiration of microorganisms in field circumstances has focused attention on understanding processes

of carbon loss from soils. This section summarizes the more recent work done on root exudates, decomposition, and fungal and bacterial activities contributing to carbon loss from forest soils.

#### 3.1 Root, Fungal, and Bacterial Respiration

Roots and mycorrhizal fungi produce about half of total respired CO<sub>2</sub>, with the balance from heterotrophic breakdown of organic matter (Ryan and Law 2005). Soil respiration is commonly partitioned between autotrophic (plant) and heterotrophic (decomposition) respiration. These lumped categories simplify complex relationships in the soil system. For example, ectomycorrhizal fungi are clearly not primary producers, yet respiration products from ectomycorrhizal fungi are lumped with autotrophic respiration due to their close coupling with root processes and dependence on recent photosynthate (Hogberg and Read 2006). Respiration is more accurately viewed as a continuum from fully autotrophic photosynthesizers to fully heterotrophic predators and decomposers (Ryan and Law 2005). Conceptual models and new techniques for partitioning soil respiration among sources are needed (Table 2.1).

Lumping of soil respiration under heterotrophic and autotrophic respiration also neglects daily and seasonal differences in CO<sub>2</sub> flux as a result of physiological differences among bacteria, fungi and plants (e.g. Bradford et al. 2008; Allison et al. 2010). Radiocarbon dating is proving useful (Cisneros-Dozal et al. 2006; Hahn et al. 2006; Schuur and Trumbore 2006), but there are big differences between results from radiocarbon dating, <sup>13</sup>C labeling and CO<sub>2</sub> efflux studies (Hogberg et al. 2005). New research suggests tight coupling of current photosynthesis with soil respiration, possibly via the supply of labile carbon at the root-soil interface (Bond-Lamberty et al. 2004; Sampson et al. 2007; Stoy et al. 2007).

Ectomycorrhizal fungi make up a large proportion of soil biomass and contribute significantly to soil respiration but respond differently to environmental change compared to either

**Table 2.1** Experimental methods employed to date for partitioning soil respiration among autotrophic and heterotrophic sources

Category	Technique	
Root exclusion	Trenching	All roots crossing the perimeter of the treatment plot are severed; membrane installed to prevent regrowth
	Girdling	Girdled trees near or within treatment plots cannot allocate photosynthate to roots
	Gap	Compare soil CO <sub>2</sub> efflux in clearcut stand to control stand
Physical separation of components	Components	Separate litter, roots and mineral soil from a soil core; incubate separately; measure CO <sub>2</sub> efflux from each component
	Root excising	Remove roots from a fresh soil core; measure CO <sub>2</sub> efflux immediately
	Live root respiration	Excavate roots while still attached to tree; isolate and measure CO <sub>2</sub> efflux <i>in situ</i>
Isotopic techniques	Isotopic labelling	<sup>13</sup> C labelling in FACE or chambers; switch C3 with C4 plants
	Radiocarbon	Radioactive decay of <sup>14</sup> C permits dating of photosynthetic event
Indirect techniques	Modelling	Bottom-up simulation of response of soil components to biotic and abiotic factors
	Mass balance	Assume soil C is at steady state; measure rates of C addition to soil from above- and belowground sources; subtract soil CO <sub>2</sub> efflux
	Subtraction	Soil CO <sub>2</sub> efflux minus other flux components from ecosystem NPP models and published values
	Root mass regression	Regress CO <sub>2</sub> efflux at multiple sites against root biomass; y-intercept is heterotrophic respiration

Source: Derived from Subke et al. (2006) and Hanson et al. (2000)

roots or bacteria, suggesting a need to separately model bacterial, mycorrhizal, and root respiration (Hogberg and Hogberg 2002; Langley and Hungate 2003; Fahey et al. 2005; Groenigen et al. 2007; Hogberg et al. 2005; Heinemeyer et al. 2007; Blackwood et al. 2007). Bacterial and fungal dominance, as well as overall faunal community composition, affects soil carbon dynamics (Jones and Bradford 2001; Bradford et al. 2002b, 2007). However, their differing responses may cancel each other out (Bradford et al. 2002a) and the evidence that bacterial-fungal ratios directly affect soil carbon stocks is only correlative (see Strickland and Rousk 2010). Further studies must clarify understanding of underlying mechanisms and environmental factors that characterize differing microbe responses (e.g. fungi, bacteria) (Chung et al. 2006; Monson et al. 2006; Blackwood et al. 2007; Fierer et al. 2007; Hogberg et al. 2007).

In addition, earthworm effects on carbon and nitrogen cycling are significant (Li et al. 2002; Marhan and Scheu 2006). Fresh inputs of carbon (i.e. priming) from organisms such as earthworms

may allow soil microbes to mine old carbon deeper in the profile (Dijkstra and Cheng 2007; Fontaine et al. 2007). This suggests that increased input from leaf productivity may boost soil heterotrophic respiration and CO<sub>2</sub> flux from soils. Priming can lead to rapid shifts in community composition (Cleveland et al. 2007; Montano et al. 2007). Low molecular weight compounds, including organic acids, amino acids and sugars, are products of microbial breakdown and root exudation, and represent a small fraction of the total mass of carbon cycling through soil. However, breakdown of low molecular weight carbon compounds may contribute up to 30% of total soil CO<sub>2</sub> efflux because of extremely rapid turnover, with residence times estimated at 1–10 h (Van Hees et al. 2005).

### 3.2 Respiration Responses to Environmental Change

Under global change scenarios, nitrate deposition from fossil fuel burning, particulate deposition from forest fires, and wind erosion of agricultural



soils, are expected to alter forest nutrient cycling. The addition of nitrogen has been shown to affect microbial breakdown of litter and SOM, the results varying with litter type and microbial community composition (Sinsabaugh et al. 2004, 2005; Waldrop et al. 2004). Litter quality is important, at least for temperate forests, where litter in high-lignin systems shows unchanged or decreased rates of decomposition under nitrogen deposition, while low-lignin, low-tannin systems tend to increase decomposition rates (Magill and Aber 2000; Gallo et al. 2005). In turn, it was shown in northern temperate forests that the composition of the microbial communities changed in response to nitrogen deposition (Waldrop et al. 2004). Based on these observations, elucidating carbon dynamics under elevated nitrogen scenarios for other biomes and across canopy tree associations should be a priority.

Fertilization by increased atmospheric CO<sub>2</sub> and the deleterious effects of ozone (O<sub>3</sub>), both resulting from burning of fossil fuels, are also expected to alter forest soil carbon cycling. In a 4-year study in experimental temperate forest stands, Loya et al. (2003) found that a simultaneous 50% increase in CO<sub>2</sub> and O<sub>3</sub> resulted in significantly lower soil carbon formation, possibly due to reduced plant detritus inputs and/or increased consumption of recent carbon by soil microbes. In another study of temperate forest soils, soil faunal communities changed composition under exposure to CO<sub>2</sub> or O<sub>3</sub> singly but, when combined, there was no main effect (Loranger et al. 2004). Fungal community composition was significantly altered as a response to elevated O<sub>3</sub> in a FACE study in Wisconsin, USA (Chung et al. 2006). The response of fungal respiration to elevated CO<sub>2</sub> is so far equivocal. One study indicated a rise in fungal activity (Phillips et al. 2002) while another recorded a decrease (Groenigen et al. 2007). As in the divergent responses under nitrogen deposition, the result may depend heavily on litter chemical properties. Soil respiration is expected to increase under increased CO<sub>2</sub> and O<sub>3</sub> (Andrews and Schlesinger 2001; King et al. 2004; Luo et al. 2001b; Pregitzer et al. 2006), but some studies show conflicting results (Suwa et al. 2004; Lichter et al. 2005) or a decrease when

combined with fertilization (Butnor et al. 2003). Overall, FACE studies indicate a net increase in carbon storage, mostly in litter and fine root mass, despite soil respiration increases (Allen et al. 2000; Hamilton et al. 2002), although cycling through litter is especially rapid and sequestration in litter is likely limited (Schlesinger and Lichter 2001).

Respiration response to temperature changes, especially pertaining to a still-hypothetical positive feedback of warming to carbon mineralization, is highly uncertain (Denman et al. 2007). The original uncertainty centered on whether the soil carbon pool should be lumped or split by rate of turnover (Davidson et al. 2000; Giardina and Ryan 2000), since (often small) portions of the soil carbon pool cycle very quickly, especially low molecular weight organic acids, and therefore may be more responsive to temperature than larger, older or adsorbed compounds. Later, evidence mounted for an acclimation of soils to heightened temperatures over time, although it now seems clear that depletion of the fast-cycling labile carbon pool under increased initial mineralization rates is partly responsible for the apparent downshifting in respiration over time (Luo et al. 2001a; Melillo et al. 2002; Eliasson et al. 2005). Further experiments are needed to test the acclimation hypothesis (see Bradford et al. 2008). Reworking the data of Giardina and Ryan (2000), others found that the response of the fast pool over experimental scales obscured the slower but ultimately more important response of the large pool of stable carbon (Knorr et al. 2005b). A consensus is still in the making concerning the impact of warming on soil respiration, although it now seems clear that the complex nature of SOC, and confounding factors, including soil water content, complicate a simple determination of the temperature effect (Davidson and Janssens 2006). Indeed, inclusion of microbial physiology in soil models can negate the projected positive feedback between warming and loss of soil carbon (Allison et al. 2010). Complicating the interpretation of field data, soil respiration is closely coupled to photosynthesis of the canopy, explaining some of the apparent causal correlation between temperature and respiration *in situ* (Sampson et al. 2007).

The effects of soil freezing, compounded by a decreased or absent snow pack predicted for some temperate and boreal regions, may decrease winter soil respiration (Monson et al. 2006). More attention has been given to drying and wetting cycles recently, which appear to substantially increase annual decomposition (Fierer and Schimel 2002; Borken et al. 2003; Jarvis et al. 2007).

## 4 Stabilization of Carbon in Forest Soils

Plant-derived organic molecules are stabilized from microbial action by biochemical resistance or by physical protection within soil aggregates or microsites (Table 2.2 and Fig. 2.6). Microbial decomposition can also, itself, facilitate stabilization through the production of secondary microbial products and the majority of carbon that is most resistant to decay has microbial – and not plant – signatures (Grandy and Neff 2008). When assessing environmental correlates, in order of importance for the measured stabilization of organic matter in soils across Ohio, USA, drainage class was the only significant determinant of SOM content in the upper 30 cm in forest soils, whereas the significance of individual site variables on SOM content in non-forested soils was firstly soil taxon, then drainage class, and lastly texture. The low significance of these other factors on forest soils suggests different drivers of SOM dynamics in forests (Tan et al. 2004).

The importance of anoxic conditions for preservation of organic matter in boreal peatlands is without doubt (Fierer and Schimel 2002; Borken et al. 2003; Jarvis et al. 2007). But in aerobic soils, dissolved organic carbon (DOC) that leaches from decomposing material is vulnerable to mineralization and respiration as CO<sub>2</sub> by bacteria or saprophytic fungi. The portion of DOM that escapes mineralization by microbes generally does so by sorption to soil minerals where it is stabilized as SOC. Carbon is also stabilized when fire produces black charcoal from organic matter. Finally, some DOC may be flushed from the soil system during periods of high soil water flow.

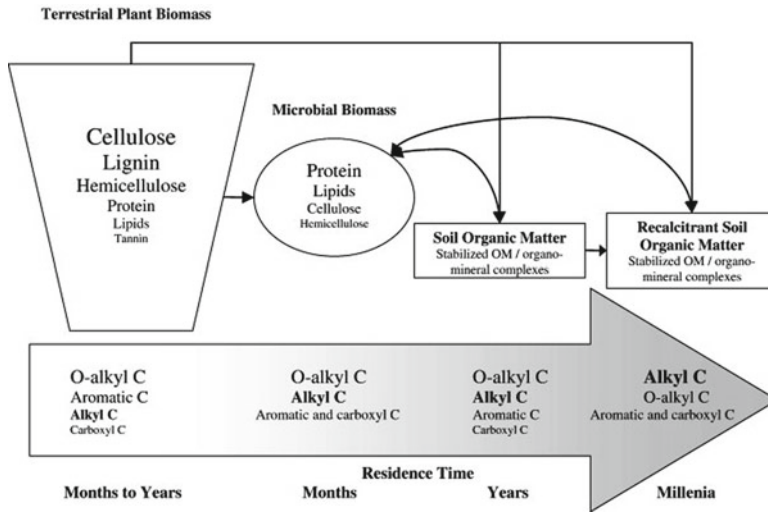
### 4.1 Sorption and Complexation of Dissolved Organic Matter

In aerobic soils, texture is considered to be the most important driver of DOC stabilization in soil, with mineralogy an important factor that is dependent on texture (Bird et al. 2002). Across a 1,000 km latitudinal transect in Siberia, SOC stocks on fine-textured soils were approximately double the stocks on coarse-textured soils (Bird et al. 2002). The layered structure of clay results in an extremely high surface area to volume ratio, and clay interlayers host a multitude of cations which provide binding sites for DOC. Clay content exerts a powerful control on the size of the older soil carbon pool in Amazonian soils (Telles et al. 2003). However, Giardina et al. (2001)

**Table 2.2** Mechanisms of carbon stabilization in forest soils (some mechanisms are specific to soil order or biome, while others are active in all soils)

Selective preservation	Inherent stability due to e.g. alkyl-C chains in lipids, aromatic structures, phenolics
Spatial segregation	Occlusion inside soil aggregates
	Sequestration within soil micropores
	Coating with hydrophobic aliphatic compounds
	Intercalation within phyllosilicates (clay)
Molecular interaction	Complexation with metal ions
	Interaction with other organic molecules through ligand exchange, polyvalent cation bridges or weak interactions
Inundation	Anoxic conditions prevent abiotic oxidation and aerobic microbial respiration
Freezing	Sub-freezing temperature stifles microbial respiration
Carbonization	Relatively inert carbon is broken down only at millennial timescales

Source: After Lorenz et al. (2007) and Lutzow et al. (2006)



**Fig. 2.6** Carbon flux through terrestrial organic matter pools (*top*) and relative enrichment of recalcitrant alkyl carbon during breakdown of more-labile compounds (*bottom*).

The relative composition of organic matter by carbon structure is represented by size of type (*Source*: Reprinted from Lorenz et al. 2007, with permission from Elsevier)

found no relation between carbon mineralization rates and clay content in laboratory-incubated upland forest soils. Clay content of soil is well-correlated with SOC generally, although other factors dominate DOC stabilization in cold or wet climates. Sorption to the mineral matrix has been shown to strongly preserve DOM (Kaiser and Guggenberger 2000). Aluminum (Al) and iron (Fe) cations are the most important interlayer mineral binders for DOM (Zinn et al. 2007). Besides binding to clay particles, colloidal and soluble organic matter can form insoluble complexes with Al and Fe cations, which precipitate (Schwesig et al. 2003; Rasmussen et al. 2006; Scheel et al. 2007). These results suggest that whole-ecosystem carbon cycle models should account for both soil texture and soil mineralogy when modeling carbon fluxes (Table 2.3). Labile DOM high in carbohydrate has a large increase in stability due to sorption, but for DOM with a greater proportion in complex aromatic organic compounds stability due to sorption is relatively small because such compounds are already relatively stable. However, irrespective of proportional increases, gross sorption of recalcitrant compounds was much larger than sorption of labile

compounds, in fact as much as four times larger (Kalbitz et al. 2005). Stabilization of OM by sorption therefore depends on particulars of the organic compounds sorbed, strong chemical bonds to the mineral soil, and/or a physical inaccessibility of OM to microorganisms (Kalbitz et al. 2005).

## 4.2 Fire as a Sequestration Mechanism

The many effects of fire on forest soils have been reviewed by Certini (2005). In areas with frequent fires, 35–40% of SOC was fire-derived black carbon. Fire can sterilize soils to depths of 10 cm or more, and effects of sterilization may last a decade, resulting in decreased microbial respiration. When fire does not remove carbon from the soil system through combustion, it tends to increase the stability of the carbon remaining through carbonization, reduction in water solubility, and relative enrichment in aromatic groups (Certini 2005). Czimeczik et al. (2003) found that in a boreal Siberian Scots pine forest, black carbon contributed a small percentage of the SOC pool while the fire reduced the mass of the forest floor by 60%. A wildfire

**Table 2.3** Characteristics of six process-based forest soil carbon models

Yasso	ROMUL	SOILN	RothC	Forest-DNDC	CENTURY
Time-step	Month	Day	Month	Day	Month
Simulation depth	Organic layer +1 m mineral soil	Any depth	Adjustable from 0 to 1 m	Adjustable from 1 to 1.5 m	20 cm
Organic matter pools					
Stand	–	Roots, stems, leaves, grains	–	Canopy, understory, groundstory	Leaves, fine roots, fine branches, coarse wood, coarse roots
Litter	Fine and coarse woody litter	1–2 per soil layer, 10–15 soil layers	Resistant and decomposable pools	Very labile, labile, and resistant pools for each soil layer	Aboveground and belowground pools divided into metabolic and structural, senescent litter and structural, senescent litter pooled based on lignin:N ratio
Soil	Extractives, celluloses, lignin-like compounds, 2 humus pools	One humus, one microbe pool per soil layer, 10–15 soil layers	Living, humic and insoluble OM pools	Two humads and humus per layer	Active, slow and passive SOM pools
Different pools for organic and mineral soil?	No	Yes	No	Yes	No
Nutrient input	–	N deposition, fertilization, N content of plant parts	–	N deposition and fertilization	N deposition and fertilization, organic N inputs, P, S
Soil texture input	–	Hydraulic properties	Clay content	Clay content	Sand, silt and clay content
Limitations	Upland forest soils only	Substantial input information required, not for peatlands	Upland forest soils only	Substantial input information required	Very shallow, not for peatlands, does not separate humified litter from mineral soil
Measurability of pools	Only extractives, celluloses and the sum of the other pools are measurable	No, pools are conceptual and cannot be directly measured	Yes, all pools measurable	No, pools are conceptual and cannot be directly measured	SOC, litter pools measurable, sub-pools conceptual only

Source: Adapted from Peltoniemi et al. (2007)

in boreal Alaska burned polysaccharide-derived compounds preferentially, resulting in a relative enrichment of lipid- and lignin-derived compounds (Neff et al. 2005). There appears to be an inverse relationship between fire frequency and complete combustion: infrequent fire return intervals and high intensity may result in less carbonization and more complete combustion than in regions with shorter fire return intervals that experience lower-intensity fires, increased carbonization, and therefore increased storage (Czimczik et al. 2005).

---

## 5 Quantifying the Carbon Under Forests

In the northern hemisphere, the carbon in soils remains the highest uncertainty in global budgeting (Goodale et al. 2002) and partitioning soil respiration among sources to identify carbon leakage/loss has proved to be one of the most difficult tasks (Ryan and Law 2005). Failure to close the soil carbon budget stems from discrepancies between measured bulk CO<sub>2</sub> fluxes and the predictions of process models of autotrophic and heterotrophic respiration (Trumbore 2006). Different methods used to accommodate study objectives and resources make comparison difficult (Wayson et al. 2006) and, as a result, many budgets leave out soil carbon and litter carbon accumulations completely (Liski et al. 2003).

### 5.1 Quantifying Carbon Additions

The turnover of organic matter in surface soil layers can be quantified by direct measurement of mass loss through litterbag studies or by <sup>14</sup>C enrichment, litter sampling and mass spectrometer analysis. However, there are known problems with both litterbag studies and <sup>14</sup>C enrichment as methodologies for measuring carbon addition to soils. Litterbags limit breakdown of litter by soil macrofauna. The <sup>14</sup>C signature measures the mean residence time of carbon in the surface layer, but not the lifetime of various recognizable litter components (e.g. from fine roots, leaves, bark) (Hanson et al. 2005). And it

has been found that <sup>14</sup>C-labeled carbon residence time in fine roots, estimated at >4 years, is much longer than the <1 year root longevity estimated by using the minirhizotron, a small camera lowered through a clear plastic tube to monitor the growth of roots over time (Strand et al. 2008).

It was previously thought that radiocarbon dating and the turnover time for roots – estimated by laborious sorting and weighing of root production year-to-year and then dividing total root biomass by annual production – could be reconciled if the age distribution of roots was positively skewed (Tierney and Fahey 2002; Trumbore and Gaudinski 2003). Current thinking on important sources of discrepancy in estimating fine root turnover are outlined by Strand et al. (2008) and include: (1) the presence of different root pools cycling at different rates; (2) the confounding effect of stored carbohydrates, which throw off radiocarbon estimates of age; (3) the skewed nature of root age distribution as pointed out in Trumbore and Gaudinski (2003); (4) lingering effects of minirhizotron installation on root growth; and (5) the use of median root longevity as an inaccurate substitute for mean longevity in minirhizotron studies. These sources of error cause radiocarbon methods to underestimate the importance of fine root turnover to soil carbon cycling and the minirhizotron method to overestimate this importance (Strand et al. 2008). Work is underway to address these shortcomings and to deepen understanding of root turnover, e.g. by partitioning root pools by branching order (Guo et al. 2008).

### 5.2 Partitioning Soil Respiration

Hanson et al. (2000) discuss in detail and outline the major classes of soil partitioning techniques (summarized in Table 2.1). A comprehensive review of research needs in measuring and modeling soil respiration has been done by Ryan and Law (2005), while Subke et al. (2006) provide an exhaustive list of soil CO<sub>2</sub> efflux partitioning studies through 2006 across all terrestrial biomes. They show that many of the techniques for partitioning have inherent methodological biases (Subke et al. 2006). For example, detection

of changes, especially depletion, of the large, slow-cycling pool of recalcitrant soil carbon represents a significant challenge and is almost always underrepresented, but it is essential to quantifying the carbon exchange between soil and the atmosphere. Additionally, multi-factor experiments must be of sufficient length to allow adjustment to treatment conditions (Ryan and Law 2005). It is therefore better to resample the same points than to randomly select new ones in long-term sampling studies and inventories. Due to the spatial variability of SOC processes, 15–20% changes in soil carbon stocks may be overlooked (Yanai et al. 2003). Site variability therefore confounds broad-scale application of flux data (Hibbard et al. 2005). There is also a trade-off between spatial and temporal resolution when using manual vs. automated CO<sub>2</sub> flux measurements. Used in combination, the two systems provide combined resolution in both dimensions, but manual measurements are sufficient for measuring integrated seasonal fluxes (Savage and Davidson 2003).

### 5.3 Modeling Soil Carbon Dynamics

Many SOC models have been created for agricultural systems, and may be modified to simulate forested systems, in order to accommodate important differences in management, disturbance regime, vegetation, and biota. To date there has been only one published model comparison for forest SOC dynamics. Peltoniemi et al. (2007) review and compare six process-based, multiple-SOC-pool models of forest SOC dynamics. The review includes an extensive comparison of model inputs and modeled processes. More work is needed to assess the accuracy of forest soil carbon models, and to adapt them or develop new ones for diverse biomes. Critically, very few countries and regions have published long-term soil carbon datasets with the ancillary data needed to verify model accuracy, and there is a total lack of such inventories for tropical regions. Most soil carbon process models do not deal explicitly with peatlands, severely limiting their applicability in some boreal regions. Wetlands versions of the *RothC* and *ROMUL* models are expected in the near future, and *Forest-DNDC*

includes a wetland component (Peltoniemi et al. 2007). The move toward process-based models of SOC dynamics is hindered by poor understanding of the different mechanisms of sequestration of diverse classes of organic biomolecules in soils. Model soil carbon pools must be derived from functional classes of compounds (which must first be characterized) with similar sequestration mechanisms, rather than from the most easily differentiated classes of SOC based on *in situ* measurement techniques or fractionation (Lutzow et al. 2006) (Table 2.3).

Empirical models must be careful to parameterize at the same time step as the output (Janssens and Pilegaard 2003). The concentration of labile carbon, its rapid turnover, and the resultant large CO<sub>2</sub> efflux can obscure the sensitivity of heterotrophic respiration to soil temperature change. Care should be taken to control for labile carbon concentrations when extrapolating field measurements of bulk soil respiration to global change scenarios (Gu et al. 2004).

The temperature dependence of soil is often described by the Q<sub>10</sub> value, which is defined by the difference in respiration rates over a 10°C interval. Q<sub>10</sub> has been found to be extremely variable, with a range from 1 (no effect of temperature on respiration) to 5 (five times higher respiration rate with a 10° rise in temperature) under different combinations of soil moisture and soil temperature (Reichstein et al. 2003). Kinetic properties of the many organic compounds in soils, plus environmental constraints such as limiting soil moisture or nutrients, complicate efforts to fully explain the temperature sensitivity of microbial respiration (Davidson and Janssens 2006). In an analysis of sources of uncertainty in the soil carbon model *SWIM*, Post et al. (2008) identified the carbon mineralization rate, carbon use efficiency, Q<sub>10</sub>, soil bulk density, and initial carbon content as the most critically sensitive parameters. Better models will have to differentiate the direct effects of drying, wetting, and carbon substrate supply to soil microbes from the indirect effects of soil water content and temperature on diffusion of carbon substrates to the microbial population (Davidson et al. 2006). Work in this area indicates that models incorporating



realistic spatial relationships, hourly time steps, and mechanistic workings give the most accurate results (Hanson et al. 2004). Not all applications will be suited to process models, however, due to the extensive inputs required (Liski et al. 2005). Yet, leaving out process may yield projections for soil carbon stocks that differ to when biological response is explicitly modeled. For example, Allison et al. (2010) showed that by making carbon use efficiency temperature sensitive, microbial biomass decreases with warming. This decrease then negates the loss of soil carbon with temperature increase that is projected with conventional models, because of the reduction in microbes that actually carry out decomposition. Indeed, the IPCC identify such responses as significant areas of uncertainty, with all eleven models coupling climate with carbon cycling omitting the soil microbiology.

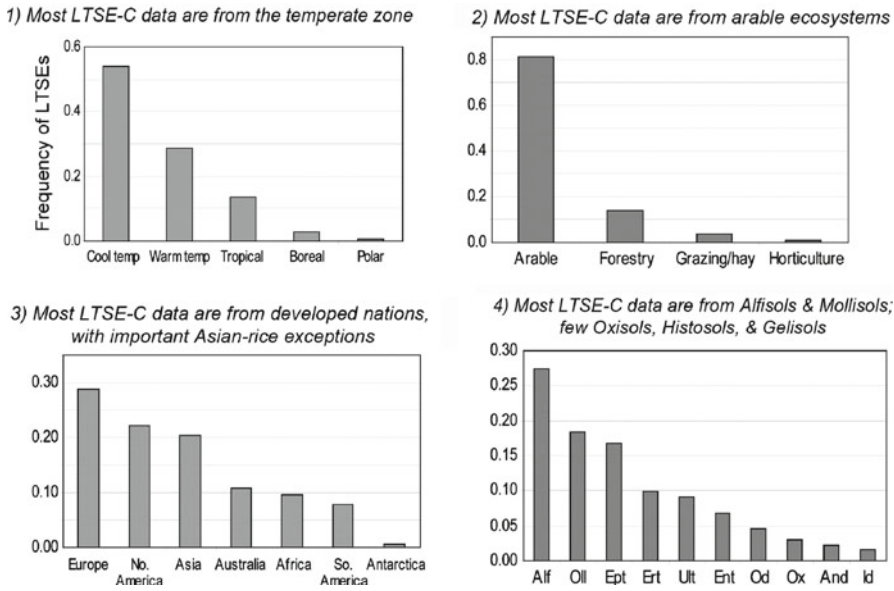
#### 5.4 The Superficial Nature of Soil Carbon Research

Studies of soil organic matter under conventional and no-till soil management in agriculture have been largely limited to the top 30 cm of soil. Now, some are suggesting the need to consider SOM deeper in the profile (Baker et al. 2007). The same argument ought to be made for forest soil research: rooting depths are far greater for many tree species than field crops. Soil depth confounds warming studies by insulating deeper soil layers (Pavelka et al. 2007) and delaying CO<sub>2</sub> efflux (Jassal et al. 2004; Drewitt et al. 2005). Also, a significant portion of below-ground carbon is deeper than 1 m (Jobbagy and Jackson 2000) and recent research indicates that roots exert powerful influences on redox activity in their vicinity, with important implications for carbon cycling deep in the soil profile (Fimmen et al. 2008).

#### 5.5 Quantifying Carbon Stocks After Land Use Change

Long-term soil experiments and inventories can elucidate SOC dynamics in ways that shorter

ones cannot. Peltoniemi et al. (2007) point out the importance of repeated soil surveys for SOC model verification and validation. Given the importance of chronosequence studies for area-based carbon budgeting under land use change (Woodbury et al. 2007), the first unified global network of long-term soil experiments (LTSEs) has been formed (<http://ltse.env.duke.edu/>). This network will ideally address the lack of uniformity of measurements of soil carbon that so complicate comparison and synthesis. There are other problems: only 20% of soil studies measuring SOC are in forested biomes; therefore, boreal, tropical and warm-temperate forests are under-represented; soil studies measuring SOC are heavily concentrated in developed countries; and long-term SOC studies on alfisols and mollisols dominate, while long-term changes on oxisols, histosols and gelsols are still poorly understood (Fig. 2.7). Chronosequences, or space-for-time substitutions, though useful for characterizing soil change over centuries or millennia, may confuse the effects of land use with weathering. Land use history can be difficult to properly control for (Richter et al. 2007) (Table 2.4). Yet perhaps of most concern, if we can standardize methods for quantifying soil carbon stocks, it is in selecting a method that can robustly quantify both absolute carbon stocks and their change with time. The currently accepted practice of measuring soil carbon concentrations in the surface 30 cm of soil suffers from the fact that soils are not static entities. For example, soil compaction following forest removal – or soil expansion following afforestation – both change the mass of soil carbon in the surface 30 cm even when the absolute mass of soil carbon at a location does not change. This means that depth-independent (i.e. mass dependent) sampling is required to resolve change in carbon stocks with time, which involves measurement of soil carbon in at least two soil cores (a surficial core and one immediately below) at a location (Gifford and Roderick 2003). In addition to this, it must be recognized that soil carbon stocks are spatially variable at the scale of only a few meters. This means that multiple samples are required to gain a spatial estimate for a site. Also, this variability causes lack of statistical power to



**Fig. 2.7** Distribution of long term soil experiments (LTSE) measuring SOC across climate zones, land uses, continents and soil orders. Note the lack of forest LTSEs despite the importance of land use change, specifically

deforestation, to national and global carbon budgets (Source: Graphs produced by Richter et al. from data at <http://ltse.env.duke.edu>. Used with permission)

**Table 2.4** Types of soil experiments that may be used to elucidate carbon dynamics and changes in carbon stocks under land-use change

Approach	Time scale (year)	Uses and strengths	Challenges and limitations
Short-term soil experiments	<1–10	Field or lab based, experimental control, versatile, short-term processes	Extrapolation to larger scales of space and time, reductionist
Long-term soil experiments	>10	Field based, direct soil observation, experimental control, sample archive	Duration before useful data, vulnerable to loss or neglect, extrapolation to larger scales
Repeated soil surveys	>10	Field based, direct soil observation, regional perspective, sample archive	Planning and operational details, very few yet conducted, monitoring
Space-for-time-substitution	>10 to >>1,000	Field based, highly time efficient	Space and time confounded
Computer models	<1 to >>1,000	Versatile, heuristic and predictive, positively interact with all approaches	Dependent on observational data

Source: Richter et al. (2007). Reprinted with permission

detect change in soil carbon; so statistically non-significant change in soil carbon does not mean that there has not been a biologically significant change (Throop and Archer 2008; Strickland et al. 2010). Lastly, soil carbon must be sampled at a landscape scale – loss of soil carbon through erosion from one area of a forest patch might simply be redistributed within that patch in another area that is aggrading carbon.

## 6 Effects of Management Regime on Soil Carbon Cycling

The Fourth Assessment Report by the IPCC Working Group III projects that, initially, reduction in deforestation will lead to the greatest positive increase in global carbon sequestration, due to the current rapid rate of deforestation and the

**Table 2.5** The generalized impact of forest management actions on carbon stocks Summary of the effects of specific forest management actions on ecosystem C stocks ('+'...increases C stock, '-'...decreases C stock; '±' neutral with respect to C stock)

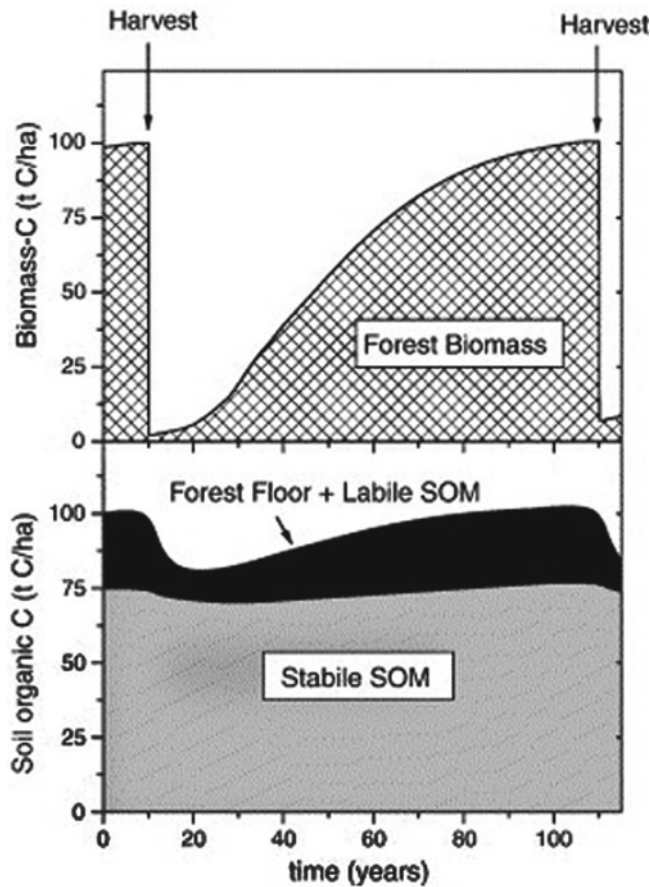
<i>Afforestation</i>	
+ Accumulation of aboveground biomass formation of a C-rich litter layer and slow build-up of the C pool in the mineral soil	
± Stand stability depends on the mixture of tree species	
– Monotone landscape, in the case of even-aged mono-species plantations	
<i>Tree species</i>	
+ Affects stand stability and resilience against disturbances; effect applies for entire rotation period; positive side-effect on landscape diversity, when mixed species stands are established	
– Effect on C storage in stable soil pools controversial and so far insufficiently proven	
<i>Stand management</i>	
+ Long rotation period ensures less disturbance due to harvesting, many forest operations aim at increased stand stability, every measure that increases ecosystem stability against disturbance	
± Different conclusions on the effect of harvesting, depending if harvest residues are counted as a C loss or a C input to the soil	
– Forests are already C-rich ecosystems – small increase in C possible; thinning increases stand stability at the expense of the C pool size; harvesting invariably exports C	
<i>Disturbance</i>	
+ Effects such as pest infestation and fire can be controlled to a certain extent	
± Low intensity fires limit the risk of catastrophic events	
– Catastrophic (singular) events cannot be controlled; probability of disturbance can rise under changed climatic conditions, when stands are poorly adapted	
<i>Site improvement</i>	
+ N fertilization affects aboveground biomass; effect on soil C depends on interaction of litter production by trees and carbon use efficiency of soil microbes	
± Drainage of peatland enables the establishment of forests (increased C storage in the biomass) and decreases CH <sub>4</sub> emissions from soil, but is linked to the increased release of CO <sub>2</sub> and N <sub>2</sub> O from the soil	
– Liming and site preparation always stimulate soil microbial activity. The intended effect of activating the nutrient cycle is adverse to C sequestration; N fertilization leads to emission of potent greenhouse gases from soils	

Source: Reprinted from Jandl et al. (2007), with permission from Elsevier

large associated CO<sub>2</sub> loss to the atmosphere. Over the long term, sustainable forest management that increases forest growing stock while also providing timber, fiber and energy will provide the greatest mitigation benefit at the lowest cost to society (IPCC 2007). But the link between different forest management activities, deforestation, reforestation and afforestation and the net carbon flux between soils and the atmosphere is not well characterized (Table 2.5).

Productivity of the forest increases litter fall and potentially sequestration; less disturbance of soil tends to preserve soil carbon stocks; and mixed species forests are more resilient and therefore better systems for securing carbon in forest soils. On the other hand, planting on agricultural soils increases carbon accumulation by soils for both conifers and broadleaf trees (Morris

et al. 2007). Although the rate of carbon accumulation and sequestration within the soil profile differs by tree species, no species effect on SOM stability has yet been reported (Jandl et al. 2007). Differences in plant anatomy lead to changes in the vertical distribution of minerals and soil carbon when there is land use or land cover change (Jackson et al. 2000). For example, in Fujian, China, conversion of natural forests to plantations has been linked to carbon loss (Yang et al. 2007). However, combined CO<sub>2</sub> sequestration and timber production can be economically maximized (Thornley and Cannell 2000). In addition, during reforestation, soils are a slower but more persistent sink than aboveground carbon, and are more stable pools than aboveground pools for actively harvested forests (Thuille et al. 2000).



**Fig. 2.8** A simulation of carbon stocks above- and belowground before and after forest harvesting, for a typical Central European Norway spruce forest. Assumptions

include a 100 year rotation for a typical Norway spruce stand with 25% labile SOM (Source: Reprinted from Jandl et al. 2007, with permission from Elsevier)

Studies in boreal forests have demonstrated that tree harvesting generally has little long-term effect on stabile soil carbon stocks (Martin et al. 2005), although evidence from temperate forests of the southeastern USA indicates that whole tree harvesting can be detrimental by removing nitrogen (Johnson et al. 2002). There are no obvious long-term effects from clearcutting that can be detected on in-stream DOC chemistry (Johnson et al. 2002), although clearcutting released a pulse of labile DOC at Hubbard Brook in New Hampshire, USA (Dai et al. 2001), probably from humic substances at the forest floor (Ussiri and Johnson 2007). Shortened rotations from 90 to 60 years in Finland increased soil carbon by increasing input of litter but did not maximize system-wide carbon seques-

tration because of increased frequency of harvest operations (Liski et al. 2001); although others have found that fresh carbon additions due to harvesting operations can stimulate microbial populations to mineralize ancient deep soil carbon (Fontaine et al. 2007; Jandl et al. 2007) (Fig. 2.8).

Plant diversity and composition effects on net primary productivity (NPP) are becoming apparent and must be accounted for (Catovsky et al. 2002). Oak forests turn SOM over faster compared to pine, which locks up more litter for longer in the surface layers (Quideau et al. 2001). Broadleaf tree plantations replacing natural forest or pasture tend not to change soil carbon stocks, while pine plantations reduce soil carbon stocks 12–15% (Guo and Gifford 2002). Conversion of forest to

pasture results in a slow but marked increase in soil carbon stocks, but this is the reverse for tilled agriculture (Cerri et al. 2003, 2004). Pasture systems are very productive and thus larger carbon fluxes from them indicate greater allocation of carbon belowground (Johnson and Curtis 2001; Johnson et al. 2002; Paul et al. 2002; Salimon et al. 2004; Thuille and Schulze 2006).

## 7 Conclusion and Summary Recommendations

This review outlined the most critical issues and impediments to characterizing belowground carbon cycling in forested biomes. To further our understanding of belowground carbon dynamics in forests, more work is needed to characterize the following:

- controls on the depth of the forest floor organic layer by leaching of dissolved organic carbon (DOC) to the mineral soil.
- responses of root carbon inputs to environmental change, such as nitrogen deposition.
- rates of fine root turnover across species and biomes.
- patterns of bacterial, fungal and plant respiration and responses to physical and biotic forcing.
- dynamics of functionally-distinct soil carbon pools, rather than the most easily measured and fractionated pools.
- the most accurate methods for quantifying forest soil carbon stocks and fluxes.

The global nature of the carbon cycle requires a globally-distributed and coordinated research program, but has thus far been largely limited to:

- the developed world
- the top 30 cm of the soil profile
- temperate biomes
- agricultural soils

Political and financial resources are being mobilized to increase the stock of carbon in forest soils despite minimal research to date about the long-term effects of land use on SOC stocks. Key research needs are to reduce the uncertainty in environmental response of the mechanisms that stabilize soil carbon inputs, and to develop and implement appropriate methods to estimate stocks

and their change with time. Such efforts will inform management strategies, ensuring effectiveness in their intended goal of sequestering carbon in forest soils.

## References

- Allen AS, Andrews JA, Finzi AC, Matamala R, Richter DD, Schlesinger WH (2000) Effects of free-air CO<sub>2</sub> enrichment (FACE) on belowground processes in a *Pinus taeda* forest. *Ecol Appl* 10:437–448
- Allison SD, Wallenstein MD, Bradford MA (2010) Soil-carbon response to warming dependent on microbial physiology. *Nat Geosci* 3:336–340
- Andrews JA, Schlesinger WH (2001) Soil CO<sub>2</sub> dynamics, acidification, and chemical weathering in a temperate forest with experimental CO<sub>2</sub> enrichment. *Glob Biogeochem Cycles* 15:149–162
- Baker JM, Ochsner TE, Venterea RT, Griffis TJ (2007) Tillage and soil carbon sequestration—what do we really know? *Agric Ecosyst Environ* 118:1–5
- Bird MI, Santruckova H, Arneith A, Grigoriev S, Gleixner G, Kalaschnikov YN, Lloyd J, Schulze ED (2002) Soil carbon inventories and carbon-13 on a latitude transect in Siberia. *Tellus B* 54:631–641
- Blackwood CB, Waldrop MP, Zak DR, Sinsabaugh RL (2007) Molecular analysis of fungal communities and laccase genes in decomposing litter reveals differences among forest types but no impact of nitrogen deposition. *Environ Microbiol* 9:1306–1316
- Bond-Lamberty B, Wang C, Gower ST (2004) A global relationship between the heterotrophic and autotrophic components of soil respiration? *Glob Change Biol* 10:1756–1766
- Borken W, Davidson EA, Savage K, Gaudinski J, Trumbore SE (2003) Drying and wetting effects on carbon dioxide release from organic horizons. *Soil Sci Soc Am J* 67:1888–1896
- Bradford MA, Jones TH, Bardgett RD, Black HIJ, Boag B, Bonkowski M, Cook R, Eggers T, Gange AC, Grayston SJ, Kandeler E, McCaig AE, Newington JE, Prosser JL, Setälä H, Staddon PL, Tordoff GM, Tscherko D, Lawton JH (2002a) Impacts of soil faunal community composition on model grassland ecosystems. *Science* 298:615–618
- Bradford MA, Tordoff GM, Eggers T, Jones TH, Newington JE (2002b) Microbiota, fauna, and mesh size interactions in litter decomposition. *Oikos* 99:317–323
- Bradford MA, Tordoff GM, Black HIJ, Cook R, Eggers T, Garnett MH, Grayston SJ, Hutcheson KA, Ineson P, Newington JE, Ostle N, Sleep D, Stott A, Jones TH (2007) Carbon dynamics in a model grassland with functionally different soil communities. *Funct Ecol* 21:690–697
- Bradford MA, Davies CA, Frey SD et al (2008) Thermal adaptation of soil microbial respiration to elevated temperature. *Ecol Lett* 11:1316–1327



- Butnor JR, Johnsen KH, Oren R, Katul GG (2003) Reduction of forest floor respiration by fertilization on both carbon dioxide-enriched and reference 17-year-old loblolly pine stands. *Glob Change Biol* 9:849–861
- Catovsky S, Bradford MA, Hector A (2002) Biodiversity and ecosystem productivity: implications for carbon storage. *Oikos* 97:443–448
- Cerri CEP, Coleman K, Jenkinson DS, Bernoux M, Victoria R, Cerri CC (2003) Modeling soil carbon from forest and pasture ecosystems of Amazon, Brazil. *Soil Sci Soc Am J* 67:1879–1887
- Cerri CEP, Paustian K, Bernoux M, Victoria RL, Melillo JM, Cerri CC (2004) Modeling changes in soil organic matter in Amazon forest to pasture conversion with the century model. *Glob Change Biol* 10:815–832
- Certini G (2005) Effects of fire on properties of forest soils: a review. *Oecologia* 143:1–10
- Chung H, Zak DR, Lilleskov EA (2006) Fungal community composition and metabolism under elevated CO<sub>2</sub> and O<sub>3</sub>. *Oecologia* 147:143–154
- Cisneros-Dozal LM, Trumbore S, Hanson PJ (2006) Partitioning sources of soil-respired CO<sub>2</sub> and their seasonal variation using a unique radiocarbon tracer. *Glob Change Biol* 12:194–204
- Cleveland CC, Nemergut DR, Schmidt SK, Townsend AR (2007) Increases in soil respiration following labile carbon additions linked to rapid shifts in soil microbial community composition. *Biogeochemistry* 82:229–240
- Czimczik CI, Preston CM, Schmidt MWI, Schulze ED (2003) How surface fire in Siberian Scots pine forests affects soil organic carbon in the forest floor: stocks, molecular structure, and conversion to black carbon (charcoal). *Glob Biogeochem Cycles* 17:20–21
- Czimczik CI, Schmidt MWI, Schulze ED (2005) Effects of increasing fire frequency on black carbon and organic matter in podzols of Siberian Scots pine forests. *Eur J Soil Sci* 56:417–428
- Dai KH, Johnson CE, Driscoll CT (2001) Organic matter chemistry and dynamics in clear-cut and unmanaged hardwood forest ecosystems. *Biogeochemistry* 54:51–83
- Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440:165–173
- Davidson EA, Trumbore SE, Amundson R (2000) Soil warming and organic carbon content. *Nature* 408:789–790
- Davidson EA, Janssens IA, Lou Y (2006) On the variability of respiration in terrestrial ecosystems: moving beyond Q10. *Glob Change Biol* 12:154–164
- Denman KL, Brasseur G, Chidthaisong A et al (2007) Couplings between changes in the climate system and biogeochemistry. 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
- Dijkstra FA, Cheng WX (2007) Interactions between soil and tree roots accelerate long-term soil carbon decomposition. *Ecol Lett* 10:1046–1053
- Don A, Kalbitz K (2005) Amounts and degradability of dissolved organic carbon from foliar litter at different decomposition stages. *Soil Biol Biochem* 37:2171–2179
- Drewitt GB, Black TA, Jassal RS (2005) Using measurements of soil CO<sub>2</sub> efflux and concentrations to infer the depth distribution of CO<sub>2</sub> production in a forest soil. *Can J Soil Sci* 85:213–221
- Eliasson PE, McMurtrie RE, Pepper DA, Stromgren M, Linder S, Agren GI (2005) The response of heterotrophic CO<sub>2</sub> flux to soil warming. *Glob Change Biol* 11:167–181
- Eswaran H, Van den Berg E, Reich P, Kimble J (1995) Global soil carbon resources. In: Lal R, Kimble JM, Levine E (eds) *Soils and global change*. CRC Press, Boca Raton, pp 27–43
- Fahey TJ, Tierney GL, Fitzhugh RD, Wilson GF, Siccama TG (2005) Soil respiration and soil carbon balance in a northern hardwood forest ecosystem. *Can J Forest Res* 35:244–253
- Fierer N, Schimel JP (2002) Effects of drying-rewetting frequency on soil carbon and nitrogen transformations. *Soil Biol Biochem* 34:777–787
- Fierer N, Bradford MA, Jackson RB (2007) Toward an ecological classification of soil bacteria. *Ecology* 88:1354–1364
- Fimmen RL, Richter DD Jr, Vasudevan D, Williams MA, West LT (2008) Rhizogenic Fe-C redox cycling: a hypothetical biogeochemical mechanism that drives crustal weathering in upland soils. *Biogeochemistry* 87:127–141
- Finzi AC, Schlesinger WH (2002) Species control variation in litter decomposition in a pine forest exposed to elevated CO<sub>2</sub>. *Glob Change Biol* 8:1217–1229
- Fontaine S, Barot S, Barre P, Bdioui N, Mary B, Rumpel C (2007) Stability of organic carbon in deep soil layers controlled by fresh carbon supply. *Nature* 450:277–280
- Froberg M, Jardine PM, Hanson PJ, Swanston CW, Todd DE, Tarver JR, Garten CT Jr (2007a) Low dissolved organic carbon input from fresh litter to deep mineral soils. *Soil Sci Soc Am J* 71:347–354
- Froberg M, Kleja DB, Hagedorn F (2007b) The contribution of fresh litter to dissolved organic carbon leached from a coniferous forest floor. *Eur J Soil Sci* 58:108–114
- Gallo ME, Lauber CL, Cabaniss SE, Waldrop MP, Sinsabaugh RL, Zak DR (2005) Soil organic matter and litter chemistry response to experimental N deposition in northern temperate deciduous forest ecosystems. *Glob Change Biol* 11:1514–1521
- Giardina CP, Ryan MG (2000) Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. *Nature* 404:858–861
- Giardina CP, Ryan MG, Hubbard RM, Binkley D (2001) Tree species and soil textural controls on carbon and nitrogen mineralization rates. *Soil Sci Soc Am J* 65:1272–1279
- Giesler R, Hogberg MN, Strobel BW, Richter A, Nordgren A, Hogberg P (2007) Production of dissolved organic carbon and low-molecular weight organic acids in soil solution driven by recent tree photosynthate. *Biogeochemistry* 84:1–12



- Gifford RM, Roderick ML (2003) Soil carbon stocks and bulk density: spatial or cumulative mass coordinates as a basis of expression? *Glob Change Biol* 9:1507–1514
- Godbold DL, Hoosbeek MR, Lukac M, Cotrufo MF, Janssens IA, Ceulemans R, Polle A, Velthorst EJ, Scarascia-Mugnozza G, De Angelis P, Miglietta F, Peressotti A (2006) Mycorrhizal hyphal turnover as a dominant process for carbon input into soil organic matter. *Plant Soil* 281:15–24
- Goodale CL, Apps MJ, Birdsey RA, Field CB, Heath LS, Houghton RA, Jenkins JC, Kohlmaier GH, Kurz W, Liu S, Nabuurs GJ, Nilsson S, Shvidenko AZ (2002) Forest carbon sinks in the Northern Hemisphere. *Ecol Appl* 12:891–899
- Grandy AS, Neff JC (2008) Molecular C dynamics downstream: the biochemical decomposition sequence and its impact on soil organic matter structure and function. *Sci Total Environ* 404:297–307
- Groenigen KJ, Six J, Harris D, Kessel CV (2007) Elevated CO<sub>2</sub> does not favor a fungal decomposition pathway. *Soil Biol Biochem* 39:2168–2172
- 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 Cycles* 18:GB1022
- Guo LB, Gifford RM (2002) Soil carbon stocks and land use change: a meta analysis. *Glob Change Biol* 8:345–360
- Guo D, Li H, Mitchell RJ, Han W, Hendricks JJ, Fahey TJ, Hendrick RL (2008) Fine root heterogeneity by branch order: exploring the discrepancy in root turnover estimates between minirhizotron and carbon isotopic methods. *New Phytol* 177:443–456
- Hagedorn F, Machwitz M (2007) Controls on dissolved organic matter leaching from forest litter grown under elevated atmospheric CO<sub>2</sub>. *Soil Biol Biochem* 39:1759–1769
- Hahn V, Hogberg P, Buchmann N (2006) <sup>14</sup>C - A tool for separation of autotrophic and heterotrophic soil respiration. *Glob Change Biol* 12:972–982
- Hamilton JG, DeLucia EH, George K, Naidu SL, Finzi AC, Schlesinger WH (2002) Forest carbon balance under elevated CO<sub>2</sub>. *Oecologia* 131:250–260
- Hanson PJ, Edwards NT, Garten CT, Andrews JA (2000) Separating root and soil microbial contributions to soil respiration: a review of methods and observations. *Biogeochemistry* 48:115–146
- Hanson PJ, Amthor JS, Wullschlegel SD, Wilson KB, Grant RF, Hartley A, Hui D, Hunt ER Jr, Johnson DW, Kimball JS, King AW, Luo Y, McNulty SG, Sun G, Thornton PE, Wang S, Williams M, Baldocchi DD, Cushman RM (2004) Oak forest carbon and water simulations: model intercomparisons and evaluations against independent data. *Ecol Monogr* 74:443–489
- Hanson PJ, Swanston CW, Garten CT Jr, Todd DE, Trumbore SE (2005) Reconciling change in Oi-horizon carbon-14 with mass loss for an oak forest. *Soil Sci Soc Am J* 69:1492–1502
- Heinemeyer A, Hartley IP, Evans SP, De la Fuente JAC, Ineson P (2007) Forest soil CO<sub>2</sub> flux: uncovering the contribution and environmental responses of ectomycorrhizas. *Glob Change Biol* 13:1786–1797
- Hibbard KA, Law BE, Reichstein M, Sulzman J (2005) An analysis of soil respiration across northern hemisphere temperate ecosystems. *Biogeochemistry* 73:29–70
- Hogberg MN, Hogberg P (2002) Extramatrical ectomycorrhizal mycelium contributes one-third of microbial biomass and produces, together with associated roots, half the dissolved organic carbon in a forest soil. *New Phytol* 154:791–795
- Högberg P, Read DJ (2006) Towards a more plant physiological perspective on soil ecology. *Trends Ecol Evol* 21:548–554
- Hogberg P, Nordgren A, Hogberg MN, Ottosson-Lofvenius M, Bhupinderpal S, Olsson P, Linder S (2005) Fractional contributions by autotrophic and heterotrophic respiration to soil-surface CO<sub>2</sub> efflux in boreal forests. *SEB Exp Biol Ser* 2005:251–267
- Hogberg MN, Hogberg P, Myrberg DD (2007) Is microbial community composition in boreal forest soils determined by pH, C-to-N ratio, the trees, or all three? *Oecologia* 150:590–601
- Hyvonen R, Agren GI (2001) Decomposer invasion rate, decomposer growth rate, and substrate chemical quality: how they influence soil organic matter turnover. *Can J Forest Res* 31:1594–1601
- IPCC (2007) Forestry. In: *Climate change 2007: mitigation. Contribution of Working Group III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*
- Jackson RB, Schenk HJ, Jobbagy EG, Canadell J, Colello GD, Dickinson RE, Field CB, Friedlingstein P, Heimann M, Hibbard K, Kicklighter DW, Kleidon A, Neilson RP, Parton WJ, Sala OE, Sykes MT (2000) Belowground consequences of vegetation change and their treatment in models. *Ecol Appl* 10:470–483
- Jandl R, Lindner M, Vesterdal L, Bauwens B, Baritz R, Hagedorn F, Johnson DW, Minkkinen K, Byrne KA (2007) How strongly can forest management influence soil carbon sequestration? *Geoderma* 137:253–268
- Janssens IA, Pilegaard K (2003) Large seasonal changes in Q10 of soil respiration in a beech forest. *Glob Change Biol* 9:911–918
- Jarvis P, Rey A, Petsikos C, Wingate L, Rayment M, Pereira J, Banza J, David J, Miglietta F, Borghetti M, Manca G, Valentini R (2007) Drying and wetting of Mediterranean soils stimulates decomposition and carbon dioxide emission: the “Birch effect”. *Tree Physiol* 27:929–940
- Jassal RS, Black TA, Drewitt GB, Novak MD, Gaumont-Guay D, Nesic Z (2004) A model of the production and transport of CO<sub>2</sub> in soil: predicting soil CO<sub>2</sub> concentrations and CO<sub>2</sub> efflux from a forest floor. *Agric Forest Meteorol* 124:219–236
- Jobbagy EG, Jackson RB (2000) The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecol Appl* 10:423–436
- Johnson DW, Curtis PS (2001) Effects of forest management on soil C and N storage: meta analysis. *Forest Ecol Manag* 140:227–238
- Johnson DW, Knoepp JD, Swank WT, Shan J, Morris LA, Van Lear DH, Kapeluck PR (2002) Effects of forest management on soil carbon: results of some long-term resampling studies. *Environ Pollut* 116:S201–S208

- Jones TH, Bradford MA (2001) Assessing the functional implications of soil biodiversity in ecosystems. *Ecol Res* 16:845–858
- Kaiser K, Guggenberger G (2000) The role of DOM sorption to mineral surfaces in the preservation of organic matter in soils. *Org Geochem* 31:711–725
- Kalbitz K, Solinger S, Park JH, Michalzik B, Matzner E (2000) Controls on the dynamics of dissolved organic matter in soils: a review. *Soil Sci* 165:277–304
- Kalbitz K, Schwesig D, Rethemeyer J, Matzner E (2005) Stabilization of dissolved organic matter by sorption to the mineral soil. *Soil Biol Biochem* 37:1319–1331
- Kalbitz K, Kaiser K, Bargholz J, Dardenne P (2006) Lignin degradation controls the production of dissolved organic matter in decomposing foliar litter. *Eur J Soil Sci* 57:504–516
- King JS, Pregitzer KS, Zak DR, Kubiske ME, Ashby JA, Holmes WE (2001) Chemistry and decomposition of litter from *Populus tremuloides* michaux grown at elevated atmospheric CO<sub>2</sub> and varying N availability. *Glob Change Biol* 7:65–74
- King JS, Hanson PJ, Bernhardt E, Deangelis P, Norby RJ, Pregitzer KS (2004) A multiyear synthesis of soil respiration responses to elevated atmospheric CO<sub>2</sub> from four forest FACE experiments. *Glob Change Biol* 10:1027–1042
- King JS, Pregitzer KS, Zak DR, Holmes WE, Schmidt K (2005) Fine root chemistry and decomposition in model communities of north-temperate tree species show little response to elevated atmospheric CO<sub>2</sub> and varying soil resource availability. *Oecologia* 146:318–328
- Knorr M, Frey SD, Curtis PS (2005a) Nitrogen additions and litter decomposition: a meta-analysis. *Ecology* 86:3252–3257
- Knorr W, Prentice IC, House JI, Holland EA (2005b) Long-term sensitivity of soil carbon turnover to warming. *Nature* 433:298–301
- Langley JA, Hungate BA (2003) Mycorrhizal controls on belowground litter quality. *Ecology* 84:2302–2312
- Li X, Fisk MC, Fahey TJ, Bohlen PJ (2002) Influence of earthworm invasion on soil microbial biomass and activity in a northern hardwood forest. *Soil Biol Biochem* 34:1929–1937
- Lichter J, Barron SH, Bevacqua CE, Finzi AC, Irving KF, Stemmler EA, Schlesinger WH (2005) Soil carbon sequestration and turnover in a pine forest after six years of atmospheric CO<sub>2</sub> enrichment. *Ecology* 86:1835–1847
- Liski J, Pussinen A, Pingoud K, Makipaa R, Karjalainen T (2001) Which rotation length is favourable to carbon sequestration? *Can J Forest Res* 31:2004–2013
- Liski J, Korotkov AV, Prins CFL, Karjalainen T, Victor DG, Kauppi PE (2003) Increased carbon sink in temperate and boreal forests. *Climatic Change* 61:89–99
- Liski J, Palosuo T, Peltoniemi M, Sievanen R (2005) Carbon and decomposition model yasso for forest soils. *Ecol Model* 189:168–182
- Loranger GI, Pregitzer KS, King JS (2004) Elevated CO<sub>2</sub> and O<sub>3</sub> concentrations differentially affect selected groups of the fauna in temperate forest soils. *Soil Biol Biochem* 36:1521–1524
- Lorenz K, Lal R, Preston CM, Nierop KGJ (2007) Strengthening the soil organic carbon pool by increasing contributions from recalcitrant aliphatic bio(macro) molecules. *Geoderma* 142:1–10
- Loya WM, Pregitzer KS, Karberg NJ, King JS, Giardina CP (2003) Reduction of soil carbon formation by tropospheric ozone under increased carbon dioxide levels. *Nature* 425:705–707
- Luo Y, Wan S, Hui D, Wallace LL (2001a) Acclimatization of soil respiration to warming in a tall grass prairie. *Nature* 413:622–625
- Luo Y, Wu L, Andrews JA, White L, Matamala R, Schafer K, Schlesinger WH (2001b) Elevated CO<sub>2</sub> differentiates ecosystem carbon processes: deconvolution analysis of Duke Forest FACE data. *Ecol Monogr* 71:357–376
- Lutzow MV, Kogel-Knabner I, Ekschmitt K, Matzner E, Guggenberger G, Marschner B, Flessa H (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
- Magill AH, Aber JD (2000) Dissolved organic carbon and nitrogen relationships in forest litter as affected by nitrogen deposition. *Soil Biol Biochem* 32:603–613
- Manning P, Saunders M, Bardgett RD, Bonkowski M, Bradford MA, Ellis RJ, Kandeler E, Marhan S, Tscherko D (2008) Direct and indirect effects of nitrogen deposition on litter decomposition. *Soil Biol Biochem* 40:688–698
- Marhan S, Scheu S (2006) Mixing of different mineral soil layers by endogeic earthworms affects carbon and nitrogen mineralization. *Biol Fert Soils* 42:308–314
- Martin JL, Gower ST, Plaut J, Holmes B (2005) Carbon pools in a boreal mixedwood logging chronosequence. *Glob Change Biol* 11:1883–1894
- Melillo JM, Steudler PA, Aber JD, Newkirk K, Lux H, Bowles FP, Catricala C, Magill A, Ahrens T, Morrisseau S (2002) Soil warming and carbon-cycle feedbacks to the climate system. *Science* 298:2173–2176
- Michalzik B, Kalbitz K, Park JH, Solinger S, Matzner E (2001) Fluxes and concentrations of dissolved organic carbon and nitrogen - a synthesis for temperate forests. *Biogeochemistry* 52:173–205
- Monson RK, Lipson DL, Burns SP, Turnipseed AA, Delany AC, Williams MW, Schmidt SK (2006) Winter forest soil respiration controlled by climate and microbial community composition. *Nature* 439:711–714
- Montano NM, Garcia-Oliva F, Jaramillo VJ (2007) Dissolved organic carbon affects soil microbial activity and nitrogen dynamics in a Mexican tropical deciduous forest. *Plant Soil* 295:265–277
- Morris SJ, Bohm S, Haile-Mariam S, Paul EA (2007) Evaluation of carbon accrual in afforested agricultural soils. *Glob Change Biol* 13:1145–1156
- Neff JC, Harden JW, Gleixner G (2005) Fire effects on soil organic matter content, composition, and nutrients in boreal interior Alaska. *Can J Forest Res* 35:2178–2187
- Park JH, Matzner E (2003) Controls on the release of dissolved organic carbon and nitrogen from a deciduous

- forest floor investigated by manipulations of above-ground litter inputs and water flux. *Biogeochemistry* 66:265–286
- Paul KI, Polglase PJ, Nyakuengama JG, Khanna PK (2002) Change in soil carbon following afforestation. *Forest Ecol Manag* 168:241–257
- Pavelka M, Acosta M, Marek MV, Kutsch W, Janous D (2007) Dependence of the Q10 values on the depth of the soil temperature measuring point. *Plant Soil* 292: 171–179
- Peltoniemi M, Thurig E, Ogle S, Palosuo T, Schrumpf M, Wutzler T, Butterbach-Bahl K, Chertov O, Komarov A, Mikhailov A, Gardenas A, Perry C, Liski J, Smith P, Makipaa R (2007) Models in country scale carbon accounting of forest soils. *Silva Fenn* 41:575–602
- Phillips RL, Zak DR, Holmes WE, White DC (2002) Microbial community composition and function beneath temperate trees exposed to elevated atmospheric carbon dioxide and ozone. *Oecologia* 131: 236–244
- Phillips RL, Finzi AC, Bernhardt ES (2011) Enhanced root exudation induces microbial feedbacks to N cycling in a pine forest under long-term CO<sub>2</sub> fumigation. *Ecol Lett* 14:187–194
- Post J, Hattermann FF, Krysanova V, Suckow F (2008) Parameter and input data uncertainty estimation for the assessment of long-term soil organic carbon dynamics. *Environ Modell Softw* 23:125–138
- Pregitzer K, Loya W, Kubiske M, Zak D (2006) Soil respiration in northern forests exposed to elevated atmospheric carbon dioxide and ozone. *Oecologia* 148: 503–516
- Pregitzer KS, Burton AJ, Zak DR, Talhelm AF (2008) Simulated chronic nitrogen deposition increases carbon storage in Northern Temperate forests. *Glob Change Biol* 14:142–153
- Pritchard SG, Rogers HH, Davis MA, Van Santen E, Prior SA, Schlesinger WH (2001) The influence of elevated atmospheric CO<sub>2</sub> on fine root dynamics in an intact temperate forest. *Glob Change Biol* 7:829–837
- Pritchard SG, Strand AE, McCormack ML, Davis MA, Finzi AC, Jackson RB, Matamala R, Rogers HH, Oren R (2008) Fine root dynamics in a loblolly pine forest are influenced by free-air- CO<sub>2</sub>-enrichment: a six-year-minirhizotron study. *Glob Change Biol* 14:588–602
- Quideau SA, Chadwick OA, Trumbore SE, Johnson-Maynard JL, Graham RC, Anderson MA (2001) Vegetation control on soil organic matter dynamics. *Org Geochem* 32:247–252
- Rasmussen C, Southard RJ, Horwath WR (2006) Mineral control of organic carbon mineralization in a range of temperate conifer forest soils. *Glob Change Biol* 12: 834–847
- Reichstein M, Rey A, Freibauer A, Tenhunen J, Valentini R, Banza J, Casals P, Cheng Y, Grunzweig JM, Irvine J, Joffre R, Law BE, Loustau D, Miglietta F, Oechel W, Ourcival JM, Pereira JS, Peressotti A, Ponti F, Qi Y, Rambal S, Rayment M, Romanya J, Rossi F, Tedeschi V, Tirone G, Xu M, Yakir D (2003) Modeling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices. *Glob Biogeochem Cycles* 17:15, 11
- Richter DD, Hofmockel M, Callahan MA Jr, Powlson DS, Smith P (2007) Long-term soil experiments: keys to managing Earth's rapidly changing ecosystems. *Soil Sci Soc Am J* 71:266–279
- Ryan MG, Law BE (2005) Interpreting, measuring, and modeling soil respiration. *Biogeochemistry* 73:3–27
- Salimon CI, Davidson EA, Victoria RL, Melo AWF (2004) CO<sub>2</sub> flux from soil in pastures and forests in southwestern Amazonia. *Glob Change Biol* 10: 833–843
- Sampson DA, Janssens IA, Yuste JC, Ceulemans R (2007) Basal rates of soil respiration are correlated with photosynthesis in a mixed temperate forest. *Glob Change Biol* 13:2008–2017
- Savage KE, Davidson EA (2003) A comparison of manual and automated systems for soil CO<sub>2</sub> flux measurements: trade-offs between spatial and temporal resolution. *J Exp Bot* 54:891–899
- Scheel T, Dorfler C, Kalbitz K (2007) Precipitation of dissolved organic matter by aluminum stabilizes carbon in acidic forest soils. *Soil Sci Soc Am J* 71:64–74
- Schlesinger WH, Lichter J (2001) Limited carbon storage in soil and litter of experimental forest plots under increased atmospheric CO<sub>2</sub>. *Nature* 411:466–469
- Schulze ED, Wirth C, Heimann M (2000) Managing forests after Kyoto. *Science* 289:2058–2059
- Schuur EAG, Trumbore SE (2006) Partitioning sources of soil respiration in boreal black spruce forest using radiocarbon. *Glob Change Biol* 12:165–176
- Schwesig D, Kalbitz K, Matzner E (2003) Effects of aluminium on the mineralization of dissolved organic carbon derived from forest floors. *Eur J Soil Sci* 54: 311–322
- Sinsabaugh RL, Zak DR, Gallo M, Lauber C, Amonette R (2004) Nitrogen deposition and dissolved organic carbon production in northern temperate forests. *Soil Biol Biochem* 36:1509–1515
- Sinsabaugh RL, Gallo ME, Lauber C, Waldrop MP, Zak DR (2005) Extracellular enzyme activities and soil organic matter dynamics for northern hardwood forests receiving simulated nitrogen deposition. *Biogeochemistry* 75:201–215
- Stoy PC, Palmroth S, Oishi AC, Siqueira MB, Juang JY, Novick KA, Ward EJ, Katul GG, Oren R (2007) Are ecosystem carbon inputs and outputs coupled at short time scales? a case study from adjacent pine and hardwood forests using impulse-response analysis. *Plant Cell Environ* 30:700–710
- Strand AE, Pritchard SG, McCormack ML, Davis MA, Oren R (2008) Irreconcilable differences: fine-root life spans and soil carbon persistence. *Science* 319: 456–458
- Strickland MS, Rousk J (2010) Considering fungal: bacterial dominance in soils – methods, controls, and ecosystem implications. *Soil Biol Biochem* 42:1385–1395

- Strickland MS, Devore JL, Maerz JC, Bradford MA (2010) Grass invasion of a hardwood forest is associated with declines in belowground carbon pools. *Glob Change Biol* 16:1338–1350
- Subke JA, Inglima I, Cotrufo MF (2006) Trends and methodological impacts in soil CO<sub>2</sub> efflux partitioning: a metaanalytical review. *Glob Change Biol* 12: 921–943
- Suwa M, Katul GG, Oren R, Andrews J, Pippen J, Mace A, Schlesinger WH (2004) Impact of elevated atmospheric CO<sub>2</sub> on forest floor respiration in a temperate pine forest. *Glob Biogeochem Cycles* 18:GB2013
- Tan ZX, Lal R, Smeck NE, Calhoun FG (2004) Relationships between surface soil organic carbon pool and site variables. *Geoderma* 121:187–195
- Telles ECC, de Camargo PB, Martinelli LA, Trumbore SE, da Costa ES, Santos J, Higuchi N, Oliveira RC Jr (2003) Influence of soil texture on carbon dynamics and storage potential in tropical forest soils of Amazonia. *Glob Biogeochem Cycles* 17:9, 1
- Thornley JHM, Cannell MGR (2000) Managing forests for wood yield and carbon storage: a theoretical study. *Tree Physiol* 20:477–484
- Throop HL, Archer SR (2008) Shrub (*Prosopis velutina*) encroachment in a semidesert grassland: spatial-temporal changes in soil organic carbon and nitrogen pools. *Glob Change Biol* 14:2420–2431
- Thuille A, Schulze ED (2006) Carbon dynamics in successional and afforested spruce stands in Thuringia and the Alps. *Glob Change Biol* 12:325–342
- Thuille A, Buchmann N, Schulze ED (2000) Carbon stocks and soil respiration rates during deforestation, grassland use and subsequent Norway spruce afforestation in the Southern Alps, Italy. *Tree Physiol* 20:849–857
- Tierney GL, Fahey TJ (2002) Fine root turnover in a northern hardwood forest: a direct comparison of the radiocarbon and minirhizotron methods. *Can J Forest Res* 32:1692–1697
- Trumbore S (2006) Carbon respired by terrestrial ecosystems - recent progress and challenges. *Glob Change Biol* 12:141–153
- Trumbore SE, Gaudinski JB (2003) The secret lives of roots. *Science* 302:1344–1345
- Uselman SM, Qualls RG, Lilienfein J (2007) Contribution of root vs. leaf litter to dissolved organic carbon leaching through soil. *Soil Sci Soc Am J* 71:1555–1563
- Ussiri DA, Johnson CE (2007) Organic matter composition and dynamics in a northern hardwood forest ecosystem 15 years after clear-cutting. *Forest Ecol Manag* 240:131–142
- Van Hees PAW, Jones DL, Finlay R, Godbold DL, Lundstrom US (2005) The carbon we do not see - the impact of low molecular weight compounds on carbon dynamics and respiration in forest soils: a review. *Soil Biol Biochem* 37:1–13
- Vogt KA, Vogt DJ, Bloomfield J (1998) Analysis of some direct and indirect methods for estimating root biomass and production of forests at an ecosystem level. *Plant Soil* 200:71–89
- Waldrop MP, Zak DR, Sinsabaugh RL (2004) Microbial community response to nitrogen deposition in northern forest ecosystems. *Soil Biol Biochem* 36:1443–1451
- Wan S, Norby RJ, Pregitzer KS, Ledford J, O'Neill EG (2004) CO<sub>2</sub> enrichment and warming of the atmosphere enhance both productivity and mortality of maple tree fine roots. *New Phytol* 162:437–446
- Wayson CA, Randolph JC, Hanson PJ, Grimmond CSB, Schmid HP (2006) Comparison of soil respiration methods in a mid-latitude deciduous forest. *Biogeochemistry* 80:173–189
- Woodbury PB, Heath LS, Smith JE (2007) Effects of land use change on soil carbon cycling in the conterminous United States from 1900 to 2050. *Glob Biogeochem Cycles* 21:GB3006
- Yanai RD, Stehman SV, Arthur MA, Prescott CE, Friedland AJ, Siccama TG, Binkley D (2003) Detecting change in forest floor carbon. *Soil Sci Soc Am J* 67: 1583–1593
- Yang Y, Chen G, Guo J, Xie J, Wang X (2007) Soil respiration and carbon balance in a subtropical native forest and two managed plantations. *Plant Ecol* 193:71–84
- Zinn YL, Lal R, Bigham JM, Resck DVS (2007) Edaphic controls on soil organic carbon retention in the Brazilian Cerrado: texture and mineralogy. *Soil Sci Soc Am J* 71:1204–1214