

**REVIEW AND
SYNTHESIS****Plant functional traits and soil carbon sequestration
in contrasting biomes**

Gerlinde B. De Deyn,^{1*} Johannes
H. C. Cornelissen² and Richard D.
Bardgett¹

¹*Institute of Environmental and
Natural Sciences, Soil and
Ecosystem Ecology, Lancaster
University, Lancaster LA1 4YQ,
UK*

²*Department of Systems
Ecology, Faculty of Earth and
Life Sciences, Institute of
Ecological Science, Vrije
Universiteit, De Boelelaan 1085,
1081 HV Amsterdam, The
Netherlands*

*Correspondence: E-mail:
g.dedeyn@lancaster.ac.uk

Abstract

Plant functional traits control a variety of terrestrial ecosystem processes, including soil carbon storage which is a key component of the global carbon cycle. Plant traits regulate net soil carbon storage by controlling carbon assimilation, its transfer and storage in belowground biomass, and its release from soil through respiration, fire and leaching. However, our mechanistic understanding of these processes is incomplete. Here, we present a mechanistic framework, based on the plant traits that drive soil carbon inputs and outputs, for understanding how alteration of vegetation composition will affect soil carbon sequestration under global changes. First, we show direct and indirect plant trait effects on soil carbon input and output through autotrophs and heterotrophs, and through modification of abiotic conditions, which need to be considered to determine the local carbon sequestration potential. Second, we explore how the composition of key plant traits and soil biota related to carbon input, release and storage prevail in different biomes across the globe, and address the biome-specific mechanisms by which plant trait composition may impact on soil carbon sequestration. We propose that a trait-based approach will help to develop strategies to preserve and promote carbon sequestration.

Keywords

Biochemical stoichiometry, biodiversity, C : N ratio, carbon budget, decomposition, ecosystem functioning, global change, plant–soil feedback, respiration, soil organic carbon.

Ecology Letters (2008) 11: 1–16

INTRODUCTION

Globally, terrestrial ecosystems contain *c.* 2100 Gt of carbon (Schulze 2006), of which over two-thirds are stored in soils (Jobbagy & Jackson 2000; Amundson 2001). Part of this soil carbon pool is highly variable in space and time, while a large ‘inert’ carbon pool may become ‘active’ when exposed to new environmental conditions. Rapid climatic changes may thus alter soils from sinks to sources for atmospheric carbon (Davidson & Janssens 2006). The large carbon-storage capacity of soils suggests a potential ‘function’ for soils to dampen increasing atmospheric CO₂ concentrations. To date, however, the mechanisms that regulate soil carbon sequestration remain unclear, and extrapolation from short-term empirical studies to long-term projections of worldwide carbon balances remains uncertain (Rustad 2006).

Net productivity of ecosystems is determined by the balance between carbon assimilation through photosynthesis and carbon loss through plant respiration and heterotrophic soil respiration. However, to determine the net ecosystem carbon balance, non-respiratory losses of

carbon also need to be considered (Schulze 2006). Soil carbon pools are the balance between carbon input via primary productivity, and output via decomposition processes, charring or burning and volatilization and leaching of organic compounds (Amundson 2001). The maximal potential of soils to sequester carbon is determined by intrinsic abiotic soil factors such as topography, mineralogy and texture, but soil carbon dynamics are also driven by biota and their interaction with climate. Here, we review the biotic aspects of soil carbon sequestration from local to the biome scale, and illustrate how the selection of plant traits by abiotic stress factors sets the different scenes within which soil biota drive carbon cycling. Our plant trait-based approach provides a mechanistic framework for understanding how different primary producers and their consumers drive soil carbon sequestration through the direct and indirect effects of their inherent traits. First, we summarize the mechanisms by which particular plant traits control assimilation of carbon, its transfer to soil, its residence time in soil, and their relation to carbon metabolism by heterotrophic soil organisms. Second, we

explore how soil carbon pools, and the key traits of plants and soil biota that control them, prevail in different terrestrial biomes across the globe. We illustrate that environmental stress factors, such as extreme temperatures and low nutrient availability, select for particular plant response traits, with major consequences for carbon cycling through associated ecosystem effect traits (Lavorel *et al.* 2007). Finally, we address the biome-specific mechanisms by which changes in the composition of plant traits may affect soil carbon sequestration by autotrophs and heterotrophs.

MECHANISMS FOR PLANT TRAIT CONTROL OF SOIL CARBON SEQUESTRATION

Plant traits that regulate soil carbon sequestration can be broadly divided into those that alter carbon input to soil, through primary productivity and belowground carbon allocation, and those that control carbon loss from soil via respiration, volatilization of organic compounds (VOC), fire and leaching (Fig. 1). We discuss these mechanisms with special focus on interactions between traits of plants and soil biota that influence the balance between input and output of soil carbon.

Plant traits and soil carbon input

Owing to the evolutionary trade-offs between acquisition and conservation of resources, plant species that can persist in stressful environments (e.g. low availability of light, nutrients, water and oxygen, and extremes in temperature and pH) by

protecting their resources, differ in growth rate, lifespan and physical and chemical composition from those plant species that mainly invest in growth potential. As a consequence, the amount and composition of carbon forms that plants return to soil, and their subsequent fate in soil, can be related to plant growth rate (Chapin 2003; Lavorel *et al.* 2007). Plant species with high inherent relative growth rates tend to have greater photosynthetic capacity than inherently slow-growing plant species, but this trades off with shorter lifespan, lower dry matter content and lower carbon concentrations of aboveground and belowground plant organs (Aerts & Chapin 2000). Soil carbon mostly originates from decaying aboveground and belowground plant tissue, but root exudates are also an important source of carbon input to soil (5–33% of daily photoassimilate), especially in actively growing plants (Bardgett *et al.* 2005). Fast-growing plant species may thus contribute to soil carbon pools through the input of large amounts of carbon to soil, whereas slow-growing species contribute through the input of low-quality plant material, i.e. highly concentrated carbon forms in nutrient poor tissues. Which plant strategy prevails within an ecosystem depends on the environmental conditions, as the dominance of species with high growth rates requires high availability of light and nutrients. Hence, in biomes with a short growing season and low nutrient availability, soil carbon input will be mainly derived from poor-quality litter, while in more productive biomes primary productivity will be the main driver of soil carbon sequestration. Besides nutrient and light limitation of primary productivity, other environmental stress factors may select for more specific plant traits that can

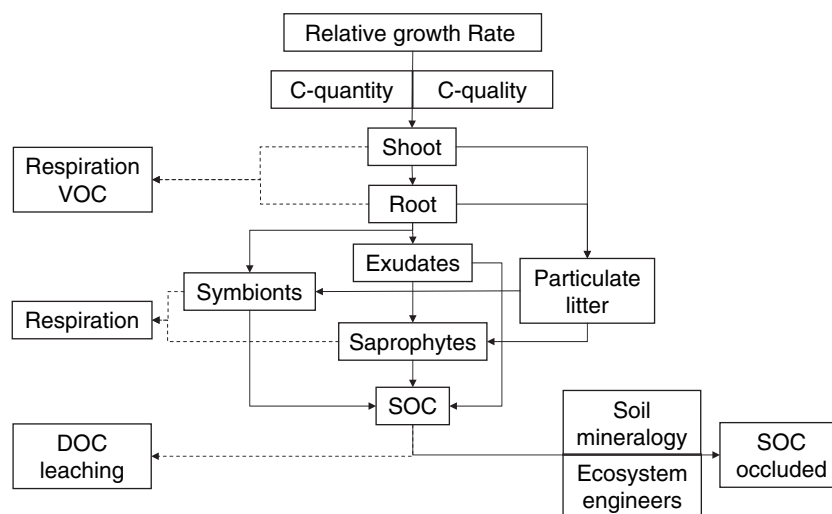


Figure 1 Soil carbon (C) in- and output by plants and associated soil heterotrophs. Net soil carbon sequestration depends on the quantity and quality of the plant and heterotroph carbon pools, which determine carbon use efficiency and soil carbon residence time. High growth rate generally corresponds with large, fast fluxes and relatively small soil carbon pools, slow growth rate with slower fluxes, more recalcitrant and more persistent carbon pools. Occlusion of carbon in soil minerals, often enhanced by rhizodeposits and ecosystem engineers, enables long residence time. Solid lines indicate carbon incorporation and dotted lines soil carbon loss; SOC: soil organic carbon, VOC: volatile organic carbon, DOC: dissolved organic carbon.

impact on carbon sequestration. For example, plant traits that govern tolerance to waterlogging and anoxia comprise aerenchyma in roots and shoots, and the formation of thick, superficial, adventitious roots rather than fine roots. These adaptations likely reduce soil carbon input by limiting root distribution through the soil profile and by reducing root mechanical strength, unless plants also invest in root sclerenchyma (Striker *et al.* 2007).

Plant traits that determine responsiveness to mutualistic symbionts are important for soil carbon input because such symbiosis can increase plant productivity through enhanced acquisition of limiting resources. Globally, the most common plant symbionts are N-fixing bacteria and mycorrhizal fungi. Species of symbiotic bacteria that incorporate N from air can live with legumes, actinorhizal plants, *Parasponia* sp., cycad tree species (Vessey *et al.* 2005) and many bryophytes and lichens (Cornelissen *et al.* 2007a). Mycorrhizal fungi, on the other hand, enhance plant nutrient acquisition from soil, especially of N and P (Smith & Read 1997). Moreover, mycorrhizal fungi can reduce soil carbon loss by immobilizing carbon in their mycelium, by extending root lifespan and by improving carbon sequestration in soil aggregates (Langley *et al.* 2006; Rillig & Mummey 2006). Mycorrhizal fungi associate with most terrestrial plant species, and host specificity is supposedly low. However, their effect on soil carbon sequestration may be highly specific to the combination of plant and symbiont species (Kiers & van der Heijden 2006) and soil fertility (Allen *et al.* 2003). The underlying traits need further elucidation, yet it appears that across ecosystems different types of mycorrhizal fungi prevail and are related to particular plant traits and growth limiting nutrients (Cornelissen *et al.* 2001; Read & Perez-Moreno 2003).

Plant traits and soil carbon loss

Soil respiration accounts for most loss of carbon from soil and results from the metabolic activity of autotrophs and heterotrophs. The precise contribution of different organisms to soil respiration is yet unknown, largely because the separation of the sources is notoriously difficult in that roots, symbionts and heterotrophs form a functional continuum rather than discrete groups (Högberg & Read 2006). However, we can identify two broad ways by which plant traits can influence respiratory processes and hence carbon loss from soil: directly through inherent variation in root respiration and VOC release and indirectly by determining the rate at which heterotrophs in soil can decompose, assimilate and respire plant-derived carbon.

Plant inherent respiration and volatilization

Fast-growing plant species are metabolically more active than slow-growing species and therefore have higher rates

of carbon loss through respiration. Shoot respiration accounts for most of this difference, because root respiration rates of slow-growing species are high due to their low efficiency of N-acquisition (Lambers *et al.* 1998). Plant traits involved in carbon and nutrient cycling appear strongly coupled: across plant functional groups, growth forms and biomes, respiration rates relate positively to N-concentration of plant tissues. The underlying cause is the high metabolic cost of maintaining active N-rich proteins involved in carbon and nutrient acquisition (Wright *et al.* 2004). Respiration by mycorrhizal and N-fixing roots on the other hand is directly coupled to belowground carbon allocation of photosynthates (Högberg & Högberg 2002; Warembourg *et al.* 2003). Respiration rates of symbionts are thus likely greater in fast- than in slow-growing plant species, but the net effect on soil carbon can be specific to the host-symbiont species combination due to differential efficiencies of the symbiosis (Allen *et al.* 2003; Kiers & van der Heijden 2006). In addition to respiration, plants lose carbon through VOCs (Kesselmeier *et al.* 2002). To date, most work on these emissions has focussed on leaves and forest canopies, but roots might also emit VOCs and their potential impact on soil carbon sequestration requires further exploration (Lin *et al.* 2007). In waterlogged systems, such as peatlands, soil carbon is lost to the atmosphere either as CH₄ or as CO₂ through aerenchyma, at rates which likely depend on the type of aerenchyma and carbon supply to roots (Ström *et al.* 2003; Striker *et al.* 2007).

Plant traits, decomposition and heterotrophic respiration

Plant functional traits strongly influence the chemical and physical composition of litter inputs, and thereby their decomposability, carbon loss through soil respiration and leaching, and carbon immobilization in humified plant residues (Cornelissen & Thompson 1997). Fast-growing plants allocate most of their carbon to photosynthetically active structures of low density and high nutrient content, yielding easily decomposable litter. In contrast, slow-growing and long-lived plants produce nutrient poor, recalcitrant litter (Aerts & Chapin 2000). These patterns of growth rate and litter quality are not limited to seed plants: most slow-growing vascular and non-vascular cryptogams, such as ferns, fern allies, bryophytes and some lichen groups, also contain high concentrations of secondary carbon compounds that retard decomposition and thereby potentially increase soil carbon storage (Cornelissen *et al.* 2007a).

Recalcitrant carbon forms, especially lignin, are beneficial for soil carbon sequestration because of their long residence time in soil, due to the specificity of lignin-degradation enzymes and limited occurrence of the soil fungi, especially white-rot fungi, that can produce them (de Boer *et al.* 2005; Zak *et al.* 2006). Lignin breakdown products (humic substances) further enhance soil carbon sequestration

through the formation of complexes with other organic molecules, such as amino acids and enzymes (Hättenschwiler & Vitousek 2000). The production of ligninolytic enzymes by white-rot fungi is suppressed by high concentrations of soil N, so that a lignin-rich litter may seem more recalcitrant in fertile than in poor soils (Waldrop & Zak 2006); such selective suppression of soil biota through N-deposition might even contribute more to soil carbon sequestration than enhanced primary productivity (Pregitzer *et al.* 2008). In addition to lignin, polyphenols and tannins can also retard decomposition, while in living plants they offer protection from herbivores and pathogens (Hättenschwiler & Vitousek 2000).

Whole-plant structure and the partitioning of carbon and nutrients between plant organs also affect soil carbon sequestration. Long-lived, woody plants allocate a high proportion of their carbon into organs that govern physical support, resulting in the production of tough, dense litter forms: coarse woody debris. This debris represents a slow-cycling, recalcitrant carbon pool, due to its high density, volume to surface ratio and chemical complexity. Some studies have indicated the importance of woody debris for carbon storage in forest ecosystems (e.g. Sitch *et al.* 2003), but little is known about how species differences in wood traits, such as wood density, specific chemical composition and bole diameter, link to wood decomposition rate, belowground carbon allocation and carbon storage in and turnover of roots. It seems, however, that the great variation in root decomposition is driven by the variation in root litter quality (Silver & Miya 2001).

Most studies on inter-specific variation in litter decomposability have focussed on aboveground tissue (Hättenschwiler & Vitousek 2000; Lavorel *et al.* 2007). The few examples that included both aboveground and belowground structures indicate that shoot and root decomposability traits might not be directly related (Wardle *et al.* 1998; Craine *et al.* 2005). Plants may even combine leaf traits typical for fast-growing 'competitors' with root traits typical for slower-growing 'stress tolerators', or the other way round, and such reciprocal trait combinations supposedly stabilize their co-existence (Personeni & Loiseau 2004). Across plant species, root litter generally appears to be of lower quality than that of shoots and thereby represents a more recalcitrant carbon pool (Craine *et al.* 2005; Tjoelker *et al.* 2005). Higher root to shoot ratios may thus indicate increased soil carbon sequestration potential.

Plants stimulate the activity of soil microbes, especially through the release of labile carbon forms contained in root exudates, and hence stimulate carbon loss through mineralization of recent as well as old, residing, soil organic carbon (SOC), a phenomenon known as 'priming' (Kuzaykov 2006). The 'priming effect' mostly operates in nutrient-poor soil where specific fungi use the labile carbon to

produce enzymes that degrade recalcitrant substrates, such as lignin (Waldrop & Zak 2006). Recently, priming of SOC was also demonstrated in productive soils and was positively related to plant productivity and negatively to root N-concentration, suggesting that plant-microbe competition for N may regulate priming (Dijkstra *et al.* 2006). On the other hand, specific plant traits such as toxin exudation can suppress priming and carbon loss by blocking the microbial activity (Dijkstra *et al.* 2006). Traits of root exudation (quantity and quality) may thus be very important with respect to the loss of SOC. However, root exudates are qualitatively very diverse in terms of the metabolites that they contain, and their contributions to priming are largely unexplored (Inderjit & Weston 2003).

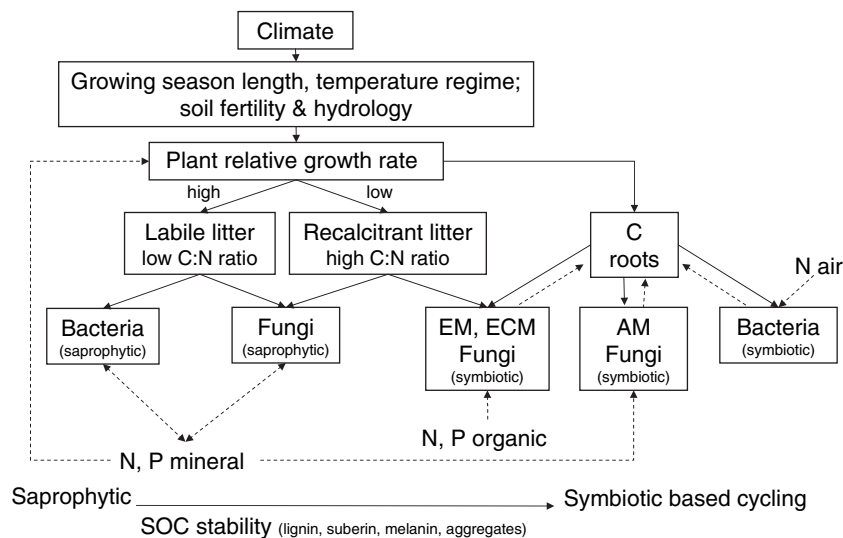
Root exudation patterns are driven by aboveground and belowground plant metabolic activity of photosynthesis and nutrient uptake (Bardgett *et al.* 2005). Therefore, exudate quantity is likely greatest in fast-growing plant species, especially those with highly branched, fine root systems (Personeni & Loiseau 2004). However, rates of net efflux are highly variable, due to for example reabsorption of exudates, plant age and cell leakiness, and interactions with herbivores that stimulate root carbon efflux (Bardgett & Wardle 2003). Therefore, traits that make plants palatable to herbivores (i.e. high nutrient concentrations) might not only promote their decomposability, but also root exudation, thereby further enhancing soil carbon loss; these ideas, however, remain untested.

Plant root rhizodeposits and root turnover may, however, also enhance soil carbon sequestration through interacting with soil minerals, especially clay particles, to form soil aggregates (Lorenz & Lal 2005; Six *et al.* 2006). Plant traits that promote the interaction between soil minerals and root products, such as deep-rooting, high root branching and exudation (Jobbagy & Jackson 2000), will thus have important effects on soil carbon sequestration via this route.

Traits of soil heterotrophs and soil carbon dynamics

As discussed above, plant traits influence soil carbon sequestration indirectly through influencing the activity of soil heterotrophs, especially bacteria, fungi and fauna. The functional traits of these soil-inhabiting heterotrophs affect soil carbon sequestration in various ways (Fig. 2). The biomass of primary consumer soil biota generally represents only a small fraction (< 7%) of the total soil carbon pool (Wardle 1992), but their metabolites can stabilize SOC and provide plant nutrients, and thereby drive carbon input from primary productivity (Six *et al.* 2006). The diversity of soil bacteria and fungi is enormous, and to date their functional roles are not fully explored. However, regarding soil carbon sequestration, we can generalize that bacteria and fungi play distinct roles because of their inherent stoichiometry, especially of C and N. The average C : N ratio in bacteria

Figure 2 Inter-dependency of labile and recalcitrant litter and mineral and organic nutrient-cycling drives abundances of different functional groups of primary consumer soil biota. Recalcitrant litter with high C : N ratio favours saprophytic fungi, while low mineral-nutrient availability in soil stimulates carbon allocation to symbiotic associations. Solid lines indicate C and dotted lines mineral N or P flow; EM: ericoid mycorrhizal, ECM: ecto-mycorrhizal, AM: arbuscular mycorrhizal.



is *c.* 4 and in fungi *c.* 10, and fungi generally respire less carbon per unit fungal biomass carbon gained, resulting in higher carbon use efficiency (CUE) in fungi than in bacteria (Six *et al.* 2006). Recent studies, however, found considerable overlap in CUE-values of bacteria and fungi, according to species and functional group identity, quantity and quality of substrates, and abiotic factors (Six *et al.* 2006). Mycorrhizal fungi may have higher CUE than saprophytic fungi and bacteria, given that they obtain carbon within plant cells and have mycelium with a C : N ratio of 20 (Wallander *et al.* 2003). Generally, carbon in fungal metabolites may reside longer in soil than those in bacteria, as fungal mycelia comprise complex, nutrient-poor carbon forms, such as chitin and melanin, while bacterial membranes mainly consist of phospholipids that are quickly reassimilated by soil biota. The mechanisms of microbial contribution to SOC sequestration are yet poorly known *in situ*, but overall increased fungal-dominance in soils is typically associated with high organic-matter content and low substrate quality, i.e. high C : N ratio (Bardgett *et al.* 2005; van der Heijden *et al.* 2008).

Ecosystem engineers residing in soil affect carbon sequestration through carbon consumption, but probably even more so through modifying soil physical structure. Soil fauna, such as earthworms, ants and termites, promote carbon sequestration by redistributing carbon through the soil profile by channelling, mixing organic and mineral soil components, and by forming relatively stable soil aggregates and casts. Soil aggregates are formed through the occlusion of organic matter in soil minerals by means of 'gluing' compounds, e.g. polysaccharides and glycoproteins, or by creating structural networks. Plant litter quality, especially low C : N ratio and adequate size, enhances soil ecosystem engineering by earthworms and termites (Lavelle *et al.* 1997; Eggleton & Tayasu 2001), while earthworms are promoted

further by high litter Ca (Reich *et al.* 2005). In addition to soil fauna, plant roots and soil fungi, especially mycorrhizae, strongly affect soil carbon sequestration via this physicochemical pathway (Rillig & Mummey 2006; Six *et al.* 2006). At the same time, soil channelling enhances decomposition, implying carbon loss, but this can be offset by stimulated plant growth.

Long-term effects on carbon sequestration through feedbacks

Long-term enhancement of soil carbon sequestration requires sustained primary productivity and hence efficient feedback between communities of plants and soil biota for carbon and nutrient cycling (Fig. 2) (Fontaine & Barot 2005). Moreover, plant–soil feedbacks, with saprophytes, mutualists and pathogens, affect carbon input quantity, quality and carbon- and nutrient-cycling rates by altering the plant community composition and thereby the prevailing plant traits (Ehrenfeld *et al.* 2005; van der Heijden *et al.* 2008). Similarly, plant community shifts by selective herbivory, aboveground and belowground, may promote soil carbon input through increased dominance of less nutritious, recalcitrant plants (Bardgett & Wardle 2003). In unproductive soils, plants strongly compete with soil microbes for mineral nutrients (Bardgett *et al.* 2003), and this interaction might promote plant species with traits that provide higher nutrient competitiveness, for example by utilizing organic nutrients (Schimel & Bennett 2004). Plants with such capabilities have low growth rates but can enhance soil carbon input through their recalcitrant litter. Associations with symbiotic fungi or bacteria, on the other hand, might reduce direct nutrient competition with free-living soil biota, and is potentially an efficient mechanism to enhance soil carbon input, given mutual exchange of

limiting nutrients (Allen *et al.* 2003). N-fixing plants tend to produce litter with a relatively high nutrient content, which can facilitate other plants and thereby primary productivity and soil carbon input at community level (Hooper *et al.* 2005). In contrast, ericoid and ecto-mycorrhizal plants produce recalcitrant litter that tends to immobilize nutrients (Cornelissen *et al.* 2001).

Plant traits that alter the soils' abiotic conditions can have strong and long-term effects on SOC sequestration. Plant canopy characteristics, which influence surface albedo, evapotranspiration, wind speed and snow cover, can thereby overrule the effects of resource quantity and quality on carbon in- and output through temperature- and moisture-mediated effects on SOC mineralization and carbon leaching (Chapin 2003). Furthermore, plant physical traits can enhance soil carbon stabilization by occlusion and reduction of erosion, for example by deep and branched rooting (Lorenz & Lal 2005). Fluctuations in soil moisture and hence ice dynamics and cycles of soil drying are strongly affected by plant traits that drive soil hydrology, but more work is required to elucidate their influence on carbon sequestration. Finally, plant traits that affect ecosystem flammability and combustibility have major impacts on fire regimes and thereby on rapid and major carbon losses (Chapin 2003).

SOIL CARBON STORAGE ACROSS BIOMES LINKED TO PLANT TRAIT COMPOSITION

At global scale, plant species of similar functional types co-occur in distinct areas forming biomes, of which the distribution is driven by temperature and precipitation regimes (Prentice *et al.* 1992; Woodward *et al.* 2004; Fig. 3). Across biomes, SOC pools vary widely (King *et al.* 1997; Amundson 2001; Fig. 3): the smallest SOC pools

(< 10 kg C m⁻²) are found in deserts and savannas, and also in warm temperate and dry tropical forests; intermediate SOC pools (±13 kg C m⁻²) are present in temperate grasslands and forest, whereas the largest SOC pools (≥ 19 kg C m⁻²) are located in wet biomes such as wet tropical and boreal forest, and tundra. Climate selects plants with specific ecophysiological traits, resulting in communities with similar response traits (Violle *et al.* 2007). Because many plant traits are inter-dependent (Eviner & Chapin 2003), climate also selects sets of plant traits that act as carbon-cycling effect traits (Violle *et al.* 2007).

Biomes rich in plant diversity do not necessarily have larger SOC pools than less species-rich systems, as illustrated by comparable SOC concentrations in tundra, boreal and tropical forests, despite large differences in plant species richness (Amundson 2001). However, within biomes, plant trait composition strongly influences soil carbon sequestration. While the relative abundances and productivities of the predominant plant functional types and their traits *per se* are probably the principal factor determining soil carbon dynamics, interactions among plant species, or the avoidance thereof, may also play some important roles. The promotion of soil carbon input relative to soil carbon loss (Fig. 4) can be achieved through complementarity or through the facilitation of plant traits that enhance carbon sequestration at community level (Hooper *et al.* 2005). Examples include distinct nutrient requirements and uptake mechanisms, differential use of physical space or other resources such as water and light, and phenological traits that promote complementarity on short (seasons) or longer time scales (years to decades). These inherent traits may act directly or can be mediated by specific associations with different symbiont types (Fig. 4). Plant trait composition may also affect carbon loss to: (1) herbivory, through the protection of palatable plants by physically or chemically

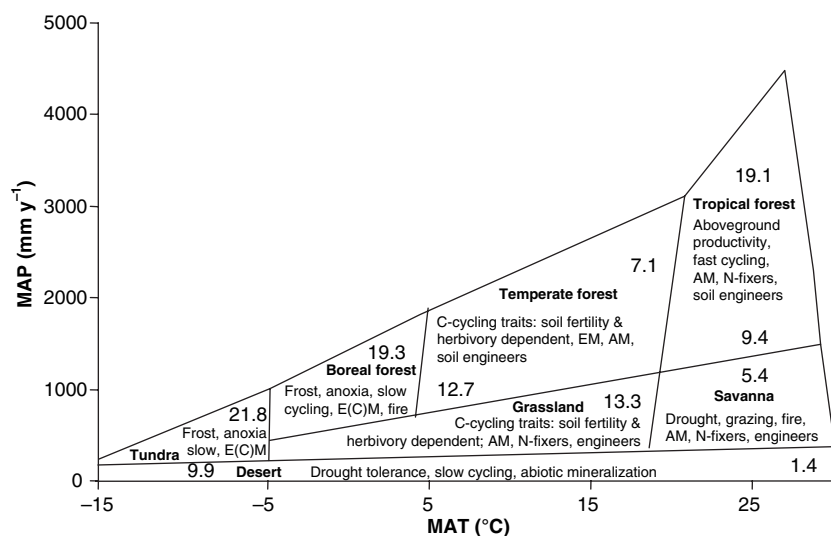


Figure 3 Soil organic carbon pools (kg C m⁻²; Amundson 2001) and drivers of plant carbon sequestration traits across biomes with characteristic MAT: mean annual temperature and MAP: mean annual precipitation. Lower and higher values within biomes represent warm- vs. cool-temperate forest, respectively, and drier vs. wet (peaty) tropical forests; EM: ecto-, ECM: ericoid- and AM: arbuscular mycorrhizal fungi; biome location after Woodward *et al.* (2004).

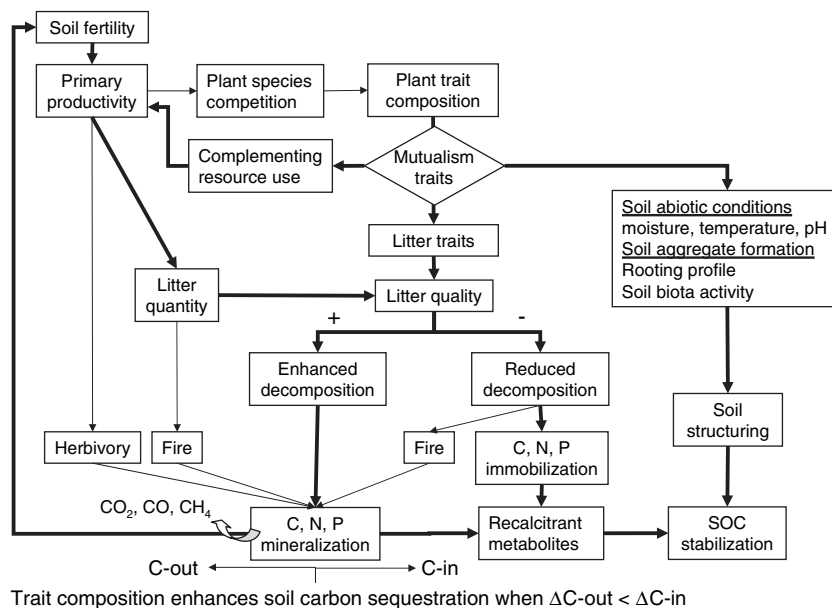


Figure 4 Potential plant trait composition effects on soil carbon sequestration, through influencing the ratio between carbon gains (C-in) and losses (C-out).

defended neighbours (Olf *et al.* 1999); (2) fire, e.g. through enhanced moisture conservation, wind breaking and recovery potential; (3) litter decomposition, e.g. through increased litter recalcitrance and enhanced CUE of decomposers; and (4) leaching, via occlusion in soil minerals through soil engineering by root proliferation and activity of heterotrophic soil biota (Fig. 4). Plant trait composition may influence soil decomposer diversity through the diversity of substrates and habitats they provide (Porazinska *et al.* 2003), and decomposer diversity in turn can affect soil carbon cycling through functional complementarity (Hättenschwiler *et al.* 2005; Wardle 2006). While interspecific variation in plant traits is a major determinant of soil carbon dynamics, there remains much uncertainty over the extent that trait interactions among plant species might influence carbon inputs and losses, because such interaction effects appear to be context dependent (Gartner & Cardon 2004; Hooper *et al.* 2005), and the factors controlling them may diverge between biomes. In this section, we explore current knowledge on biome-specific plant traits across a range of biomes and identify the main mechanisms by which plant trait composition may influence soil carbon input and output, and hence soil carbon storage.

Tundra

In tundra, very low temperature, short growing seasons, low nutrient availability and waterlogging are major plant stressors (Prentice *et al.* 1992; Fig. 3). Favourable plant traits hence must govern cold and waterlogging tolerance and minimize nutrient loss, and are associated with slow growth and input of low amounts of poor-quality carbon to

soil. The nutrient poor litter feeds back negatively to primary productivity, but traits that enable the uptake of organic nutrients without (Schimel & Bennett 2004) or with mycorrhizal fungi (Read & Perez-Moreno 2003), or of inorganic N through symbiosis with N-fixers, as in cryptogams (Cornelissen *et al.* 2007a), can bypass nutrient limitation. Plant traits that reduce SOC loss through decomposition in tundra are production of specific secondary chemicals associated with poor litter quality and modification of abiotic conditions (e.g. soil acidification and promotion of waterlogging) as demonstrated for cryptogams, especially *Sphagnum* species (Cornelissen *et al.* 2007a).

Plants often have certain traits that enhance, and other traits that reduce SOC sequestration. For example, shrubs enhance SOC loss through improved winter and spring soil temperature or soil moisture regimes for decomposition, while the low decomposability of their litter creates a negative feedback on carbon cycling (Cornelissen *et al.* 2007b). Similarly, graminoids may promote SOC sequestration through high root and rhizome biomass, but can stimulate SOC loss through high rates of root exudation, high litter quality, and air channels in roots and stems (Eviner & Chapin 2003; Cornelissen *et al.* 2007b).

The composition of plant traits in tundra can affect soil carbon input through complementarity in root distributions, such as between and within graminoids, shallow-rooting shrubs and cryptogams, which only have rhizoids loosely attached to the soil surface. Here, trait complementarity in nutrient uptake, directly or through association with mutualist symbionts such as ectomycorrhizae in shrubs and N-fixers in, or on, cryptogams, may also prevail.

Hemiparasitic plants, on the other hand, promote nutrient cycling by transferring nutrients locked up in vascular plant roots into high-quality hemiparasite litter (Quesada *et al.* 2003), which may facilitate primary productivity and soil carbon input. Other mechanisms of facilitation may be reduced environmental stress, such as low temperature and waterlogging, through diverse plant and litter traits that affect evapotranspiration and soil warming. Plant trait interactions in species mixtures may reduce carbon loss by retarding litter decomposition through non-additive antagonistic effects, such as through the activity of toxic compounds (e.g. cryptogam litter), whereas synergistic effects and enhanced carbon loss can be expected through nutrient transfer and improved microclimate. The prevalence and importance of such (above- and belowground) litter mixing effects on decomposition rates remain to be tested in tundra (Gartner & Cardon 2004; Hättenschwiler *et al.* 2005), but is likely to be minor compared with the great differences in litter quality among plant species and types (Cornelissen *et al.* 2007b).

Overall, soil carbon input in tundra is slow, but a high proportion of plant carbon is allocated belowground (root : shoot ratio of 6.6; Jackson *et al.* 1996), albeit mainly contained in the soil surface due to permafrost (Jobbagy & Jackson 2000; Schenk & Jackson 2002a). Carbon output is slow due to poor litter quality, low temperatures and often soil anoxia, yielding old but large carbon pools in poorly decomposed litter (Hobbie 1996; Mack *et al.* 2004). Richness of (vascular) plants is low, but the range of traits that affect carbon cycling is wide due to distinct effects of shrubs, cryptogams and graminoids that differ in secondary chemistry and in how they affect microclimate (Hobbie 1996; Hättenschwiler *et al.* 2005).

Boreal forest

Boreal forests replace tundra where growing seasons are longer, but where low minimum temperature and nutrient availability remain major stressors for plant growth (Prentice *et al.* 1992; Fig. 3). Typical traits of the vegetation, i.e. coniferous forests and peatlands, are cold tolerance, low mineral nutrient requirements and, where permafrost prevails, tolerance to drought, shallow soil and seasonal waterlogging. As in tundra, these adaptations require long-lived, nutrient-poor plant organs, yielding low carbon input quantity and quality to soil. Where winters are less severe, deciduous trees, such as larch, birch, aspen and diverse understory species also occur. These species have traits that enhance carbon input quantity, being deciduous, and improve litter by their high nutrient content (Aerts & Chapin 2000; Nilsson & Wardle 2005).

As for tundra, association with mutualist symbionts, such as ericoid- but especially ecto-mycorrhizal fungi, may

enhance soil carbon input (Smith & Read 1997; Read & Perez-Moreno 2003), while direct utilization of amino acids from soil appears also common in boreal forest dominants (Kielland *et al.* 2006). Soil microbes only represent 1% of SOC (Wardle 1992). However, estimates of soil microbial carbon poorly capture the contribution of symbiotic organisms in soil, and mycorrhizal fungi are expected to account for a considerable proportion of the total soil carbon pool (Högberg & Högberg 2002; Wallander *et al.* 2003). Moreover, saprophytic soil biota significantly complement mycorrhizal fungi in plant growth promotion through mineralization of litter (Lindahl *et al.* 2007) and of themselves during freeze–thaw cycles (Bardgett *et al.* 2005).

Carbon loss through wildfires is common in boreal forests, albeit at lower frequency than in grassland ecosystems. Wildfires not only consume carbon in standing plant biomass, but also reduce older carbon pools by burning litter. Plant traits that may reduce such immediate carbon loss comprise reduced plant and litter flammability (e.g. through lower resin content, lower litter quantity or higher litter quality that reduces litter layer thickness), while other traits may reduce losses after fire through enhanced charcoal formation and rapid forest rejuvenation (Nilsson & Wardle 2005; Preston & Schmidt 2006).

In boreal forests, competition for light is important, given tall trees and dense canopy. Trait complementarity in light interception between under- and overstorey vegetation may therefore increase carbon input. Trait complementarity in nutrient use may be achieved through symbiosis with mutualists that differ in nutrient-uptake strategy. Some boreal plant species host N-fixers, while ericoid mycorrhizae are widespread in understory shrubs and ectomycorrhizae in overstorey trees (Smith & Read 1997; Read & Perez-Moreno 2003).

Boreal forest carbon loss through decomposition is strongly affected by highly specific plant traits, such as litter allelopathy. Litter of the understory dominant *Empetrum nigrum* thereby yields non-additive antagonistic effects in litter mixtures (Nilsson & Wardle 2005). However, non-additive facilitative effects of litter mixing on decomposition rates are also common, mostly through improved microclimate for decomposers and with a key role of feather mosses (Nilsson & Wardle 2005). Overall, in boreal forests, the presence of specific plant traits rather than the diversity of the traits present, appear to direct the outcome of litter diversity effects on decomposition (Hättenschwiler *et al.* 2005; Nilsson & Wardle 2005). In living plants, carbon losses to herbivores may be reduced through the facilitation of plants with unpalatable tissues of high C : N ratio and secondary metabolite content (Bardgett & Wardle 2003). Trait composition may also affect carbon loss to fires, e.g. through traits that reduce the chance of fire striking highly flammable plants and litter, and by enhanced recovery after

fire through traits that govern resilience to fire (Bond *et al.* 2005; Preston & Schmidt 2006).

In conclusion, boreal forests contain a large, slow-cycling SOC pool, which exceeds the carbon pool in vegetation (King *et al.* 1997; Amundson 2001; Fig. 3). In contrast to tundra, most carbon in plant biomass is located above-ground (root : shoot ratio of 0.3), but root biomass, and SOC as a whole, still represent a large and recalcitrant soil carbon pool, despite its often shallow distribution (Jackson *et al.* 1996; Jobbagy & Jackson 2000). Plant species richness of higher plants is relatively low, but deciduous and evergreen vascular plants and cryptogams have distinct SOC effect traits through the difference in carbon form quantity and quality for decomposability and flammability. Moreover, rates of carbon cycling do not directly relate to plant species richness, and effects of species and functional groups strongly depend on abiotic and historic factors, as demonstrated in long-term removal experiments in this biome (Wardle & Zackrisson 2005).

Temperate forest

Temperate forests form in climates with moderate winter frost and regular precipitation. Typical vegetation comprises evergreen or deciduous–coniferous and broadleaved trees (Prentice *et al.* 1992; Fig. 3). Compared with boreal forests, plant traits associated with growth rate and litter quantity and quality promote fast soil carbon cycling, but plants are less cold-tolerant.

In temperate forest, plant traits that determine carbon input quantity and quality are diverse within and between plant species and seasons (Lauenroth & Gill 2003). Litter quality from broadleaf trees is generally higher than that from needle leaf trees (Silver & Miya 2001), but differences between species or even between genotypes may be as large due to specific plant compounds (Lauenroth & Gill 2003; Whitham *et al.* 2006). In this biome, the interaction between soil fertility and traits of litter quality and of decomposers may drive longer-term soil carbon sequestration (Pregitzer *et al.* 2008). Most studies on the role of plant traits in carbon and nutrient cycling have focussed on aboveground litter, while only recently the major importance of belowground litter for soil carbon cycling in temperate forests has become apparent (Högberg & Read 2006; Pollierer *et al.* 2007; but see Matamala *et al.* 2003). In particular, the need to account for SOC priming, by which increased carbon inputs from roots could result in a net loss of SOC through the interaction with soil biota, is an important new finding with longer-term implications for soil carbon balance in forests (Dijkstra & Cheng 2007).

High litter decomposability of high-quality litter implies higher carbon mineralization and loss in temperate than in boreal forests. However, the net effect on SOC sequestra-

tion depends on the efficiency of nutrient mineralization and re-use in primary production. Plant traits that enhance nutrient use efficiency in temperate forests include association with mutualist symbionts, such as ectomycorrhizae in coniferous (poorer litter quality) and ecto- and arbuscular mycorrhizal fungi in broadleaved forests (Cornelissen *et al.* 2001; Read & Perez-Moreno 2003). A trade-off of this association may be a rapid pathway for carbon loss of recent photosynthate through soil respiration (Högberg & Read 2006), but the amount lost via this route differs between tree species due to yet unknown traits (Steinmann *et al.* 2004). The efficiency with which carbon is sequestered also depends strongly on forest age-structure. Growth decline with stand age does not, however, directly relate to growth rate or lifespan, but rather to stand height (Mencuccini *et al.* 2007), suggesting that tree height might be an important trait for soil carbon sequestration.

In temperate forests, traits that stimulate ecosystem engineers (e.g. low litter C : N ratio and favourable microclimate) can be important for longer-term soil carbon sequestration through enhanced soil aggregation, litter distribution and nutrient mineralization (Lavelle *et al.* 1997). Their net effect on soil carbon sequestration, however, strongly depends on the complementarity of the traits of soil fauna and vegetation, as illustrated by the sharp decline in soil carbon pools caused by the invasive earthworms in North-American temperate forests that resulted in much faster litter decomposition than in non-invaded forests (Bohlen *et al.* 2004).

Longer growing seasons and greater productivity in temperate compared with boreal forests further increases the importance of light competition and complementarity in light interception and thus likely contributes to soil carbon input. In deciduous forests, seasonal understory vegetation uses irradiation before overstory vegetation can and thereby adds carbon to the system (Aerts & Chapin 2000). Understory vegetation, deciduous and evergreen trees may also have complementary types of mycorrhizal symbionts, which may further enhance carbon and nutrient input to soil. However, in this biome, saprophytes may be the most important mediators of nutrient availability, and their interaction with mycorrhizae may be facilitative as well as competitive (Read & Perez-Moreno 2003; Hättenschwiler *et al.* 2005).

Carbon loss in temperate forest is mainly due to decomposition and major disturbances (e.g. fire, storm damage, outbreaks of insects or disease). Trait compositions that enhance resistance and resilience to these disturbance factors (e.g. seed and seedling longevity, tolerance to shade, herbivores and pathogens, resprouting ability) may thus yield enhanced carbon sequestration on the longer term. To date, litter-mixing effects on decomposition rate remain unpredictable. However, some data point to a possible role

for trait complementarity in litter nutrient content (e.g. balanced nitrogen availability) and a modification of the abiotic environment (e.g. improved humidity) for decomposer soil fungi, bacteria and fauna (Hättenschwiler *et al.* 2005); consequent effects on plant growth have hardly been investigated (Ehrenfeld *et al.* 2005).

Overall plant biomass accounts for a large portion of the total carbon pool and is stored in large woody aboveground organs and deep, coarse root systems (Jackson *et al.* 1996; Jobbagy & Jackson 2000; Schenk & Jackson 2002a), and plant biomass carbon exceeds SOC due to rapid rates of carbon mineralization (King *et al.* 1997). Plant traits that enhance soil carbon sequestration thus require enhanced nutrient use efficiency and carbon incorporation into deeper soil layers and soil aggregates. Litter inputs are diverse, ranging from recalcitrant structural tissue to labile rhizodeposits, and differ markedly in quality, quantity and seasonality between plant species, especially between evergreens and deciduous broad-leaf trees, and even between plant genotypes. Litter quantity and quality can strongly influence SOC sequestration through stimulating decomposers, mutualist symbionts or ecosystem engineers that, depending on their traits, may enhance as well as reduce soil carbon sequestration.

Tropical forest

Tropical forests occur in humid climate zones with minimal temperatures above 15 °C (Prentice *et al.* 1992; Fig. 3). Plant carbon assimilation rates are high and year-round, but this trades off with high carbon loss through respiration and production of VOCs (Kesselmeier *et al.* 2002). Given continuous plant growth, traits that optimize acquisition and efficient use of solar radiation and nutrients throughout the forest complex canopy are very important for sustained ecosystem carbon input (Schieving & Poorter 1999). Carbon allocation to aboveground supportive plant organs is high, while the climate is favourable for carbon mineralization and hence significantly more carbon is stored in vegetation than in soil (King *et al.* 1997).

In tropical forests, plant traits that enable the acquisition of limiting nutrients, especially P, likely enhance soil carbon input through primary productivity. Such traits may be extensive root foraging and/or association with arbuscular mycorrhizal fungi (Smith & Read 1997; van der Heijden *et al.* 2008) and may also reduce SOC loss through increased carbon stabilization within mycorrhizal networks and enhanced carbon infiltration in soil. Nutrient-rich litter further stimulates carbon incorporation in soil by ecosystem engineers, especially earthworms and termites (Lavelle *et al.* 1997; Eggleton & Tayasu 2001). Increased soil incorporation of surface litter may further reduce carbon loss through reduced probability of intense forest fires, which also in rainforests cause huge carbon losses (Cochrane 2003).

Except for forest areas with very high tree diversity, most of the standing carbon stock is often attributed to relatively few, tall and dense-wooded species (Ter Steege *et al.* 2006). However, trait complementarity in light and aboveground water and nutrient interception, e.g. by overstory plants and the species inhabiting forest canopies such as epiphytes and lianas or understory vegetation, may increase soil carbon and nutrient input quantity and quality (Santiago & Wright 2007). Also, trait compositions that enhance nutrient uptake, especially of P (e.g. through diverse associations with arbuscular mycorrhizal fungi), may enhance the quantity of soil carbon input. As in other forest biomes, reduced carbon loss can be attained by trait compositions that promote protection of plants from tissue loss (e.g. diverse defences) and that optimize regeneration after tissue loss (e.g. rapid regrowth or seeding). Many of such plant traits trade off against each other in individual plants, but can be unified and maintained at plant community level (Johnson & Stinchcombe 2007). In tropical forests, reproduction and thus regeneration of many plant species strongly depend on specialist pollinators and seed dispersers, which may require a set of resources only provided by functionally diverse plant communities (Mayfield *et al.* 2006). To date, the impact of species loss for SOC storage in tropical forests is largely unknown, but simulation studies on aboveground carbon stocks indicate that especially shifts in species composition, and hence trait composition, will have strong effects (Bunker *et al.* 2005).

Overall, carbon pools in tropical forests are large and diverse, due to the variety of growth forms and canopy complexity, especially in humid systems. Rates of carbon cycling are high due to favourable climatic conditions for plant growth and, at least in mesic soils, litter decomposition (Aerts & Chapin 2000; Chapin 2003). Increases in SOC sequestration may thus be achieved by minimizing soil carbon loss and enhanced incorporation of carbon in the soil profile, through deep-rooting, association with mycorrhizal fungi and stimulation of ecosystem engineers. Short-term carbon losses through disturbances, such as small fires and local windthrows, may partly be compensated by the stimulation of sequestration in the long term by creating regeneration niches, charcoal and release of mineral nutrients. Essential plant traits to buffer against long-term net carbon loss at the community level will thus be a combination of traits that enable resistance to disturbance, persistence until canopy opening and resilience through quick recovery and use of freed-up resources.

Grassland

Grasslands occur over a wide range of temperature zones, where seasonal droughts and fire, or regular removal of aboveground plant biomass by grazing or mowing prevent

forest development (Bond *et al.* 2005). The relative importances of factors that regulate carbon sequestration vary between temperate and tropical grassland systems, and are therefore discussed separately.

Temperate grassland

Temperate grasslands occur at lower average temperatures than tropical savannas and are mainly composed by C3 and C4 grasses and C3 forbs and shrubs. The prevalence of plant traits that drive carbon input quantity and quality, such as growth rate, litter C : N ratio and lignin content, strongly depend on water and nutrient availability and herbivory. Generally, when water or nutrients are limiting plant growth, slow-growing species with poor quality litter and high root to shoot ratio dominate, hence carbon cycling is slow and SOC builds up (Aerts & Chapin 2000; Tjoelker *et al.* 2005). In temperate grasslands, herbivory strongly affects carbon loss through defoliation and priming of SOC (Bardgett & Wardle 2003). Carbon loss to herbivores, however, depends both on plant and on herbivore traits, i.e. their selectivity and grazing pressure. Hence, different plant traits may reduce carbon loss to herbivores through escape (e.g. prostrate growth form), deterrence (structural or chemical defences) or traits that enable regrowth after herbivore damage (Diaz *et al.* 2006). Hemiparasitic plants, which typically suppress the growth of fast-growing graminoids, also have the potential to strongly affect soil carbon storage in grassland by altering both the quantity and quality of carbon input to soil, and ultimately the activity of the soil microflora (Bardgett *et al.* 2006).

Ecosystem engineers are of particular importance for grassland productivity and carbon sequestration, by promoting carbon occlusion in soil aggregates and by mineralizing nutrients and enhancing soil structure. Carbon sequestration through these interactions can be promoted through high plant litter quality for earthworms and ants, as provided by grassland forbs and legumes (Cornelissen & Thompson 1997). Also, other plant traits that determine food quality for ecosystem engineers, for example, quality of seeds, nectar and aphid honeydew, may be significant for ant-mediated carbon sequestration.

In temperate grasslands, primary productivity is mostly constrained by N and/or P availability. Composition of nutrient use traits, e.g. root architecture, root phenology or association with different mutualist symbionts, such as N-fixers and species of arbuscular mycorrhizal fungi, can strongly affect carbon input quantity. Complementarity (van der Heijden *et al.* 1998; Allen *et al.* 2003) and facilitation in such traits (van Groenigen *et al.* 2006) can enhance carbon inputs significantly. Reductions in carbon loss through herbivory may result from selective grazing, which may promote plant traits typical for slow and conservative carbon and nutrient cycling (Bardgett & Wardle 2003).

Overall, temperate grasslands have high SOC concentrations, often exceeding that in temperate forests (Amundson 2001; Fig. 3). Carbon pools in aboveground vegetation are small relative to that in soil (King *et al.* 1997), due to high belowground carbon allocation, the virtual absence of persistent woody structures aboveground, and generally higher decomposability of shoot than root tissue (Aerts & Chapin 2000; Lauenroth & Gill 2003).

Tropical savanna

Tropical savannas occur at latitudes with annual temperatures of 20 °C or higher, hot, wet summers and cool, dry winters. Savannas are primarily composed by C4 grasses and C3 shrubs and trees, and the net soil carbon input is mainly constrained by low water availability and large carbon losses to herbivory and fire. Given the strong impact of shrub encroachment on carbon SOC and the sensitivity of shrub and tree seedlings to grazing, plant traits that may promote soil carbon sequestration comprise deep rooting, production of woody structures and herbivore defence traits (Jobbagy & Jackson 2000; Ehrenfeld *et al.* 2005). Carbon loss to fire can be reduced by traits of fire resistance (bark thickness, wood density, lignin concentration and litter build-up) and fire resilience (fire tolerant seeds, resprouting, germination and seedling growth ability after fire), which reduce fire intensity and frequency and maximize carbon input after fire. Presence of these traits may not be unifiable at individual level but can be at community level (Bond *et al.* 2005).

In arid grasslands, ecosystem engineers such as termites can promote soil carbon sequestration through mixing soil organic and mineral fractions, thereby not only increasing carbon occlusion in aggregates, but also enhancing water retention. High litter quality for termites, i.e. low C : N ratio and adequate litter fragment size (Eggleton & Taysu 2001), is therefore likely very important for enhancing SOC sequestration and alleviating plant water stress in savannas. Enhanced water retention and water use efficiency may also be achieved through more direct and more specific plant associations with mycorrhizal fungi (Smith & Read 1997).

Plant trait composition may influence soil carbon input through community water use, where diverging root distributions may promote water use complementarity. Efficient use of nutrients and precipitation is down to traits that govern adequate root and canopy structure and physiology (Hunt & Colasanti 2007), which may be enhanced further by association with mutualist symbionts, such as N-fixers and mycorrhizal fungi. The contribution of N-fixing bacteria to plant productivity, and hence carbon input to soil, is especially important in tropical savanna where they contribute up to 20% of all plant N that is annually acquired by vegetation (Cleveland *et al.* 1999; van der Heijden *et al.* 2008).

Overall, savanna soils have lower carbon content compared with temperate grasslands (Fig. 3), due to more favourable temperatures for carbon mineralization (Davidson & Janssens 2006). Savanna vegetation is, however, deeper rooting than temperate grassland and as climate acts most strongly on carbon loss in the top soil, total soil profile SOC pools may be underestimated (Jobbagy & Jackson 2000; Schenk & Jackson 2002a). Water availability, fire and grazing are major controls of carbon input quantity and quality in grassland; hence traits that may promote carbon sequestration comprise traits that govern resistance and resilience to drought, fire and grazing and promote ecosystem engineers.

Desert

Deserts form across temperature zones where soil moisture restricts plant growth (Prentice *et al.* 1992; Fig. 3). Here, traits that enable the survival and growth under the extreme precipitation and temperature regimes, through opportunistic or persistence strategies (Ogle & Reynolds 2004), and traits that govern carbon distribution through the soil profile (Jobbagy & Jackson 2000; Schenk & Jackson 2002b) directly impact on SOC sequestration through primary productivity and carbon stabilization in soil.

Traits of litter quality vary from highly decomposable, in short-lived species with high nutrient content, to mostly poor, in longer-lived species with woody and leathery tissue, high C : N ratios and/or high wax content (Kemp *et al.* 2003). Generally, most litter is of recalcitrant form and given low soil moisture and soil fertility carbon loss through biotic decomposition is slow. However, carbon loss through abiotic mineralization (on the surface or often still attached to the plants) driven by solar radiation and mechanical forces (e.g. sand storms) is considerable (Austin & Vivanco 2006). In arid systems, plant traits that enhance resistance to oxidation through solar radiation, such as the quantity and quality of waxes (Arriaga & Maya 2007) and UV-protecting phenolic compounds (Zepp *et al.* 2007), may thus be very important for reducing carbon loss. At community level, potentially important traits comprise the protection of surface litter from solar radiation, such as canopy structure or enhanced incorporation of surface litter into soil by ecosystem engineers, through favourable litter quality and environmental conditions, especially for termites (Lavelle *et al.* 1997).

In deserts, trait complementarity and facilitation in water use and in protection from drought and solar radiation are most likely to enhance soil carbon sequestration (Schenk & Jackson 2002b). Traits that enable opportunistic use of precipitation events, for example, through quick growth and reproduction, and survival of drought periods through dormancy, as found in annual species, may complement plants with persistent traits, as found in xerophytes, which

enable the survival and growth through water storage or restricted water loss, or prevent overheating or damage from abrasion by sand blows. Amongst xerophytes, trait composition in terms of rooting depth and canopy structure is important; divergence in these traits could lead to complementarity or facilitation of smaller by taller species, through the interception of precipitation, litter and thus nutrient input and protection from UV damage. A structurally diverse canopy may also reduce carbon loss through reduced abiotic mineralization by shading and, together with improved litter quality, by enhancing the ecosystem engineer activity (Arriaga & Maya 2007).

Overall, SOC pools in deserts are very small, yet surprisingly high in cold deserts, explained by historic and exogenous carbon input, low soil and plant respiration rates and high abundance of microbes with low activity (Wardle 1992), while also in warm deserts carbon in soil exceeds carbon stored in vegetation (King *et al.* 1997). A key feature of deserts is the highly heterogeneous distribution of carbon in space and time and therefore the importance of specific plant traits, but generally deep-rooting and slow-decomposing roots and the incorporation of surface litter by termites are major pathways of soil carbon input (Arriaga & Maya 2007).

SYNTHESIS AND FURTHER RESEARCH NEEDS

Plant traits that drive carbon sequestration mainly operate through high primary productivity (high carbon input quantity) or slow decomposition (low carbon output) routes that generally appear to trade-off at the level of individuals (Aerts & Chapin 2000). Across biomes, environmental factors select for plant traits that enable plant persistence in specific regimes of temperature, precipitation and light availability. Generally, where soil resources (nutrients, water, oxygen, pH) limit growth, plant traits that govern carbon and nutrient conservation dominate: slow growth, high C : N and root : shoot ratios, high secondary metabolite content, long (organ) lifespan and long litter residence time. In contrast, plants with opposite traits dominate under favourable soil, but light limiting conditions. Plant associations with soil organisms are crucial for supporting carbon input from primary productivity as well as for carbon output and carbon stabilization in soil. Carbon cycling traits of soil biota directly relate to plant traits through host suitability (symbionts), and indirectly through plant litter quality and modification of abiotic soil conditions (temperature, moisture, aeration and pH). Soil carbon sequestration is enhanced by maximizing the balance between soil carbon input and output, hence by carbon use efficiency of decomposers and of mineralized nutrients by plants, and by improved interaction between organic and mineral soil fractions throughout the soil profile (via deep rooting and

ecosystem engineers). In fire prone and grazed systems, traits that reduce carbon and nutrient loss through these disturbances are also favoured.

Clearly many plant traits are relevant to soil carbon sequestration through a variety of pathways, but traits of individual plants are often conflicting: high input quantity and fast nutrient mineralization trade off with short carbon residence times; long carbon residence time of poor quality litter trades off with low nutrient mineralization and poor litter incorporation. However, at the community level, traits that promote nutrient availability and support primary productivity can be combined with traits that promote soil carbon stabilization through slow decomposition and incorporation to mineral soil. This depends on the co-existence of species with different growth rates, e.g. through patchy resource distribution, disturbances or differential trait combinations of above vs. belowground structures (Personeni & Loiseau 2004; Hooper *et al.* 2005).

We still know remarkably little about the links between aboveground and belowground plant traits and soil biota to be able to make accurate predictions about their impact on soil carbon sequestration, or their response to global change. We therefore propose seven key research challenges that require further investigation:

- (1) Aboveground and belowground plant traits involved in carbon cycling appear to be weakly coupled, which is a major drawback for modelling and predicting global carbon cycling (Owen *et al.* 2007). Therefore, we need to identify easily measurable, cost-effective, aboveground traits that capture belowground carbon dynamics across different spatial and temporal scales.
- (2) Conceptual carbon pools used in models are not directly measurable, because current methodologies are unable to selectively isolate functional carbon pools with specific residence times and stabilization mechanisms (von Lützow *et al.* 2007). Enhanced mechanistic understanding of the coupling between plant traits and soil biotic traits can aid bridging between concepts and practice by providing a framework for newly developing techniques, such as compound tracing, aimed at identifying functional soil carbon pools.
- (3) We need long-term carbon-tracing experiments, especially in under-investigated biomes, because soil carbon sequestration is a 'fast-out, slow-in' process with high variation due to regulation by environmental factors (Schulze 2006).
- (4) We need to be open to yet undiscovered plant traits and pathways of carbon flow, especially with respect to soil biota (Zak *et al.* 2006).
- (5) Under-investigated carbon pathways, such as VOCs produced above- and belowground, may prove important components of carbon cycling; a mechanistic understanding of their inter-dependency with other plant traits is warranted.
- (6) Traits of carbon sequestration are governed by the expression of genes in structured communities (Zak *et al.* 2006). Hence, a mechanistic understanding of ecosystem carbon sequestration requires the understanding of traits and trade-offs across trophic levels, bridging the expression of genes to ecosystem processes in space and feedback time.
- (7) Global changes impact upon carbon cycling pathways, but to date these have only been studied in few biomes. Therefore, we need to identify the impact of climatic and human driven changes on the various carbon cycling processes in all biomes. We propose that a trait-based framework can provide a common platform for empirical and theoretical carbon cycling research across them.

ACKNOWLEDGEMENTS

We are grateful to Ian Dicky for thoughtful comments on earlier figures. We also thank the three anonymous referees and James Grace whose comments helped to improve this manuscript. The UK BBSRC Agri-Food Committee provided financial support for this work.

REFERENCES

- Aerts, R. & Chapin, F.S. III (2000). The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Adv. Ecol. Res.*, 30, 1–67.
- Allen, M.F., Swenson, W., Querejeta, J.I., Egerton-Warburton, L.M. & Treseder, K.K. (2003). Ecology of mycorrhizae: a conceptual framework for complex interactions among plants and fungi. *Annu. Rev. Phytopathol.*, 41, 271–303.
- Amundson, R. (2001). The carbon budget in soils. *Annu. Rev. Earth Planet. Sci.*, 29, 535–562.
- Arriaga, L. & Maya, Y. (2007). Spatial variability in decomposition rates in a desert scrub of Northwestern Mexico. *Plant Ecol.*, 189, 213–225.
- Austin, A.T. & Vivanco, L. (2006). Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. *Nature*, 442, 555–558.
- Bardgett, R.D. & Wardle, D.A. (2003). Herbivore-mediated linkages between aboveground and belowground communities. *Ecology*, 84, 2258–2268.
- Bardgett, R.D., Streeter, T. & Bol, R. (2003). Soil microbes compete effectively with plants for organic nitrogen inputs to temperate grasslands. *Ecology*, 84, 1277–1287.
- Bardgett, R.D., Bowman, W.D., Kaufmann, R. & Schmidt, S.K. (2005). A temporal approach to linking aboveground and belowground ecology. *Trends Ecol. Evol.*, 20, 634–641.
- Bardgett, R.D., Smith, R.S., Shiel, R.S., Peacock, S., Simkin, J.M., Quirk, H. *et al.* (2006). Parasitic plants indirectly regulate belowground properties in grassland ecosystems. *Nature*, 439, 969–972.

- de Boer, W., Folman, L.B., Summerbell, R.C. & Boddy, L. (2005). Living in a fungal world: impact of fungi on soil bacterial niche development. *FEMS Microbiol. Rev.*, 29, 795–811.
- Bohlen, P.J., Scheu, S., Hale, C.M., McLean, M.A., Migge, S., Groffman, P.M. *et al.* (2004). Non-native invasive earthworms as agents of change in northern temperate forests. *Front. Ecol. Evol. Environ.*, 2, 427–435.
- Bond, W.J., Woodward, F.I. & Midgley, G.F. (2005). The global distribution of ecosystems in a world without fire. *New Phytol.*, 165, 525–538.
- Bunker, D.E., DeClerck, F., Bradford, J.C., Colwell, R.K., Perfecto, I., Phillips, O.L. *et al.* (2005). Species loss and aboveground carbon storage in a tropical forest. *Science*, 310, 1029–1031.
- Chapin, F.S. (2003). Effects of plant traits on ecosystem and regional processes: a conceptual framework for predicting the consequences of global change. *Ann. Bot.*, 91, 455–463.
- Cleveland, C.C., Townsend, A.R., Schimel, D.S., Fisher, H., Howarth, R.W., Hedin, L.O. *et al.* (1999). Global patterns of terrestrial biological nitrogen (N₂) fixation in natural ecosystems. *Global Biogeochem. Cycles*, 13, 623–645.
- Cochrane, M.A. (2003). Fire science for rainforests. *Nature*, 421, 913–919.
- Cornelissen, J.H.C. & Thompson, K. (1997). Functional leaf attributes predict litter decomposition rate in herbaceous plants. *New Phytol.*, 135, 109–114.
- Cornelissen, J.H.C., Aerts, R., Cerabolini, B., Werger, M.J.A. & van der Heijden, M.G.A. (2001). Carbon cycling traits of plant species are linked with mycorrhizal strategy. *Oecologia*, 129, 611–619.
- Cornelissen, J.H.C., Lang, S.I., Soudzilovskaia, N.A. & During, H.J. (2007a). Comparative cryptogam ecology: a review of bryophyte and lichen traits that drive biogeochemistry. *Ann. Bot.*, 99, 987–1001.
- Cornelissen, J.H.C., van Bodegom, P.M., Aerts, R., Callaghan, T.V., van Logtestijn, R.S.P., Alatalo, J. *et al.* (2007b). Global negative feedback to climate warming responses of leaf litter decomposition rates in cold biomes. *Ecol. Lett.*, 10, 619–627.
- Craine, J.M., Lee, W.G., Bond, W.J., Williams, R.J. & Johnson, L.C. (2005). Environmental constraints on a global relationship among leaf and root traits of grasses. *Ecology*, 86, 12–19.
- Davidson, E.A. & Janssens, I.A. (2006). Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*, 440, 165–173.
- Diaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanovess, F., Milchunas, D.G. *et al.* (2006). Plant trait response to grazing – a global synthesis. *Glob. Chang. Biol.*, 12, 1–29.
- Dijkstra, F.A. & Cheng, W.X. (2007). Interactions between soil and tree roots accelerate long-term soil carbon decomposition. *Ecol. Lett.*, 10, 1046–1053.
- Dijkstra, F.A., Hobbie, S.E. & Reich, P.B. (2006). Soil processes affected by sixteen grassland species grown under different environmental conditions. *Soil Sci. Soc. Am. J.*, 70, 770–777.
- Eggleton, P. & Tayasu, I. (2001). Feeding groups, lifetypes and the global ecology of termites. *Ecol. Res.*, 16, 941–960.
- Ehrenfeld, J.G., Ravit, B. & Elgersma, K. (2005). Feedback in the plant-soil system. *Annu. Rev. Environ. Resour.*, 30, 75–115.
- Eviner, V.T. & Chapin, F.S. (2003). Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. *Annu. Rev. Ecol. Evol. Syst.*, 34, 455–485.
- Fontaine, S. & Barot, S. (2005). Size and functional diversity of microbe populations control plant persistence and long-term soil carbon accumulation. *Ecol. Lett.*, 8, 1075–1087.
- Gartner, T.B. & Cardon, Z.G. (2004). Decomposition dynamics in mixed-species leaf litter. *Oikos*, 104, 230–246.
- van Groenigen, K.J., Six, J., Hungate, B.A., de Graaff, M.A., van Breemen, N. & van Kessel, C. (2006). Element interactions limit soil carbon storage. *Proc. Natl. Acad. Sci. U.S.A.*, 103, 6571–6574.
- Hättenschwiler, S. & Vitousek, P.M. (2000). The role of polyphenols in terrestrial ecosystem nutrient cycling. *Trends Ecol. Evol.*, 15, 238–243.
- Hättenschwiler, S., Tiunov, A.V. & Scheu, S. (2005). Biodiversity and litter decomposition in terrestrial ecosystems. *Annu. Rev. Ecol. Evol. Syst.*, 36, 191–218.
- van der Heijden, M.G.A., Klironomos, J.N., Ursic, M., Moutoglou, P., Streitwolf-Engel, R., Boller, T. *et al.* (1998). Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature*, 396, 69–72.
- van der Heijden, M.G.A., Bardgett, R.D. & van Straalen, N.M. (2008). The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecol. Lett.*, 11, 296–310.
- Hobbie, S.E. (1996). Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecol. Monogr.*, 66, 503–522.
- Högberg, M.N. & Högberg, 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, D.J. (2006). Towards a more plant physiological perspective on soil ecology. *Trends Ecol. Evol.*, 21, 548–554.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S. *et al.* (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.*, 75, 3–35.
- Hunt, R. & Colasanti, R.L. (2007). Self-assembling plants and integration across ecological scales. *Ann. Bot.*, 99, 1023–1034.
- Inderjit & Weston, L.A. (2003). Root exudates: an overview. In: *Root Ecology* (eds de Kroon, H. & Visser, E.J.W.). Ecological Studies, 168. Springer, Berlin, pp. 235–255.
- Jackson, R.B., Canadell, J., Ehleringer, J.R., Mooney, H.A., Sala, O.E. & Schulze, E.D. (1996). A global analysis of root distributions for terrestrial biomes. *Oecologia*, 108, 389–411.
- Jobbagy, E.G. & Jackson, R.B. (2000). The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecol. Appl.*, 10, 423–436.
- Johnson, M.T.J. & Stinchcombe, J.R. (2007). An emerging synthesis between community ecology and evolutionary biology. *Trends Ecol. Evol.*, 22, 250–257.
- Kemp, P.R., Reynolds, J.F., Virginia, R.A. & Whitford, W.G. (2003). Decomposition of leaf and root litter of Chihuahuan desert shrubs: effects of three years of summer drought. *J. Arid Envi.*, 53, 21–29.
- Kesselmeier, J., Ciccioli, P., Kuhn, U., Stefani, P., Biesenthal, T., Rottenberger, S. *et al.* (2002). Volatile organic compound emissions in relation to plant carbon fixation and the terrestrial carbon budget. *Global Biogeochem. Cycles*, 16, 4, Art. no. 1156.

- Kielland, K., McFarland, J. & Olson, K. (2006). Amino acid uptake in deciduous and coniferous taiga ecosystems. *Plant Soil*, 288, 297–307.
- Kiers, E.T. & van der Heijden, M.G.A. (2006). Mutualistic stability in the arbuscular mycorrhizal symbiosis: exploring hypotheses of evolutionary cooperation. *Ecology*, 87, 1627–1636.
- King, A.W., Post, W.M. & Wullschlegel, S.D. (1997). The potential response of terrestrial carbon storage to changes in climate and atmospheric CO₂. *Clim. Change*, 35, 199–227.
- Kuzyakov, Y. (2006). Sources of CO₂ efflux from soil and review of partitioning methods. *Soil Biol. Biochem.*, 38, 425–448.
- Lambers, H., Scheurwater, I., Mata, C. & Nagel, O.W. (1998). Root respiration of fast- and slow-growing plants, as dependent on genotype and nitrogen supply: a major clue to the functioning of slow-growing plants. In: *Inherent Variation in Plant Growth, Physiological Mechanisms and Ecological Consequences* (eds Lambers, H., Poorter, H. & Van Vuren, M.). Backhuys Publishers, Leiden, pp. 139–157.
- Langley, J.A., Chapman, S.K. & Hungate, B.A. (2006). Ectomycorrhizal colonization slows root decomposition: the post-mortem fungal legacy. *Ecol. Lett.*, 9, 955–959.
- Lauenroth, W.K. & Gill, R. (2003). Turnover of root systems. In: *Root Ecology* (eds de Kroon, H. & Visser, E.J.W.). Ecological Studies, 168. Springer, Berlin, pp. 61–89.
- Lavelle, P., Bignell, D., Lepage, M., Wolters, V., Roger, P., Ineson, P. *et al.* (1997). Soil function in a changing world: the role of invertebrate ecosystem engineers. *Eur. J. Soil Biol.*, 33, 159–193.
- Lavorel, S., Díaz, S., Cornelissen, J.H.C., Garnier, E., Harrison, S.P., McIntyre, S. *et al.* (2007). Plant functional types: are we getting any closer to the Holy Grail? In: *Terrestrial Ecosystems in a Changing World* (eds Canadell, J., Pitelka, L.F. & Pataki, D.). Springer, Berlin, pp. 171–186.
- Lin, C., Owen, S.M. & Penuelas, J. (2007). Volatile organic compounds in the roots and rhizosphere of *Pinus* spp.. *Soil Biol. Biochem.*, 39, 951–960.
- Lindahl, B.D., Ihrmark, K., Boberg, J., Trumbore, S.E., Höglberg, P., Stenlid, J. *et al.* (2007). Spatial separation of litter decomposition and mycorrhizal nitrogen uptake in a boreal forest. *New Phytol.*, 173, 611–620.
- Lorenz, K. & Lal, R. (2005). The depth distribution of soil organic carbon in relation to land use and management and the potential of carbon sequestration in subsoil horizons. *Adv. Agron.*, 88, 35–66.
- von Lützow, M., Kögel-Knabner, I., Ekschmitt, K., Flessa, H., Guggenberger, G., Matzner, E. *et al.* (2007). SOM fractionation methods: relevance to functional pools and to stabilization mechanisms. *Soil Biol. Biochem.*, 39, 2183–2207.
- Mack, M.C., Schuur, E.A.G., Bret-Harte, M.S., Shaver, G.R. & Chapin, F.S. III (2004). Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature*, 431, 440–443.
- Matamala, R., Gonzalez-Meler, M.A., Jastrow, J.D., Norby, R.J. & Schlesinger, W.H. (2003). Impacts of fine root turnover on forest NPP and soil C sequestration potential. *Science*, 302, 1385–1387.
- Mayfield, M.M., Ackerly, D. & Daily, G.C. (2006). The diversity and conservation of plant reproductive and dispersal functional traits in human-dominated tropical landscapes. *J. Ecol.*, 94, 522–536.
- Mencuccini, M., Martinez-Vilalta, J., Hamid, H.A., Korakaki, E. & Vanderklein, D. (2007). Evidence for age- and size-mediated controls of tree growth from grafting studies. *Tree Physiol.*, 27, 463–473.
- Nilsson, M.C. & Wardle, D.A. (2005). Understorey vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. *Front. Ecol. Environ.*, 3, 421–428.
- Ogle, K. & Reynolds, J.F. (2004). Plant responses to precipitation in desert ecosystems: integrating functional types, pulses, thresholds, and delays. *Oecologia*, 141, 282–294.
- Olf, H., Vera, F.W.M., Bokdam, J., Bakker, E.S., Gleichman, J.M., de Maeyer, K. *et al.* (1999). Shifting mosaics in grazed woodlands driven by the alternation of plant facilitation and competition. *Plant Biol.*, 1, 127–137.
- Owen, K.E., Tenhunen, J., Reichsten, M., Wang, Q., Falge, E., Geyer, R. *et al.* (2007). Linking flux network measurements to continental scale simulations: ecosystem carbon dioxide exchange capacity under non-water-stressed conditions. *Glob. Chang. Biol.*, 13, 734–760.
- Personeni, E. & Loiseau, P. (2004). How does the nature of living and dead roots affect the residence time of carbon in the root litter continuum? *Plant Soil*, 267, 129–141.
- Pollierer, M.M., Langel, R., Korner, C., Maraun, M. & Scheu, S. (2007). The underestimated importance of belowground carbon input for forest soil animal food webs. *Ecol. Lett.*, 10, 729–736.
- Porazinska, D.L., Bardgett, R.D., Blaauw, M.B., Hunt, W.H., Parsons, A., Seastedt, T.R. *et al.* (2003). Relationships at the aboveground-belowground interface: plants, soil microflora and microfauna, and soil processes. *Ecol. Monogr.*, 73, 377–395.
- Pregitzer, K.S., Burton, A.J., Zak, D.R. & Talhelm, A.F. (2008). Simulated chronic nitrogen deposition increases carbon storage in northern temperate forests. *Glob. Chang. Biol.*, 14, 142–153.
- Prentice, I.C., Cramer, W., Harisson, S.P., Leemans, R., Monsrud, R.A. & Solomon, A.M. (1992). A global biome model based on plant physiology and dominance, soil properties and climate. *J. Biogeogr.*, 19, 117–134.
- Preston, C.M. & Schmidt, M.W.I. (2006). Black (pyrogenic) carbon: a synthesis of current knowledge and uncertainties with special consideration of boreal regions. *Biogeosciences*, 3, 397–420.
- Quested, H.M., Press, M.C. & Callaghan, T.V. (2003). Litter of the hemiparasite *Bartsia alpina* enhances plant growth: evidence for a functional role in nutrient cycling. *Oecologia*, 135, 606–614.
- Read, D.J. & Perez-Moreno, J. (2003). Mycorrhizas and nutrient cycling in ecosystems – a journey towards relevance? *New Phytol.*, 157, 475–492.
- Reich, P.B., Oleksyn, J., Modrzyński, J., Mrozinski, P., Hobbie, S.E., Eissenstat, D.M. *et al.* (2005). Linking litter calcium, earthworms and soil properties: a common garden test with 14 tree species. *Ecol. Lett.*, 8, 811–818.
- Rillig, M.C. & Mummey, D.L. (2006). Mycorrhizas and soil structure. *New Phytol.*, 171, 41–53.
- Rustad, L.E. (2006). From transient to steady-state response of ecosystems to atmospheric CO₂-enrichment and global climate change: conceptual challenges and need for an integrated approach. *Plant Ecol.*, 182, 43–62.
- Santiago, L.S. & Wright, S.J. (2007). Leaf functional traits of tropical forest plants in relation to growth form. *Funct. Ecol.*, 21, 19–27.

- Schenk, H.J. & Jackson, R.B. (2002a). The global biogeography of roots. *Ecol. Monogr.*, 72, 311–328.
- Schenk, H.J. & Jackson, R.B. (2002b). Rooting depths, lateral spreads, and below-ground/above-ground allometries of plants in water-limited ecosystems. *J. Ecol.*, 90, 480–494.
- Schieving, F. & Poorter, H. (1999). Carbon gain in a multispecies canopy: the role of specific leaf area and photosynthetic nitrogen-use efficiency in the tragedy of the commons. *New Phytol.*, 143, 201–211.
- Schimel, J.P. & Bennett, J. (2004). Nitrogen mineralization: challenges of a changing paradigm. *Ecology*, 85, 591–602.
- Schulze, E.D. (2006). Biological control of the terrestrial carbon sink. *Biogeosciences*, 3, 147–166.
- Silver, W.L. & Miya, R.K. (2001). Global patterns in root decomposition: comparisons of climate and litter quality effects. *Oecologia*, 129, 407–419.
- Sitch, S., Smith, B., Prentice, I.C., Arneth, A., Bondeau, A., Cramer, W. *et al.* (2003). Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Glob. Chang. Biol.*, 9, 161–185.
- Six, J., Frey, S.D., Thiet, R.K. & Batten, K.M. (2006). Bacterial and fungal contributions to carbon sequestration in agroecosystems. *Soil Sci. Soc. Am. J.*, 70, 555–569.
- Smith, S.E. & Read, D.J. (1997). *Mycorrhizal Symbiosis*, 2nd edn. Cambridge University Press, London.
- Steinmann, K.T.W., Siegwolf, R., Saurer, M. & Körner, C. (2004). Carbon fluxes to the soil in a mature temperate forest assessed by C-13 isotope tracing. *Oecologia*, 141, 489–501.
- Striker, G.G., Insausti, P., Grimoldi, A.A. & Vega, A.S. (2007). Trade-off between root porosity and mechanical strength in species with different types of aerenchyma. *Plant Cell Environ.*, 30, 580–589.
- Ström, L., Ekberg, A., Mastepanov, M. & Christensen, T.R. (2003). The effect of vascular plants on carbon turnover and methane emissions from a tundra wetland. *Glob. Chang. Biol.*, 9, 1185–1192.
- Ter Steege, H., Pitman, N.C.A., Phillips, O.L., Chave, J., Sabatier, D., Duque, A. *et al.* (2006). Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature*, 443, 444–447.
- Tjoelker, M.G., Craine, J.M., Wedin, D., Reich, P.B. & Tilman, D. (2005). Linking leaf and root trait syndromes among 39 grassland and savannah species. *New Phytol.*, 167, 493–508.
- Vessey, J.K., Pawlowski, K. & Bergman, B. (2005). Root-based N-2-fixing symbioses: legumes, actinorhizal plants, *Parasponia* sp. and cycads. *Plant Soil*, 274, 51–78.
- Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. *et al.* (2007). Let the concept of trait be functional! *Oikos*, 116, 882–892.
- Waldrop, M.P. & Zak, D.R. (2006). Response of oxidative enzyme activities to nitrogen deposition affects soil concentrations of dissolved organic carbon. *Ecosystems*, 9, 921–933.
- Wallander, H., Nilsson, L.O., Hagerberg, D. & Rosengren, U. (2003). Direct estimates of C:N ratios of ectomycorrhizal mycelia collected from Norway spruce forest soils. *Soil Biol. Biochem.*, 35, 997–999.
- Wardle, D.A. (1992). A comparative assessment of factors which influence microbial biomass carbon and nitrogen levels in soil. *Biol. Rev. Camb. Philos. Soc.*, 67, 321–358.
- Wardle, D.A. (2006). The influence of biotic interactions on soil biodiversity. *Ecol. Lett.*, 9, 870–886.
- Wardle, D.A. & Zackrisson, O. (2005). Effects of species and functional group loss on island ecosystem properties. *Nature*, 435, 806–810.
- Wardle, D.A., Barker, G.M., Bonner, K.I. & Nicholson, K.S. (1998). Can comparative approaches based on plant ecophysiological traits predict the nature of biotic interactions and individual plant species effects in ecosystems? *J. Ecol.*, 86, 405–420.
- Warembourg, F.R., Roumet, C. & Lafont, F. (2003). Differences in rhizosphere carbon-partitioning among plant species of different families. *Plant Soil*, 256, 347–357.
- Whitham, T.G., Bailey, J.K., Schweitzer, J.A., Shuster, S.M., Bangert, R.K., Leroy, C.J. *et al.* (2006). A framework for community and ecosystem genetics: from genes to ecosystems. *Nat. Rev. Genet.*, 7, 510–523.
- Woodward, F.I., Lomas, M.R. & Kelly, C.K. (2004). Global climate and the distribution of plant biomes. *Proc. R. Soc. Lond., B, Biol. Sci.*, 359, 1465–1476.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F. *et al.* (2004). The worldwide leaf economics spectrum. *Nature*, 428, 821–827.
- Zak, D.R., Blackwood, C.B. & Waldrop, M.P. (2006). A molecular dawn for biogeochemistry. *Trends Ecol. Evol.*, 21, 288–295.
- Zepp, R.G., Erickson, D.J., Paul, N.D. & Sulzberger, B. (2007). Interactive effects of solar UV radiation and climate change on biogeochemical cycling. *Photochem. Photobiol. Sci.*, 6, 286–300.

Editor, James Grace

Manuscript received 14 January 2008

Manuscript accepted 15 January 2008