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# Carbon allocation and carbon isotope fluxes in the plant-soil-atmosphere continuum: a review

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## Abstract

The terrestrial carbon (C) cycle has received increasing interest over the past few decades, however, there is still a lack of understanding of the fate of newly assimilated C allocated within plants and to the soil, stored within ecosystems and lost to the atmosphere. Stable carbon isotope studies can give novel insights into these issues. In this review we provide an overview of an emerging picture of plant-soil-atmosphere C fluxes, as based on C isotope studies, and identify processes determining related C isotope signatures. The first part of the review focuses on isotopic fractionation processes within plants during and after photosynthesis. The second major part elaborates on plant-internal and plant-rhizosphere C allocation patterns at different time scales (diel, seasonal, interannual), including the speed of C transfer and time lags in the coupling of assimilation and respiration, as well as the magnitude and controls of plant-soil C allocation and respiratory fluxes. Plant responses to changing environmental conditions, the functional relationship between the physiological and phenological status of plants and C transfer, and interactions between C, water and nutrient dynamics are discussed. The role of the C counterflow from the rhizosphere to the aboveground parts of the plants, e.g. via $CO_2$ dissolved in the xylem water or as xylem-transported sugars, is highlighted. The third part is centered around belowground C turnover, focusing especially on above- and belowground litter inputs, soil organic matter formation and turnover, production and loss of dissolved organic C, soil respiration and $CO_2$ fixation by soil microbes. Furthermore, plant controls on microbial communities and activity via exudates and litter production as well as microbial community effects on C mineralization are reviewed. The last part of the paper is dedicated to physical interactions between soil $CO_2$ and the soil matrix, such as $CO_2$ diffusion and dissolution processes within the soil profile. From the presented evidence we conclude that there exists a tight coupling of physical, chemical and biological processes involved in C cycling and C isotope fluxes in the plant-soil-atmosphere system. Generally, research using information from C isotopes allows an integrated view of the different processes

involved. However, complex interactions among the range of processes complicate or impede the interpretation of isotopic signals in $CO_2$ or organic compounds at the plant and ecosystem level. This is where new research approaches should be aimed at.

## 1 Introduction

The flux of carbon dioxide between the atmosphere and the terrestrial biosphere and back is ≈15–20 times larger than the anthropogenic release of $CO_2$ (IPCC, 2007). This large bidirectional biogenic $CO_2$ flux has a significant imprint on the carbon isotope signature of atmospheric $CO_2$ (Randerson et al., 2002), which in turn helps to understand the controls of $CO_2$ fluxes and to predict how they will respond to global change. There is a lack of knowledge on how plant physiological as well as soil biological, physical and chemical processes interact with and affect ecosystem processes, such as net ecosystem primary production and carbon sequestration as well as the larger scale carbon balance. The vegetation is not only the original source of soil organic matter, thus contributing to long-term carbon accumulation in the organic soil layers, but it also determines belowground processes such as soil respiration over the short term through transport of photosynthates to the roots and to the soil (Bahn et al., 2010; Mencuccini and Hölttä, 2010a; Högberg et al., 2010). For an assessment of the adaptability of stands and ecosystems as well as for the development of strategies for forest and landscape management that aims at minimizing the negative effects of the predicted climate change and maintaining the carbon sequestration potential, we have to deepen our knowledge on the processes determining plant-carbon relations.

Due to the slight difference in atomic mass, physical and chemical properties of substances containing different stable isotopes (isotopologues, such as $^{12}CO_2$ and $^{13}CO_2$) vary, resulting in different reaction kinetics and thermodynamic properties. These result in the "preference" of chemical and physical processes for one isotopologue, usually the lighter one, over the other (e.g. preference for $^{12}CO_2$ over $^{13}CO_2$) and hence in so-called *fractionation* events. Two major fractionation types can be distinguished, which





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are *kinetic fractionation* and *equilibrium fractionation*. *Kinetic fractionation* occurs during an irreversible process, either during physical events, like diffusion of $CO_2$ in air or phase transitions with constant removal of one phase, or during chemical reactions, like the conversion of a substance to another, e.g. $CO_2$ into plant carbohydrates. *Equilibrium fractionation* occurs when a chemical reaction or a physical process is reversible and continues to occur in both directions, and the different isotopes accumulate on either side of the reaction or process according to their mass-dependent binding energies in substrate(s) and product(s) or aggregate states, e.g. evaporation and condensation of $H_2O$. As a result of the different isotope fractionation processes along the pathway of carbon from the atmosphere through the plant into the soil, associated with phase transition, diffusion and enzyme activities in leaves, non-green plant parts and soil, the natural abundance of carbon isotopes at different stages of the pathway is the key to understanding and integrating the complexity of plant-soil interactions in the global terrestrial carbon cycle and to predicting future atmospheric carbon dioxide levels under global change. The analysis of temporal variations in the isotopic composition of different chemical compounds in different ecosystem compartments provides tools to assess the fate of carbon in plant, soil and atmosphere. In addition, the physiological information encoded in the isotope signature due to fractionation processes allows in principle to link whole ecosystem carbon dynamics with changes in carbon metabolism on the biochemical scale. The aim of this review is to aggregate the state-of-the-art knowledge of carbon isotope fluxes and fractionation patterns in terrestrial ecosystems with a special emphasis on plant-soil interactions and their impact on soil carbon turnover and storage capacity.

## 2 Carbon isotope fractionation in plants

Mainly due to historical reasons carbon isotope fractionation in plants has been separated into photosynthetic carbon isotope fractionation, including $CO_2$ diffusion, carboxylation, as well as dark and photorespiration (Farquhar et al., 1982), and into





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post-photosynthetic fractionation (von Caemmerer et al., 1997). However, if the distinction between the main fractionation step by RubisCO activity and all downstream fractionation steps should be made, the latter can be collectively addressed as post-carboxylation fractionation (Gessler et al., 2008), the terminology applied in the following. Figure 1 summarises photosynthetic and post-carboxylation carbon isotope fractionations (and some other processes such as mixing of sugars during phloem transport), which affect the carbon isotope composition of plant organic matter and respired $CO_2$. In the following sections we will explore these particular processes, their effects on $\delta^{13}C$ as well as the environmental and physiological information encoded in the isotopic signals.

## 2.1 Photosynthetic carbon isotope fractionation and its temporal variation

Generally, carbon isotope fractionation during photosynthesis (1 in Fig. 1) is described according to the following equation (Farquhar et al., 1982):

$$\Delta^{13}C = a_b \frac{p_a - p_s}{p_a} + a \frac{p_s - p_i}{p_a} + (e_s + a_l) \frac{p_i - p_c}{p_a} + b \frac{p_c}{p_a} - \left( \frac{eR_d/k}{p_a} + \frac{f\Gamma^*}{p_a} \right) \quad (1)$$

where $p_a$, $p_s$, $p_i$ and $p_c$ are the $CO_2$ partial pressures in ambient air, at the leaf surface, in the leaf intercellular airspace and in the chloroplasts, respectively. $a_b$ and $a$ describe the carbon isotope fractionation during diffusion through the boundary layer (2.9‰) and into the leaves through the stomata (4.4‰), respectively. $e_s$ is the fractionation occurring as $CO_2$ enters an aqueous solution (1.1‰ at 25 °C) and $a_l$ the fractionation during diffusion through the liquid phase (0.7‰ at 25 °C), $k$ is the carboxylation efficiency and $b$ the net fractionation during carboxylation. $R_d$ is the respiration rate in the light, $\Gamma^*$ is the $CO_2$ compensation point in the absence of day respiration, and $e$ and $f$ are the fractionation factors during day respiration and photorespiration. The mechanisms of photosynthetic carbon isotope fractionation have been reviewed elsewhere (Farquhar et al., 1989; Brugnoli and Farquhar, 2000), so that only some central points are discussed here.





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In literature, often a simplified model of Eq. (2), assuming a two-stage model (diffusion through the stomata followed by carboxylation), is applied to estimate photosynthetic carbon isotope fractionation:

$$\Delta_i = a + (b - a)\frac{p_i}{p_a} \tag{2}$$

Due to the relationship between photosynthetic carbon isotope fractionation and the ratio of intercellular airspace and ambient $CO_2$ partial pressures ($p_i/p_a$), which is often expressed as a $CO_2$ concentration ratio ($c_i/c_a$), newly assimilated organic matter can be generally used to characterise environmental effects on the physiology of photosynthesis. Stomatal closure due to water deficit generally reduces $c_i$, leading to an increase in $\delta^{13}C$ (e.g., Farquhar et al., 1982; Korol et al., 1999). As light limitation of photosynthesis increases $c_i$, $\delta^{13}C$ can also depend on radiation (Leavitt and Long, 1986; McCarroll and Pawellek, 2001) under particular conditions, but also combined influences of water and light availability have been observed (Gessler et al., 2001).

Von Caemmerer and Evans (1991) established the relation between assimilation rate ($A$) and mesophyll (internal) $CO_2$ transfer conductance ($g_m$) as follows:

$$A = \frac{g_m(p_i - p_c)}{P} \tag{3}$$

where $P$ is the atmospheric pressure. However, only recently it was observed that $g_m$ and its reaction to environmental conditions can vary among functional plant groups (Warren, 2008), and also within cultivars of a particular species (Flexas et al., 2008), not strictly related to $A$. In addition, $g_m$ of a given species and/or cultivar might change with plant and leaf age. Such changes in $g_m$ might partially constrain the application of the simplified carbon isotope fractionation models (Warren and Adams, 2006; Gessler et al., 2008). Since mesophyll conductance is not included in the widely used two-step model (Eq. 2) for photosynthetic carbon isotope fractionation (Farquhar et al., 1982), and $p_i$ and not the $CO_2$ partial pressure inside the chloroplast ($p_c$) is used as a basis for calculation, any variation in $g_m$ will constrain the classical way of calculating





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carbon isotope fractionation (Seibt et al., 2008) when the relationship between $g_m$ and assimilation rate is not constant (Warren and Adams, 2006).

Similarly, it has been shown by several authors (see Gillon and Griffiths, 1997; Igamberdiev et al., 2004; Tcherkez, 2006) that the isotope effect associated with photorespiration can be quite high ($f \approx 10‰$) and thus can have a significant impact given that $\Gamma^*/p_a$ equals $\approx 0.1$. In contrast, the day respiratory fractionation, $e$, is thought to be less significant because the factor $R_d/(kp_a)$ is much smaller (typically 0.02).

Recent direct online measurements under field conditions, applying novel laser spectroscopy techniques, revealed high variations of photosynthetic carbon isotope fractionation over the day, between days and over the growing season (Wingate et al., 2010). Over the whole growing season, photosynthetic carbon isotope fractionation for branches of maritime pine amounted to 10 to 35‰. These values well agree with the range of photosynthetic carbon isotope fractionation under various light conditions determined for wheat and bean under controlled conditions (Gillon and Griffiths, 1997). The highest values typically occurred at dusk throughout the growing season, but also in the early morning of June and July and throughout the day during the winter months. During summer, diel variations of photosynthetic fractionation amounted to more than 15‰ (Wingate et al., 2010). Changes in weather conditions among days also caused clear variations in $\delta^{13}C$, which then could be traced in the newly produced organic matter transported through the plant. On the basis of day-to-day variations in the photosynthetic carbon isotope fractionation, the transport of new assimilates through the plant and within the ecosystem has been tracked as soil respired $CO_2$ (Ekblad and Högberg, 2001; Knohl et al., 2005; Mortazavi et al., 2005; Brandes et al., 2006; Gessler et al., 2007) and transport times have been assessed (Mencuccini and Hölttä, 2010a) (see Sect. 3.5). As demonstrated by Brandes et al. (2007) and Wingate et al. (2010), such techniques can be applied throughout the whole growing season and have the additional advantage – compared to $^{13}C$ pulse labeling experiments – that the information on leaf physiology encoded in $\delta^{13}C$ can be additionally analysed. As mentioned above and discussed by Warren and Adams (2006), it might, however, not be possible





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to directly relate $\delta^{13}C$ to $p_i/p_a$ or water-use efficiency due to potential variations in $g_m$. Despite this potential constraint, $\delta^{13}C$ of basipetally transported assimilates have been successfully applied to characterise variation in stomatal conductance in different tree species (e.g., Cernusak et al., 2003; Keitel, 2003; Scartazza et al., 2004; Keitel et al., 2006).

However, it also has to be stated that the natural abundance technique failed tracking the fate of new assimilates in particular species mainly when environmental conditions were not very different among days (Kodama et al., 2008, 2011). It has been suggested that post-carboxylation fractionation and mixing of sugars of different metabolic history during phloem transport might blur the rather weak initial isotopic signal from photosynthetic fractionation in these cases.

## 2.2 Post-carboxylation fractionation

Post-carboxylation isotopic fractionation is defined as all isotope effects associated with the metabolic pathways downstream RubisCO carboxylation and with export of organic matter out of particular tissues (Hobbie and Werner, 2004; Badeck et al., 2005). Fractionation due to equilibrium and kinetic isotope effects results in differences in isotopic signatures between metabolites and in intramolecular isotopic distribution (Schmidt, 2003; Tcherkez and Farquhar, 2005). Post-carboxylation fractionation is also thought to be responsible for differences in $\delta^{13}C$ between plant organs (for a recent review see Cernusak et al., 2009). Beside photosynthetic also post-carboxylation carbon isotope fractionation might account for diel variations in the isotopic composition of carbon exported from the leaves to heterotrophic tissues (Tcherkez et al., 2004; Brandes et al., 2006) and of respired $CO_2$ (Tcherkez et al., 2003; Werner and Gessler, 20011). The following section will give an overview of the main fractionation mechanisms and the consequences for research on plant and ecosystem carbon balances.

One of the first post-carboxylation fractionation steps occurs in the Calvin cycle during aldolase condensation (i.e. synthesis of fructose 1,6-bisphosphate from triose





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phosphates), enriching $^{13}$C in the $C_3$ and $C_4$ atom positions of hexoses while leaving behind the light triose phosphates (Rossmann et al., 1991; Gleixner and Schmidt, 1997). A model developed by Tcherkez et al. (2004) and based on the isotope effects of both aldolase, reported by Gleixner and Schmidt (1997), and transketolase (estimated values), fits well the reproducible non-statistical $^{13}$C distribution in hexose molecules reported by Rossmann et al. (1991). The intra-molecular carbon isotope distribution in Calvin cycle hexoses also depends on the relative activity of the glyoxylate cycle (photorespiration) because of decarboxylation of a $^{13}$C-rich carbon atom position and fractionation during glycine decarboxylation (Tcherkez et al., 2004). This intra-molecular $^{13}$C pattern in hexose and thus in pyruvate molecules is considered to be the main origin of the so-called "fragmentation fractionation" (see Tcherkez et al., 2004) during dark respiration, which will be discussed below.

Another effect of the fractionation by aldolase and transketolase is the $^{13}$C-enrichment in transitory starch in the chloroplasts (2 in Fig. 1) and $^{13}$C-depletion in cytosolic sucrose (Schmidt and Gleixner, 1998). Indeed, as explained above, the fractionations of these enzymes in the Calvin cycle favour $^{13}$C in hexoses and thus in transitory starch in the chloroplasts while leaving behind $^{13}$C-depleted trioses, which will form sucrose in the cytosol. Accordingly, the phloem sugars are $^{13}$C-enriched during night-time (originating from transitory starch degradation), while the daytime sugars in the phloem originating from the trioses left behind by aldolase/transketolase reactions are $^{13}$C-depleted. Such a diel change in $^{13}$C content of phloem sugars modelled by Tcherkez et al. (2004) was observed experimentally by Gessler et al. (2008) in *Ricinus* plants.

Data available in the literature on the carbon isotope difference between starch and sugars (mainly sucrose) are scarce, and experimental protocols for their determination still need to be scrutinized (Richter et al., 2009). However, expected technical progress will open new avenues for studies of the variability of fractionation due to transitory starch synthesis with the rate of starch synthesis and with environmental conditions (Tcherkez et al., 2004). Thus, measurements of intra-molecular patterns of $\delta^{13}$C and





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diel variation in sugar $\delta^{13}C$ can potentially be used in ecological studies as indicators of assimilate allocation.

Carbon isotope fractionation during plant respiration (3 and 7 in Fig. 1) is a widely observed phenomenon (see reviews by Ghashghaie et al., 2003; Badeck et al., 2005; Bowling et al., 2008). There are several enzyme-catalyzed reactions involved in respiratory metabolism that can lead to isotope fractionation.

Due to the non-statistical $^{13}C$ distribution in glucose, the $\delta^{13}C$ of respired $CO_2$ highly depends on the intra-molecular position of the C atom used for decarboxylation. Consequently, $CO_2$ produced during different respiratory processes is often relatively enriched or depleted in $^{13}C$ compared to the associated substrate (Ghashghaie et al., 2003). This fragmentation fractionation (Tcherkez et al., 2004) may occur at a number of metabolic branching points along plant respiratory pathways (Barbour and Hanson, 2009).

Coupled to the glycolysis pathway, decarboxylation of pyruvate by the pyruvate dehydrogenase complex (PDH) releases relatively $^{13}C$-enriched $CO_2$, using the $C_3$ and $C_4$ atoms of glucose (DeNiro and Epstein, 1977; Melzer and Schmidt, 1987). Consequently, acetyl-CoA is relatively depleted in $^{13}C$, as are fatty acids or $CO_2$ released during the tricarboxylic acid cycle (TCA). Partitioning acetyl-CoA to fatty acid synthesis and TCA leads to an overall higher contribution of PDH than TCA activity to total $CO_2$ efflux, which may explain the often-observed $^{13}C$-enrichment of $CO_2$ efflux compared to respiratory substrate (Ghashghaie et al., 2003). Imbalances between TCA and PDH may also account for diel changes in $\delta^{13}C$ of plant respiration (Kodama et al., 2008; Priault et al., 2009; Kodama et al., 2011). In addition, fractionation by PDH and TCA cycle enzymes may further change the isotopic signature of respired $CO_2$ (Tcherkez and Farquhar, 2005). These effects depend on the relative flux strengths at the associated metabolic branching points.

Another decarboxylation reaction of glucose takes place within plastids during the oxidative stage of the pentose phosphate pathway (PPP). The PPP releases $^{13}C$-depleted $C_1$ atoms of glucose as $CO_2$ (Dieuaide-Noubhani et al., 1995; Bathellier et al.,





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2009). Moreover, this decarboxylation reaction fractionates against $^{13}C$ by about 9.6‰ (kinetic isotope effect; Rendina et al., 1984) or against $^{12}C$ by 4‰ (equilibrium isotope effect; Rendina et al., 1984). Accordingly, the $\delta^{13}C$ of $CO_2$ produced during PPP is relatively depleted in $^{13}C$ compared to respiratory substrate. High PPP activity reported for roots could explain the $^{13}C$ depletion in root-respired $CO_2$ (Bathellier et al., 2008) compared to $^{13}C$-enriched $CO_2$ respired by leaves (Duranceau et al., 1999; Tcherkez et al., 2003).

High activity of phosphoenolpyruvate carboxylase (PEPc) is also known to occur in roots (8 in Fig. 1) and has recently been detected also in aboveground $C_3$ plant tissues (Berveiller and Damesin, 2008; Gessler et al., 2009a). PEPc carboxylates PEP using $HCO_3^-$ as substrate (stemming either from respiratory or external $CO_2$) to malic acid (via oxaloacetate), which may enter the mitochondria to sustain TCA activity. This so-called "anaplerotic" supply is assumed to refill the TCA when citrate intermediates of the TCA are used, e.g. for amino acid synthesis (Tcherkez and Hodges, 2008; Bathellier et al., 2009). PEPc discriminates against $^{12}C$ by 5.7‰ (Farquhar, 1983), leading to $^{13}C$ enrichment of plant $CO_2$ efflux (Gessler et al., 2009a), as long as malic acid is not immediately decarboxylated again (Cernusak et al., 2009). Consequently, the high $^{13}C$ enrichment of respiratory $CO_2$ evolved from leaves shortly after darkening may be explained by rapid decarboxylation of highly enriched malic acid pools, derived from PEPc during illumination (light-enhanced dark respiration – LEDR; see Barbour et al., 2007). However, the overall quantitative effect of the before-mentioned fractionation processes in combination with temporal changes in the respiratory substrates on $\delta^{13}C$ of plant $CO_2$ efflux is still a matter of debate (Tcherkez, 2010; Werner, 2010).

It is now well established that plant organs differ in their isotopic signature. Several recent reviews (Badeck et al., 2005; Bowling et al., 2008; Cernusak et al., 2009) have shown that heterotrophic organs (branches, stems and roots) are enriched in $^{13}C$ compared to autotrophic organs, which supply them with carbon. Branches and woody stems of $C_3$ species are on average 1.9‰ enriched in $^{13}C$ compared to leaves (Badeck et al., 2005), whereas roots show an average enrichment varying between

1.1‰ (Badeck et al., 2005) and 2‰ (Bowling et al., 2008). Several mechanisms have been proposed to explain these differences in isotopic signatures of plant organs and respired $CO_2$ (cf. Badeck et al., 2005, and Cernusak et al., 2009, for detailed review of these processes). One of the reasons for differences in $^{13}C$ content between different plant organs is that the metabolites used for export (e.g. sucrose) are enriched in $^{13}C$ with respect to the photosynthetic products, leading to differences in $^{13}C$ content of heterotrophic tissues compared with leaves. Fragmentation of molecules with heterogeneous intra-molecular $^{13}C$ distribution and kinetic isotope effects at metabolic branching points associated with the enzymatic reactions leading to the respective products are known to cause compound-specific differences (4 and 9 in Fig. 1). When compounds, which become $^{13}C$-depleted as a consequence of such processes (e.g. lipids), remain in the leaves, whereas relatively $^{13}C$-enriched compounds are exported, the inter-organ differences will then be related to the chemical composition of organs.

Other potential reasons for organ-specific differences might be seasonal asynchrony of growth of photosynthetic and heterotrophic tissues, with corresponding variation in photosynthetic discrimination against $^{13}C$ due to different environmental and ontogenetic conditions (Bathellier et al., 2008; Salmon et al., 2011), and developmental variation in photosynthetic fractionation against $^{13}C$ during leaf expansion. In addition, seasonal variations in starch storage and remobilisation (6 in Fig. 1) and the preferential use of $^{13}C$-enriched, starch-derived organic matter in a particular organ might be responsible for more positive $\delta^{13}C$ values. As, however, also $^{13}C$ enrichment of particular compounds (e.g. phloem sucrose) was detected in basipetal direction (Gessler et al., 2009b), independent of ontogeny or development, other additional factors must be responsible for this observation. These might include differential use of daytime vs. night-time sucrose between leaves and sink tissues, with daytime sucrose being relatively $^{13}C$-depleted and night-time sucrose $^{13}C$-enriched (Tcherkez et al., 2004), as well as fractionation associated with the transport of assimilates. The transport processes (such as phloem loading or phloem transport; 5 in Fig. 1) are not likely to discriminate against $^{13}C$. It is rather assumed that repeated sugar unloading along the phloem

transport path, metabolic conversion of part of this sugar pool, and reloading of the remaining unreacted sugars into the sieve tubes might contribute to the basipetal $^{13}C$ enrichment (for details see Gessler et al., 2009b). In addition, differences in fractionation during dark respiration in heterotrophic vs. autotrophic tissues (Bathellier et al., 2008), and higher carbon fixation by PEP carboxylase in roots might explain the inter-organ differences. The organ-specific spatial variation of the carbon isotope signal, i.e. the basipetal enrichment, which is not necessarily constant over the growing season (Gessler et al., 2009b), challenges the calculation of intrinsic water-use efficiency or $p_i/p_a$ from organic material of heterotrophic organs (e.g. in tree rings). However, temporal variations in $\delta^{13}C$ of organic matter and respired $CO_2$ as a consequence of post-carboxylation isotope fractionation have been related to starch synthesis and remobilization (e.g., Tcherkez et al., 2004) and other switches between metabolic pathways (Priault et al., 2009) and may, therefore, provide a way to identify changes in metabolic processes related to changes in carbon allocation patterns in plants and ecosystems.

In conclusion, post-carboxylation fractionation produces additional changes and variations in carbon isotope signals on top of the original photosynthetic signal. On the one hand, this complicates the tracking of the fate of carbon within the plant-soil system and might partially uncouple the isotope composition in heterotrophic tissues from leaf level processes. On the other hand, the post-carboxylation isotope fractionation processes are likely to give additional information on processes in heterotrophic tissues. It is, however, crucial to disentangle particular processes and quantify their contribution to post-carboxylation isotope fractionation and to link the plant-level processes, assessed with isotope techniques, with processes at the ecosystem level.

## 3 Carbon allocation in the plant-soil system

As reviewed in Sect. 2, stable carbon isotope ratios of recently assimilated C contain valuable information about environmental conditions which can be tracked through the





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plant-soil system and are imprinted in respired $CO_2$. However, temporal changes in C allocation can strongly affect this relationship between environmental conditions and $\delta^{13}C$. In the following section, studies are reviewed and discussed that document how C allocation in the plant-soil system varies on diel, seasonal and annual to interannual time scales and how it influences isotope signals in plant biomass and soil respiration.

### 3.1 Plant-internal C allocation

Carbon transport through the phloem and xylem, and the underlying physiological mechanisms as affected by environmental and plant-internal factors, are a major point of uncertainty in understanding the patterns of assimilate distribution within plants and of plant-soil C coupling. Partitioning of the newly assimilated carbohydrates within the plant occurs via loading of sugars into the phloem, transport in the sieve tube system and unloading at the sites of demand. The pressure-driven mass flow system of the phloem allows C compounds to be transported over long distances in the plant from source to sink tissues (Van Bel, 2003). Consequently, the C partitioning is controlled by the supply of assimilates via photosynthesis, but also depends on the ability of different organs to utilise the available supply (Wardlaw, 1969). While these general principles are well known, the molecular background of the regulation of carbohydrate partitioning and of the transporters involved is less understood (Slewinski and Braun, 2010). Redox control of sugar transport and sugar plus phytohormone signalling seem to be at least involved in coordinating carbohydrate partitioning (Rolland et al., 2006). In such a manner, whole plant physiology can also exert a feedback sink control over leaf level photosynthesis, even overriding direct control by light and $CO_2$ (Paul and Foyer, 2001).

Considering the phloem just as a static tube for organic matter transport is inappropriately simplified (Fisher, 2002). The modified dynamic version of the Münch mass flow model (Münch, 1930), as reviewed by Van Bel (2003), assumes that assimilates are translocated in the plant via the phloem through “leaky pipes” – a metaphor for the sieve tube companion cell complexes. According to this model, the solute content in the phloem – and as a consequence the pressure – are controlled by release/retrieval





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mechanisms in the sieve element/companion cell complexes. During transport, sugars are released from the sieve tubes and part of them are retrieved again (Minchin and Thorpe, 1987). The differential release/retrieval balances not only control the net influx or efflux of sugars, but also the flux of water in different phloem zones. In the collection phloem in source tissues, the influx of sugars and water will dominate, whereas in the release phloem in the sink tissues the efflux of sugars and water will prevail. In summary, as in the original Münch model, the driving force to control phloem transport is the source-sink turgor difference. In contrast, Thompson (2006) assumes that the "inability of decentralized organisms such as plants to control phloem translocation centrally disqualifies such [pressure] differentials as control variables". In addition, the author argues that the maximum efficiency of phloem transport is achieved if the pressure differentials are small, and that homogeneous turgor and rapid long-distance distribution of local disturbances in turgor and solute concentration are a prerequisite for the sieve element/companion cell complexes to operate in a non-centralized manner and to serve both long distance transport and local supply of surrounding tissues.

Mencuccini and Hölttä (2010a) advanced towards a mechanistic understanding of the phloem as a "bottleneck" to C flow below ground. They provide evidence that specific phloem properties (path length, specific conductivity and turgor pressure differences) and transport velocities are crucial to explain the linkage between canopy photosynthesis and belowground processes. Furthermore, they put forward the hypothesis of Ferrier et al. (1975) and Thompson and Holbrook (2004) that pressure/concentration waves travelling through the phloem are responsible for a very fast transfer of information, coupling assimilation to belowground processes. Pressure wave fronts are assumed to travel several orders of magnitude faster than the phloem solution and the solutes within, thus creating a signal that is rapidly transferred through the plant via the phloem. If pressure concentration waves completely mediated the coupling between (canopy) carbon assimilation and soil respiration, the tracking of isotope signals – either as natural abundance isotope composition or as highly enriched $^{13}$C label – would not be suited to characterize this link (Mencuccini and Hölttä, 2010a; Sect. 3.5).



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Soil respiration as an example would already be up-regulated hours or days before the newly assimilated substrate arrives belowground and could imprint its $\delta^{13}C$ signature upon the respired $CO_2$. Kayler et al. (2010a) postulated, however, that the time of arrival of carbon molecules belowground conveys more important information than a hypothetic pressure concentration wave. This is because the time it takes for a carbon molecule to pass through the plant indicates the status of plant storage pools, the impact of water availability on biological activity and plant nutrient status. The authors thus concluded that the time-lag between carbon fixation during photosynthesis and its loss through respiration belowground carries real physiological information about the carbon use within plants as well as about the degree to which plants and soil are coupled and that this information is exactly the one derived from studies of the isotopic composition of recent assimilates, other short- or long-lived carbon pools and respired $CO_2$.

### 3.2 Carbon transfer to soil biota

A large fraction of C fixed by plant photosynthesis is allocated belowground, where C can be: (1) invested into biomass or respired by roots; (2) released as exudates and respired during or allocated to growth of soil microorganisms in the rhizosphere (Kuzyakov and Domanski, 2000; Kuzyakov et al., 2000; Walker et al., 2003); or (3) incorporated as litter into soil organic matter that may be respired by heterotrophic soil microorganisms. In this section we focus on pathways 1 and 2. Pathway 3 will be discussed in Sect. 4.

Carbon allocated to roots can stimulate exudation, which in turn increases microbial respiration in the rhizosphere (Kuzyakov and Cheng, 2001; Bowling et al., 2002; Tang et al., 2005). Up to 40% of photosynthates are exudated by roots and are rapidly respired or invested in biomass by rhizosphere microorganisms (Whipps, 1990; Meharg, 1994; Kuzyakov and Cheng, 2001). The rhizosphere is a narrow zone in the vicinity of the roots characterized by the presence of mycorrhizal fungi and other rhizosphere microorganisms that depend on root exudates as a C substrate source (Cheng





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et al., 1996; Jones et al., 2009). Among rhizosphere microorganisms, mycorrhizal fungi are of great relevance to plant-soil C interactions (Finlay and Söderström, 1992; Stuart et al., 2009; Jones et al., 2009). Several studies indicate that mycorrhizal fungi can use up to 30% of recent plant photosynthates (Högberg and Högberg, 2002; Johnson et al., 2002; Leake et al., 2006; Heinemeyer et al., 2007; Chapin et al., 2009). It has been shown that C turnover in mycorrhyzal fungi ranges from 5 to 9 days, indicating that there is a very rapid flux of C through mycorrhizal hyphae (Staddon et al., 2003; Goldbold et al., 2006; Vandenkoornhuyse et al., 2007). The C turnover in microbial biomass ranges from 7 to 95 days, indicating a slower turnover compared to mycorrhizal fungi (Ocio et al., 1991; Ostle et al., 2003; Kaštovská and Šantrůčková, 2007). The large variability in C turnover times of soil microorganisms could be associated with a switch between different functional groups of microbes, as e.g. rhizosphere bacteria and mycorrhizal mycelium can be used as C substrates by other soil microorganisms (Jones et al., 2009).

Soil macrofauna (e.g. earthworms) are dependent on plant exudates as a C source in addition to above- and belowground plant litter inputs as shown by Ostle et al. (2007), using $^{13}$C-pulse labeling. Turnover times of C in earthworms range from 12 to 37 days (Bouche, 1984; Dyckmans et al., 2005). Also collembola (springtails) were found to feed on very recently assimilated C in contrast to Acari (e.g. mites) and Enchytraeidae (Högberg et al., 2010).

Overall, the C flux to soil biota in the rhizosphere is large and C is typically lost from the system within days to months. Environmental conditions imprinted in $\delta^{13}$C of photosynthates are thus translated through organisms in the rhizosphere and remain detectable in the autotrophic part of soil respiration ($R_a$; see Sect. 3.3).

### 3.3 Carbon losses via plant and rhizosphere respiration and BVOC emissions

Respiration of plant tissues and rhizosphere microorganisms constitutes a major C loss in terrestrial ecosystems and can make up to 80% of gross primary production (Janssens et al., 2001). Also the emission of biogenic volatile organic C compounds



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(BVOCs) can be a considerable drain of C from the vegetation, especially under stress conditions such as drought, continuing even when net assimilation has ceased (Brüggemann and Schnitzler, 2002). However, BVOC emission rates differ strongly among plant species and thus only play a role for the C budget of particular species (Sharkey et al., 2008).

Plant respiration and BVOC emissions are normally not fuelled by a homogeneous substrate, but by several C pools with different turnover times and metabolic histories (Schnyder et al., 2003; Ghirardo et al., 2011; Kuptz et al., 2011a). Lehmeier et al. (2008) identified three major C pools distinguishable by their half-life, which fed dark respiration in shoots and roots of perennial rye grass. Only 43% of respiration was directly driven by current photosynthates, thus pointing to the importance of short-term storage pools with half-lives of a few hours to more than a day. This finding is in agreement with observations made by Nogués et al. (2004) for French bean, showing that the leaf respiratory substrate is a mixture in which current photosynthates are not the main components. Changes in the N supply (Lehmeier et al., 2010), but presumably also in other environmental conditions, can change the mean residence time of the respiratory substrate pool mainly due to different contributions from storage.

In summary, plant respiratory $CO_2$ losses are largely, but not exclusively fuelled by recently assimilated C with valuable information imprinted in its $\delta^{13}C$. However, temporal changes in substrate use (e.g., Hymus et al., 2005; Nogués et al., 2006) and post-carboxylation isotope fractionation in leaves and heterotrophic tissues can partially uncouple the isotope composition of $CO_2$ from assimilates (Sect. 2.2). Furthermore, measurements in tall stature plants are technically challenging, explaining why field studies are scarce.

Soil $CO_2$ efflux is dominated by two major sources of soil respiration: an autotrophic component ($R_a$, roots, mycorrhizal fungi and other root-associated microbes dependent on recent C photosynthates) and a heterotrophic component ($R_h$, organisms decomposing soil organic matter; see Sect. 4). A large array of methods for partitioning $R_a$ and $R_h$ exists, the advantages and disadvantages of which have been extensively





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reviewed elsewhere (Hanson et al., 2000; Kuzyakov, 2006; Subke et al., 2006; Trumbore, 2006). On average, $R_a$ and $R_h$ contribute equal amounts to total soil respiration, ranging from 10 to 90% in single studies (Hanson et al., 2000), with the contribution of $R_a$ increasing with annual soil $CO_2$ efflux (Subke et al., 2006; Bond-Lamberty, 2010).

5 While many experiments suggest that $R_a$ strongly depends on recent photosynthates as indicated by rapid and pronounced declines in soil respiration after clipping, shading or phloem girdling (Craine et al., 1999; Högberg et al., 2001; Wan and Luo, 2003), other studies have reported only minor effects (Hibbard et al., 2005; Zhou et al., 2007; Bond-Lamberty and Thomson, 2010). These latter studies indicate that root C stores
10 might serve as respiratory substrates for $R_a$ and allow to maintain respiration rates at least temporarily (Bahn et al., 2006). This is supported by radiocarbon analysis of root respired $CO_2$, which showed that roots partly respire older C (Cisneros-Dozal et al., 2006; Czimczik et al., 2006; Schuur and Trumbore, 2006). In contrast, respiration by microbes in the rhizosphere is not buffered by carbohydrate reserves and may decline
15 more rapidly after interruption of assimilate supply (Bahn et al., 2006).

In strongly seasonal ecosystems at high latitudes, dramatic increases in $R_a$ have been found in late as opposed to early summer (Högberg et al., 2010), indicating that $R_a$ is dependent on plant phenology and/or the season. Higher $R_a$ is likely dominated by increased growth respiration, while maintenance respiration is assumed to undergo
20 less seasonal change (Wieser and Bahn, 2004). Although higher temperatures in late summer undoubtedly play a role in the observed increase in $R_a$, the occurrence of hysteresis, expressed as different respiration rates measured at the same soil temperatures (Bhupinderpal-Sing et al., 2003; Olsson and Johnson, 2005; Högberg et al., 2009), suggests that additional factors, such as phenology, control $R_a$. Yet, changes in
25 physical transport processes of $CO_2$ and heat hold an alternative explanation for the occurrence of hysteresis (Subke and Bahn, 2010; Phillips et al., 2011).

Nutrient availability can also exert a strong control on $R_a$. In N-poor systems, addition of N fertilizer reduces $R_a$ (Högberg et al., 2010), associated with an increase in aboveground C allocation (Olsson et al., 2005). Responses in total soil respiration rates





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have been found to increase, decrease or remain unaltered as reviewed by Janssens et al. (2010). The discrepancy in these results may reflect the combined responses of plants and soil to N fertilization.

Many studies show a pronounced effect of soil moisture on $R_a$ relative to total soil respiration. During a dry summer, the amount of recent C respired decreased in an evergreen forest (Andrews et al., 1999), possibly as a result of a reduction in C supply from above ground. Similarly, Ruehr et al. (2009) found less labeled C respired in drought experiments (see also Sect. 3.6). In contrast, an increase in the fraction of recent C was measured in soil $CO_2$ during an exceptionally dry summer in a temperate deciduous forest (Keel et al., 2006). These different results might be explained by interacting effects of soil moisture and temperature on C supply for respiration (Davidson et al., 2006) or changes in $CO_2$ transport rates in the soil (Phillips et al., 2011).

Despite the importance of rhizospheric respiration to the terrestrial C cycle, little is known about the biotic and abiotic factors that regulate their activity (Högberg and Read, 2006; Chapin et al., 2009). Carbone et al. (2007) showed that $^{14}$C-labeled assimilates respired by rhizosphere microorganisms had a mean residence time of 15 days, but 30 days after the labeling, the signal was still detectable in soil respiration. Moyano et al. (2008) suggested that factors controlling mycorrhizal respiration are similar to those that control root respiration. However, recent studies indicate that mycorrhizal respiration may be less sensitive to temperature than root respiration (Heinemeyer et al., 2007; Moyano et al., 2007; Nottingham et al., 2010).

Overall, the autotrophic component of soil respiration is closely coupled to assimilate supply and is sensitive to factors that control C uptake (e.g. phenology, N availability, and shading) and C allocation patterns. Root respiration can also be supplied by stored C, if assimilate supply is interrupted. How C stores contribute to $R_a$ under normal conditions will affect the plant-soil respiratory $\delta^{13}$C linkage. It can be concluded that the link should be tightest during periods of high C supply and in plant species with small C stores.





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### 3.4 Temporal C allocation patterns

From correlation-based flux studies it is not consistently clear and currently debated to which extent commonly observed diel variations in soil respiration are temperature- (and moisture) independent and thus possibly related to rapid allocation of C from recent photosynthesis to respiration (Tang et al., 2005; Bahn et al., 2008; Subke and Bahn, 2010; Vargas et al., 2010; Philipps et al., 2011). Also $\delta^{13}C$ of soil $CO_2$ efflux has been shown to exhibit diel variations (e.g., Kodama et al., 2008; Bahn et al., 2009; but see Betson et al., 2007), which may reflect a number of processes including: changes in vapor pressure deficit that affect photosynthetic discrimination against $^{13}C$ (Brugnoli et al., 1988; Farquhar et al., 1989; see Sect. 2.1), changes in respiratory C isotope fractionation as demonstrated for $CO_2$ respired by leaves (Hymus et al., 2005) as well as trunks (Kodama et al., 2008), diurnal changes in respiratory carbon source (Tcherkez et al., 2004; Gessler et al., 2007; Bahn et al., 2009) and diffusion processes (Moyes et al., 2010). For a detailed mechanistic analysis of the origin of diel variations in the $\delta^{13}C$ see Werner and Gessler (2011).

In both annual and perennial plants, initial growth and respiration are supplied from storage C in seeds (Bathellier et al., 2008). Carbon isotope ratios of young plants will thus be dominated by storage compounds (e.g. $^{13}C$-depleted lipids or $^{13}C$-enriched carbohydrates; see Sect. 2.2). Similarly, leaf growth in deciduous trees relies on stored C (mainly starch) during the first phase of leaf development (Lacointe et al., 2004; Kagawa et al., 2006a; Asaeda et al., 2008), which in some species can be rather short (Keel and Schädel, 2010). Damesin and Lelarge (2003) have documented the switch from $^{13}C$-enriched starch to more $^{13}C$-depleted assimilates for young beech leaves. In contrast, new foliage of evergreen species is typically considered to be made almost entirely of recent assimilates (Hansen and Beck, 1994; Cerasoli et al., 2004).

Early radial growth of stems is often supplied by reserves as well (Helle and Schleser, 2004; Kagawa et al., 2006b; Skomarkova et al., 2006). However, distinct differences in the use of recent vs. stored C for radial growth have been documented for deciduous





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trees, with some species incorporating negligible amounts of reserves (Keel et al., 2006). During summer, photosynthates are allocated mainly above ground (Mordacq et al., 1986; Olsrud and Christensen, 2004), supplying shoot elongation (Schier, 1970; Hansen and Beck, 1994), radial growth (Gordon and Larson, 1968), further foliage development (Dickson et al., 2000; Lamade et al., 2009) and flowering and fruiting (Mor and Halevy, 1979; Hoch and Keel, 2006). Possibly as a result of rapid mixing between old and new C (Keel et al., 2007) there is a carry-over of stores for wood growth in most species (Kagawa et al., 2006b; Keel et al., 2006; von Felten et al., 2007), which may impair the use of isotope tree-ring data as proxy for environmental processes.

Changes in the relative contributions of different C sources throughout phenological plant development entail remarkable seasonal variations in the $\delta^{13}C$ of different plant organs (Damesin and Lelarge, 2003; Helle and Schleser, 2004). Such variations may hinder the interpretation of $\delta^{13}C$ in plants as indicator for environmental conditions (Cavender-Bares and Bazzaz, 2000; Helle and Schleser, 2004). The contribution of new C to foliage production is highly variable in deciduous species (Keel et al., 2006), but on average close to the c. 70% reported for evergreen *Pinus uncinata* trees (von Felten et al., 2007). The amount of new C used for stem growth ranges from 35% (*Quercus petraea* saplings; Palacio et al., 2011) to 71% (average of 5 deciduous tree species, Keel et al., 2006). Diffuse porous species allocate significantly higher amounts of new C to wood than ring-porous species (52% vs. 35%, respectively; Palacio et al., 2011). Thus, differences between evergreen and deciduous species may be smaller than initially thought and, in some cases, overridden by inter-species variability.

Carbon allocation patterns are known to vary not only throughout the life cycle of plants but also with the age of the different plant organs (Kozlowski, 1992). These changes are particularly relevant for long-lived perennial species. In general, older plants tend to decrease allocation belowground, and to increase allocation to maintenance (increased standing biomass and respiration) (Kozlowski, 1971), storage pools (Lusk and Piper, 2007; Genet et al., 2010), defense mechanisms (Boege, 2005; Boege





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and Marquis, 2005) and reproduction (Genet et al., 2010). Changes in C allocation to plant organs entail quantitative and qualitative differences in their C composition with age. Consequently, the C isotope composition of plant respiratory $CO_2$ (Maunoury et al., 2007; Kuptz et al., 2011b) or of bulk material (Helle and Schleser, 2004; Skomarkova et al., 2006; Salmon et al., 2011) may change with season and ontogeny. For example, leaves of adult plants tend to be enriched in $^{13}C$, showing higher $\delta^{13}C$ than leaves of young plants (Donovan and Ehleringer, 1994; Cavender-Bares and Bazzaz, 2000; Fessenden and Ehleringer, 2002). Information on the age-related variations of $\delta^{13}C$ in the different organs of plants (including not only leaves but also roots or stems for which data are mostly absent) is crucial for scaling $\delta^{13}C$ results on young plants to mature individuals.

Belowground plant parts are supplied by both recent photosynthates and C reserves (Joslin et al., 2006; Carbone et al., 2007). Recent investigations estimated that up to 55% of fine root C comes from storage, although such stored C is of young age (≈0.4 years) (Gaudinski et al., 2009). Belowground allocation of newly fixed C increases dramatically towards the end of the growing season (Smith and Paul, 1988; Stewart and Metherell, 1999; Högberg et al., 2010), competing with storage accumulation in aboveground parts for winter dormancy and frost hardiness (Hansen and Beck, 1990; Skomarkova et al., 2006; Kuptz et al., 2011a). In evergreen species, a second maximum of belowground allocation is often observed in early spring, shortly before bud break (Shiroya et al., 1966; Ziemer, 1971). During winter, deciduous species maintain their living tissue mainly from reserve pools (Dickson, 1989; Maunoury et al., 2007), whereas evergreen trees may produce new substrate for respiration (mainly maintenance respiration) by active photosynthesis during warmer periods within the cold season (Hansen et al., 1996; Hu et al., 2010; Kuptz et al., 2011b). Similar to the cold season, summer drought might induce a seasonal allocation pattern with regularly occurring favorable and unfavorable growth conditions, leading to seasonal changes in growth and in the contribution of growth and maintenance respiration to $R_a$. Such phases are likely to be associated with variations in $\delta^{13}C$ of plant respired $CO_2$. If





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assimilate supply decreases, $^{13}C$-enriched stores can serve as substrates for respiration leading to increases in $\delta^{13}C$ of released $CO_2$.

Compared to the wealth of studies on seasonal changes in C allocation, relatively little is known about interannual variations. Carbon allocation to radial stem growth is typically correlated with climatic conditions such as precipitation and air temperature, a relationship used for climate reconstructions by dendrochronologists. Interestingly, Rocha et al. (2006) found no correlation between gross ecosystem production (a measure for photosynthesis at the stand scale) with tree ring width, suggesting that radial growth is not directly related to the availability of recent C, but also depends on the amount of carbohydrate stored.

Although significant advances have been made in recent years to characterize the use of stored C in plants, there are still important knowledge gaps to fill. For example, the relationship between the age of plant stores and remobilization is still not fully understood, raising the question of how much of the C stored by plants can actually be remobilized (Millard et al., 2007), and how long these stores can be remobilized before they are ultimately sequestered in plant tissues or lost as $CO_2$ or BVOC. It is also not known how stores are mobilized in relation to the time (phenology and age) they were built up (but see initial results by Lacointe et al., 1993), or how these processes are affected by environmental stress and disturbance. These key questions have to be answered before the role of plants in ecosystem C cycling can be fully understood.

### 3.5 Time lags between $CO_2$ assimilation, C allocation and respiration

The time lag caused by C translocation from aboveground sites of assimilation (leaves) to belowground sites of respiration ($R_a$ and $R_h$) has been extensively reviewed (Davidson and Holbrook, 2009; Kuzyakov and Gavrichkova, 2010; Mencuccini and Hölttä, 2010a) since photosynthesis has been identified as a key driver of soil respiration (Högberg et al., 2001). There is ongoing controversy about the main mechanism describing the speed of link between assimilation and respiration (Kayler et al., 2010a;

Mencuccini and Hölttä, 2010b; see also Sect. 3.1). The information is either directly conveyed by the phloem sugar concentration change or by the propagation of pressure/concentration waves within the phloem (Thompson and Holbrook, 2004; Kayler et al., 2010a; see Sect. 3.1). However, empirical evidence in support of the latter hypothesis is still pending. Generally, time lags determined as propagation of fluctuations in $\delta^{13}$C at natural abundance increase with tree height, showing transport rates between 0.07 and 0.5 m h$^{-1}$ (Kuzyakov and Gavrichkova, 2010; Mencuccini and Hölttä, 2010a). Carbon isotope labeling experiments suggest a longer transport time in gymnosperms compared to angiosperm trees (Kuzyakov and Gavrichkova, 2010), due to structural differences in the phloem. The differences between the two groups can be considerable, despite the heterogeneity in environmental conditions the experiments were conducted at. The observed patterns suggest a separate consideration of gymnosperm and angiosperm tree species in the future. Furthermore, also time lag studies in grasses need to be considered independently, as – in contrast to tree species – time lags generally decreased with plant height at least in *Lolium perenne* (Kuzyakov and Gavrichkova, 2010).

Carbon translocation velocities are often higher in tall plants (Lang, 1979; Thompson and Holbrook, 2003; Van Bel and Hafke, 2005; Mencuccini and Hölttä, 2010a), potentially due to stronger root C sinks associated with a larger belowground biomass. However, considerable seasonal changes in belowground C allocation did not affect time lags (Horwath et al., 1994; Högberg et al., 2010), suggesting that phloem path length and structural differences are the main determinants of C transfer velocity.

### 3.6 Sensitivity of C allocation to environmental stress

The general responses of plant ecophysiology to environmental stress (e.g. resource limitations in light, water or nutrients) have been well known for many years (Larcher, 2003). Ecophysiological responses often involve changes at different organizational levels, ranging from cellular mechanisms to whole plant carbon-water or carbon-nutrient relations to sustain plant performance and plant fitness under stress. Stable





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carbon isotopes have been shown to be sensitive indicators of leaf stress responses involving stomatal regulations, changes in mesophyll conductance and (photo)respiration (Farquhar et al., 1989; Dawson and Siegwolf, 2007, and references therein). For example, leaf carbon discrimination was shown to increase under light stress for $C_3$ (Brugnoli and Farquhuar, 2000) and $C_4$ plants (Buchmann et al., 1996), but decrease under water limitations (Dawson et al., 2002).

Recently, studies demonstrated that drought stress not only reduced C assimilation but often also increased the mean residence time of recently assimilated C in leaf biomass. Furthermore, the C transfer velocity was reduced in saplings and the trunk of some tree species, leading to a reduced coupling between canopy photosynthesis and belowground processes under water stress (Ruehr et al., 2009; Dannoura et al., 2011). Similarly, shading has been shown to reduce the speed of link between photosynthesis and soil respiration in grassland (Bahn et al., 2009). Mechanisms underlying these short-term responses to stress are possibly related to source-sink relationships, as at low photosynthetic rates a decrease of phloem loading at the collection phloem end will lower the pressure gradient and hence decrease the downward transport rates (Lee, 1981). Furthermore, soil moisture influences the quantity of water supplied by the xylem to the collection phloem, affecting the turgor pressure differences between two phloem ends. Potentially, all environmental factors which affect photosynthesis (vapor pressure deficit, radiation, $CO_2$ concentration, etc.) might have similar consequences. However, more studies, including also compound-specific carbon isotope analyses, are needed to further elucidate the biochemical and physiological mechanisms responsible for these patterns.

While application of the widespread isotope ratio mass spectrometry technique for analyzing time series of carbon isotopic signatures in plant materials and respired $CO_2$ is costly and labor-intensive, new cutting-edge technologies for stable isotope analysis of $^{13}C$ and $^{18}O$ in $CO_2$, like isotope-specific infrared laser absorption spectroscopy, provide great opportunities to measure changes in carbon and oxygen isotopic signatures in $CO_2$ at the chamber and ecosystem level at high temporal resolution in situ

(Bowling et al., 2003; Bahn et al., 2009; Plain et al., 2009). This will help improve our understanding of environmental effects on C uptake and storage capacity of terrestrial ecosystems, which will be particularly important in the future with higher frequency and magnitude of extreme events (IPCC, 2007).

### 3.7 Bi-directional C transport processes

Efflux of $CO_2$ from the soil to the atmosphere is not the only escape way of carbon out of the soil. It has been shown with isotopically labeled $CO_2$ that roots can take up $CO_2$ and deliver it to aboveground parts of the plant via the transpiration stream (Ford et al., 2007; Moore et al., 2008). It is known since many years that $CO_2$ concentrations in the xylem sap of plants can be up to three orders of magnitude higher than in the atmosphere (Eklund, 1990; Hari et al., 1991; Levy et al., 1999; Teskey et al., 2008 and citations therein). In addition to root uptake of soil $CO_2$, root respiration adds $CO_2$ to the xylem water, followed by stem respiration, i.e. in the inner bark (consisting of the periderm and the phloem), in the cambium and in the ray cells of the xylem (Teskey et al., 2008). As especially the cambium, but also the cell walls of the xylem are strong diffusion barriers, very high $CO_2$ partial pressure ($pCO_2$) can build up inside the stem.

The high xylem $pCO_2$ has significant effects on stem, branch and leaf $CO_2$ exchange. Martin et al. (1994) found temperature-independent fluctuations in stem $CO_2$ efflux in loblolly pine (*Pinus taeda* L.) seedlings, with flux rates being 6.7% lower during periods of high transpiration associated with high temperatures, as compared with periods of low transpiration. They could identify transport of respiratory $CO_2$ in and diffusive loss from the transpiration stream as the most likely cause of this unexpected observation. Levy et al. (1999) calculated a contribution of xylem-transported $CO_2$ to leaf photosynthetic rates of 0.5 to 7.1%, and a contribution of up to 12% to apparent stem respiration rates. Teskey and McGuire (2002, 2005) observed a linear relationship between stem $CO_2$ efflux and xylem sap $CO_2$ concentrations. They could evoke rapid and reversible changes of stem $CO_2$ efflux by manipulating xylem sap $CO_2$ concentrations, explaining up to 77% of the stem efflux variation. The negative relationship of xylem sap $pCO_2$





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with xylem sap velocities or volume flow presents an explanation for the frequently observed midday depression of stem $CO_2$ efflux, when xylem sap flow is highest and, hence, xylem $CO_2$ concentration is lowest (Teskey and McGuire, 2002; Aubrey and Teskey, 2009). Overall, it has to be acknowledged that xylem-mediated $CO_2$ transport from the soil to the atmosphere can be substantial, in some cases equaling soil $CO_2$ efflux (Aubrey and Teskey, 2009).

By far not all of the xylem $CO_2$, be it soil-, root- or stem-derived, is released via stem efflux. It was shown already a long time ago that not only leaves, but also woody tissue can assimilate $CO_2$ via photosynthesis (e.g., Wiebe, 1975; Foote and Schaedle, 1976; Pfanz et al., 2002). Albeit this corticular photosynthesis usually does not lead to a net $CO_2$ uptake, it can compensate for most of the respiratory loss during the light period (Foote and Schaedle, 1976; Pfanz et al., 2002; Cernusak and Marshall, 2000; Wittmann et al., 2006). Given the high xylem $pCO_2$, it is likely that most of the $CO_2$ fixed by the woody tissue is derived from the stem-internal $CO_2$ pool, as could be shown in a $^{13}CO_2$ labeling study with sycamore (McGuire et al., 2009). However, as the transpiration stream ends in the leaves of a plant, the remaining $CO_2$ will be subject to photosynthetic fixation here, which was demonstrated in a labeling study with a 1 mM $^{14}$C-bicarbonate solution fed to excised leaves of *Populus deltoides* (Stringer and Kimmerer, 1993). If soil $CO_2$ taken up by the roots is fixed during photosynthesis, this will have implications for the carbon isotopic signature of photosynthates due to the much lower $\delta^{13}$C of the soil-derived $CO_2$, depending on the amount of $CO_2$ transported with the transpiration stream.

Beside phloem transport, large amounts of C can also be transported via the transpiration stream, even in periods when leaves are fully developed and re-mobilization of C from storage pools is unlikely to occur. In pedunculate oak (*Quercus robur* L.) saplings, Heizmann et al. (2001) found a contribution of xylem-transported carbohydrates, mainly sucrose, glucose and fructose, to the total C budget of leaves of up to 91%, with the highest values occurring during midday depression of photosynthesis at high temperature. In grey poplar, xylem transport of carbohydrates contributed 9%

to 28% to the total C delivered to the leaves (Mayrhofer et al., 2004). This xylem-transported C can form a major constituent of leaf C metabolism, as was shown in labeling experiments with $^{13}$C-glucose in pedunculate oak (Kreuzwieser et al., 2002) and in grey poplar (Schnitzler et al., 2004; Ghirardo et al., 2011). The cycling of C within the plant through the phloem down to the roots and back to the aboveground parts of the plants via the xylem makes the supply of carbohydrates to heterotrophic tissues independent of short-term fluctuations of photosynthetic performance of the plants, as hypothesized by Heizmann et al. (2001), but also leads to a dampening of photosynthetic carbon isotope signals sent from the leaves down to the roots.

## 4 Belowground C turnover

Stable isotopes have proven to be a technique to address the complex carbon transformations in the soil (Kuzyakov et al., 2000; Bowling et al., 2008; Paterson et al., 2009; Kayler et al., 2010a). Here, we extend the view of isotopes in belowground research beyond methodology, but limit the scope of our discussion of carbon isotopes to the investigation of plant-soil interactions with a specific emphasis on plant direct and indirect controls on microbial metabolism, organo-mineral interactions, dynamic soil carbon pools, and microbial markers.

### 4.1 Heterotrophic soil respiration

Heterotrophic soil respiration ($R_h$) is mainly affected by soil temperature and moisture. However, recent studies have shown the importance of soil C availability as a driver of heterotrophic respiration (Vance and Chapin, 2001; Trueman and Gonzalez-Meler, 2005; Scott-Denton et al., 2006). There is evidence that fresh C input into soil can increase, decrease or have little or no effect on $R_h$ (Kuzyakov et al., 2000; Fontaine et al., 2007). This variability of the $R_h$ response to soil C availability may arise in part because soil organic matter (SOM) consists of several functional C pools with different

levels of protection and recalcitrance (Six and Jastrow, 2002). Furthermore, the diversity found in soil microbial communities may result in different preferential usage of soil organic carbon (SOC) sources contributing to the difficulty in correlating changes in $R_h$ in response to soil C availability.

### 4.2 Patterns of SOM $\delta^{13}$C isotopic enrichment with soil depth

Bulk soil organic matter (SOM) is a large-scale representation of belowground biogeochemistry in that isotopic values of SOM integrate processes over a large scale of both space and time. Across many ecosystems SOM becomes increasingly $^{13}$C-enriched (1 to 3‰) with depth. Ehleringer et al. (2000) offered four hypotheses to describe this pattern: (1) the Suess effect – i.e. the decrease in $\delta^{13}$C of atmospheric $CO_2$ due to the admixture of anthropogenic, isotopically depleted $CO_2$ – which accounts for about 1‰ from the litter to about 6 cm depth (Boström et al., 2007); (2) microbial fractionation; (3) preferential microbial decomposition of litter and SOM; and (4) soil carbon mixing. Wynn et al. (2005) included microbes as precursors of SOM and variable mobility and sorption of DOC with variable isotopic values. Identification of which of these hypotheses correctly explains the variation of $\delta^{13}$C with depth will potentially reveal important biogeochemical mechanisms of carbon flow that are common to all ecosystems. Yet, part of the difficulty in validating these different hypotheses is the relatively small change of the vast pool of SOM over a short period of time. However, recent experiments have been carried out that provide direct and indirect evidence of the importance of each process in describing patterns of SOM enrichment with depth.

Studies using the Rayleigh distillation equation (Fry, 2008) have shown some success towards explaining the patterns in SOM $\delta^{13}$C enrichment (Accoe et al., 2002; Wynn et al., 2005, 2006; Diochon and Kellman, 2008). In this case, the Rayleigh distillation equation describes kinetic isotope fractionation (i.e. unidirectional reactions) in an open substrate reservoir and a product (Wynn et al., 2006). The distillation model is a first order reaction that describes the change in $\delta^{13}$C of SOM as a function of the initial SOM carbon content at the surface, the fraction of SOM remaining in the





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soil with depth, and the ratio of the decomposition of $^{12}C$ substrate to $^{13}C$ substrate. The Rayleigh distillation equation is a function of fractionation resulting from two processes: microbial metabolism or differential sorption of organic components to mineral surfaces. From these studies (Wynn et al., 2005, 2006; Diochon and Kellman, 2008), it is apparent that the pattern of $^{13}C$ enrichment of SOM with depth is dependent on the fractionation parameter in the Rayleigh model which is limited in the ability to distinguish between the two fractionation mechanisms.

### 4.3 Fractionation due to microbial metabolism

The carbon metabolism of microbes is crucial to understanding autotrophic and heterotrophic contributions of soil respiration. Thus, if isotopes are to be an effective tool to estimate heterotrophic respiration then we need to quantify the fractionation by microbes to back-calculate the isotopic source that is respired (i.e. old vs. new carbon sources or, more precisely, soil organic matter or root exudates). Microbial $^{13}C$ fractionation is a challenge to measure, but is nonetheless very important to accurately quantify because it can confound the interpretation of results from experiments using $^{13}C$ pulse labeling or natural $^{13}C$ abundance. Fractionation is commonly calculated by quantifying the difference between the isotopic signature of microbial biomass and the isotopic signature of the substrate (i.e. SOM, DOC, culture) and products (i.e. $CO_2$) (Fry, 2008). There is a wide range of estimates of fractionation by microbes from studies implementing this approach (Fig. 5). However, Lerch et al. (2011) found fractionation to vary over time when calculated in this manner, and while changes in substrate could account for this pattern it is also likely that the active microbial community is changing. Fast changes in microbial composition have been documented after addition of labile substrate (Cleveland et al., 2007), rapidly changing environmental conditions (Gordon et al., 2008), and other environmental stresses (Schimel et al., 2007). The question arises whether this variation in microbial fractionation is real, or whether estimates of fractionation are possibly confounded by different soil substrates or microbial community composition.





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A recent review of belowground fractionation (Werth and Kuzyakov, 2010) suggests that fractionation occurs during both microbial uptake and respiration of carbon. The specific processes associated with each are: (1) uptake, associated with enzymatic breakdown of organic matter and transport of monomers into cell walls; and (2) respiration associated with kinetic $^{13}C$ fractionation. The authors listed variation in the availability and molecular composition of substrates as a possible fractionation mechanism during uptake, but this is better defined by mixing processes and microbial community dynamics. Mixing, because soil organic matter is a mixture of chemical compounds, representing different stages of decomposition and availability, which is dependent on the activity and the composition of the microbial community present (see below). They also suggested that preferential substrate utilization of easily degraded compounds results in fractionation during respiration, which may well result in differences between the $^{13}C$ signature of substrate and products (microbial biomass, remaining SOC or $CO_2$). However, the mechanisms behind this are not well defined or understood. Perhaps, microbial substrate selectivity is a function of the enzymes available to break down substrate.

As discussed above, organic matter sources that contain multiple carbon moieties confound accurate estimates of fractionation resulting from microbial metabolism. Experiments that observe biochemical pathways within microbes by utilizing a controlled substrate provide a more precise picture of fractionation. Hayes (2001) compiled a comprehensive review of carbon fractionation in biosynthetic processes. In this review, he shows how fractionation occurring in chemical reactions, pathways and branch points within a cell results in the isotopic composition of carbohydrates, amino acids, nucleic acids, and lipids among different organisms. The often cited study on *Escherichia coli* by Blair et al. (1985) documented fractionation between the acetate and fatty acid synthesis, most likely with the conversion of acetyl phosphate to acetyl-CoA as regulated by phosphotransacetylase. Building on previous studies on plants (Ghashghaie et al., 2003), two mechanisms of fractionation, leading to $\delta^{13}C$ values of $CO_2$ that are different from the initial substrate or microbial biomass, were





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hypothesized: (1) the non-uniform distribution of $^{13}C$ within hexose molecules (or other substrate) (Hobbie and Werner, 2004), which leads to $^{13}C$-enriched $CO_2$; and (2) fractionation during the pyruvate dehydrogenase reaction (Blair et al., 1985), which leads to $^{13}C$ depletion of $CO_2$.

Microbial metabolism type will also affect the magnitude and direction of isotopic fractionation. Differences in biosynthetic pathways result in a diverse isotopic composition of extracted soil microbial biomass. For example, oxygen availability determines in part the level of anaerobic versus aerobic respiration by microbes, which in turn affects the isotopic composition of microbial biomass and fatty acids (Teece et al., 1999; Cifuentes and Salata, 2001). Carbon fixation by heterotrophs, which is estimated to be 4% to 7% of net microbial respiration (Miltner et al., 2004, 2005), is another pathway that leads to different isotopic composition of amino acids and fatty acids (Feisthauer et al., 2008) and could have a significant impact on the overall isotopic signal of microbial biomass and the $CO_2$ respired. Methodologies to study microbial biosynthesis and metabolomics are becoming increasingly more sophisticated (Tang et al., 2009), and studies using these techniques may provide a clear basis from which isotopic differences between substrate and microbial biomass and overall microbial fractionation could be understood.

Studies that assess the isotopic composition of soil microbial biomass usually treat soil microbes as a single C pool without differentiating between metabolically active and dormant microorganisms (Šantrůčková et al., 2000; Lerch et al., 2011). Soil microbial biomass is composed of both active and dormant microorganisms, yet, $CO_2$ respired from microorganisms derives solely from those that are metabolically active (Stenstrom et al., 2001; Werth and Kuzyakov, 2008, 2009; Millard et al., 2010; Werth and Kuzyakov, 2010). Hence, comparing isotopic composition of soil microorganisms as a single C pool to soil $CO_2$ respired could lead to a misinterpretation of the real isotopic effects of fractionation during soil respiration. Furthermore, soil microorganisms as well as roots accumulate C reserves (Plateau and Blanquet, 1994; Ekblad and Högberg, 2000; Sylvia et al., 2005). This is especially true as soil microorganisms

have the capacity to undergo dormancy in sudden adverse environmental conditions. To cope with these conditions, accumulated C in soil microorganisms can be replaced and released by adding readily available C (Bremer and van Kessel, 1990; Wu et al., 1993; Ekblad and Högberg, 2000; Ekblad et al., 2002). Therefore, due to the internal C reserves of microbes, a mixing occurs between available and stored C respiratory substrate, and, consequently, a flawed interpretation of kinetic fractionation during soil microbial respiration may result.

When fractionation of belowground carbon pools is calculated, the uncertainty increases with an increasing degree of metabolic separation between the actual substrate respired and the specific organism respiring. In fact, researchers have already recognized the limitation in defining fractionation as the difference between SOC and microbial biomass by referring to the estimate as "apparent fractionation". This term implies an unknown level of ambiguity and perhaps it is best to avoid its use in favor of discussing potential fractionation due to biogeochemistry and microbial metabolism. Ultimately, the research question asked will drive the level of detail to which fractionation is discussed. For example, in research describing patterns at the ecosystem scale the difference in $\delta^{13}$C between the actual C respired (detected in $\delta^{13}$C of $CO_2$) and SOM may suffice to understand belowground C dynamics in soils at larger scales. However, if the research requires a high degree of precision in estimating microbial fractionation, in partitioning studies for example, then a more sophisticated methodology and quantification is required.

### 4.4 Interactions with mineral surfaces

As found in studies of SOM $\delta^{13}$C patterns with depth, isotopic enrichment occurs with an increase in fine soil particles (Solomon et al. 2002; Bird et al., 2003). Moreover, Wynn et al. (2005) found that in coarse textured soils Rayleigh fractionation did not account for patterns of SOM $^{13}$C enrichment with depth, raising the question of the effect of soil texture, soil mineralogy and chemistry on the pattern of SOM $^{13}$C enrichment with depth. Soil texture also plays a predominant role in carbon stabilization in soil for



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which the mechanisms are not entirely understood (Plante et al., 2006). However, stabilization studies using $\delta^{13}C$ have shed light on the carbon dynamics of organo-mineral association (Kayler et al., 2011) and the role plants play in carbon stabilization below ground.

Analysis of stable isotopes in soil fractions has given some insight into the mechanisms behind SOM stabilization. Studies that have analyzed the isotopic signature of SOM fractions (beyond $C_3$/$C_4$ labeling techniques) have found patterns of enrichment of $\delta^{13}C$ and $\delta^{15}N$ with increasing density of sequentially separated SOM fractions (Huygens et al., 2008; Sollins et al., 2009; Marin-Spiotta et al., 2009). Using several chemical techniques including isotopes, Mikutta et al. (2006) showed that organo-mineral interactions accounted for over 70% of the carbon stabilized in the soils they analyzed. Organo-mineral interactions refer to the bonding of organic matter via polyvalent cations to mineral surfaces (von Lützow et al., 2006). Using isotopes, Mikutta et al. (2006) also substantiated the role of microbial exudates and biomass providing coatings over minerals allowing for more efficient sorption (Kleber et al., 2005) as well creating chemically resistant organic matter. The authors also found that recently deposited organic material can be stabilized with mineral surfaces, suggesting that plant-soil interactions can also directly lead to carbon stabilization, long thought of as a slow process driven by decomposition only.

While changes in soil organic matter appear slow, because the pool is so vast, the processes of carbon loss and stabilization occur relatively rapidly. Questions still remain concerning how strongly organic matter is bonded to the mineral surface and to surrounding layers of the organo-mineral complex (Kleber et al., 2005). However, this research does suggest that plants may play a pivotal role in the fast cycles of carbon stabilization (Trumbore, 2006). Isotopes used toward identification of carbon stabilization mechanisms belowground are just in their infancy, and with the help of models (Kleber et al., 2007) and soil properties, we will be able to explain not only patterns of the $\delta^{13}C$ of SOM with depth, but also questions regarding carbon accumulation and stabilization (Kleber et al., 2011).





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## 4.5 Transfer of C from leaf litter and DOC to soil and microbes

Apart from the primary flux of C from plant assimilates into soil, plant litter degradation and the subsequent C distribution into soil carbon pools and microbial communities provide an important secondary flow of carbon into the soil (Elfstrand et al., 2008). For example, soil microbial dynamics are controlled through complex interactions with plants and are influenced by a range of organic compounds added to soils from plants as root exudates and as litter inputs (Butler et al., 2004; Bardgett et al., 2005; Kaštovská and Šantrůčková, 2007; Elfstrand et al., 2008; Denef et al., 2009; Esperschütz et al., 2009). Thus, a key issue in studies investigating soil carbon dynamics has been tracing the carbon input into soil from leaf litter decomposition (Liski et al., 2002; Dungait et al., 2010).

Litter decomposition is the breakdown of highly organized plant tissue to complex organic compounds that is regulated by both biotic and abiotic processes. Since decomposition is slow, the litter layer of an ecosystem is composed of a continuum of fresh litter to unrecognizable organic matter and serves as a bottleneck for a significant portion of primary productivity sent belowground. But there still remain a series of questions of (1) how the carbon in the litter layer reaches the mineral soil, (2) how the biogeochemical processes determine the fate of organic matter, either remaining in the litter layer or being transported into the soil profile, and (3) which mechanisms control litter-microbe interactions and dynamics. These questions have important ramifications for the carbon cycling of ecosystems and for the use of isotopes to elucidate the complex chemical nature of litter decomposition and incorporation into soil organic matter.

Mechanisms behind the isotopic patterns in leaf litter are considered to be (1) selective preservation of recalcitrant compounds that are depleted in $^{13}$C, (2) preferential consumption of $^{12}$C by microbes, (3) incorporation of exogenous organic matter, and (4) transport of dissolved organic matter within the soil profile (Nadelhoffer and Fry, 1988). Preston et al. (2009) found that patterns in the isotopic signal of leaf litter located on the soil surface depend on the degree of decomposition. The decomposing



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leaf litter tended to become more $^{13}$C-depleted with a decrease in the amount of the original litter mass. Only after about < 30% of the original litter material was remaining, the isotopic composition shifted towards an enriched signal. They attributed this shift to sorption of older soil organic carbon to the remaining leaf litter. Osono et al. (2008), found a similar depletion of litter over a three-year period of decomposition. However, they inferred isotopic patterns of leaf litter were a result of selective C loss as a function of lignin concentration. Thus, patterns in the isotopic signature of leaf litter are a function of decomposition and the degree to which it is integrated with mineral soil, an important consideration when using litter carbon as a tracer source for studies of carbon belowground.

Isotopic studies of the role of leaf litter input into the mineral soil has yielded a better understanding of carbon cycling and stabilization at the soil surface and carbon transported to deeper soil horizons. Bird et al. (2008) found more than half of the needle carbon had been lost from the top 5 cm of soil after 1.5 years, similar to loss rates reported by Müller et al. (2009). Furthermore, the $^{13}$C of decomposed leaf litter remained in the light fraction of pools and was not physically protected within soil aggregates. Similarly, Rubino et al. (2010) found in a decomposition experiment with $^{13}$C-labeled litter that up to one third of the litter mass was lost as $CO_2$, while the rest was transported into the mineral soil. Within the mineral soil, Kramer et al. (2010) found that microbes used < 10% of leaf litter carbon for respiration or growth and did not utilize dissolved organic carbon (DOC) from the organic horizon as a carbon source.

The carbon in the leaf litter can be characterized to have three fates: initial mineralization by microbes and soil fauna, stored as readily available substrate in the upper mineral horizons, and transported to deeper horizons (Froegberg et al., 2007; Sanderman and Amundson, 2008; Kindler et al., 2011).

Carbon compounds from aboveground litter are one source of DOC (Kindler et al., 2011), and roots are a significant, if not the predominant, contributor as well (Kramer et al., 2010). Up to 70% of the DOC originating from leaf litter can be degraded within four weeks (Müller et al., 2009), which illustrates how fast this pool turns over and



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supports the notion that DOC production is the rate-limiting step of soil respiration (Bengtson and Bengtsson, 2007; Cleveland et al., 2007). Because of the high turnover of DOC (2 to 3 times per day; Bengtson and Bengtsson, 2007; Giesler et al., 2007; Kalbitz et al., 2000) it is difficult to measure concentrations and isotopic composition in the litter layer, though general patterns have been observed. Sanderman et al. (2008) found a pattern of DOC $^{13}C$ enrichment with depth. Using batch adsorption experiments, they found that the $^{13}C$ enrichment of DOC with depth was best explained by exchange of organic matter between the liquid and the solid phase, as the soil solution moves through the soil profile, independent of net adsorption or net desorption of DOC. This finding substantiates the hypothesis that the mechanism behind DOC $^{13}C$ enrichment with depth is a continuous exchange of carbon in the soil solution and older organic matter in the soil. Regardless whether the carbon originates from aboveground or belowground litter, DOC is an important driver of rapid carbon cycling belowground and also a fast moving pool of old and new carbon that contributes to the isotopic signature of stabilized soil carbon.

Microbial communities are also regulated by litter input (Eilers et al., 2010), and communities can change rapidly depending on the available substrate (Cleveland et al., 2007). Through stable isotope probing it is now possible to characterize microbial communities utilizing carbon from litter. Using $^{13}C$-enriched litter in a poplar plantation, Rubino et al. (2010) have shown that Gram-positive bacteria are primarily involved in litter degradation compared to other microbial groups (Gram-negative bacteria, actinomycetes and fungi). This finding was based on detection of significant levels of $^{13}C$ in all PLFAs, indicating high amounts of litter C incorporated into the whole soil microbial biomass. Gram-positive bacteria were the dominant group in the soil and contained around 75% litter-derived C assimilated by the soil microbial biomass after one year. However, after 11 months, similar $\delta^{13}C$ values across all the microorganisms illustrated either (1) a similar litter C incorporation by all microbial communities, or (2) that the system had been at steady state after 11 months such that incorporated litter C was being recycled within the soil microbial biomass.





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Uncertainty still remains in microbial community analysis and potential carbon sources. For example, Kramer et al. (2010) showed that the source of carbon in the biomarkers present in their incubation studies did not originate from litter or SOM, leaving only roots as the primary source. Using fatty acid methyl ester isotopic composition, Lerch et al. (2011) found a switch in the active microbial community from Gram-negative bacteria initially, which consumed the easily degradable and water-soluble substrates, to Gram-positive bacteria and fungi later. Based on their isotopic measurements, Lerch et al. (2011) also suggested that there is a potential lag between changes in the bacteria actually consuming carbon belowground, and the community structure as a whole.

## 5 Physical interactions in soil-atmosphere $CO_2$ exchange

Section 4 illustrates the complexity of carbon sources belowground; yet, understanding how C is released from a stabilized state in soil and released as $CO_2$ is a priority to determine soil as a net source or sink of C to the global greenhouse budget. Measuring soil respiration is arguably the best method to quantify the release of active C from these belowground organic and mineral sources. Thus, the C isotopic signature of soil respiration ($\delta^{13}C_{R_s}$) can be a promising tool to partition C sources of soil respiration, monitor belowground biological activity, and potentially identify and quantify the mechanisms of C stabilization and release. One of the inherent limitations of isotopic partitioning of respiration is the similar isotopic composition of potential sources, thus, achieving precise estimates of the $\delta^{13}C$ of soil $CO_2$ efflux ($\delta^{13}C_{R_s}$) requires the reduction of measurement artifacts as well as validation of measurement assumptions. This is why it is important to recognize the potential physical interactions of $\delta^{13}C_{R_s}$ with the soil and the potential outcomes which can manifest in isotopic fractionation, time lags from production sources, and non-steady-state events.

There are several physical processes that occur along the pathway of soil $CO_2$ from soil to surface which can lead to fractionation including physical and chemical effects on





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gas transport as well as $CO_2$ production rates and near-surface atmospheric boundary conditions (Severinghaus et al., 1996; Bowling et al., 2009; Nickerson and Risk 2009a,b; Kayler et al., 2010b; Moyes et al., 2010; Gamnitzer et al., 2011). Gaseous diffusion of $CO_2$ can lead to the most $^{13}C$-enriched signal when Knudsen diffusion (where diffusive transport is dominated by the collision of $CO_2$ molecules with pore walls instead of other gas molecules) dominates, or it can lead to incorrect estimates of fractionation if transport is not at steady state (Bowling et al., 2009; Kayler et al., 2010b). Correctly or not (Clifford and Hillel, 1986), gaseous diffusion is assumed to dominate soil gas transport. However, estimates of the diffusion coefficient ($D_s$) are often a parameter of high uncertainty. In a detailed analysis of soil production estimates made from profile $CO_2$ measurements, Koehler et al. (2010) demonstrated that the models used to interpolate diffusion over soil depth are highly dependent on the functions used to describe the distribution of $D_s$. Furthermore, they suggest that water within soil aggregates may result in $CO_2$ storage that is not accounted for in current models. Models of diffusion that incorporate the van Genuchten function of soil hydraulic conductivity (van Genuchten, 1980) have shown initial success in accounting for soil moisture effects on diffusion (Resurreccion et al., 2008). However, these strategies have yet to be developed for isotopic fractionation and mixing.

Transport of $CO_2$ to the soil surface induced by pressure pumping during fluctuations in wind speed or background atmospheric conditions can be a considerable component of total surface flux (Lewicki et al., 2003; Takle et al., 2003, 2004; Poulsen and Møldrup, 2006). Only a few studies exist that describe $\delta^{13}C$ behavior of $CO_2$ during advective gas transport. A sustained bulk flow, due to advection, will transport $^{13}CO_2$ and $^{12}CO_2$ at the same rate leading to a $\delta^{13}C$ of $CO_2$ at the surface that is similar to the soil gas (Camarda et al., 2007). However, advection due to small pressure perturbations associated with chamber placement on the surface could also result in a higher representation of $^{13}C$-enriched $CO_2$ from the soil pore space in the mixture that arrives in the surface chamber leading to biased estimates of $\delta^{13}C_{R_s}$ (Kayler et al,. 2010b; Phillips et al., 2010). A difficult challenge is quantifying and modeling soil

surface concentrations (Moyes et al. 2010; Kayler et al., 2011). The dynamics at the surface can be attributed to potential evening concentration build-up, or fluctuations in surface wind speed. Indeed, in a well-controlled study, Moyes et al. (2010) found the physical dynamics at the soil surface to drive the diel fluctuations at their site. Evidence also exists of bias in estimates of $\delta^{13}C_{R_s}$ due to advection from wind events in snow in a subalpine forest (Bowling et al., 2009). However, there are very few isotopic studies that have observed and quantified the effects of alternative gas transport mechanisms in soil nor, for that matter, have corrections been developed.

It is clear that gas transport can have a strong impact on the relative gradient between $^{13}CO_2$ and $^{12}CO_2$ in the soil profile, but gradients in soil temperature and water vapor can also result in changes in the concentration gradient, independent of diffusive or advective transport mechanisms. In the case of temperature, the lighter isotope tends to move toward the warmer end of the gradient, while the heavier isotope moves toward the cooler end (Grew and Ibbs, 1952). Likewise, an enrichment in soil gas isotopic composition occurs with an increase in water vapor flux from soil (Severinghaus et al., 1996) and has been calculated to $^{13}C$ fractionation of $CO_2$ of 0.12‰ (Kayler et al., 2011). Moreover, in the same study, several estimates of $\delta^{13}C_{R_s}$ were driven out of steady state by the soil temperature gradient, which can be corrected for (Severinghaus et al., 1996). These findings are based on discrete measurement of $\delta^{13}C_{R_s}$ and the dominant factors that impact isotope fractionation during $^{13}CO_2$ efflux may be further resolved when continuous measurements of both $\delta^{13}C_{R_s}$ and soil physical factors are analyzed.

Although it has been known that these fractionation mechanisms exist, the problem remains how to recognize them in the field. This is difficult to overcome when relying solely on the flux off the soil surface, as with chamber measurements, because the information contained in this flux is the end-product of many processes occurring belowground, processes that are assumed to be at steady-state during the measurement period (Livingston et al., 2005). To account for this black box approach, dynamic production-transport models are used, but these do not account for most of the





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potential fractionation mechanisms described previously, nor do they include the uncertainty surrounding the parameters (e.g. diffusion) used to model soil gas isotopic fractionation and transport. Subsurface gas measurements have shown promise for achieving robust estimates of $\delta^{13}C_{R_s}$, and allowing analysis for fractionation and validation of steady-state assumptions (Andrews et al., 2000; Steinmann et al., 2004; Kayler et al., 2008, 2010b; Moyes et al., 2010; Kayler et al., 2011). However, questions still remain concerning this approach. Is, for instance, the flux from the litter layer well represented? Or, is the assumption of a homogenously mixed source gas realistic? Related to this latter point is the use of isotopic mixing models. Kayler et al. (2010c) have shown that respiration measurements, such as from soil, tend to be more accurate and precise when the Miller-Tans model used with the geometric mean regression is applied to the data, because of the relatively large measurement error that occurs with measuring high $CO_2$ concentration gas. The Keeling mixing models used with chambers have also been shown to have a bias that results in enriched estimates of $\delta^{13}C_{R_s}$ with increasing sampling time (Nickerson and Risk, 2009b). Until a robust method for measuring $\delta^{13}C_{R_s}$ is developed that accounts for these physical processes, future studies will need to incorporate all three approaches: soil chamber, $CO_2$ profile and transport-production models (e.g., Moyes et al., 2010).

Physical isotopic fractionation and mixing processes do not occur independently, and they often interact with changes in soil biological processes posing a further challenge to studies of $\delta^{13}C_{R_s}$. For example, changes in rates of production also alter the isotopic signal at the soil surface, the faster diffusing $^{12}CO_2$ isotopologue arrives at equilibrium first, thus, an increase in production results in a depleted signal and a decrease in production results in an enriched signal (Amundson et al., 1998; Nickerson and Risk, 2009a). The way forward in $\delta^{13}C_{R_s}$ research is to account for these effects associated with soil physical properties, so that biological phenomena related to the soil-plant-atmosphere continuum can be characterized accurately.



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## 6 Conclusions and outlook

This review has aggregated the complex meshwork of carbon transformation and transport processes in the plant-soil-atmosphere continuum and their implications for carbon isotopic signatures of the different compounds at different stages and locations (Fig. 4). It has given evidence of the tight coupling of processes in the plant-soil system, which calls for more integrated multidisciplinary approaches towards understanding plant and ecosystem C dynamics, combining the fields of (eco)physiology, microbiology and soil sciences. Furthermore, this review has demonstrated that research using information from C isotopes is a powerful tool permitting both tracing of C molecules and an integrated view of physical, chemical and biological processes in ecosystems across space and time. However, the review has also shown the current limitations and frontiers in the field, indicating that multiple interactions between biochemical processes at the cellular level, whole-plant physiology including plant-internal C translocation, biotic interactions as well as physiological and physical fractionation steps may complicate the interpretation of isotopic signatures at the plant and ecosystem scale. Here, tracer experiments using highly $^{13}$C-enriched or depleted substrates have provided and will yield novel insights, especially when combined with the recent developments in instrumentation, including laser absorption spectroscopy, compound-specific C isotope analysis and nanoSIMS, i.e. sary ion mass spectrometry, which allows determination of stable isotope ratios at the nanometer scale.

Amongst the emerging research questions that may need to be addressed in the near future we highlight the following:

1. How do environmental factors and plant physiology affect post-carboxylation C isotope fractionation? How do changes in these fractionation processes translate into metabolic flux information?

2. How do changes in metabolic fluxes scale to ecosystem C fluxes?

3. What is the relationship between the age of plant C stores and their remobilization





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potential, and how is it affected by plant age, phenology, and environmental conditions?

4. What processes determine the coupling of photosynthesis and respiration, especially between canopy and soil? What is the role of the transfer of C via sugars in the phloem versus indirect signaling effects (including pressure concentration waves)? Are such effects universal or do they differ between plant species/functional types and seasons?

5. What is the role of physical (diffusion, dissolution) and physiological (re-fixation) processes as co-determinants of $\delta^{13}C$ measured in plant- and soil-respired $CO_2$ and how do these processes affect isotopic time lags between photosynthesis and respiration?

6. How does environmental stress affect C fluxes in the plant-soil system?

7. How pronounced is the upward $CO_2$ transport from roots to aboveground plant organs across plant species/functional types and seasons, and how does it affect plant and ecosystem C dynamics and C isotope signatures?

8. How strongly do plant-microbe interactions and related priming effects influence SOM turnover, C retention in microbial biomass and SOC isotope composition? How much are they determined by vegetation composition and how are they modified by changing environmental conditions?

Addressing these questions with the emerging technologies will likely permit major progress towards our understanding of environmental effects on C uptake, allocation, storage and release in the plant-soil system and thereby contribute to improving our projections of the C cycle in a rapidly changing environment.





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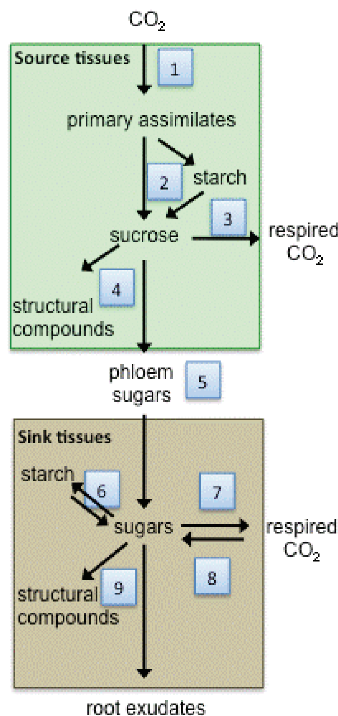
Isotope composition

Fractionation and other processes affecting the isotope composition




1 Photosynthetic C-isotope fractionation

2 Post-carboxylation C-isotope fractionation in autotrophic tissues related to transitory starch metabolism (aldolase and transketolase fractionation)

3 Respiratory fractionation

4 Post-carboxylation C-isotope fractionation leading to compound specific differences

2 + 3 + 4 Post-carboxylation C-isotope fractionation in photosynthetic tissues

5 Mixing processes during phloem transport

6 Fractionation associated with seasonal starch metabolism

7 Respiratory fractionation

8 Fractionation associated with PEPc (re)fixation

9 Post-carboxylation C-isotope fractionation leading to compound specific differences

6 + 7 + 9 Post-carboxylation C-isotope fractionation in non-green tissues

**Fig. 1.** Summary of the plant-related processes that potentially influence the carbon isotopic composition of organic matter and $CO_2$. Carbon isotope fractionation and other processes (i.e. mixing of pools), which influence the isotope composition are listed on the right side of the figure. In addition to the listed fractionation processes, the carbon isotope composition of atmospheric $CO_2$ influences $\delta^{13}C$ of organic matter. The figure is adapted from Gessler et al. (2009b).





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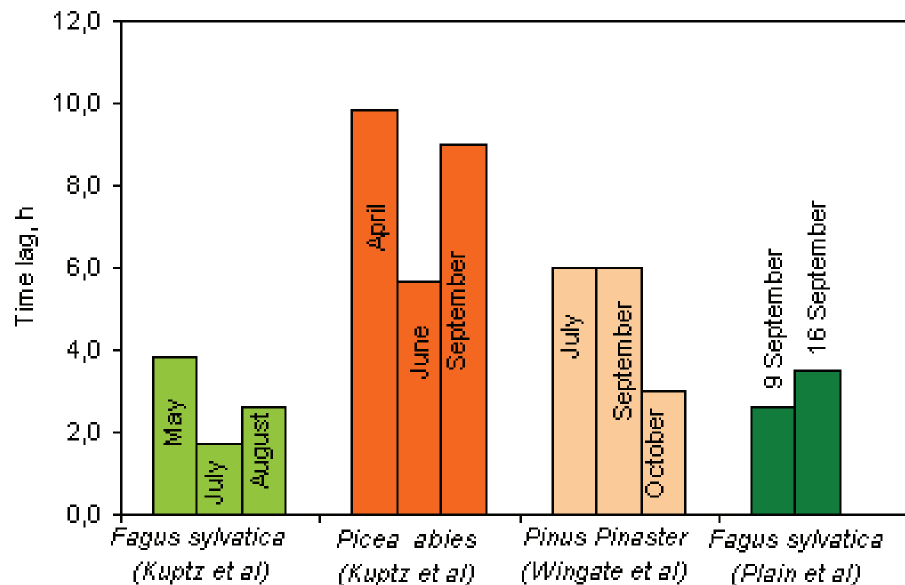


**Fig. 2.** Seasonal changes in time lag measured by tracing variations in $\delta^{13}C$ at natural abundance level (Wingate et al., 2010; Kuptz et al., 2011a) or after $^{13}CO_2$ pulse-labeling (Plain et al., 2009) in soil respiration and trunk respiration (at 1 m height; Kuptz et al., 2011a). Average values were calculated based on monthly ranges reported in Wingate et al. (2010).





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**Fig. 3.** Estimates of respiration fractionation from different experimental approaches (grey bars: from $C_3$ plants; dark grey bars: Rayleigh distillation methods, black bars: $C_4$ plants). The dashed line is the mean of all estimates. Data sources: Werth and Kuzyakov (2010); Wynn et al. (2005, 2006); Diochon and Kellman (2008).





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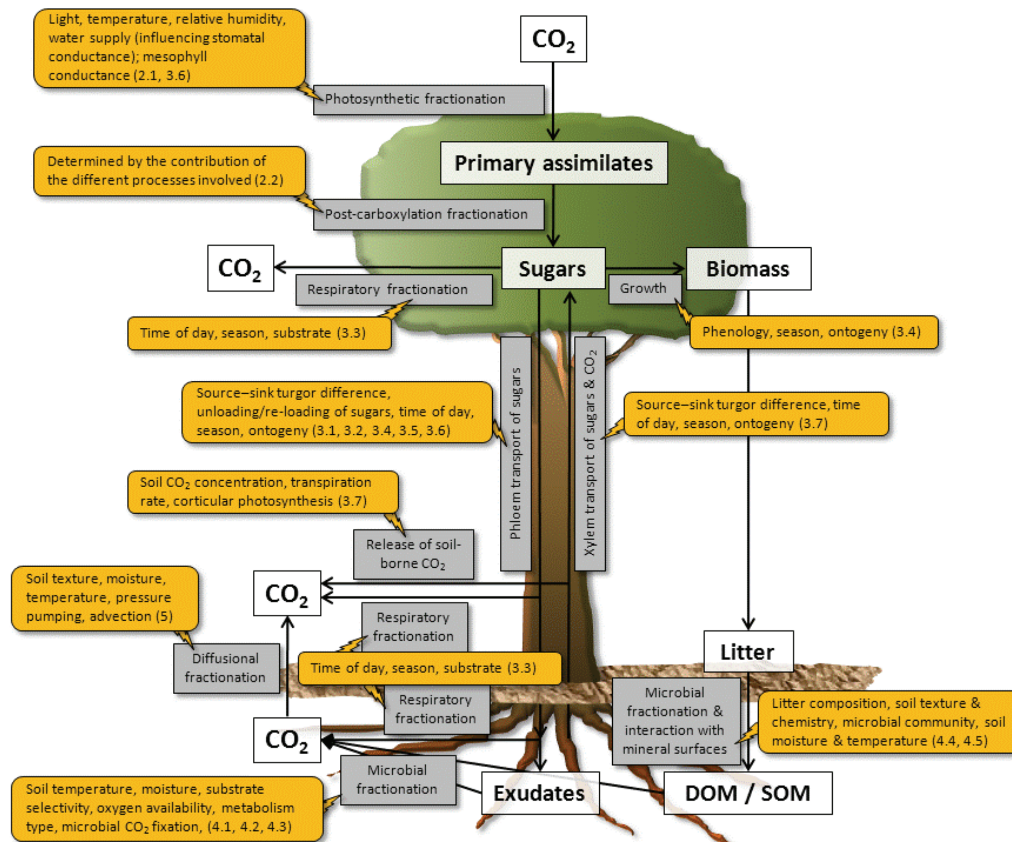


**Fig. 4.** Overview of processes and factors determining the isotope signature of C pools and fluxes in space and time in the plant-soil-atmosphere continuum. White boxes represent pools, gray boxes show fractionation or other processes determining the C isotope composition of the involved compounds, and orange boxes depict control factors. The numbers in parentheses refer to the respective chapters of the review.





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