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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

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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. A further 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. Finally, we highlight state-of-the-art stable isotope methodologies and their latest developments. 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 currently impede the interpretation of isotopic signals in CO_2 or organic compounds at the plant and ecosystem level. This review tries to identify present knowledge gaps in correctly interpreting carbon stable isotope signals in the plant-soil-atmosphere system and how future research approaches could contribute to closing these gaps.

1 Introduction

The flux of carbon dioxide between the atmosphere and the terrestrial biosphere and back is approx. 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 primary 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, 2010; 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 and atmospheric composition changes and maintaining the carbon sequestration potential, we have to deepen our knowledge on the processes determining plant-arbon 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, which change the isotopic composition of compounds involved in such processes. The carbon isotope composition is usually expressed in δ notation (in ‰ units), relative to the international standard Vienna Pee Dee Belemnite (VPDB) (Hut, 1987). The carbon isotopic composition $\delta^{13}C$ of any sample is thus expressed as deviation from VPDB as shown in Eq. (1):

$$\delta^{13}C = \frac{R_{sample}}{R_{VPDB}} - 1 \quad (1)$$

where R is the isotope (abundance) ratio ($^{13}C/^{12}C$) of a given sample (R_{sample}) and of VPDB ($R_{VPDB} = 0.0111802$; from Werner and Brand, 2001), respectively.

The notation for isotope fractionation is the capital Greek letter Δ. Carbon isotope discrimination ($\Delta^{13}C$) is defined as the depletion of ^{13}C during any process preferring the lighter isotopologue:

$$\Delta^{13}C = \frac{\delta^{13}C_s - \delta^{13}C_p}{1 + \delta^{13}C_p} \quad (2)$$

where $\delta^{13}C_s$ is the carbon isotope signature of the source (or the substrate entering a reaction; e.g. CO_2 when photosynthetic fractionation is considered) and $\delta^{13}C_p$ is the isotopic signature of the product of a process (Farquhar et al., 1982).

Two major fractionation types can be distinguished, which 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 diffusion, phase transition 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 atmosphere-plant-soil interactions in the global terrestrial carbon cycle and to predicting future atmospheric carbon dioxide levels under global change. The physiological information encoded in the isotope signature due to fractionation processes allows in principle to link changes in carbon metabolism on the biochemical scale with whole ecosystem carbon dynamics. In addition, the analysis of temporal variations in the isotopic composition of different chemical compounds in different ecosystem compartments provides a tool to assess the fate of carbon in plant, soil and atmosphere. However, as the isotopic signatures of carbon compounds transported in the plant-soil-atmosphere system do not necessarily remain unchanged during transport, it is important to know all relevant processes involved in generating and altering theses signatures. 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.

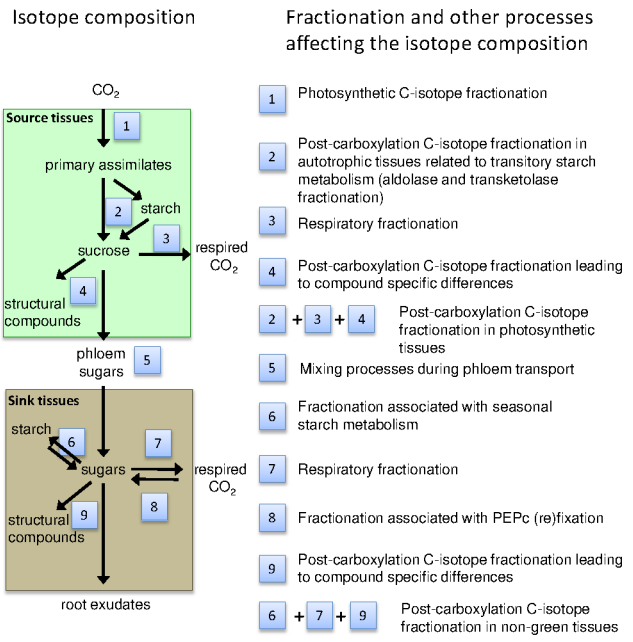

Fig. 1. Summary of the plant-related processes that potentially influence the carbon isotopic composition of organic matter and CO_2. Carbon isotope fractionation and other processes (i.e. mixing of pools), which influence the isotope composition are listed on the right side of the figure. In addition 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).

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 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) in C_3 plants is described according to the following equation (Farquhar et al., 1982):

$$\Delta^{13}C = a_b\frac{p_a - p_s}{p_a} + a\frac{p_s - p_i}{p_a} + (e_s + a_l)\frac{p_i - p_c}{p_a} + b\frac{p_c}{p_a} - \left(\frac{eR_d/k}{p_a} + \frac{f\Gamma*}{p_a}\right) \quad (3)$$

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.

In literature, often a simplified version of the model presented in Eq. (3), assuming a two-stage model (diffusion through the stomata followed by carboxylation, is applied to estimate photosynthetic carbon isotope fractionation:

$$\Delta_i = a + (b - a)\frac{p_i}{p_a} \quad (4)$$

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:

$$A = \frac{g_m(p_i - p_c)}{P} \quad (5)$$

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. 4) 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 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≈10 ‰) and thus can have a significant impact given that Γ^*/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).

Carbon isotope discrimination related to C_4 photosynthesis is much smaller and less variable compared to the C_3 pathway. Net fractionation of the CO_2 fixation by the enzyme phosphoenolpyruvate carboxylase (PEPc) in the mesophyll cell is −5.7 ‰, i.e. there is a discrimination against the lighter carbon, ^{12}C (Farquhar, 1983). This is mainly due to the fact that PEPc uses HCO_3^- as substrate and the dissolution plus hydration of CO_2 enriches ^{13}C in HCO_3^- by 7.9 ‰ (at 25 °C; Mook et al., 1974), and that PEPc discriminates by only 2.2 ‰ against ^{13}C. The PEPc-fixed CO_2 will be released again in the bundle sheath cells, where it is re-fixed by Rubisco. Since part of the CO_2 released in the bundle sheath tissue leaks out to the mesophyll (Hatch, 1995), a (metabolic) branching point is formed, which allows ^{13}C discrimination by Rubisco (Farquhar, 1983). Farquhar (1983) developed the following (simplified) equation to describe the carbon isotope discrimination of C_4 photosynthesis:

$$\Delta = a + (b_4 + b_3\phi - a)\frac{p_i}{p_a} \quad (6)$$

where b_4 describes the discrimination of the fixation of gaseous CO_2 in equilibrium with HCO_3^- (at 25 °C) by PEPc (for details see Farquhar, 1983 and Farquhar et al., 1989), ϕ is the relative proportion of the carbon fixed by PEPc that leaks out of the bundle sheath ("bundle sheath leakiness"; Farquhar, 1983) and b_3 describes the discrimination by Rubisco.

The Crassulacean acid metabolism (CAM) as a particular modification of the photosynthetic carbon fixation also imprints a specific carbon isotope signal on the assimilates (O'Leary, 1988). The most simple description of the CAM according to Lüttge (2004) is that there is nocturnal uptake of CO_2 via open stomata, CO_2 fixation by PEPc and vacuolar storage of organic acid assimilates, mainly malic acid (phase I; Osmond, 1978), and daytime remobilization of vacuolar organic acids, decarboxylation and re-fixation of the released CO_2 behind closed stomata by Rubisco (phase III). The malate stored at night will show the same discrimination as for C_4 species without bundle sheath leakiness and since CO_2 evolution during phase III is assumed to be negligible, the carbon isotope discrimination in phase I and III might be described by Eq. 6 assuming ϕ to be 0 (Farquhar et al., 1989). In the early light period (phase II) and in the late light period, when organic acids are exhausted (phase VI), however, stomata are open and external CO_2 can be fixed by Rubisco (Osmond, 1978; Farquhar et al., 1989). Both, phase II and phase IV are very sensitive to environmental parameters (Lüttge 2004) and thus the relative contribution of PEPc- (phase II and III) and Rubisco-driven (mainly phase IV) discrimination might also vary with the environment.

High variations of photosynthetic carbon isotope fractionation in C_3 species over the day, between days and over the growing season were recently revealed by direct online isotope measurements under field conditions, which allow data acquisition with high temporal resolution by applying novel laser spectroscopy techniques (Wingate et al., 2010). Over the whole growing season, photosynthetic carbon isotope fractionation for branches of maritime pine at a field site in France amounted to 10 to 35 ‰. These values agree well 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 as occurring in C_3 plants, 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, 2010) (see 3.4). 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 to directly relate $\delta^{13}C$ to p_i/p_a or water-use efficiency in C_3 species 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; 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, 2011). 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 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 intramolecular patterns of $\delta^{13}C$ and 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; Werner and Gessler, 2011). 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).

Decarboxylation of pyruvate by the pyruvate dehydrogenase complex (PDH), coupled to the glycolysis pathway, 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 δ^{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, and only recently Werner et al. (2011) argued that the impermeability of the inner chloroplast membrane for acetyl-CoA as well as the channeling principle of the TCA cycle enzymes prevent the enzymatic reactions in the TCA cycle to effectively fractionate against ^{13}C in vivo.

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., 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 δ^{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 PEPc is also known to occur in roots (8 in Fig. 1) and has also 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). Net discrimination of PEPc against ^{12}C of 5.7 ‰ (including the equilibrium hydration of CO_2) (Farquhar, 1983), enriches organic matter in ^{13}C and leaves ^{13}C-depleted CO_2 molecules behind (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 ^{13}C-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 δ^{13}C of plant CO_2 efflux is still a matter of debate (Tcherkez, 2010; Werner, 2010; Werner et al., 2011).

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 (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 in δ^{13}C 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 δ^{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 (see 3.1). 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 δ^{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 as well as their dependency on environmental and plant physiological processes and to quantify their contribution to post-carboxylation isotope fractionation. Moreover it is urgently needed 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 plant-soil system and are imprinted in respired CO_2. The process of C transport in the plant itself is not assumed to fractionate against the ^{13}C-isotopologues of the transported compounds. However, temporal changes in C allocation and metabolic processes along the transport pathways can strongly affect this relationship between environmental conditions and δ^{13}C. For example, it has been observed that phloem sucrose is ^{13}C-enriched in the trunk compared to the twig phloem of trees (e.g. Brandes et al., 2006, 2007). It is likely that metabolic processes associated with phloem transport (such as phloem loading, unloading and mixing; 5 in Fig. 1) but not the transport itself is responsible for these patterns. Since phloem-allocated sucrose is the main carbon source for all processes in non-green plant parts, spatial variations in δ^{13}C along the plant axis and the processes involved need to be taken into account when interpreting respiratory isotope signals. Moreover, transport dynamics determine the coupling of the isotope signals above- and belowground and thus an understanding of the underlying processes is crucial to interpret carbon isotope signals on the ecosystem scale. 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 these variations can influence 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 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). This mechanism of carbon release and partial retrieval might also explain the often observed ^{13}C enrichment of phloem sugars during transport in basipetal direction (Gessler et al., 2009b). Part of the sugars released might undergo metabolic conversion in reactions fractionating against the heavier isotopologue.

Due to mass balance reasons the unreacted sugars, which are reloaded in the phloem, will be ^{13}C-enriched (Hobbie and Werner, 2004).

The differential release/retrieval balances in the phloem 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 noncentralized manner and to serve both long distance transport and local supply of surrounding tissues.

Mencuccini and Hölttä (2010) 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, 2010). Soil respiration as an example would already be upregulated hours or days before the newly assimilated substrate arrives belowground and could imprint its δ^{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.

The time lag caused by C translocation from leaves to belowground sites of respiration has been extensively reviewed (Davidson and Holbrook, 2009; Kuzyakov and Gavrichkova, 2010; Mencuccini and Hölttä, 2010) since photosynthesis has been identified as a key driver of soil respiration (Högberg et al., 2001). Generally, time lags determined as propagation of fluctuations in δ^{13}C at natural abundance increase with tree height, with transport rates between 0.07 and 0.5 m h^{-1} (Kuzyakov and Gavrichkova, 2010; Mencuccini and Hölttä, 2010), although carbon translocation velocities are often higher in tall plants (Lang, 1979; Thompson and Holbrook, 2003; Van Bel and Hafke, 2005; Mencuccini and Hölttä, 2010), potentially due to stronger root C sinks associated with a larger belowground biomass. In certain studies, seasonal changes in belowground C allocation had no effect on the time lag between assimilation and use of assimilates in belowground respiration (Horwath et al., 1994; Högberg et al., 2010), suggesting that phloem path length and structural differences were the main determinants of C transfer velocity. In contrast, other studies reported considerable variation of the time lag during the growing season in the same trees (Plain et al., 2009; Wingate et al. 2010; Dannoura et al., 2011; Epron et al., 2011; Kuptz et al., 2011a) (Fig. 2). However, the mechanisms behind such variability are still unknown even though seasonal variations of carbon storage and remobilization in the trunk are the most likely mechanisms to affect the transfer of carbon as well as the conveyance of the carbon isotope signal from the canopy in basipetal direction over the growing season (Offermann et al., 2011).

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 may even decrease with increasing plant height as has been shown for *Lolium perenne* (Kuzyakov and Gavrichkova, 2010).

Recently Vargas et al. (2011) observed multi-temporal correlation between photosynthesis and soil respiration across different ecosystems with time periods between 1 and 16 days. Based on a comprehensive time series analysis of flux data they concluded that multiple biophysical drivers are likely to coexist for the regulation of allocation and transport speed of carbon. Strong correlations both within a 1-day

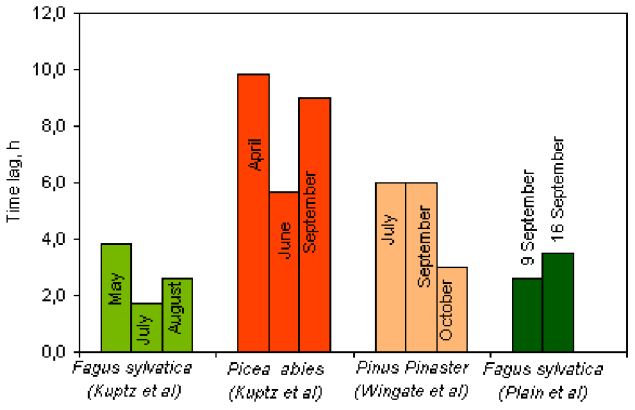

Fig. 2. Seasonal changes in time lag measured by tracing variations in $\delta^{13}C$ at natural abundance level (Wingate et al., 2010; Kuptz et al., 2011a) or after $^{13}CO_2$ pulse-labeling (Plain et al., 2009) in soil respiration and trunk respiration (at 1 m height; Kuptz et al., 2011a). Average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

period and within periods >1d for forests suggest that the link between assimilation and soil respiration might potentially involve both the propagation of pressure-concentration waves in the phloem and the actual transport of new assimilates from the leaves to belowground tissues. In addition, the correlations with longer time periods might be a result of transient storage and remobilisation of carbon in the plant tissues. Moreover, Heinemeyer et al. (2011) reported differences for particular components of soil respiration (root and mycorrhizal respiration) in their temporal relation and response to gross primary production. The authors assume that carbon storage in roots and/or fungi over days to weeks and later allocation to mycorrhizae might explain the correlation between photosynthesis and mycorrhizal respiration at longer temporal scales.

As a consequence, not only phloem transport but also short-term storage/remobilisation and transfer to rhizosphere biota (see 3.2) have to be considered for the interpretation of the speed of link or degree of coupling (cf. Kayler et al., 2010a) between above- and belowground processes.

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 allocated to 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 4.2.

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 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 plant-derived C flux into (Vandenkoornhuyse et al., 2007) and through arbuscular mycorrhizal hyphae (Staddon et al., 2003; Goldbold et al., 2006) is rapid, i.e. in the range of only a few days. Also for ectomycorrhizal hyphae a fast turnover of freshly assimilated C was found (Godbold et al., 2006), which has been confirmed recently also on the basis of several years of respiration data at high temporal resolution from a deciduous oak forest in southeastern England (Heinemeyer et al., 2011). However, in forests dominated by ectomycorrhiza this linkage seems to vary considerably during seasons and years, suggesting alternative C sources for ectomycorrhizal metabolism such as litter decomposition (Heinemeyer et al., 2011), but there are too few high temporal resolution flux data available to allow a generalization. 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).

It has been shown with ^{13}C-pulse labeling that also soil macrofauna (e.g. earthworms) may quickly incorporate plant exudates as a C source in addition to above- and belowground plant litter inputs, probably by incorporating ^{13}C-labeled microorganisms (Ostle et al., 2007). 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 3.3).

3.3 Carbon losses via plant 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). Plant respiration is 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. 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 respired CO_2 from assimilates (see also 2.2), and imprint valuable information in its $\delta^{13}C$. However, as measurements in tall stature plants are technically challenging, data on plant respiration and its isotopic composition from field studies, especially from forests, are scarce.

Also the emission of biogenic volatile organic compounds (BVOC) can constitute a considerable loss of C from vegetation in the range of a few percent of the current net assimilation rate under non-stress conditions, but can reach or even exceed net assimilation rates under stress conditions, such as drought, and continue even when net assimilation has ceased (e.g., Brüggemann and Schnitzler, 2002), using alternative carbon sources like xylem-transported sugars and breakdown of starch (Loreto and Schnitzler, 2010). However, BVOC emission rates differ strongly among plant species and genera, and thus only play a role for the C budget of particular species, e.g. for isoprene-emitting poplar, oak and willow species (Sharkey et al., 2008). In view of the predicted future increases in temperature and drought periods, BVOC might play an increasing role in determining the C budget of ecosystems that are dominated by BVOC-emitting plant species, although elevated atmospheric CO_2 has been found to counteract temperature effects on BVOC emission (cf. Peñuelas and Staudt, 2010, for a review).

The carbon isotopic signature of isoprene has been found moderately ^{13}C-depleted by 2 to 3 ‰ as compared to recently fixed carbon (Sharkey et al., 1991; Rudolph et al., 2003) or stronger depleted by 4 to 11 ‰ (Affek and Yakir, 2003). The reason for this observation might be fractionation along the isoprene biosynthesis pathway, but also the fact that isoprene biosynthesis is, like plant respiration, not solely fuelled from recent assimilates, but also from alternative sources, such as xylem-transported sugars (Kreuzwieser et al., 2002; Ghirardo et al., 2011), which might be ^{13}C-depleted as compared to recent assimilates at the time of their use in isoprene biosynthesis. Once released to the atmosphere, isoprene does not preserve its original ^{13}C signature, as it is highly reactive and undergoes fast oxidation reactions with ozone and hydroxyl radicals, leading to a ^{13}C-enrichment in the remaining isoprene (Iannone et al., 2010). This has to be considered when interpreting atmospheric isoprene carbon isotope signals.

Most other BVOC are also characterized by ^{13}C signatures close to that of the leaf material they were emitted from (Goldstein and Shaw, 2003). The only major exception are methyl halides, which are derived in plants from the methoxy groups of pectin, which themselves are already significantly ^{13}C-depleted as compared to the bulk leaf material (Keppler et al., 2004).

3.4 Temporal C allocation patterns

Also the $\delta^{13}C$ 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). However, from correlation-based flux studies it is not consistently clear to which extent they 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). It is also not clear to which extent these diel variations of $\delta^{13}C$ of soil CO_2 efflux reflect the number of processes potentially involved, including changes in vapor pressure deficit that affect photosynthetic discrimination against ^{13}C (Brugnoli et al., 1988; Farquhar et al., 1989; see 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; Barthel et al. 2011) 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).

Initial growth and respiration are supplied from storage C in seeds in both annual and perennial plants (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 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 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; Palacio et al, 2011), 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 δ^{13}C of different plant organs (Damesin and Lelarge, 2003; Helle and Schleser, 2004). Such variations may hinder the interpretation of δ^{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). Within deciduous plants, 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 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 δ^{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 δ^{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 δ^{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; Carbon and Trumbore, 2007). Recent investigations estimated that up to 55 % of fine root C comes from storage, although such stored C seems of young age (approx. 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; Epron et al., 2011), 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 of recent C 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 δ^{13}C of plant respired CO_2. If assimilate supply decreases, ^{13}C-enriched stores can serve as substrates for respiration leading to increases in δ^{13}C of released CO_2.

Relatively little is known about interannual variations compared to the wealth of studies on seasonal changes in C allocation. 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

(represented by "Starch" in Fig. 4), 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 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 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.

3.6 Sensitivity of C allocation to environmental stress

The general responses of plant ecophysiological processes 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 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, it was 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; Barthel et al. 2011; 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.

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 rhizosphere respiration, microbial metabolism, organo-mineral interactions, dynamic soil carbon pools, and microbial markers.

4.1 Rhizosphere respiration

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). A large array of methods for partitioning R_a and R_h exists, the advantages and disadvantages of which have been extensively 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 and Thomson, 2010).

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; Bahn et al., 2009; Bond-Lamberty and Thomson, 2010). These latter studies indicate that root C stores 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 more rapidly after interruption of assimilate supply (Bahn et al., 2006).

Dramatic increases in R_a have been found in strongly seasonal ecosystems at high latitudes 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 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 in different seasons (Högberg et al., 2009), suggests that additional factors, such as phenology, control R_a. At shorter time scales, changes in 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 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 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), different contributions of the individual component fluxes to total soil respiration, or changes in CO_2 transport rates in the soil (Phillips et al., 2011).

Little is known about the biotic and abiotic factors that regulate rhizosphere respiration despite its importance for the terrestrial C cycle (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 δ^{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.

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. Details on SOM turnover and isotopic discrimination associated with it will be given in the following chapters.

4.2 Patterns of SOM δ^{13}C isotopic enrichment with soil depth

Bulk 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 δ^{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 δ^{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 δ^{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 Rayleigh distillation equation from Wynn et al. (2006) is a first order reaction model described by the isotopic

$$F = \left[\frac{\frac{\delta^{13}C_f}{1000}+1}{\frac{\delta^{13}C_i}{1000}+1}\right]^{\left(\frac{1}{\left[\frac{\alpha(1+e)(t-1)}{[\alpha(e-1)(t-1)]+t}\right]-1}\right)} \quad (7)$$

signature of SOM ($\delta^{13}C_f$), the isotopic composition of biomass input ($\delta^{13}C_i$), the fractionation factor between SOM and respired CO_2 (α), and the SOM fraction remaining. 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

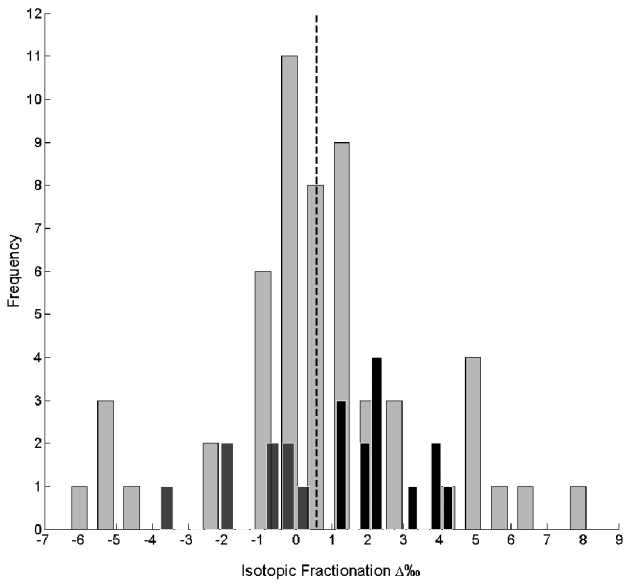

Fig. 3. Estimates of apparent fractionation associated with soil microbial respiration determined by different experimental approaches (grey bars: from C_3 plants; dark grey bars: Rayleigh distillation methods, black bars: C_4 plants). The dashed line is the mean of all estimates. Data sources: Werth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

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. 3). 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.

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 that lead to $\delta^{13}C$ values of CO_2 that are different from the initial substrate or microbial biomass were 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

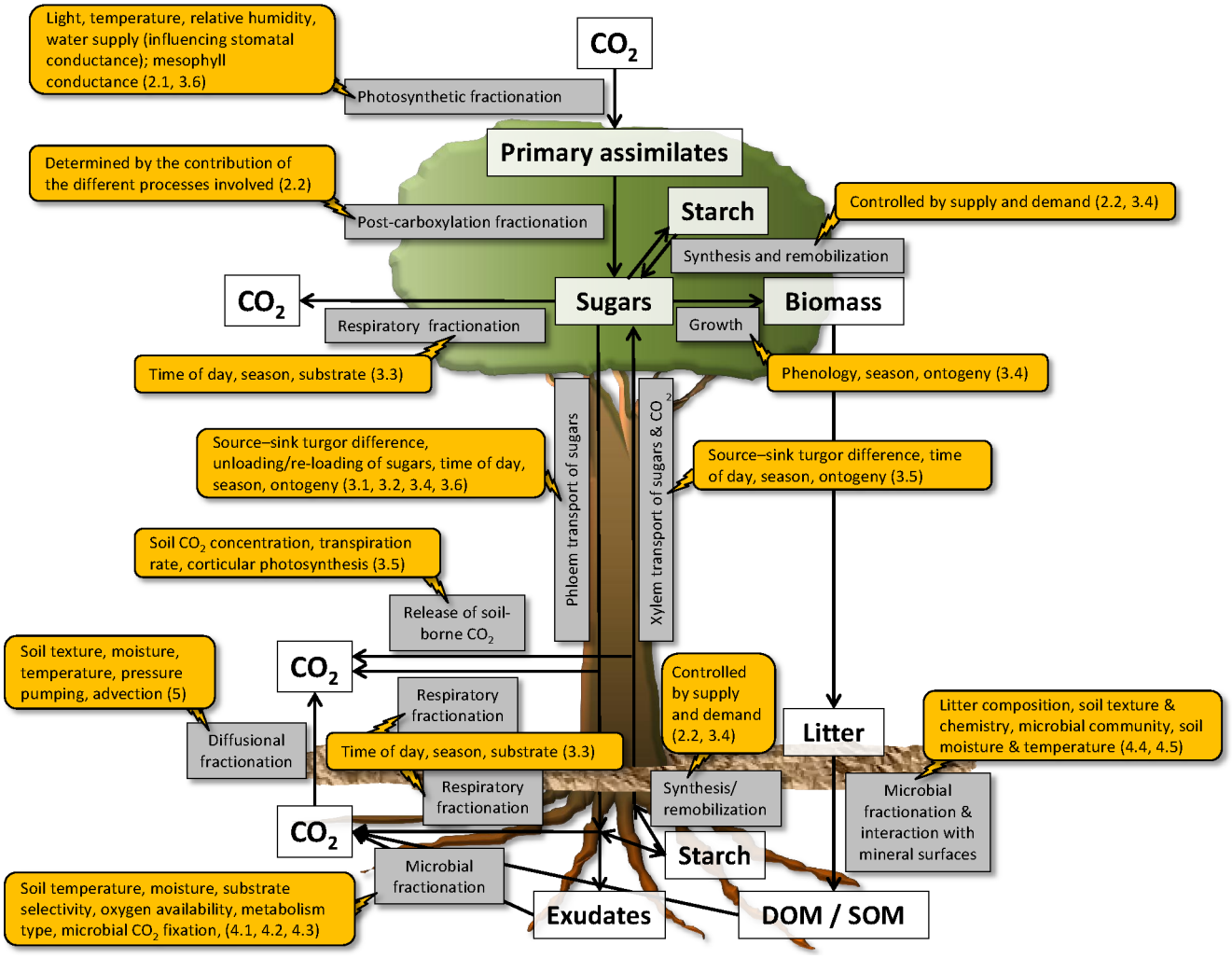

Fig. 4. Overview of processes and factors determining the isotope signature of C pools and fluxes in space and time in the plant-soil-atmosphere continuum. White boxes represent pools, gray boxes show fractionation or other processes determining the C isotope composition of the involved compounds, and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

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. Furthermore, autotrophic and photoautotrophic CO_2-fixation must be considered in terms of C fractionation. On the one hand, the 3-hydroxypropionate pathway causes smaller isotopic fractionation (−13 to 14 ‰) compared to the Calvin cycle (−20 to −25 ‰, van der Meer et al., 2007, and references therein), which is of special importance in systems where microbial mats and cyanobacteria play a large role in C translocation to soil and soil microbial biomass. On the other hand, autotrophic organisms may express a high level of isotopic fractionation, and fractionation has been reported to be interestingly high within the context of inorganic C fixation (Cowie et al., 2009).

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. For example, the use of positional labeling of carbon in glucose has given metabolic insight into carbon pathways in mycorrizhae (Scandellari et al., 2009). 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 δ^{13}C between the actual C respired (detected in δ^{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 δ^{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 which the mechanisms are not entirely understood (Plante et al., 2006). However, stabilization studies using δ^{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 δ^{13}C and δ^{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 δ^{13}C of SOM with depth, but also questions regarding carbon accumulation and stabilization (Kleber et al., 2011).

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).

Leaf 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 aboveground litter layer of an ecosystem is composed of a continuum of fresh litter to completely

humified 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 (i) how the carbon in the aboveground litter layer reaches the mineral soil, (ii) how the biogeochemical processes determine the fate of organic matter, either remaining in the aboveground litter layer or being transported into the soil profile, and (iii) which mechanisms control leaf 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.

To a large extent, the isotopic composition of leaf litter is determined by the plant organs and tissues deposited as well as the post-carboxylation fractionation that occurred during their synthesis (see Sect. 2.2). For example, roots and woody stems are generally enriched in ^{13}C when compared to leaves, and the isotopic signature of organic matter in the litter layer is often close in value to the isotopic composition of aboveground plant organs (Badeck et al., 2005). Thus, the different ^{13}C signals of heterotrophic and autotrophic plant organs and their turnover times may affect the isotopic composition of the litter layer. Scartazza et al. (2004) found no significant variation in $\delta^{13}C$ of the litter layer in a beech forest in the central Apennine Mountains, Italy, when there was a significant seasonal change in $\delta^{13}C$ values in leaves and in phloem sap sugar. In the study by Scartazza et al. (2004), there was a significant relationship between leaf sugar $\delta^{13}C$ and ecosystem-respired $^{13}CO_2$. Thus, the different ^{13}C signals of heterotrophic and autotrophic plant organs may control $^{13}CO_2$ produced from the ecosystem for some extent, but in terms of litter layer ^{13}C, other C sources may be determining the $\delta^{13}C$ of litter layer (e.g. lipids), and C with a short turn over time (e.g. sugars) may not influence the $\delta^{13}C$ of litter layer.

Beyond the initial composition of litter, 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 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 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; Kalbitz et al., 2000; Bengtson and Bengtsson, 2007; Giesler et al., 2007) 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 (SIP), i.e. detecting and quantifying isotopic tracers in DNA of the organisms of interest, it is now possible to characterize microbial communities utilizing carbon from ^{13}C-labeled litter or continuous ^{13}C-labeling. 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 δ^{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.

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.

Leaf and root litter are important links coupling the short- and long-term carbon cycles belowground, and many open questions remain in resolving their dynamics. Of particular interest will be the fate of organic molecules derived from plant litter as they travel through the many branching points belowground. How these molecules vary spatially and temporally and whether or not they are available as substrate or physically occluded in the soil matrix are other challenges to elucidating plant-soil interactions. Isotopes will remain an important tool in tracing the carbon continuum, especially with the advent of new tools that give higher resolution spatially, for example nanoSIMS, and temporally, for example infrared laser absorption spectroscopy (Sect. 6).

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 δ^{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 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 δ^{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 δ^{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). 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‰. 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 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 of fractionation and validation of steady-state assumptions (Andrews et al., 2000; Steinmann et al., 2004; Kayler et al., 2008, 2010b; Moyes et al., 2010). 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). Therefore, 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.

6 Stable isotope methodologies for characterizing C fluxes in the plant-soil-atmosphere continuum

Steady-state ^{13}C isotope labeling techniques have been successfully applied to assessing C fluxes in metabolic networks on a cell or on tissue level. Carbon fluxes are determined by measuring the redistribution of label after the system has reached an isotopic steady state (Allen et al., 2009). Steady-state $^{13}CO_2$ labeling in combination with the application of compartmental models have been used to characterize different metabolic pools with distinct turnover times, feeding growth (Lattanzi et al., 2005) or respiration (Lehmeier et al., 2008) of leaves or heterotrophic plant parts.

A more detailed analysis of δ^{13}C in particular metabolites – going beyond the separation into different C pools (e.g. Xu et al., 2004; Gessler et al., 2009a) – is possible with modern continuous-flow coupling of liquid chromatography (LC-IRMS; cf. Godin et al., 2007) or gas chromatography (GC-IRMS; cf. Sessions, 2006) with isotope-ratio mass spectrometry and, when high levels of ^{13}C label are applied, also with LC-MS/MS (LC coupled to tandem mass spectrometer) systems. These techniques may be combined with pulse or steady-state labeling and metabolic flux analysis models

(e.g. Nöh et al., 2007) to provide deeper insights into cellular to whole-plant partitioning and transport of metabolites. In addition, compound-specific analyses of the C isotope composition at natural abundance levels over time might give insights into the turnover times and partitioning of C between metabolites and metabolite groups (e.g. leaf waxes; Gessler et al., 2007)

The natural variation of stable isotope signatures has been tracked through different plant organic matter pools (e.g. starch, water-soluble organic matter) in order to characterize the short-term partitioning of recent assimilates (e.g. Barbour et al., 2005; Brandes et al., 2006; Gessler et al., 2007; Kodama et al., 2008; see also 2.1). On an ecosystem scale, the interpretation of isotopic signals at the natural abundance level is challenging, as too many processes affect the isotopic signatures of the compounds of interest. Therefore, partitioning and transport of newly assimilated C within the plant-soil system have been mainly determined with pulse labeling experiments. In these experiments, plants are exposed to ^{13}C-enriched CO_2 for a short time period (minutes to a few hours), and the fate of the assimilated C tracer is tracked in various plant organs and/or in plant- and soil-respired CO_2 over time (Bahn et al., 2009; Plain et al., 2009; Ruehr et al., 2009; Ghirardo et al., 2011). In addition, nanoSIMS, i.e. secondary ion mass spectrometry, which allows determination of stable isotope ratios at the nanometer scale, could contribute to understanding carbon allocation in the rhizosphere.

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, isotope-specific infrared laser absorption spectroscopy, e.g. for the analysis of ^{13}C and ^{18}O in CO_2, which equals or even exceeds the performance of isotope ratio mass spectrometry, provides 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). The continuous and simultaneous analysis of photosynthetic fractionation in the canopy (e.g. carried out with leaf or twig chambers) or its proxies and of δ^{13}C of CO_2 respired from heterotrophic plant parts and the soil with laser-based isotope analyzers provides information on the time lag between above- and belowground processes and the magnitude of C fluxes between canopy and soil as well as on their variability during the growing season or as influenced by environmental factors. 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).

7 Conclusions and outlook

This review has provided a comprehensive overview of the complex network of interlinked 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.

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

- 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?
- How do changes in metabolic fluxes scale to ecosystem C fluxes?
- What is the relationship between the age of plant C stores and their remobilization potential, and how is it affected by plant age, phenology, and environmental conditions?
- 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?
- What is the role of physical (diffusion, dissolution) and physiological (re-fixation) processes as co-determinants of δ^{13}C measured in plant- and soil-respired CO_2 and how do these processes affect isotopic time lags between photosynthesis and respiration?
- How does environmental stress affect C fluxes in the plant-soil system?
- 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?

– 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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