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Permalink
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Journal
New Phytologist, 178(1)

ISSN
0028-646X

Authors
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Publication Date
2008-04-01

DOI
10.1111/j.1469-8137.2007.02342.x

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New Phytologist

Tansley review

Carbon isotopes in terrestrial ecosystem pools and CO_2 fluxes

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Received: *23 August 2007*
Accepted: *11 November 2007*

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Summary

Stable carbon isotopes are used extensively to examine physiological, ecological, and biogeochemical processes related to ecosystem, regional, and global carbon cycles and provide information at a variety of temporal and spatial scales. Much is known about the processes that regulate the carbon isotopic composition ($\delta^{13}C$) of leaf, plant, and ecosystem carbon pools and of photosynthetic and respiratory carbon dioxide (CO_2) fluxes. In this review, systematic patterns and mechanisms underlying variation in $\delta^{13}C$ of plant and ecosystem carbon pools and fluxes are described. We examine the hypothesis that the $\delta^{13}C$ of leaf biomass can be used as a reference point for other carbon pools and fluxes, which differ from the leaf in $\delta^{13}C$ in a systematic fashion. Plant organs are typically enriched in ^{13}C relative to leaves, and most ecosystem pools and respiratory fluxes are enriched relative to sun leaves of dominant plants, with the notable exception of root respiration. Analysis of the chemical and isotopic composition of leaves and leaf respiration suggests that growth respiration has the potential to contribute substantially to the observed offset between the $\delta^{13}C$ values of ecosystem respiration and the bulk leaf. We discuss the implications of systematic variations in $\delta^{13}C$ of ecosystem pools and CO_2 fluxes for studies of carbon cycling within ecosystems, as well as for studies that use the $\delta^{13}C$ of atmospheric CO_2 to diagnose changes in the terrestrial biosphere over annual to millennial time scales.

Key words: carbon dioxide (CO_2), organic, plant, photosynthesis, respiration, soil.

New Phytologist (2008) **178**: 24–40

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doi: 10.1111/j.1469-8137.2007.02342.x

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I. Introduction

Differences in the stable carbon (C) isotopic composition ($\delta^{13}C$) of organic and inorganic compounds are useful for studying processes that control C cycling within and between plants, animals, and ecosystems, and exchanges between these and other reservoirs and the atmosphere and hydrosphere. $\delta^{13}C$ is defined by the equation $\delta^{13}C = (R_{sample}/R_{VPDB} - 1) \times 1000‰$, where R is the molar ratio of $^{13}C/^{12}C$ and VPDB is the Vienna Pee Dee Belemnite laboratory standard. For a review of isotope terminology, see Farquhar *et al.* (1989). Here we use $\delta^{13}C$ to refer to isotopic composition in general, and $\delta^{13}CO_2$ to refer to the isotopic composition of CO_2.

Plants are isotopically 'lighter' than CO_2 in air, meaning that they contain less ^{13}C relative to ^{12}C in their tissues than atmospheric CO_2. This is a result of differences in diffusion rates of $^{12}CO_2$ and $^{13}CO_2$ into leaves, and especially differences in reaction rates with Rubisco during carboxylation. There is a rich understanding of the processes that control the C isotope discrimination (Δ) associated with photosynthesis, and C isotope studies have made important contributions to much of our understanding of plant physiology and ecosystem ecology. Isotope discrimination is defined as the isotope effect in the conversion from substrate to product: $\Delta = (\delta_{substrate} - \delta_{product})/(1 + \delta_{product}/1000)$. For photosynthesis, the substrate is CO_2 in air, and the product is either bulk leaf biomass or photosynthetic sugars. For respiration, the substrate is harder to define, and the product (respiratory CO_2) is usually compared with possible substrates for respiration (glucose, starch, lipids, etc.). For this reason, respiratory discrimination is usually referred to as *apparent* respiratory discrimination. In this paper, we use Δ_A to refer to discrimination associated with photosynthesis.

A host of processes influence the $\delta^{13}C$ of bulk leaf material, including light, photosynthetic capacity, water availability, atmospheric humidity, and others, which have been thoroughly reviewed (Farquhar *et al.*, 1989; Brugnoli & Farquhar, 2000; Dawson *et al.*, 2002). Here we explore the hypothesis that *bulk leaf $\delta^{13}C$, which is controlled by physiological and ecological factors, can be used as a reference point from which there are predictable differences in the $\delta^{13}C$ of plant and ecosystem C pools and fluxes*. Such differences can be utilized to make inferences about ecosystem C cycling and related effects on the isotopic composition of atmospheric CO_2. This hypothesis has strong support when comparing the isotopic composition of leaf metabolites to that of the bulk leaf, as noted by others (e.g. Boutton, 1996). In this review, we will show that it also appears valid when comparing bulk leaf biomass to specific plant tissue classes (e.g. phloem sap organics, wood, or roots), to ecosystem C pools (e.g. bulk soil organic matter or fungal biomass) and to respiratory fluxes (from leaves, roots, soil, and whole forests). While the concepts developed here may have applicability to C_4 systems, we have restricted our analysis to vascular plants and associated ecosystems that are dominated by the C_3 photosynthetic pathway.

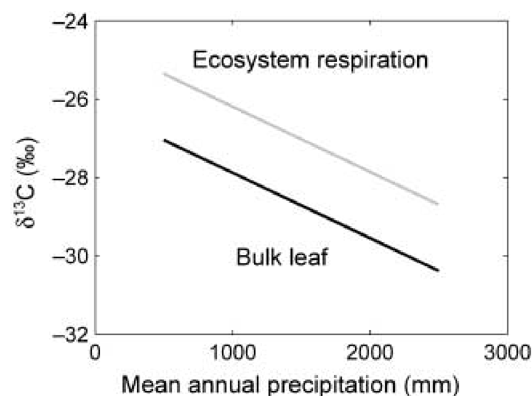

Fig. 1 A conceptual relationship among the carbon isotopic composition ($\delta^{13}C$) of bulk leaf biomass (black line, which is hypothetical), ecosystem respiration (gray line, which is observed) and mean annual precipitation (MAP). The ecosystem respiration line is a regression of data points below 2300 mm MAP from fig. 10 of Pataki *et al*. (2003); $y = -0.00167x - 24.5$; $r^2 = 0.94$. The hypothetical bulk leaf line is offset from the ecosystem respiration line by the mean offset (1.7‰) between them found in the present study and shown in Fig. 4. Pataki *et al*. (2003) showed a similar offset between leaves and ecosystem respiration in their fig. 6, but the actual relationships between MAP and the $\delta^{13}C$ of leaves and of ecosystem respiration are more complex than this simplified example implies.

Our choice of bulk leaf tissue as the isotopic reference point is one of pragmatism. One could argue that triose phosphates or leaf sugars would be a better choice, as they are more directly linked to photosynthetic discrimination than the bulk leaf tissue. Alternatively, leaf or wood cellulose might be appropriate because of its stability. While appealing, these are not commonly measured in the majority of studies relevant to this review. The most commonly measured organic component $\delta^{13}C$ in plant and ecosystem studies is the bulk leaf tissue, and for this reason we use it as our common unit for comparison.

A conceptual example helps to illustrate our central theme (Fig. 1). The isotopic composition of atmospheric CO_2 (which we denote $\delta^{13}CO_2$) currently averages *c.* –8‰, while the $\delta^{13}C$ of C_3 plants ranges from –20 to –35‰ because of variability in photosynthetic discrimination (Dawson *et al.*, 2002). As a consequence, the C that returns to the atmosphere through release of respiratory CO_2 from plants and animals is depleted in $^{13}CO_2$ relative to the atmosphere, and therefore the $\delta^{13}C$ of whole-forest respiration in C_3 ecosystems ranges from –24 to –30‰. ('Enriched' and 'depleted' refer to the relative amount of each isotope in one sample relative to another. Sample A is enriched (or depleted) relative to sample B if $^{13}C/^{12}C$ for sample A is larger (or smaller) than for sample B. In δ notation, sample A is enriched (or depleted) relative to sample B if $\delta^{13}C_A$ is less (or more) negative than $\delta^{13}C_B$.) Several studies have shown that $\delta^{13}C$ of leaves varies across broad gradients of precipitation, with the general pattern that plants in wetter ecosystems tend

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to have more negative $\delta^{13}C$ in their leaves than those in drier regions (Read & Farquhar, 1991; Stewart *et al.*, 1995; but see Schulze *et al.*, 1998). As we will show, there is substantial post-photosynthetic discrimination against ^{13}C during plant tissue synthesis, and the relationship between respiration and bulk leaf composition shown in Fig. 1 follows as a result. A similar pattern in $\delta^{13}C$ of respiration has been observed across a wide range of biomes; for sites that ranged in mean annual precipitation from 200 to 2300 mm, the $\delta^{13}C$ of ecosystem respiration ranged from −24 to −30‰ (Fig. 1, and Pataki *et al.*, 2003). Therefore, ecological factors (precipitation in this example) influence the $\delta^{13}C$ of photosynthate, which influences the $\delta^{13}C$ of plant tissues, plant respiration, and ecosystem respiration. We present evidence in this paper that many C pools and fluxes show systematic offsets from bulk leaf $\delta^{13}C$.

Isotopic mass balance at the leaf, plant, and ecosystem scales is unattainable at present because of gaps in our understanding of several processes. Ideally, to fully utilize the information contained in the $\delta^{13}C$ of terrestrial ecosystems, an understanding of all the processes that influence the $\delta^{13}C$ of C pools and fluxes is necessary. In this review we summarize the current understanding of the factors that influence the C isotopic composition of plant and ecosystem C pools and fluxes, with an emphasis on systematic patterns of the $\delta^{13}C$ of pools and fluxes relative to bulk leaf organic matter. The first section is a discussion of the isotopic composition of plant metabolites and leaf respiration, followed by a review of observed patterns in $\delta^{13}C$ of plant and ecosystem C pools. Next, we examine the isotope content of assimilation and respiration fluxes, and then discuss these fluxes at various spatial scales, with an emphasis on interpreting the atmospheric record of $\delta^{13}CO_2$. We conclude with a discussion of important areas for future research.

II. Isotopic composition of plant metabolites and autotrophic respiration

1. Variability in $\delta^{13}C$ of plant metabolites

The factors that affect photosynthetic discrimination and the isotopic composition of bulk leaf biomass and organic compounds within leaves and other plant organs have been reviewed in detail (O'Leary, 1981; Farquhar *et al.*, 1989; Dawson *et al.*, 2002; Ghashghaie *et al.*, 2003; Hobbie & Werner, 2004). Photosynthetic discrimination is often estimated with the simplified model $\Delta_A = a + (b - a)c_i/c_a$, where a is diffusive fractionation (4.4‰), b is enzymatic fractionation, primarily Rubisco (27‰), and c_i/c_a is the ratio of CO_2 in the intercellular air space to that outside the leaf. This model (or the more detailed form) is commonly called the Farquhar *et al.* model after a highly influential paper by Graham Farquhar, Marion O'Leary, and Joe Berry (Farquhar *et al.*, 1982). Hence, discrimination varies in response to factors that influence the balance between photosynthetic drawdown of CO_2 in the substomatal cavity and the diffusion of CO_2 into the leaf, and therefore in response to c_i/c_a. For example, the influence of light availability on photosynthetic capacity leads to variation in the $\delta^{13}C$ of leaves at different heights within a forest, with most negative values of $\delta^{13}C$ in leaves near the ground and least negative values at the top of the canopy (e.g. Martinelli *et al.*, 1998; Pate & Arthur, 1998). Environmental conditions that result in stomatal closure such as drought, low atmospheric humidity, or nutrient stress generally decrease Δ_A, causing plant biomass and leaf sugars to be relatively enriched under these conditions (e.g. Brugnoli *et al.*, 1988; Madhavan *et al.*, 1991; Gaudillere *et al.*, 2002).

Within a plant, the $\delta^{13}C$ of organic compounds varies (e.g. Gleixner *et al.*, 1998), as a result primarily of isotope effects expressed at branch points in biochemical pathways. No fractionation is observed if *all* of a particular substrate is converted to a product. Biosynthesis of reduced compounds from photosynthetic sucrose involves numerous biochemical pathways in which enzymatic and positional isotope effects may be expressed, resulting in fairly systematic, compound-specific values of $\delta^{13}C$ for plant organic compounds (Fig. 2). For example, sucrose and starch are isotopically enriched relative to bulk leaves, while lipids and lignin are generally depleted (Fig. 2). The depletion of lipids appears to originate in the oxidation of pyruvate to acetyl CoA by the pyruvate dehydrogenase complex (DeNiro & Epstein, 1977). All metabolic products derived from acetyl CoA are expected to be isotopically depleted as a result of enzymatic fractionation.

2. Isotope effects influencing leaf respiration

The isotope effects addressed above for biosynthetic pathways may also directly influence the $\delta^{13}C$ of respiratory CO_2, as the biochemical pathways are interrelated. Positional isotope effects refer to nonrandom, intramolecular distributions of heavy and light isotopes. For example, C at position 4 of glucose tends to be enriched relative to the whole molecule, while position 6 tends to be depleted (Rossmann *et al.*, 1991). In addition, there may be kinetic effects in respiratory enzymes such as pyruvate dehydrogenase, which are temperature and substrate dependent (DeNiro & Epstein, 1977; Melzer & Schmidt, 1987). The net result of these effects is that isotopic depletion or enrichment of biosynthetic products must be balanced by opposing effects elsewhere in the plant, including evolved CO_2. In the case of acetyl-CoA synthesis, oxidation of pyruvate releases CO_2 that is enriched relative to the pyruvate substrate, as the acetyl CoA is generally depleted (DeNiro & Epstein, 1977; Melzer & Schmidt, 1987).

In reviews of the early literature on the $\delta^{13}C$ of dark respiration, O'Leary (1981) and Farquhar *et al.* (1982) noted that comparisons of respiratory CO_2 and plant biomass yielded inconsistent differences, with respiration sometimes more enriched or more depleted than leaves (Park & Epstein, 1961; Smith, 1971; Troughton *et al.*, 1974). Therefore, it was assumed

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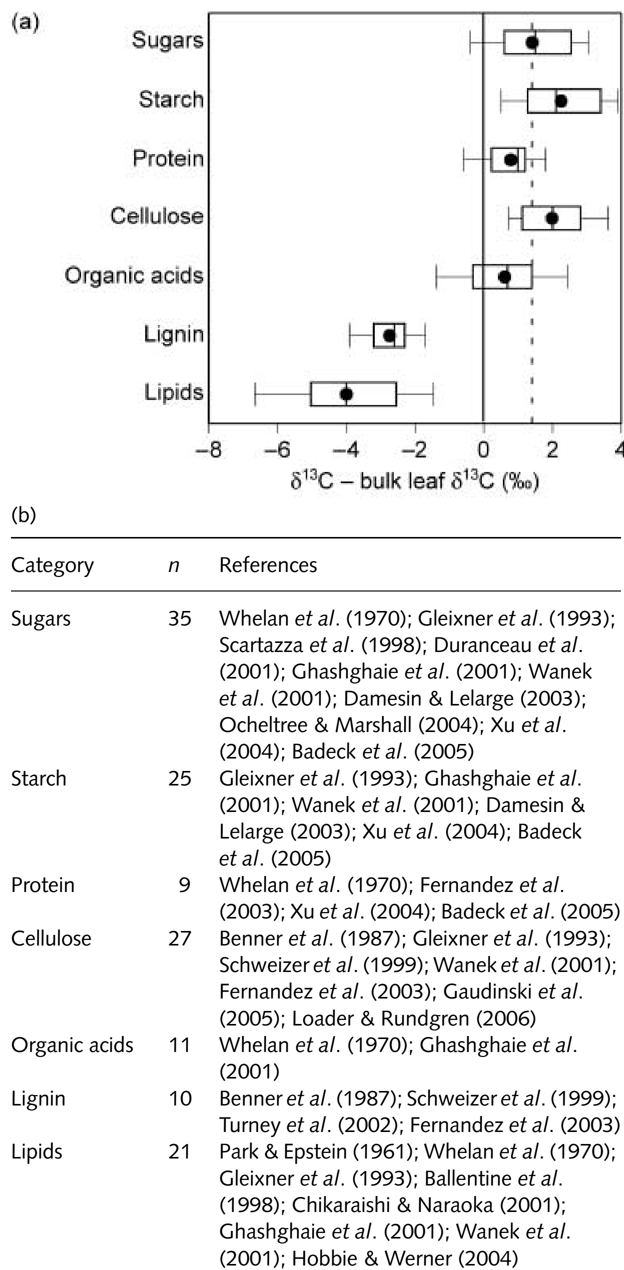

Category	*n*	References
Sugars	35	Whelan *et al*. (1970); Gleixner *et al*. (1993); Scartazza *et al*. (1998); Duranceau *et al*. (2001); Ghashghaie *et al*. (2001); Wanek *et al*. (2001); Damesin & Lelarge (2003); Ocheltree & Marshall (2004); Xu *et al*. (2004); Badeck *et al*. (2005)
Starch	25	Gleixner *et al*. (1993); Ghashghaie *et al*. (2001); Wanek *et al*. (2001); Damesin & Lelarge (2003); Xu *et al*. (2004); Badeck *et al*. (2005)
Protein	9	Whelan *et al*. (1970); Fernandez *et al*. (2003); Xu *et al*. (2004); Badeck *et al*. (2005)
Cellulose	27	Benner *et al*. (1987); Gleixner *et al*. (1993); Schweizer *et al*. (1999); Wanek *et al*. (2001); Fernandez *et al*. (2003); Gaudinski *et al*. (2005); Loader & Rundgren (2006)
Organic acids	11	Whelan *et al*. (1970); Ghashghaie *et al*. (2001)
Lignin	10	Benner *et al*. (1987); Schweizer *et al*. (1999); Turney *et al*. (2002); Fernandez *et al*. (2003)
Lipids	21	Park & Epstein (1961); Whelan *et al*. (1970); Gleixner *et al*. (1993); Ballentine *et al*. (1998); Chikaraishi & Naraoka (2001); Ghashghaie *et al*. (2001); Wanek *et al*. (2001); Hobbie & Werner (2004)

Fig. 2 (a) An update of the analysis of fig. 4 in Boutton (1996) comparing the isotopic composition of compounds isolated from leaves of C_3 vascular plants, expressed relative to bulk leaf biomass. The boxes encompass the upper and lower quartiles of the data, the line shows the median, the symbol shows the arithmetic mean, and the error bars show the upper and lower 10th percentiles of the data. The vertical dashed line is included for easy reference to the $\delta^{13}C$ of leaf sugars. (b) Number of samples (*n*) and references used for each category.

that fractionation in autotrophic respiration was negligible and could be neglected in assessing the major factors controlling the isotopic composition of plants. Lin & Ehleringer (1997) found that the $\delta^{13}C$ of CO_2 evolved from isolated mesophyll protoplasts matched that of their sugar substrates, implying that the $\delta^{13}C$ of respiratory CO_2 is not changed by biochemical reactions of the Krebs cycle, and thus should reflect the respiratory substrate. This differs fundamentally from photosynthetic discrimination, where a biochemical fractionation dominates. Previous literature showing fractionation in dark respiration of up to 8‰ (Park & Epstein, 1961) was attributed to differences in respiratory substrates, such as oxidation of glucose vs lipids (Lin & Ehleringer, 1997).

Several studies have subsequently tested the effects of respiratory substrate by measuring the isotopic composition of CO_2 evolved during dark respiration and comparing it to that of plant compounds such as sugars, starch, and lipids (see review by Ghashghaie *et al.*, 2003). Duranceau *et al.* (1999, 2001) found that respiratory CO_2 was enriched by 2–6‰ relative to sucrose in *Phaseolus vulgaris* and *Nicotiana sylvestris*, while Ghashghaie *et al.* (2001) found enrichment of respiratory CO_2 in *N. sylvestris* and *Helianthus annuus* relative to all measured carbohydrates, organic acids, and lipids.

Tcherkez *et al.* (2003) further assessed the role of respiratory substrate with simultaneous laboratory measurements of $\delta^{13}C$ of dark respiration (leaves in the dark for 2 h or longer) and the respiratory quotient (RQ), the ratio of CO_2 produced to O_2 consumed during respiration. Oxidation of carbohydrates results in RQ values close to 1, while oxidation of highly reduced compounds results in RQ < 1. At low leaf temperature, the $\delta^{13}C$ of respiration in *Phaseolus vulgaris* was 4‰ enriched relative to sucrose, while RQ was close to 1 (Fig. 3). RQ declined with increasing leaf temperature, suggesting that, as an increasing proportion of reduced respiratory substrates was consumed, the $\delta^{13}C$ of respiration became more depleted. These results suggest that the $\delta^{13}C$ of dark respiration varies with respiratory substrate, but they also indicate that the $\delta^{13}C$ of the CO_2 evolved in respiration is offset from the $\delta^{13}C$ of the substrate. The mostly likely explanation is fractionation at metabolic branch points between oxidation of pyruvate to CO_2 in the Krebs cycle and biosynthetic pathways such as fatty acid synthesis from acetyl CoA. Indeed, the only known process that can account for large enrichments of respiratory CO_2 of 6‰ or greater relative to sucrose is the synthesis of equally depleted compounds in lipid production.

Field experiments with *Quercus ilex*, *Quercus cerris*, and *Pinus elliottii* have found a strong pattern of diurnal enrichment in $\delta^{13}C$ of CO_2 evolved by leaves that were removed from the light and placed in the dark for several minutes (Hymus *et al.*, 2005; Prater *et al.*, 2006; also see Wingate *et al.*, 2007). Respiratory CO_2 near the end of the daily photoperiod was enriched by up to 7‰ relative to predawn, and always enriched relative to possible respiratory substrates. These diel changes could not be reconciled with changes in the $\delta^{13}C$ of possible respiratory substrates within the leaf, or with environmental changes in Δ_A throughout the day (Hymus *et al.*, 2005). There may be differences in the diel pattern of respiratory enrichment in woody vs herbaceous plants. A recent study with *Ricinus communis* showed that some of the respiratory

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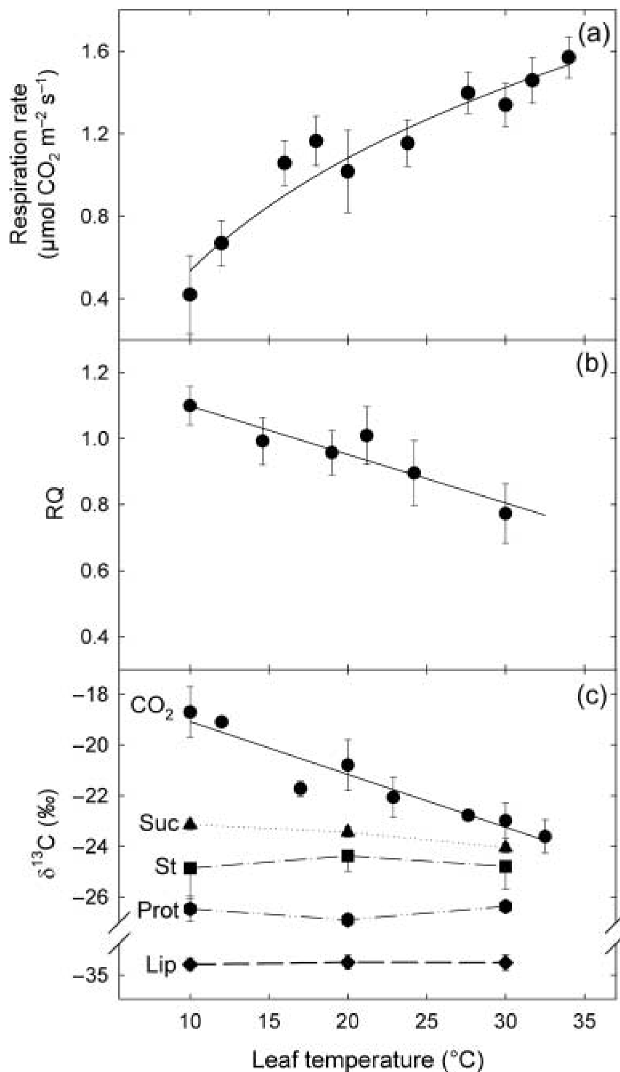

Fig. 3 Leaf respiration rate, respiratory quotient (CO_2 produced/O_2 consumed; RQ), and isotopic composition of leaf sucrose (Suc), starch (St), proteins (Prot), and lipids (Lip), and leaf-respired CO_2 in *Phaseolus vulgaris* under varying leaf temperature. Reproduced with permission from Tcherkez *et al*. (2003). ©American Society of Plant Biologists.

enrichment during the first 10–15 min following transfer to darkness was transient, and suggested that during the initial dark period the mitochondrial malate pool may be decarboxylated, causing the large initial enrichment (Barbour *et al.*, 2007). Some enrichment always persisted following the transient enrichment.

While important biochemical details associated with the $\delta^{13}C$ of leaf respiration remain to be unraveled, a generalization can be made: leaf dark respiration is more enriched in ^{13}C than the bulk leaf tissue. Figure 4 summarizes the results of a literature survey of studies where comparisons of the $\delta^{13}C$ of bulk leaf tissue were possible with the $\delta^{13}C$ of other categories of plant or ecosystem C pools or respiratory fluxes. Evidence from a large number of studies suggests that leaf dark respiration is usually enriched relative to bulk leaf tissue (Fig. 4), whether the leaves are in the dark for a few minutes or for several hours or days. Other categories in Fig. 4 will be discussed as they are introduced.

3. Relative importance of growth and maintenance respiration

Allocation of C to autotrophic respiration in different ecosystems and under varying environmental conditions remains a source of major uncertainty in the terrestrial C cycle. Autotrophic respiration involves many possible biochemical pathways for generating ATP, NAD(P)H, and biosynthetic intermediates, and is therefore more complex to represent in plant and ecosystem models than photosynthesis (Cannell & Thornley, 2000). A useful concept for modeling autotrophic respiration has been the distinction between growth and maintenance respiration. Growth respiration provides energy, reducing power, and C skeletons for biosynthesis of plant compounds, while maintenance respiration supports existing biomass through replacement of proteins, membranes, and ion gradients (see reviews by Amthor, 2000; Thornley & Cannell, 2000; Gifford, 2003). Although the metabolic pathways for growth and maintenance respiration are the same, growth respiration is theoretically fixed for a given set of plant compounds because of their inherent construction costs, while maintenance respiration varies with environmental conditions such as temperature (Amthor, 1984; Ryan, 1991). Temporal and spatial variability in the $\delta^{13}C$ of autotrophic respiration may provide important information about mechanisms underlying variation in growth and maintenance respiration.

Bulk leaf tissue is slightly depleted relative to the sugar substrates from which leaf compounds are produced (Fig. 2). Mass balance dictates that this depletion must be opposed by an enriched pool of C which may leave the leaf via respiration (as discussed) or phloem export. Phloem sap sugars tend to be more enriched than bulk leaf tissue and leaf sugars by a few ‰ (Fig. 4), possibly as a result of fractionation during phloem loading, unloading, or transport (Damesin & Lelarge, 2003; Scartazza *et al.*, 2004), although the mechanisms are not known. In addition, while starch, proteins, and cellulose tend to be enriched relative to bulk leaf material, lignin and lipids can be depleted by several ‰ (Fig. 2). Lignin and lipids constitute *c.* 10% of the biomass of herbaceous leaves on average, and 20% of the biomass of leaves of woody plants, which tend to have high lignin content (Poorter & Villar, 1997). While these fractions are not large, the synthesis of lipids evolves more CO_2 per gram than other compounds. For example, synthesis of 1 g of cellulose evolves *c.* 3 mmol CO_2 in comparison to 36 mmol for 1 g of lipids (Poorter & Villar, 1997). Hence, a small isotopic enrichment relative to sucrose is expected for respiratory CO_2 associated with growth.

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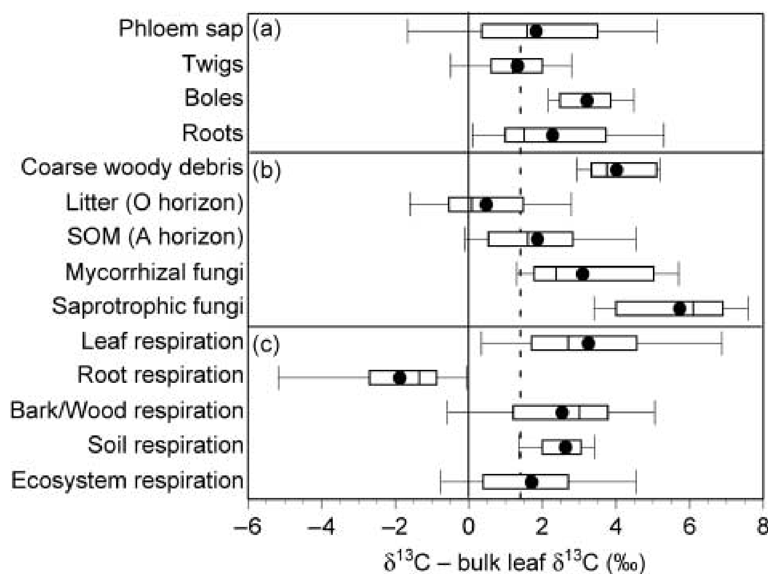

(d)

Category	*n*	References
Phloem sap	72	Pate & Arthur (1998); Gessler *et al*. (2001); Keitel *et al*. (2003, 2006); Scartazza *et al*. (2004); Barbour *et al*. (2005); Cernusak *et al*. (2005)
Twigs	86	Cernusak *et al*. (2001); Damesin & Lelarge (2003); Schuur *et al*. (2003); Trudell *et al*. (2004); Hemming *et al*. (2005)
Boles	9	Martinelli *et al*. (1998); Hobbie *et al*. (1999); Schuur *et al*. (2003); Scartazza *et al*. (2004); Trudell *et al*. (2004)
Roots	45	Hobbie *et al*. (1999); Bowling *et al*. (2002, 2003); Scartazza *et al*. (2004); Hemming *et al*. (2005); Klumpp *et al*. (2005)
Coarse woody debris	6	Kohzu *et al*. (1999); Hobbie *et al*. (2001); Trudell *et al*. (2004)
Litter	23	Buchmann *et al*. (1997); Martinelli *et al*. (1998); Hobbie *et al*. (1999, 2001); Kohzu *et al*. (1999); Bowling *et al*. (2002); Scartazza *et al*. (2004); Trudell *et al*. (2004); Barbour *et al*. (2005)
Soil organic matter (SOM)	113	Flanagan *et al*. (1996); Buchmann *et al*. (1997); Hobbie *et al*. (1999, 2001); Kohzu *et al*. (1999); Bowling *et al*. (2002, 2003); Scartazza *et al*. (2004); Trudell *et al*. (2004); Barbour *et al*. (2005); Hemming *et al*. (2005)
Mycorrhizal fungi	15	Hobbie *et al*. (1999, 2001); Högberg *et al*. (1999); Kohzu *et al*. (1999); Trudell *et al*. (2004); Hart *et al*. (2006)
Saprotrophic fungi	15	Hobbie *et al*. (1999, 2001); Högberg *et al*. (1999); Kohzu *et al*. (1999); Trudell *et al*. (2004); Hart *et al*. (2006)
Leaf respiration	69	Cernusak *et al*. (2001); Bowling *et al*. (2003); McDowell *et al*. (2004a); Ocheltree & Marshall (2004); Xu *et al*. (2004); Badeck *et al*. (2005); Klumpp *et al*. (2005); Mortazavi *et al*. (2005); Schnyder & Lattanzi (2005); Prater *et al*. (2006)
Root respiration	14	Badeck *et al*. (2005); Klumpp *et al*. (2005); Schnyder & Lattanzi (2005)
Bark/wood respiration	5	Cernusak *et al*. (2001); Damesin & Lelarge (2003)
Soil respiration	38	Flanagan *et al*. (1996); Buchmann *et al*. (1997); Mortazavi & Chanton (2002); Bowling *et al*. (2003); Fessenden & Ehleringer (2003); McDowell *et al*. (2004a); Mortazavi *et al*. (2005)
Ecosystem respiration	117	Flanagan *et al*. (1996); Buchmann *et al*. (1997); Bowling *et al*. (2002, 2003); Mortazavi & Chanton (2002); Fessenden & Ehleringer (2003); McDowell *et al*. (2004a); Scartazza *et al*. (2004); Barbour *et al*. (2005); Hemming *et al*. (2005); Mortazavi *et al*. (2005)

Fig. 4 A comparison of the isotopic composition of plant and ecosystem carbon pools and respiratory fluxes, expressed relative to bulk leaf biomass. Where studies reported sun and shade leaf carbon isotopic composition ($\delta^{13}C$), only sun leaf values were used. The boxes encompass the upper and lower quartiles of the data, the line shows the median, the symbol shows the arithmetic mean, and the error bars show the upper and lower 10th percentiles of the data. The vertical dashed line is included for easy reference to the $\delta^{13}C$ of leaf sugars. Horizontal lines separate (a) plant pools, (b) ecosystem pools, and (c) respiratory fluxes. This figure is not meant to be an exhaustive compilation of all relevant studies, rather a compilation large enough to indicate general patterns. No study has examined all of these categories at a single site. Other studies are relevant, but bulk leaf $\delta^{13}C$ is not always reported. (d) Number of samples (*n*) and references used for each category. As some studies reported means and others reported individual sample values, the values of *n* shown are minima and the actual number of samples is much larger in most cases. SOM, soil organic matter.

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Table 1 Values used in the calculation of the isotope ratio of growth respiration: the average concentration of compounds in herbaceous and woody leaves, the per cent carbon in each compound, the CO_2 produced in the synthesis of each compound, the average carbon isotope ratio ($\delta^{13}C$) of each compound relative to leaf sugars, and the $\delta^{13}C$ of growth respiration relative to leaf sugars

Compound	Herbaceous concentration[1] (mg g^{-1})	Woody concentration[1] (mg g^{-1})	Per cent carbon in compound[2]	CO_2 produced[1] (mmol g^{-1})	$\delta^{13}C$ relative to sugar (‰)[3]	$\delta^{13}C$ of growth respiration relative to sugar (‰)
Lipids	45	56	77.3	36.5	–5.4	10
Protein	222	131	46.8	37.9	–0.6	1
Lignin	44	113	66.6	13.1	–4.2	18
TSC	253	189	40.0	2.8	0.6	–7
TNC	176	131	40.0	1.8	0.0	0
Organic acids	83	51	41.9	–1.0	–0.8	–28

TSC, total structural carbohydrates; TNC, total nonstructural carbohydrates.
[1]From Poorter & Villar (1997).
[2]From Randerson *et al.* (2006).
[3]From Fig. 2.

Using data on the chemical composition of leaves and their construction costs compiled by Poorter & Villar (1997), the C content of different plant compounds from Randerson *et al.* (2006), and the data in Fig. 2, the isotopic composition of growth respiratory CO_2 for an average leaf can be calculated (Table 1). This involves the simplifying assumptions that phloem transport can be neglected and that the mass of each isotope in the compounds created and in the respiratory flux is conserved. Undoubtedly, the first of these assumptions is incorrect, as sugar export is certain to be significant and metabolic and biosynthetic pathways are intricately linked. Nevertheless, this exercise is informative. Starting with photosynthetic sugars with an isotopic composition of –26.0‰, for example, an herbaceous leaf may be expected to have an isotope ratio of –26.9‰, with individual components varying widely, including the fairly depleted lipids (–31.4‰) and lignin (–30.2‰) and enriched cellulose (–25‰) (Fig. 2). The flux-weighted average respiratory CO_2 evolved from synthesis of structural and nonstructural carbohydrates, lipids, protein, organic acids, and lignin is –23.5‰ for an herbaceous leaf and –20.9‰ for a woody plant leaf, or 2.5 and 5.1‰ enriched, respectively, relative to leaf sugar. Relative to the bulk leaf these differences are even larger (3.4 and 6.8‰) and imply that growth respiration has the potential to contribute substantially to the offset observed between the $\delta^{13}C$ values of ecosystem respiration and the bulk leaf. (Figs 1, 4).

In practice, larger enrichments of respiratory CO_2 relative to sucrose have been reported, with values as high as 6‰ (Duranceau *et al.*, 1999; Ghashghaie *et al.*, 2001; Ghashghaie *et al.*, 2003). This implies a large flux of respiratory CO_2 from synthesis of depleted compounds, given the relatively small pool of lipids and lignin in most leaves. The largest component of maintenance respiration is protein turnover, which can account for 60% of maintenance costs (Penning de Vries, 1975). The isotopic composition of amino acids is widely variable (Abelson & Hoering, 1961; Smallwood *et al.*, 2003), reflecting multiple biosynthetic pathways in photosynthesis, glycolysis, and the Krebs cycle (Lea & Ireland, 1999). In higher plants, individual amino acids have been found to be both enriched and depleted relative to the bulk leaf by 6‰ or more (Whelan *et al.*, 1970; Smallwood *et al.*, 2003); an isotopic depletion similar to that of lipids may be expected for amino acids synthesized from Krebs cycle intermediates. Protein turnover may involve recycling of amino acids in addition to the synthesis of new ones (Amthor, 2000), and the effects of both processes on C isotope fractionation have not been well examined. There is a great potential to gain a process-level understanding of maintenance respiration and its variations through evaluation of natural abundance C isotope effects in plant respiration and biosynthetic fractions. Detailed examination of positional isotope effects in various compounds, including amino acids which have a pronounced enrichment in carboxyl groups, may prove particularly useful in the future (Brenna, 2001; Schmidt, 2003; Savidge & Blair, 2004).

A role for maintenance respiration in isotopic enrichment of respiratory CO_2 is supported by Ocheltree & Marshall (2004), who found a negative correlation between respiratory enrichment and relative growth rate (RGR). *Helianthus annuus* growing in low light with low RGR showed enrichment of respiratory CO_2 of 6‰ relative to soluble carbohydrates, while plants in high light with high RGR showed enrichment of only 2‰. Maintenance respiration is a larger proportion of total respiratory CO_2 in slow-growing as opposed to fast-growing plants (Amthor, 1984), which may explain this pattern. Furthermore, the protein-turnover component of maintenance respiration has been correlated with protein content (Penning de Vries, 1975; Amthor, 1984; Ryan, 1991), which is lower in roots than in shoots (Poorter & Villar, 1997), although roots

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have a high ion uptake maintenance cost (Amthor, 1984). Klumpp *et al.* (2005) found that, while the respiratory CO_2 of shoots was enriched relative to shoot biomass, root respiratory CO_2 was depleted relative to root biomass in *H. annuus*, *Medicago sativa*, and *Lolium perenne*. These findings support a role for maintenance respiration in isotopic enrichment of shoot respiratory CO_2; in addition, there are interesting implications for consideration of the isotopic composition of whole-plant respiration. The opposing isotope effects in root and shoot respiration were nearly balanced, so the difference in $\delta^{13}C$ between whole-plant respiration and whole-plant biomass was small or negligible (Klumpp *et al.*, 2005). The generality of these results remains to be seen, particularly as the allocation of C to aboveground vs belowground biomass and metabolism may differ for other taxa.

III. Isotopic composition of plant and ecosystem carbon pools

1. Plant carbon pools

Plant tissues exhibit systematic differences in their C isotopic composition relative to the leaf (Boutton, 1996; Hobbie & Werner, 2004; Badeck *et al.*, 2005). As mentioned, phloem sap sugars and bulk phloem sap are generally enriched relative to bulk leaf material (Fig. 4) for unknown reasons. Additionally, in a *Pinus sylvestris* forest phloem sap in boles was more enriched (by 1.1‰) than phloem sap in twigs, a difference that persisted in both summer and winter (Brandes *et al.*, 2007).

The $\delta^{13}C$ of phloem sap also varies in response to environmental influences on photosynthetic C isotope discrimination. Pate & Arthur (1998) showed seasonal variability of up to 8‰ in the $\delta^{13}C$ of phloem sap of *Eucalyptus globulus* that matched the seasonal pattern of plant water stress (more enriched during months of low precipitation). Gessler *et al.* (2001) found that the relationship between leaf water potential and the $\delta^{13}C$ of phloem sap was additionally modified by light availability, both in the short term and with aspect relative to the sun. The $\delta^{13}C$ of phloem sap has also been related to sap flux-derived canopy conductance (Keitel *et al.*, 2003; Gessler *et al.*, 2004), and to c_i/c_a from leaf gas exchange (Brandes *et al.*, 2006), further indication that Δ_A influences short-term variability. Diel variability in the $\delta^{13}C$ of water-soluble C in leaves and phloem sap in twigs and boles of *P. sylvestris* has been observed (Brandes *et al.*, 2006), with peak enrichment occurring during the night/early morning. Correlations have been found between the $\delta^{13}C$ of phloem sap and the seasonal pattern of the $\delta^{13}C$ of total ecosystem respiration (Scartazza *et al.*, 2004), although the linkages appear quite complex and sometimes are not observed (Barbour *et al.*, 2005).

The systematic offset between the $\delta^{13}C$ values of wood and leaf tissue has long been known (Leavitt & Long, 1982). This is apparent as a mean enrichment in woody tissue of boles of 3.2‰, and in twigs of 1.3‰ (Fig. 4). Note, however, that the $\delta^{13}C$ of new wood growth is not constant over time. Environmental variation in Δ_A is transferred to tree rings (e.g. Pate & Arthur, 1998), providing one basis for paleo-ecological environmental studies. There are consistent systematic patterns in the $\delta^{13}C$ of wood within annual rings that are independent of photosynthetic fractionation and are likely related to the relative use of stored C reserves vs new photosynthate (Helle & Schleser, 2004). Root tissues are generally enriched relative to leaf tissue, by 2.3‰ on average (Fig. 4). The difference in enrichment among twigs, boles, and roots is not well understood, although it appears fairly robust based on the sample sizes in Fig. 4. Cernusak *et al.* (2005) reported that newly formed xylem tissue in *E. globulus* was isotopically similar to phloem sap, suggesting that the enrichment of phloem sap is not associated with wood formation.

2. Ecosystem carbon pools

After aboveground woody tissue senesces and begins decomposing as coarse woody debris, there may be additional enrichment of the dead woody tissue (Fig. 4). Possible reasons for this enrichment are unknown. Laboratory incubation of beech (*Fagus crenata*) wood with the saprotrophic fungus *Trametes versicolor* resulted in no change in the $\delta^{13}C$ of the remaining wood despite a mass loss of 69% and a 2‰ enrichment in the $\delta^{13}C$ of fungal respiration over time (Kohzu *et al.*, 1999). Decomposition studies with various plant materials have shown that the $\delta^{13}C$ of the remaining undecomposed tissues becomes more (not less) negative as mass is lost, at least in part as a result of the higher relative abundance of isotopically light lignin (Fernandez *et al.*, 2003; Preston *et al.*, 2006).

Among the categories listed in Fig. 4, the $\delta^{13}C$ of litter (organic horizon) was most closely related to that of bulk leaf tissue. This is not surprising, as surface litter in forests is composed primarily of leaves in varying stages of decomposition. Decomposition of above- and belowground C_3 plant materials in litterbags in the field has shown enrichment of bulk material as mass is lost, despite increases in lignin proportion (Wedin *et al.*, 1995). Wedin *et al.* (1995) suggested that incorporation of C from soil organic matter (SOM) into the bulk matrix was the cause of enrichment over time. In general, SOM within the top 10 cm of mineral soil, or the A-horizon, is enriched relative to leaves by *c.* 2‰ (Fig. 4). This enrichment varies with depth in the soil profile; possible reasons for this have been recently reviewed (Ehleringer *et al.*, 2000).

The biomass of soil microbes, invertebrates, and other heterotrophic organisms, at least the smallest ones, are a small component of the bulk SOM values reported in Fig. 4. It is difficult to estimate the isotopic composition of the soil microbial biomass pool separately from that of the dead organic material in the soil, but the microbial biomass pool is probably enriched by 1–2.5‰ relative to total SOM (Santruckova *et al.*, 2000; Dijkstra *et al.*, 2006). In general, the $\delta^{13}C$ of

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animals reflects the $\delta^{13}C$ of their food source. The $\delta^{13}C$ of larger soil organisms such as earthworms can be enriched relative to litter by a few ‰ (Uchida *et al.*, 2004). Fungivorous micro-arthropods, consuming enriched hyphae of both mycorrhizal and saprotrophic fungi, can be enriched above leaves by more than 10‰ (Hobbie *et al.*, 2007).

The isotopic composition of sporocarps (mushrooms) of soil-dwelling fungi has been examined extensively. Fungi that form mycorrhizal symbioses with host plants are enriched relative to bulk leaves by *c.* 3‰, and saprotrophic fungi are even more enriched, by nearly 6‰ above the leaves of the dominant plants in the forests (Fig. 4). Fungal mycelia, however, are not as enriched as the sporocarps (Wallander *et al.*, 2004; Bostrom *et al.*, 2007). Similar patterns of enrichment are found in nitrogen (N) isotopes, and C and N isotopes are often used together to distinguish the trophic status of fungal species (Högberg *et al.*, 1999; Hobbie *et al.*, 2001). There are poorly understood but consistent differences between fungal taxa at the genus and species levels (Taylor *et al.*, 2003; Trudell *et al.*, 2004). Although there is some evidence for fractionation upon fungal uptake of sucrose in culture (Henn & Chapela, 2000; Henn *et al.*, 2002), it is likely that the difference in the $\delta^{13}C$ values of mycorrhizal and saprotrophic fungi reflects a difference in C sources (Henn & Chapela, 2001). The mycorrhizal fungi use C provided by the roots, and the decomposers utilize more enriched soil organic compounds (Fig. 4). The isotopic composition of the root compounds that are provided to the mycorrhizal fungi is unknown but is likely to reflect recent photosynthate that is hours to days old (Högberg *et al.*, 2001; Johnson *et al.*, 2002). The isotopic composition of 'recent' photosynthate is difficult to measure, but studies of phloem isotopic composition (e.g. Brandes *et al.*, 2006) provide a reasonable estimate.

A final C pool that deserves attention is the dissolved organic carbon (DOC) in the soil solution. Carbon isotopes are used widely by the limnological community to infer the origin and transport of organic materials from terrestrial to aquatic ecosystems (e.g. Hood *et al.*, 2005), but there have been few studies of the $\delta^{13}C$ of DOC within the soil solution in terrestrial ecosystems (Ludwig *et al.*, 2000). One recent study compared the isotopic compositions of leaves, soil, soil solution, and stream water in catchments with deciduous and coniferous vegetation (Amiotte-suchet *et al.*, 2007). SOM was enriched relative to leaves as shown in Fig. 4. The $\delta^{13}C$ of the soil solution was *c.* 1‰ depleted relative to SOM under deciduous vegetation, and *c.* 1‰ enriched relative to SOM in coniferous forests. Variation with depth in the relationship between the $\delta^{13}C$ values of SOM and DOC appears to be important (Ludwig *et al.*, 2000); see Tu & Dawson (2005) for further discussion. We cannot yet provide a range for the isotopic composition of the soil DOC pool, but it may be important in determining overall isotopic mass balance in terrestrial ecosystems (especially for those with high precipitation).

IV. Isotopic composition of assimilation and respiration fluxes

With the exception of studies of the *leaf level* photosynthetic discrimination of net assimilation (leaf uptake – leaf respiration), now routinely measured in the laboratory via online discrimination (Evans *et al.*, 1986), the $\delta^{13}C$ of the assimilation flux is difficult to measure. Direct measurements of Δ_A at the leaf or branch level in the field are very rare (Harwood *et al.*, 1998; Wingate *et al.*, 2007), and to our knowledge there has been only one attempt to scale such field measurements to an entire vegetation canopy (Tissue *et al.*, 2006). More typically in the field, gas exchange measurements (without isotopes) are used to measure c_i/c_a, and then Δ_A is calculated using the Farquhar *et al.* model or a variant (e.g. Hymus *et al.*, 2005). Researchers have used tower-based water vapor flux measurements and a Penman–Monteith inversion to calculate a canopy conductance and the Farquhar *et al.* model or a variant to compute Δ_A for a whole forest (Bowling *et al.*, 2001; Ogee *et al.*, 2003; Knohl & Buchmann, 2005). This approach tends to underestimate Δ_A relative to estimates that come from multi-layer biophysical models (e.g. compare the results of Bowling *et al.*, 2001 and Baldocchi & Bowling, 2003 for the same forest).

Other studies have used the $\delta^{13}C$ of nocturnal whole-ecosystem respiration as a proxy from which to derive Δ_A, either directly or indirectly (e.g. Flanagan *et al.*, 1996; Bowling *et al.*, 2002; Alstad *et al.*, 2007). While reasonable, results obtained using this approach differ fundamentally from those obtained using a variety of other measurement and modeling methods that examined c_i/c_a at different scales in a temperate rainforest (Tissue *et al.*, 2006). The difference may be attributable to a systematic offset in $\delta^{13}C$ between assimilation and respiration fluxes, including the expected enrichment from plant growth respiration described in Section II 'Isotopic composition of plant metabolites and autotrophic respiration', or to the fact that the $\delta^{13}C$ of the assimilation flux is poorly quantified at present at spatial scales larger than a single leaf. Ultimately, the $\delta^{13}C$ of the assimilation flux is likely to be more closely related to the isotopic composition of leaf sugars (Fig. 2) or the organics exported from the leaf in the phloem (Fig. 4) than the $\delta^{13}C$ of bulk leaves or ecosystem respiration, because of the fractionations associated with leaf respiration, biosynthesis and C allocation discussed above.

Although the biochemical process of mitochondrial respiration does not appear to lead to direct fractionation (Lin & Ehleringer, 1997), the $\delta^{13}C$ of respiration differs from that of the bulk organic material that is respiring (such as a leaf or stem) or being decomposed. Theoretical calculations suggest that there may be inherent biochemical fractionations in the Krebs cycle (Tcherkez & Farquhar, 2005). As discussed, leaf respiration is enriched on average above bulk leaf composition by more than 3‰ (Fig. 4).

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The isotopic composition of root respiration fluxes is difficult to measure and, to our knowledge, measurements of the $\delta^{13}C$ of respiration from intact roots in the field have not been reported. Tu & Dawson (2005) reported a $\delta^{13}C$ of root respiration from detached roots that was mildly enriched relative to sun leaves at the top of a *Sequoia sempervirens* canopy, a result that differs markedly from those of laboratory studies. Klumpp *et al.* (2005) and Schnyder & Lattanzi (2005) used a special gas exchange system to measure the $\delta^{13}C$ of respiration from whole-shoot and whole-root tissues in herbaceous annuals and perennials. They found that root respiration was in general depleted in $\delta^{13}C$ relative to bulk leaf (whole shoot) biomass. In partial agreement with these laboratory studies, Badeck *et al.* (2005) reported that the $\delta^{13}C$ of root respiration in *P. vulgaris* was depleted relative to root sucrose, but not relative to bulk leaf material. Root respiration is the only quantity shown in Fig. 4 that is consistently more negative in $\delta^{13}C$ than leaves; a mechanism to explain this trend is lacking. Our understanding of the $\delta^{13}C$ of root respiration is limited at present and more studies are needed to determine whether root respiratory CO_2 is consistently depleted under field conditions.

The isotopic composition of respiration from stems and boles of living plants is also poorly understood. While woody tissue respiration represents only a few per cent of total ecosystem respiration (e.g. Law *et al.*, 1999), there is evidence to suggest that the CO_2 evolved may originate not only from the living cells within the stem, but also from respiration elsewhere (presumably roots) the products of which are transported in the xylem stream (Teskey & McGuire, 2007). Studies that have reported the $\delta^{13}C$ of respiration of woody tissue have shown an enrichment relative to the associated bulk leaf tissue (Fig. 4, Cernusak *et al.*, 2001; Damesin & Lelarge, 2003; Brandes *et al.*, 2006). A recent study with *Q. petraea* identified pronounced seasonal and diurnal variability in the $\delta^{13}C$ of respiration of woody tissue (Maunoury *et al.*, 2007). Seasonal changes were attributed to phenology and the relative contributions of growth and maintenance respiration. Diurnal changes were greatest in winter when there were no leaves on the trees.

In general, the $\delta^{13}C$ of heterotrophic respiration by microbes and other soil organisms cannot be measured in the field without experimental manipulations such as isotopic labeling, stem girdling, or trenching or other means of root exclusion. Incubation studies with decomposing organic materials generally show a $\delta^{13}C$ of microbial respiration that is initially depleted (relative to the material being decomposed), then becomes enriched, and eventually stabilizes over many months as the labile C is consumed (Andrews *et al.*, 1999; Schweizer *et al.*, 1999; Fernandez & Cadisch, 2003; Fernandez *et al.*, 2003; Crow *et al.*, 2006). A similar pattern of enrichment in respired CO_2 over time has been found with CO_2 evolved as fungi decompose wood (Kohzu *et al.*, 1999). Changes in $\delta^{13}C$ over time during incubations are potentially quite useful in identifying the $\delta^{13}C$ of the labile vs recalcitrant C pools in the soil (Andrews *et al.*, 1999), but their applicability to understanding the $\delta^{13}C$ of respiratory fluxes in the field may be limited as the connection to the rapidly cycling C pool (Högberg *et al.*, 2001) has been lost.

In general, the soil respiration flux (measured from chambers on the soil surface) is enriched relative to leaves of the dominant trees in a forest by an average of 2.6‰ (Fig. 4). Variability in the $\delta^{13}C$ of soil respiration has been linked to environmental conditions, presumably through meteorological influences on the Δ_A of whole forests (Ekblad & Högberg, 2001; Ekblad *et al.*, 2005; Mortazavi *et al.*, 2005). Linkages with weather involve time lags of a few days; that is, a particular weather event influences the $\delta^{13}C$ of soil respiration a few days later. Reasons for the time lags are not well understood, but presumably involve the time necessary for C transport belowground and C exchange with root symbionts. There is evidence that there are several pools of respiratory metabolites with differing turnover times in plants (Nogues *et al.*, 2004, 2006).

The isotopic composition of whole-ecosystem respiration (measured with the Keeling-plot technique; Pataki *et al.*, 2003) is enriched relative to bulk leaf tissue across a wide variety of biomes, by an average of 1.7‰ (Fig. 4). As mentioned, factors such as mean annual precipitation strongly influence the $\delta^{13}C$ of leaves, and the $\delta^{13}C$ of ecosystem respiration corresponds to mean annual precipitation as a result (Fig. 1). The variability in the $\delta^{13}C$ of ecosystem respiration at a particular site, however, shows important variation on a time scale of days to months that has been linked to a variety of factors. These include soil moisture (Lai *et al.*, 2005), atmospheric humidity and radiation (Bowling *et al.*, 2002; Knohl *et al.*, 2005), and air or soil temperatures (Bowling *et al.*, 2002; McDowell *et al.*, 2004b). A more complete listing of studies that have shown these linkages and related discussion can be found in Schaeffer *et al.* (in press).

A lack of complete understanding of the isotopic composition of C pools and fluxes in terrestrial ecosystems is apparent in the trends shown in Fig. 4. While no study has yet measured the $\delta^{13}C$ values of leaf, root, wood, soil, and ecosystem respiration simultaneously, a few have measured several of these fluxes at once (Bowling *et al.*, 2003; McDowell *et al.*, 2004a; Mortazavi *et al.*, 2005) and do not usually achieve mass balance. Root respiration makes up a significant component of soil respiration (Subke *et al.*, 2006), and as root respiration is fairly depleted in $\delta^{13}C$ (*c.* –2‰ relative to leaves; Fig. 4) an unidentified but enriched source of CO_2 is required to explain the enriched values of soil respiration shown in Fig. 4 (a +2.6‰ enrichment relative to leaves). CO_2 originating from decomposition of SOM is unlikely to be enriched relative to SOM; such a fractionation could not be sustained over long periods of time without gradual isotopic depletion of the soil C pool. The enriched source may come from fungal respiration, as the biomass of fungi is enriched relative to other ecosystem components (Fig. 4), but to our knowledge the $\delta^{13}C$ of fungal respiration has not been measured in the field. This

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mass balance dilemma extends to the whole ecosystem as well. How can total ecosystem respiration be 1.7‰ enriched relative to leaves on average if both leaf respiration and soil respiration are more enriched than ecosystem respiration (Fig. 4)? This problem does not result from the compilation of disparate studies in Fig. 4 – it has been observed in individual ecosystems (Bowling *et al.*, 2003; McDowell *et al.*, 2004a).

Many studies have examined the $\delta^{13}C$ of bulk soil surface respiration, using a wide variety of methods (see references in Fig. 4). The relatively small variability in the $\delta^{13}C$ of soil respiration (Fig. 4) is encouraging given the various methods used, but it is quite possible that they all are in error. Because of diffusive fractionation, CO_2 in the soil gas is enriched relative to the flux leaving the soil by 4.4‰ (Cerling *et al.*, 1991). If enriched CO_2 was inadvertently advected from the soil during flux measurements, the resulting $\delta^{13}C$ of measured soil surface flux would be too enriched (Bowling *et al.*, 2003; McDowell *et al.*, 2004a). Subtracting 4.4‰ from the soil respiration value in Fig. 4 places it much closer to the $\delta^{13}C$ of root respiration, although root respiration studies have been relatively few and should be compared with other ecosystem fluxes in a greater variety of ecosystems and environmental conditions.

V. Ecosystem to global scale issues – isotopic composition of gross primary production, net primary production, and net ecosystem production

Variations in the $\delta^{13}C$ of ecosystem C pools and fluxes (Fig. 4) provide a context for understanding how the isotopic compositions of gross primary production (GPP), net primary production (NPP), and net ecosystem production (NEP) are likely to differ. They are also critical for interpreting temporal and spatial variability in the isotopic composition of atmospheric CO_2. The isotopic composition of NPP begins with the $\delta^{13}C$ of assimilates from GPP, including the sensitivity of Δ_A to environmental conditions, but depends additionally on post-assimilation fractionation during tissue synthesis. As a result, plant-to-plant and ecosystem-to-ecosystem differences in C allocation and tissue chemistry are likely to simultaneously influence the $\delta^{13}C$ of plant respiration and the biomass increment that ultimately provides the substrate for the heterotrophic community. The $\delta^{13}C$ variations caused by allocation are not necessarily small compared with those arising from environmental regulation of GPP: the mean difference between bole and bulk leaf $\delta^{13}C$ values is 3.2‰ (Fig. 4) and is of comparable magnitude to variability in the $\delta^{13}C$ of whole-forest respiration (Bowling *et al.*, 2002; Lai *et al.*, 2005). The isotopic composition of NEP starts with the $\delta^{13}C$ of C flow from NPP, but depends additionally on the variable decomposition rates of different plant tissues (Parton *et al.*, 2007), and on the biosynthesis of new compounds by the soil microbial community. In terms of the net effect of terrestrial ecosystems on atmospheric (and oceanic) $\delta^{13}C$, other fluxes including fire, leaching of dissolved organic C compounds, and erosion can be important in some instances and are a part of the net ecosystem C balance.

The use of atmospheric $\delta^{13}CO_2$ and CO_2 measurements to partition land and ocean C sinks takes advantage of large differences in discrimination associated with C uptake by terrestrial ecosystems and by the oceans (Quay *et al.*, 1992; Tans *et al.*, 1993; Francey *et al.*, 1995; Keeling *et al.*, 1995; Heimann & Maier-Reimer, 1996). In past work, GPP-weighted estimates of Δ_A have been used as estimates of discrimination associated with the net terrestrial C sink (Ciais *et al.*, 1995), with recent work accounting for interannual variability in climate (Randerson *et al.*, 2002a; Scholze *et al.*, 2003; Suits *et al.*, 2005) and time-varying contributions from C_3 and C_4 ecosystems (Townsend *et al.*, 2002; Still *et al.*, 2003). GPP-weighted estimates of Δ_A are only appropriate for use with the net terrestrial sink when fractionations during plant tissue synthesis, C allocation and transport, and decomposition are negligible and when C storage is proportional to GPP. In light of the evidence provided here for substantial discrimination processes in terrestrial C cycling, manifested as systematic differences in $\delta^{13}C$ among different plant and ecosystem C pools (Fig. 4), there are both conceptual and practical limits to the use of GPP-weighted Δ_A in global C cycle studies. More generally, what is needed for interpreting the atmospheric record is the $\delta^{13}C$ associated with the net exchange (net storage or release) of C from terrestrial ecosystems. The challenge is that the C pools that contribute to net storage vary considerably with the time scale of the net exchange – with consequences for $\delta^{13}C$ of the net exchange. The discussion that follows is diagrammed conceptually in Fig. 5. For a fully developed forest canopy at midday over a period of a few minutes, for example, net C gain is probably dominated by photosynthesis and so the discrimination associated with net storage is near Δ_A. On this time scale, most of the C storage is associated with expanding pools of sucrose and starch in leaves. During the night, by contrast, the discrimination inferred from ecosystem respiration (nighttime Keeling plots; Fig. 5) may be smaller than the actual Δ_A during the day, as a result of contributions from growth respiration associated with the construction of more reduced plant compounds (Section II, 'Isotopic composition of plant metabolites and autotrophic respiration'). This explanation may resolve the contradiction in c_i/c_a estimates using different methods identified by Tissue *et al.* (2006).

Over seasonal time scales, the contribution of plant respiration to the atmospheric record probably becomes less important because of its rapid turnover. Several lines of evidence show that plant respiration is composed mostly of recent assimilates that have a turnover time of days to a few weeks (Ekblad & Högberg, 2001; Högberg *et al.*, 2001; Bowling *et al.*, 2002; Brandes *et al.*, 2006; Carbone *et al.*, 2007). As a

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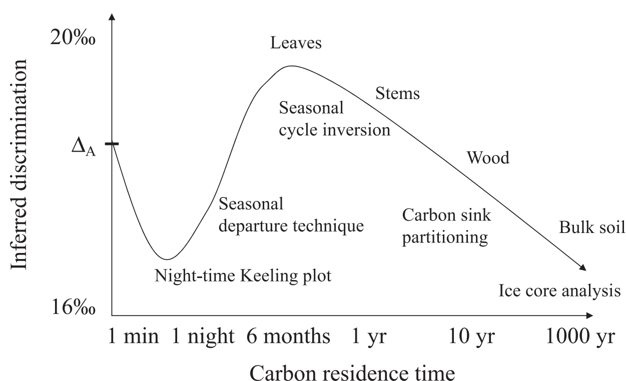

Fig. 5 Conceptual model of inferred discrimination as a function of carbon residence time. At midday over a forest, the net flux is dominated by net assimilation and so the inferred discrimination approaches the discrimination associated with photosynthesis (Δ_A). Over a period of days to weeks, biosynthesis of leaves and other plant tissues contributes to an enriched respiratory flux and, simultaneously, the construction of depleted leaf bulk tissue. Inferring discrimination from nocturnal Keeling plots thus leads to an underestimate of Δ_A. By contrast, inferring discrimination from seasonal changes in atmospheric CO_2 isotopic composition ($\delta^{13}CO_2$) may lead to an overestimate of Δ_A because the growth and decomposition of leaf and small stem tissues play an important role in shaping biosphere–atmosphere exchange over a period of months. On interannual to decadal time scales, the net terrestrial flux is dominated by the expansion or loss of woody biomass, implying that isotopic measurements of woody biomass may be most appropriate for use in 'double deconvolution' carbon partitioning studies.

result, plant respiration probably contributes only negligibly to the seasonal cycle of $\delta^{13}CO_2$ in the northern hemisphere, as the minimum in late spring (typically April or May) is separated from the maximum (typically August or September) by ~3–4 months (Trolier *et al.*, 1996), a time interval an order of magnitude larger than the turnover time of the C pool associated with plant respiration. Instead, the seasonal atmospheric enrichment (and concurrent drawdown of CO_2) has to be driven primarily by growth from assimilates that have been transformed into longer-lived compounds associated with new plant tissues such as leaves, roots, or stems. Leaf and fine-root components of NPP are probably the most important contributors to the seasonal exchange because their combined growth is often 60–80% of total NPP (Saugier *et al.*, 2001). As a result, discrimination inferred from a seasonal cycle inversion based on flask measurements of the seasonal cycle of $\delta^{13}CO_2$ and CO_2 (e.g. Randerson *et al.*, 2002b) may be larger than GPP-weighted Δ_A (Fig. 5). In fact, it may be substantially larger than that inferred from nighttime Keeling plots (Fig. 5) or approaches that take advantage of synoptic CO_2 variability, including the departure of CO_2 and $\delta^{13}CO_2$ from a mean seasonal cycle (Bakwin *et al.*, 1998; Miller *et al.*, 2003), because sucrose and other recent assimilates contribute proportionally more to atmospheric CO_2 variability on these shorter time scales and are enriched relative to bulk leaf and litter biomass pools (Figs 2, 4).

While leaf and fine-root dynamics contribute substantially to seasonal exchange, they are less important for C storage on decadal time scales because leaf and fine-root litter pools decompose relatively rapidly and thus have little long-term storage capacity. On decadal time scales, woody biomass and coarse woody debris pools play important roles in C storage of many terrestrial ecosystems. A primary mechanism contributing to the northern hemisphere terrestrial sink at the end of the 20th century, for example, was the accumulation of woody biomass in forest ecosystems as a result of decreasing fires and other forms of disturbance (Goodale *et al.*, 2002; Hurtt *et al.*, 2002). In the tropics, a primary contemporary loss pathway is deforestation, with the largest flux originating from the aboveground woody biomass pool (Houghton *et al.*, 2000; Achard *et al.*, 2002; Saatchi *et al.*, 2007). Thus, even though changes in the wood pool have a relatively small effect on the $\delta^{13}C$ of ecosystem respiration or on seasonal exchange, because of their role in long-term C storage the isotopic composition of the wood pool may be the most appropriate to assign to the net terrestrial C sink in partitioning studies that assess variability on interannual to decadal timescales.

On centennial to millennial timescales, C storage in wood is eclipsed by C storage in soils, and so for interpretation of Holocene or glacial-interglacial changes in the C cycle using ice core records (Trudinger *et al.*, 1999; Kohler *et al.*, 2006), a weighted combination of the $\delta^{13}C$ of the wood and soil pools may be the most appropriate to assign to the net terrestrial flux. More generally, the isotopic composition of the terrestrial flux is likely to vary with its temporal scale and the measurement techniques used to diagnose it (Fig. 5).

VI. Conclusions and suggestions for further research

We have provided evidence to support the hypothesis that bulk leaf $\delta^{13}C$ acts as an isotopic reference point from which there are predictable differences in the $\delta^{13}C$ of plant and ecosystem C pools and fluxes. From this work, we have identified several questions or topics that merit additional research. These topics are compelling enough to move our understanding of C cycling forward substantially, and detailed investigations of these issues will likely lead to an enhanced understanding of plant and ecosystem C cycling and allocation patterns.

- What are the factors controlling the $\delta^{13}C$ of respiration in plants?
- Why is the $\delta^{13}C$ of phloem sap enriched relative to leaves? What factors control this enrichment?
- How does growth respiration contribute to the enrichment of ecosystem respiration?
- Where does assimilation fit on Fig. 4, at whole-forest, regional, and global scales?

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- How does the $\delta^{13}C$ of whole-forest respiration compare with that of whole-forest assimilation, and how does the $\delta^{13}C$ of these fluxes change seasonally or interannually?
- Is root respiration generally as depleted as in Fig. 4? Are soil chamber isotope methods artifact-free, and if so, what is the source of enriched CO_2 that balances the depleted root respiration?

New and complementary tools for studying ecosystem C cycling will provide additional insight into the factors that cause isotopic variability in C pools and fluxes. Bomb (and experimentally added) radiocarbon is useful to study C cycling, particularly in longer-lived reservoirs such as wood and soils, but also in respiratory fluxes (Trumbore, 2000; Hahn *et al.*, 2006; Schuur & Trumbore, 2006). Combined studies with ^{13}C and ^{14}C will yield very complementary information about C cycle processes (Carbone & Trumbore, 2007). Isotope labels can be applied to whole trees or whole ecosystems over periods from hours to years (Steinmann *et al.*, 2004; Taneva *et al.*, 2006; Carbone *et al.*, 2007), and can be applied in very small amounts to investigate particular ecosystem processes (Ekblad *et al.*, 2002; Czimczik *et al.*, 2005). Real-time measurements of $\delta^{13}C$ of CO_2 are now possible in air (Bowling *et al.*, 2005), and isotopic flux measurements can be made in real time using chambers (Barbour *et al.*, 2007). Combinations of these methods with more traditional isotope sampling approaches are likely to be especially fruitful.

Acknowledgements

This review is dedicated to the memory of our colleague and friend Professor Elizabeth W. Sulzman. Thanks to Claudia Keitel, Behzad Mortazavi, Troy Ocheltree and Hans Schnyder for sharing data, and to Andrew Moyes and Sean Schaeffer for reading and improving drafts of this manuscript. DRB was supported during this time by the Office of Science (BER), US Department of Energy, Grant No. DE-FG02-04ER63904. DEP was supported by the US National Science Foundation Grants 0620176 and 0624342. JTR was supported by the US National Science Foundation (0628637), NASA (NNG04GK49G), and the NOAA Climate Program Office (NA03OAR4310059). Ideas for this review originated at conferences in Orvieto, Italy (2003), and Interlaken, Switzerland (2004), which were supported by the Biosphere-Atmosphere Stable Isotope Network (funded by the US National Science Foundation) and the Stable Isotopes in Biospheric-Atmospheric Exchange network (funded by the European Science Foundation). We thank our colleagues for their inspirational ideas and thoughtful discussions at these conferences.

References

Abelson PH, Hoering TC. 1961. Carbon isotope fractionation in formation of amino acids by photosynthetic organisms. *Proceedings of the National Academy of Sciences, USA* 47: 623–632.

Achard F, Eva HD, Stibig HJ, Mayaux P, Gallego J, Richards T, Malingreau JP. 2002. Determination of deforestation rates of the world's humid tropical forests. *Science* **297**: 999–1002.

Alstad KP, Lai C-T, Flanagan LB, Ehleringer JR. 2007. Environmental controls on the carbon isotope composition of ecosystem-respired CO_2 in contrasting forest ecosystems in Canada and the USA. *Tree Physiology* **27**: 1361–1374.

Amiotte-suchet P, Linglois N, Leveque J, Andreux F. 2007. ^{13}C composition of dissolved organic carbon in upland forested catchments of the Morvan Mountains (France): influence of coniferous and deciduous vegetation. *Journal of Hydrology* **335**: 354–363.

Amthor JS. 1984. The role of maintenance respiration in plant growth. *Plant, Cell & Environment* 7: 561–569.

Amthor JS. 2000. The McCree-de Wit-Penning de Vries-Thornley respiration paradigms: 30 years later. *Annals of Botany* **86**: 1–20.

Andrews JA, Harrison KG, Matamala R, Schlesinger WH. 1999. Separation of root respiration from total soil respiration using carbon-13 labeling during Free-Air Carbon Dioxide Enrichment (FACE). *Soil Science Society of America Journal* **63**: 1429–1435.

Badeck FW, Tcherkez G, Nogues S, Piel C, Ghashghaie J. 2005. Post-photosynthetic fractionation of stable carbon isotopes between plant organs – a widespread phenomenon. *Rapid Communications in Mass Spectrometry* **19**: 1381–1391.

Bakwin PS, Tans PP, White JWC, Andres RJ. 1998. Determination of the isotopic (C-13/C-12) discrimination by terrestrial biology from a global network of observations. *Global Biogeochemical Cycles* **12**: 555–562.

Baldocchi DD, Bowling DR. 2003. Modelling the discrimination of $^{13}CO_2$ above and within a temperate broad-leaved forest canopy on hourly to seasonal time scales. *Plant, Cell & Environment* **26**: 231–244.

Ballentine DC, Macko SA, Turekian VC. 1998. Variability of stable carbon isotopic compositions in individual fatty acids from combustion of C_4 and C_3 plants: implications for biomass burning. *Chemical Geology* **152**: 151–161.

Barbour MM, Hunt JE, Dungan RJ, Turnbull MH, Brailsford GW, Farquhar GD, Whitehead D. 2005. Variation in the degree of coupling between $\delta^{13}C$ of phloem sap and ecosystem respiration in two mature *Nothofagus* forests. *New Phytologist* **166**: 497–512.

Barbour MM, McDowell NG, Tcherkez G, Bickford CP, Hanson DT. 2007. A new measurement technique reveals rapid post-illumination changes in the carbon isotope composition of leaf-respired CO_2. *Plant, Cell & Environment* **30**: 469–482.

Benner R, Fogel ML, Sprague EK, Hodson RE. 1987. Depletion of ^{13}C in lignin and its implications for stable carbon isotope studies. *Nature* **329**: 708–710.

Bostrom B, Comstedt D, Ekblad A. 2007. Isotope fractionation and ^{13}C enrichment in soil profiles during the decomposition of soil organic matter. *Oecologia* **153**: 89–98.

Boutton TW 1996. Stable carbon isotope ratios of soil organic matter and their use as indicators of vegetation and climate change. In: Boutton TW, Yamasaki S, eds. *Mass spectrometry of soils*. New York, NY, USA: Marcel Dekker, 47–82.

Bowling DR, Burns SP, Conway TJ, Monson RK, White JWC. 2005. Extensive observations of CO_2 carbon isotope content in and above a high-elevation subalpine forest. *Global Biogeochemical Cycles* **19**: GB3023. doi: 10.1029/2004GB002394

Bowling DR, McDowell NG, Bond BJ, Law BE, Ehleringer JR. 2002. ^{13}C content of ecosystem respiration is linked to precipitation and vapor pressure deficit. *Oecologia* **131**: 113–124.

Bowling DR, Pataki DE, Ehleringer JR. 2003. Critical evaluation of micrometeorological methods for measuring ecosystem–atmosphere isotopic exchange of CO_2. *Agricultural and Forest Meteorology* **116**: 159–179.

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Bowling DR, Tans PP, Monson RK. 2001. Partitioning net ecosystem carbon exchange with isotopic fluxes of CO_2. *Global Change Biology* 7: 127–145.

Brandes E, Kodama N, Whittaker K, Weston C, Rennenberg H, Keitel C, Adams MA, Gessler A. 2006. Short-term variation in the isotopic composition of organic matter allocated from the leaves to the stem of *Pinus sylvestris*: effects of photosynthetic and postphotosynthetic carbon isotope fractionation. *Global Change Biology* 12: 1922–1939.

Brandes E, Wenninger J, Koeniger P, Schindler D, Rennenberg H, Leibundgut C, Mayer H, Gessler A. 2007. Assessing environmental and physiological controls over water relations in a Scots pine (*Pinus sylvestris* L.) stand through analyses of stable isotope composition of water and organic matter. *Plant, Cell & Environment* 30: 113–127.

Brenna JT. 2001. Natural intramolecular isotope measurements in physiology: elements of the case for an effort toward high-precision position-specific isotope analysis. *Rapid Communications in Mass Spectrometry* 15: 1252–1262.

Brugnoli E, Farquhar GD 2000. Photosynthetic fractionation of carbon isotopes. In: Leegood RC, Sharkey TD, von Caemmerer S, eds. *Photosynthesis: physiology and metabolism*. Dordrecht, the Netherlands: Kluwer, 399–434.

Brugnoli E, Hubick KT, von Caemmerer S, Wong SC, Farquhar GD. 1988. Correlation between the carbon isotope discrimination in leaf starch and sugars of C_3 plants and the ratio of intercellular and atmospheric partial pressures of carbon dioxide. *Plant Phsyiology* 88: 1418–1424.

Buchmann N, Guehl J-M, Barigah TS, Ehleringer JR. 1997. Interseasonal comparison of CO_2 concentrations, isotopic composition, and carbon dynamics in an Amazonian rainforest (French Guiana). *Oecologia* 110: 120–131.

Cannell MGR, Thornley JHM. 2000. Modelling the components of plant respiration: some guiding principles. *Annals of Botany* 85: 45–54.

Carbone MS, Czimczik CI, McDuffee KE, Trumbore SE. 2007. Allocation and residence time of photosynthetic products in a boreal forest using a low-level ^{14}C pulse-chase labeling technique. *Global Change Biology* 13: 466–477.

Carbone MS, Trumbore SE. 2007. Contribution of new photosynthetic assimilates to respiration by perennial grasses and shrubs: residence times and allocation patterns. *New Phytologist* 176: 124–135.

Cerling TE, Solomon DK, Quade J, Bowman JR. 1991. On the isotopic composition of carbon in soil carbon dioxide. *Geochimica et Cosmochimica Acta* 55: 3403–3405.

Cernusak LA, Farquhar GD, Pate JS. 2005. Environmental and physiological controls over oxygen and carbon isotope composition of Tasmanian blue gum, *Eucalyptus globulus*. *Tree Physiology* 25: 129–146.

Cernusak LA, Marshall JD, Comstock JP, Balster NJ. 2001. Carbon isotope discrimination in photosynthetic bark. *Oecologia* 128: 24–35.

Chikaraishi Y, Naraoka H. 2001. Organic hydrogen-carbon isotope signatures of terrestrial higher plants during biosynthesis for distinctive photosynthetic pathways. *Geochemical Journal* 35: 451–458.

Ciais P, Tans PP, White JWC, Trolier M, Francey RJ, Berry JA, Randall DR, Sellers PJ, Collatz JG *et al.* 1995. Partitioning of ocean and land uptake of CO_2 as inferred by $\delta^{13}C$ measurements from the NOAA Climate Monitoring and Diagnostics Laboratory Global Air Sampling Network. *Journal of Geophysical Research* 100: 5051–5070.

Crow SE, Sulzman EW, Rugh WD, Bowden RD, Lajtha K. 2006. Isotopic analysis of respired CO_2 during decomposition of separated soil organic matter pools. *Soil Biology and Biochemistry* 38: 3279–3291.

Czimczik CI, Treseder KK, Carbone MS, Trumbore SE. 2005. Radiocarbon – a low-impact tool to study nutrient transport by soil fungi under field conditions. *New Phytologist* 166: 595–600.

Damesin C, Lelarge C. 2003. Carbon isotope composition of current-year shoots from *Fagus sylvatica* in relation to growth, respiration and use of reserves. *Plant, Cell & Environment* 26: 207–219.

Dawson TE, Mambelli S, Plamboeck AH, Templer PH, Tu KP. 2002. Stable isotopes in plant ecology. *Annual Review of Ecology and Systematics* 33: 507–559.

DeNiro MJ, Epstein S. 1977. Mechanism of carbon isotope fractionation associated with lipid synthesis. *Science* 197: 261–263.

Dijkstra P, Ishizu A, Doucett R, Hart SC, Schwartz E, Menyailo OV, Hungate BA. 2006. ^{13}C and ^{15}N natural abundance of the soil microbial biomass. *Soil Biology and Biochemistry* 38: 3257–3266.

Duranceau M, Ghashghaie J, Badeck F, Deleens E, Cornic G. 1999. $\delta^{13}C$ of CO_2 respired in the dark in relation to $\delta^{13}C$ of leaf carbohydrates in *Phaseolus vulgaris* L. under progressive drought. *Plant, Cell & Environment* 22: 515–523.

Duranceau M, Ghashghaie J, Brugnoli E. 2001. Carbon isotope discrimination during photosynthesis and dark respiration in intact leaves of *Nicotiana sylvestris*: comparisons between wild type and mitochondrial mutant plants. *Australian Journal of Plant Physiology* 28: 65–71.

Ehleringer JR, Buchmann N, Flanagan LB. 2000. Carbon isotope ratios in belowground carbon cycle processes. *Ecological Applications* 10: 412–422.

Ekblad A, Bostrom B, Holm A, Comstedt D. 2005. Forest soil respiration rate and $\delta^{13}C$ is regulated by recent above ground weather conditions. *Oecologia* 143: 136–142.

Ekblad A, Högberg P. 2001. Natural abundance of ^{13}C in CO_2 respired from forest soils reveals speed of link between tree photosynthesis and root respiration. *Oecologia* 127: 305–308.

Ekblad A, Nyberg G, Högberg P. 2002. ^{13}C-discrimination during microbial respiration of added C_3, C_4 and ^{13}C-labelled sugars to a C_3-forest soil. *Oecologia* 131: 245–249.

Evans JR, Sharkey TD, Berry JA, Farquhar GD. 1986. Carbon isotope discrimination measured concurrently with gas exchange to investigate CO_2 diffusion in leaves of higher plants. *Australian Journal of Plant Physiology* 13: 281–292.

Farquhar GD, Ehleringer JR, Hubick KT. 1989. Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology* 40: 503–537.

Farquhar GD, O'Leary MH, Berry JA. 1982. On the relationship between carbon isotope discrimination and the intracellular carbon dioxide concentration in leaves. *Australian Journal of Plant Physiology* 9: 121–137.

Fernandez I, Cadisch G. 2003. Discrimination against ^{13}C during degradation of simple and complex substrates by two white rot fungi. *Rapid Communications in Mass Spectrometry* 17: 2614–2620.

Fernandez I, Mahieu N, Cadisch G. 2003. Carbon isotopic fractionation during decomposition of plant materials of different quality. *Global Biogeochemical Cycles* 17: 1075. doi: 10.1029/2001GB001834

Fessenden JE, Ehleringer JR. 2003. Temporal variation in $\delta^{13}C$ of ecosystem respiration in the Pacific Northwest: links to moisture stress. *Oecologia* 136: 129–136.

Flanagan LB, Brooks JR, Varney GT, Berry SC, Ehleringer JR. 1996. Carbon isotope discrimination during photosynthesis and the isotope ratio of respired CO_2 in boreal forest ecosystems. *Global Biogeochemical Cycles* 10: 629–640.

Francey RJ, Tans PP, Allison CE, Enting IG, White JWC, Trolier M. 1995. Changes in oceanic and terrestrial carbon uptake since 1982. *Nature* 373: 326–330.

Gaudillere JP, Van Leeuwen C, Ollat N. 2002. Carbon isotope composition of sugars in grapevine, an integrated indicator of vineyard water status. *Journal of Experimental Botany* 53: 757–763.

Gaudinski JB, Dawson TE, Quideau S, Schuur EAG, Roden JS, Trumbore SE, Sandquist DR, Oh SW, Wasylishen RE. 2005. Comparative analysis of cellulose preparation techniques for use with ^{13}C, ^{14}C, and ^{18}O isotopic measurements. *Analytical Chemistry* 77: 7212–7224.

Gessler A, Rennenberg H, Keitel C. 2004. Stable isotope composition of organic compounds transported in the phloem of European beech – Evaluation of different methods of phloem sap collection and assessment of gradients in carbon isotope composition during leaf-to-stem transport. *Plant Biology* 6: 721–729.

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Gessler A, Schrempp S, Matzarakis A, Mayer H, Rennenberg H, Adams MA. 2001. Radiation modifies the effect of water availability on the carbon isotope composition of beech (*Fagus sylvatica*). *New Phytologist* **150**: 653–664.

Ghashghaie J, Badeck F-W, Lanigan G, Nogues S, Tcherkez G, Deleens E, Cornic G, Griffiths H. 2003. Carbon isotope fractionation during dark respiration and photorespiration in C_3 plants. *Phytochemistry Reviews* **2**: 145–161.

Ghashghaie J, Duranceau M, Badeck F-W, Cornic G, Adeline M-T, Deleens E. 2001. $\delta^{13}C$ of CO_2 respired in the dark in relation to $\delta^{13}C$ of leaf metabolites: comparison between *Nicotiana sylvestris* and *Helianthus annuus* under drought. *Plant, Cell & Environment* **24**: 505–515.

Gifford RM. 2003. Plant respiration in productivity models: conceptualisation, representation, and issues for global terrestrial carbon-cycle research. *Functional Plant Biology* **30**: 171–186.

Gleixner G, Danier H-J, Werner RA, Schmidt H-L. 1993. Correlations between the ^{13}C content of primary and secondary plant products in different cell compartments and that in decomposing basidiomycetes. *Plant Physiology* **102**: 1287–1290.

Gleixner G, Scrimgeour C, Schmidt H-L, Viola R. 1998. Stable isotope distribution in the major metabolites of source and sink organs of *Solanum tuberosum* L.: a powerful tool in the study of metabolic partitioning in intact plants. *Planta* **207**: 241–245.

Goodale CL, Apps MJ, Birdsey RA, Field CB, Heath LS, Houghton RA, Jenkins JC, Kohlmaier GH, Kurz W, Liu S *et al.* 2002. Forest carbon sinks in the Northern Hemisphere. *Ecological Applications* **12**: 891–899.

Hahn V, Högberg P, Buchmann N. 2006. ^{14}C – a tool for separation of autotrophic and heterotrophic soil respiration. *Global Change Biology* **12**: 972–982.

Hart SC, Gehring CA, Selmants PC, Deckert RJ. 2006. Carbon and nitrogen elemental and isotopic patterns in macrofungal sporocarps and trees in semiarid forests of the south-western USA. *Functional Ecology* **20**: 42–51.

Harwood KG, Gillon JS, Griffiths H, Broadmeadow MSJ. 1998. Diurnal variation of $\Delta^{13}CO_2$, $\Delta C^{18}O^{16}O$ and evaporative site enrichment of $\delta H_2{}^{18}O$ in *Piper aduncum* under field conditions in Trinidad. *Plant, Cell & Environment* **21**: 269–283.

Heimann M, Maier-Reimer E. 1996. On the relations between oceanic uptake of CO_2 and its carbon isotopes. *Global Biogeochemical Cycles* **10**: 89–110.

Helle G, Schleser GH. 2004. Beyond CO_2-fixation by Rubisco – an interpretation of $^{13}C/^{12}C$ variations in tree rings from novel intra-seasonal studies on broad-leaf trees. *Plant, Cell & Environment* **27**: 367–380.

Hemming D, Yakir D, Ambus P, Aurela M, Besson C, Black K, Buchmann N, Burlett R, Cescatti A, Clement R *et al.* 2005. Pan-European $\delta^{13}C$ values of air and organic matter from forest ecosystems. *Global Change Biology* **11**: 1065–1093.

Henn MR, Chapela IH. 2000. Differential C isotope discrimination by fungi during decomposition of C_3-and C_4-derived sucrose. *Applied and Environmental Microbiology* **66**: 4180–4186.

Henn MR, Chapela IH. 2001. Ecophysiology of ^{13}C and ^{15}N isotopic fractionation in forest fungi and the roots of the saprotrophic-mycorrhizal divide. *Oecologia* **128**: 480–487.

Henn MR, Gleixner G, Chapela IH. 2002. Growth-dependent stable carbon isotope fractionation by basidiomycete fungi: $\delta^{13}C$ pattern and physiological process. *Applied and Environmental Microbiology* **68**: 4956–4964.

Hobbie EA, Macko SA, Shugart HH. 1999. Insights into nitrogen and carbon dynamics of ectomycorrhizal and saprotrophic fungi from isotopic evidence. *Oecologia* **118**: 353–360.

Hobbie EA, Rygiewicz PT, Johnson MG, Moldenke AR. 2007. ^{13}C and ^{15}N in microarthropods reveal little response of Douglas-fir ecosystems to climate change. *Global Change Biology* **13**: 1386–1397.

Hobbie EA, Weber NS, Trappe JM. 2001. Mycorrhizal vs saprotrophic status of fungi: the isotopic evidence. *New Phytologist* **150**: 601–610.

Hobbie EA, Werner RA. 2004. Intramolecular, compound-specific, and bulk carbon isotope patterns in C_3 and C_4 plants: a review and synthesis. *New Phytologist* **161**: 371–385.

Högberg P, Nordgren A, Buchmann N, Taylor AFS, Ekblad A, Högberg MN, Nyberg G, Ottosson-Lofvenius M, Read DJ. 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature* **411**: 789–792.

Högberg P, Plamboeck AH, Taylor AFS, Fransson PMA. 1999. Natural ^{13}C abundance reveals trophic status of fungi and host-origin of carbon in mycorrhizal fungi in mixed forests. *Proceedings of the National Academy of Sciences, USA* **96**: 8534–8539.

Hood E, Williams MW, McKnight DM. 2005. Sources of dissolved organic matter (DOM) in a Rocky Mountain stream using chemical fractionation and stable isotopes. *Biogeochemistry* **74**: 231–255.

Houghton RA, Skole DL, Nobre CA, Hackler JL, Lawrence KT, Chomentowski WH. 2000. Annual fluxes or carbon from deforestation and regrowth in the Brazilian Amazon. *Nature* **403**: 301–304.

Hurtt GC, Pacala SW, Moorcroft PR, Caspersen J, Shevliakova E, Houghton RA, Moore B. 2002. Projecting the future of the US carbon sink. *Proceedings of the National Academy of Sciences, USA* **99**: 1389–1394.

Hymus GJ, Maseyk K, Valentini R, Yakir D. 2005. Large daily variation in ^{13}C-enrichment of leaf-respired CO_2 in two *Quercus* forest canopies. *New Phytologist* **167**: 377–384.

Johnson D, Leake JR, Ostle N, Ineson P, Read DJ. 2002. *In situ* $^{13}CO_2$ pulse-labelling of upland grassland demonstrates a rapid pathway of carbon flux from arbuscular mycorrhizal mycelia to the soil. *New Phytologist* **153**: 327–334.

Keeling CD, Whorf TP, Wahlen M, van der Plicht J. 1995. Interannual extremes in the rate of rise of atmospheric carbon dioxide since 1980. *Nature* **375**: 666–670.

Keitel C, Adams MA, Holst T, Matzarakis A, Mayer H, Rennenberg H, Gessler A. 2003. Carbon and oxygen isotope composition of organic compounds in the phloem sap provides a short-term measure for stomatal conductance of European beech (*Fagus sylvatica* L.). *Plant, Cell & Environment* **26**: 1157–1168.

Keitel C, Matzarakis A, Rennenberg H, Gessler A. 2006. Carbon isotopic composition and oxygen isotopic enrichment in phloem and total leaf organic matter of European beech (*Fagus sylvatica* L.) along a climate gradient. *Plant, Cell & Environment* **29**: 1492–1507.

Klumpp K, Schäufele R, Lötscher M, Lattanzi FA, Feneis W, Schnyder H. 2005. C-isotope composition of CO_2 respired by shoots and roots: fractionation during dark respiration? *Plant, Cell & Environment* **28**: 241–250.

Knohl A, Buchmann N. 2005. Partitioning the net CO_2 flux of a deciduous forest into respiration and assimilation using stable carbon isotopes. *Global Biogeochemical Cycles* **19**: GB4008. doi: 10.1029/2004GB002301

Knohl A, Werner RA, Brand WA, Buchmann N. 2005. Short-term variations in $\delta^{13}C$ of ecosystem respiration reveals link between assimilation and respiration in a deciduous forest. *Oecologia* **142**: 70–82.

Kohler P, Fischer H, Schmitt J, Munhoven G. 2006. On the application and interpretation of Keeling plots in paleo climate research – deciphering $\delta^{13}C$ of atmospheric CO_2 measured in ice cores. *Biogeosciences* **3**: 539–556.

Kohzu A, Yoshioka T, Ando T, Takahashi M, Koba K, Wada E. 1999. Natural ^{13}C and ^{15}N abundance of field-collected fungi and their ecological implications. *New Phytologist* **144**: 323–330.

Lai C-T, Ehleringer JR, Schauer AJ, Tans PP, Hollinger DY, Paw UKT, Munger JW, Wofsy SC. 2005. Canopy-scale $\delta^{13}C$ of photosynthetic and respiratory CO_2 fluxes: observations in forest biomes across the United States. *Global Change Biology* **11**: 633–643.

Law BE, Ryan MG, Anthoni PM. 1999. Seasonal and annual respiration of a ponderosa pine ecosystem. *Global Change Biology* **5**: 169–182.

 © The Authors (2008). Journal compilation © *New Phytologist* (2008)

Lea PJ, Ireland RJ 1999. Nitrogen metabolism in higher plants. In: Singh BK, ed. *Plant amino acids*. New York, NY, USA: Marcel Dekker, 1–47.
Leavitt S, Long A. 1982. Evidence for $^{13}C/^{12}C$ fractionation between tree leaves and wood. *Nature* **298**: 742–744.
Lin G, Ehleringer JR. 1997. Carbon isotopic fractionation does not occur during dark respiration in C_3 and C_4 plants. *Plant Physiology* **114**: 391–394.
Loader NJ, Rundgren M. 2006. The role of inter-specific, micro-habitat and climatic factors on the carbon isotope ($\delta^{13}C$) variability of a modern leaf assemblage from northern Scandinavia: implications for climate reconstruction. *Boreas* **35**: 188–201.
Ludwig B, Heil B, Flessa H, Beese F. 2000. Dissolved organic carbon in seepage water – Production and transformation during soil passage. *Acta Hydrochimica et Hydrobiologica* **28**: 77–82.
Madhavan S, Treichel I, O'Leary MH. 1991. Effects of relative humidity on carbon isotope fractionation in plants. *Botanica Acta* **104**: 292–294.
Martinelli LA, Almeida S, Brown IF, Moreira MZ, Victoria RL, Sternberg LSL, Ferreira CAC, Thomas WW. 1998. Stable carbon isotope ratio of tree leaves, boles and fine litter in a tropical forest in Rondonia, Brazil. *Oecologia* **114**: 170–179.
Maunoury F, Berveiller D, Lelarge C, Pontailler JY, Vanbostal L, Damesin C. 2007. Seasonal, daily and diurnal variations in the stable carbon isotope composition of carbon dioxide respired by tree trunks in a deciduous oak forest. *Oecologia* **151**: 268–279.
McDowell NG, Bowling DR, Bond BJ, Irvine J, Law BE, Anthoni P, Ehleringer JR. 2004a. Response of the carbon isotopic content of ecosystem, leaf, and soil respiration to meteorological and physiological driving factors in a *Pinus ponderosa* ecosystem. *Global Biogeochemical Cycles* **18**: GB1013. doi: 10.1029/2003GB00249
McDowell NG, Bowling DR, Schauer A, Irvine J, Bond BJ, Law BE, Ehleringer JR. 2004b. Associations between carbon isotope ratios of ecosystem respiration, water availability and canopy conductance. *Global Change Biology* **10**: 1767–1784.
Melzer E, Schmidt H-L. 1987. Carbon isotope effects on the pyruvate dehydrogenase reaction and their importance for relative carbon-13 depletion in lipids. *Journal of Biological Chemistry* **262**: 8159–8164.
Miller JB, Tans PP, White JWC, Conway TJ, Vaughn BW. 2003. The atmospheric signal of terrestrial carbon isotopic discrimination and its implication for partitioning carbon fluxes. *Tellus* **55B**: 197–206.
Mortazavi B, Chanton JP. 2002. Carbon isotopic discrimination and control of nighttime canopy $\delta^{18}O$-CO_2 in a pine forest in the southeastern United States. *Global Biogeochemical Cycles* **16**: 1008. doi: 10.1029/2000GB001390
Mortazavi B, Chanton JP, Prater JL, Oishi AC, Oren R, Katul G. 2005. Temporal variability in ^{13}C of respired CO_2 in a pine and a hardwood forest subject to similar climatic conditions. *Oecologia* **142**: 57–69.
Nogues S, Damesin C, Tcherkez G, Maunoury F, Cornic G, Ghashghaie J. 2006. $^{13}C/^{12}C$ isotope labelling to study leaf carbon respiration and allocation in twigs of field-grown beech trees. *Rapid Communications in Mass Spectrometry* **20**: 219–226.
Nogues S, Tcherkez G, Cornic G, Ghashghaie J. 2004. Respiratory carbon metabolism following illumination in intact french bean leaves using C-13/C-12 isotope labeling. *Plant Physiology* **136**: 3245–3254.
O'Leary MH. 1981. Carbon isotope fractionation in plants. *Phytochemistry* **20**: 553–567.
Ocheltree TW, Marshall JD. 2004. Apparent respiratory discrimination is correlated with growth rate in the shoot apex of sunflower (*Helianthus annuus*). *Journal of Experimental Botany* **55**: 2599–2605.
Ogee J, Peylin P, Ciais P, Bariac T, Brunet Y, Berbigier P, Roche C, Richard P, Bardoux G, Bonnefond J-M. 2003. Partitioning net ecosystem carbon exchange into net assimilation and respiration using $^{13}CO_2$ measurements: a cost-effective sampling strategy. *Global Biogeochemical Cycles* **17**: 1070. doi: 10.1029/2002GB001995
Park R, Epstein S. 1961. Metabolic fractionation of C^{13} and C^{12} in plants. *Plant Physiology* **36**: 133–138.
Parton W, Silver WL, Burke IC, Grassens L, Harmon ME, Currie WS, King JY, Adair EC, Brandt LA, Hart SC *et al.* 2007. Global-scale similarities in nitrogen release patterns during long-term decomposition. *Science* **315**: 361–364.
Pataki DE, Ehleringer JR, Flanagan LB, Yakir D, Bowling DR, Still CJ, Buchmann N, Kaplan JO, Berry JA. 2003. The application and interpretation of Keeling plots in terrestrial carbon cycle research. *Global Biogeochemical Cycles* 17: 1022. doi: 10.1029/2001GB001850
Pate J, Arthur D. 1998. $\delta^{13}C$ analysis of phloem sap carbon: novel means of evaluating seasonal water stress and interpreting carbon isotope signatures of foliage and trunk wood of *Eucalyptus globulus*. *Oecologia* **117**: 301–311.
Penning de Vries FWT. 1975. The cost of maintenance processes in plant cells. *Annals of Botany* **39**: 77–92.
Poorter H, Villar R 1997. The fate of acquired carbon in plants: chemical composition and construction costs. In: Bazzaz FA, Grace J, eds. *Plant Resource Allocation*. San Diego, CA, USA: Academic Press, 39–72.
Prater JL, Mortazavi B, Chanton JP. 2006. Diurnal variation of the $\delta^{13}C$ of pine needle respired CO_2 evolved in darkness. *Plant, Cell & Environment* **29**: 202–211.
Preston CM, Trofymow JA, Flanagan LB. 2006. Decomposition, $\delta^{13}C$, and the 'lignin paradox'. *Canadian Journal of Soil Science* **86**: 235–245.
Quay PD, Tilbrook B, Wong CS. 1992. Oceanic uptake of fossil fuel CO_2: Carbon-13 evidence. *Science* **256**: 74–79.
Randerson JT, Collatz GJ, Fessenden JE, Munoz AD, Still CJ, Berry JA, Fung IY, Suits N, Denning AS. 2002a. A possible global covariance between terrestrial gross primary production and ^{13}C discrimination: consequences for the atmospheric ^{13}C budget and its response to ENSO. *Global Biogeochemical Cycles* **16**: 1136. doi: 10.1029/2001GB001845
Randerson JT, Masiello CA, Still CJ, Rahn T, Poorter H, Field CB. 2006. Is carbon within the global terrestrial biosphere becoming more oxidized? Implications for trends in atmospheric O_2. *Global Change Biology* **12**: 260–271.
Randerson JT, Still CJ, Balle JJ, Fung IY, Doney SC, Tans PP, Conway TJ, White JWC, Vaughn B, Suits N *et al.* 2002b. Carbon isotope discrimination of arctic and boreal biomes inferred from remote atmospheric measurements and a biosphere-atmosphere model. *Global Biogeochemical Cycles* **16**: 1028. doi: 10.1029/2001GB001435, 2002.
Read J, Farquhar G. 1991. Comparative studies in *Nothofagus* (Fagaceae).I. Leaf carbon isotope discrimination. *Functional Ecology* **5**: 684–695.
Rossmann A, Butzenlechner M, Schmidt H-L. 1991. Evidence for a nonstatistical carbon isotope distribution in natural glucose. *Plant Physiology* **96**: 609–614.
Ryan MG. 1991. Effects of climate change on plant respiration. *Ecological Applications* **1**: 157–167.
Saatchi SS, Houghton RA, Dos Santos Alvala RC, Soares JV, Yu Y. 2007. Distribution of aboveground live biomass in the Amazon basin. *Global Change Biology* **13**: 816–837.
Santruckova H, Bird MI, Lloyd J. 2000. Microbial processes and carbon-isotope fractionation in tropical and temperate grassland soils. *Functional Ecology* **14**: 108–114.
Saugier B, Roy J, Mooney HA. 2001. Estimations of global terrestrial productivity: converging toward a single number? In: Roy J, Saugier, B, Mooney HA, eds. *Terrestrial Global Productivity*. San Diego, CA, USA: Academic Press, 543–557.
Savidge WB, Blair NE. 2004. Patterns of intramolecular carbon isotopic heterogeneity within amino acids of autotrophs and heterotrophs. *Oecologia* **139**: 178–189.
Scartazza A, Lauteri M, Guido MC, Brugnoli E. 1998. Carbon isotope discrimination in leaf and stem sugars, water-use efficiency and mesophyll conductance during different developmental stages in rice subjected to drought. *Australian Journal of Plant Physiology* **25**: 489–498.
Scartazza A, Mata C, Matteucci G, Yakir D, Moscatello S, Brugnoli E. 2004. Comparisons of $\delta^{13}C$ of photosynthetic products and ecosystem

respiratory CO_2 and their response to seasonal climate variability. *Oecologia* **140**: 340–351.

Schaeffer SM, Anderson DE, Burns SP, Monson RK, Sun J, Bowling DR. (in press). Canopy structure and atmospheric flows in relation to the $\delta^{13}C$ of respired CO_2 in a subalpine coniferous forest. *Agricultural and Forest Meteorology*. doi: 10.1016/j.agrformet.2007.11.003

Schmidt H-L. 2003. Fundamentals and systematics of the nonstatistical distributions of isotopes in natural compounds. *Naturwissenschaften* **90**: 537–552.

Schnyder H, Lattanzi FA. 2005. Partitioning respiration of C_3–C_4 mixed communities using the natural abundance ^{13}C approach – testing assumptions in a controlled environment. *Plant Biology* **7**: 592–600.

Scholze M, Kaplan JO, Knorr W, Heimann M. 2003. Climate and interannual variability of the atmosphere-biosphere $^{13}CO_2$ flux. *Geophysical Research Letters* **30**: 1097.

Schulze E-D, Williams RJ, Farquhar GD, Schulze W, Langridge J, Miller JM, Walker BH. 1998. Carbon and nitrogen isotope discrimination and nitrogen nutrition of trees along a rainfall gradient in northern Australia. *Australian Journal of Plant Physiology* **25**: 413–425.

Schuur EAG, Trumbore SE. 2006. Partitioning sources of soil respiration in boreal black spruce forest using radiocarbon. *Global Change Biology* **12**: 165–176.

Schuur EAG, Trumbore SE, Mack MC, Harden JW. 2003. Isotopic composition of carbon dioxide from a boreal forest fire: inferring carbon loss from measurements and modeling. *Global Biogeochemical Cycles* **17**. doi: 10.1029/2001GB001840

Schweizer M, Fear J, Cadisch G. 1999. Isotopic (^{13}C) fractionation during plant residue decomposition and its implications for soil organic matter studies. *Rapid Communications in Mass Spectrometry* **13**: 1284–1290.

Smallwood BJ, Wooller MJ, Jacobson ME, Fogel ML. 2003. Isotopic and molecular distributions of biochemicals from fresh and buried *Rhizophora mangle* leaves. *Geochemical Transactions* **4**: 38–46.

Smith BN. 1971. Carbon isotope ratios of respired CO_2 from castor bean, corn, peanut, pea, radish, squash, sunflower and wheat seedlings. *Plant and Cell Physiology* **12**: 451–455.

Steinmann K, Siegwolf RTW, Saurer M, Korner C. 2004. Carbon fluxes to the soil in a mature temperate forest assessed by ^{13}C isotope tracing. *Oecologia* **141**: 489–501.

Stewart GR, Turnbull MH, Schmidt S, Erskine PD. 1995. ^{13}C natural abundance in plant communities along a rainfall gradient: a biological integrator of water availability. *Australian Journal of Plant Physiology* **22**: 51–55.

Still CJ, Berry JA, Collatz GJ, DeFries RS. 2003. Global distribution of C_3 and C_4 vegetation: carbon cycle implications. *Global Biogeochemical Cycles* **17**: 1006. doi: 10.1029/2001GB001807

Subke J-A, Inglima I, Cotrufo MF. 2006. Trends and methodological impacts in soil CO_2 efflux partitioning: a metaanalytical review. *Global Change Biology* **12**: 921–943.

Suits NS, Denning AS, Berry JA, Still CJ, Kaduk J, Miller JB, Baker IT. 2005. Simulation of carbon isotope discrimination of the terrestrial biosphere. *Global Biogeochemical Cycles* **19**: GB1017. doi: 10.1029/2003GB002141

Taneva L, Pippen JS, Schlesinger WH, Gonzalez-Meler MA. 2006. The turnover of carbon pools contributing to soil CO_2 and soil respiration in a temperate forest exposed to elevated CO_2 concentration. *Global Change Biology* **12**: 983–994.

Tans PP, Berry JA, Keeling RF. 1993. Oceanic $^{13}C/^{12}C$ observations: a new window on ocean CO_2 uptake. *Global Biogeochemical Cycles* **7**: 353–368.

Taylor AFS, Fransson PM, Högberg P, Högberg MN, Plamboeck AH. 2003. Species level patterns in ^{13}C and ^{15}N abundance of ectomycorrhizal and saprotrophic fungal sporocarps. *New Phytologist* **159**: 757–774.

Tcherkez G, Farquhar GD. 2005. Carbon isotope effect predictions for enzymes involved in the primary carbon metabolism of plant leaves. *Functional Plant Biology* **32**: 277–291.

Tcherkez G, Nogues S, Bleton J, Cornic G, Badeck F, Ghashghaie J. 2003. Metabolic origin of carbon isotope composition of leaf dark-respired CO_2 in French bean. *Plant Physiology* **131**: 237–244.

Teskey RO, McGuire MA. 2007. Measurement of stem respiration of sycamore (*Platanus occidentalis* L.) trees involves internal and external fluxes of CO_2 and possible transport of CO_2 from roots. *Plant, Cell & Environment* **30**: 570–579.

Thornley JHM, Cannell MGR. 2000. Modelling the components of plant respiration: representation and realism. *Annals of Botany* **85**: 55–67.

Tissue DT, Barbour MM, Hunt JE, Turnbull MH, Griffin KL, Walcroft AS, Whitehead D. 2006. Spatial and temporal scaling of intercellular CO_2 concentration in a temperate rain forest dominated by *Dacrydium cupressinum* in New Zealand. *Plant, Cell & Environment* **29**: 497–510.

Townsend AR, Asner GP, White JWC, Tans PP. 2002. Land use effects on atmospheric ^{13}C imply a sizable terrestrial CO_2 sink in tropical latitudes. *Geophysical Research Letters* **29**: 1426.

Trolier M, White JWC, Tans PP, Masarie KA, Gemery PA. 1996. Monitoring the isotopic composition of atmospheric CO_2: measurements from the NOAA Global Air Sampling Network. *Journal of Geophysical Research – Atmospheres* **101**: 25897–25916.

Troughton JH, Card KA, Hendy CH. 1974. Photosynthetic pathways and carbon isotope discrimination by plants. *Carnegie Institution of Washington Yearbook* **73**: 768–80.

Trudell SA, Rygiewicz PT, Edmonds RL. 2004. Patterns of nitrogen and carbon stable isotope ratios in macrofungi, plants and soils in two old-growth conifer forests. *New Phytologist* **164**: 317–335.

Trudinger CM, Enting IG, Francey RJ, Etheridge DM, Rayner PJ. 1999. Long-term variability in the global carbon cycle inferred from a high-precision CO_2 and $\delta^{13}C$ ice-core record. *Tellus* **51B**: 233–248.

Trumbore S. 2000. Age of soil organic matter and soil respiration: radiocarbon constraints on belowground C dynamics. *Ecological Applications* **10**: 399–411.

Tu KP, Dawson TE 2005. Partitioning ecosystem respiration using stable carbon isotope analyses of CO_2. In: Flanagan LB, Ehleringer JR, Pataki DE, eds. *Stable isotopes and biosphere–atmosphere interactions: processes and biological controls*. Amsterdam, the Netherlands: Elsevier, 125–153.

Turney CSM, Hunt JE, Burrows C. 2002. Deriving a consistent $\delta^{13}C$ signature from tree canopy leaf material for palaeoclimatic reconstruction. *New Phytologist* **155**: 301–311.

Uchida T, Kaneko N, Ito MT, Futagami K, Sasaki T, Sugimoto A. 2004. Analysis of the feeding ecology of earthworms (Megascolecidae) in Japanese forests using gut content fractionation and $\delta^{15}N$ and $\delta^{13}C$ stable isotope natural abundances. *Applied Soil Ecology* **27**: 153–163.

Wallander H, Goransson H, Rosengren U. 2004. Production, standing biomass and natural abundance of ^{15}N and ^{13}C in ectomycorrhizal mycelia collected at different soil depths in two forest types. *Oecologia* **139**: 89–97.

Wanek W, Heintel S, Richter A. 2001. Preparation of starch and other carbon fractions from higher plant leaves for stable carbon isotope analysis. *Rapid Communications in Mass Spectrometry* **15**: 1136–1140.

Wedin DA, Tieszen LL, Dewey B, Pastor J. 1995. Carbon isotope dynamics during grass decomposition and soil organic matter formation. *Ecology* **76**: 1383–1392.

Whelan T, Sackett WM, Benedict CR. 1970. Carbon isotope discrimination in a plant possessing the C_4 dicarboxylic acid pathway. *Biochemical and Biophysical Research Communications* **41**: 1205–1210.

Wingate L, Seibt U, Moncrieff JB, Jarvis PG, Lloyd J. 2007. Variations in ^{13}C discrimination during CO_2 exchange by *Picea sitchensis* branches in the field. *Plant, Cell & Environment* **30**: 600–616.

Xu C, Lin G, Griffin KL, Sambrotto RN. 2004. Leaf respiratory CO_2 is ^{13}C-enriched relative to leaf organic components in five species of C_3 plants. *New Phytologist* **163**: 499–505.

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