Annu. Rev. Ecol. Syst. 2002. 33:507–59
doi: 10.1146/annurev.ecolsys.33.020602.095451

First published online as a Review in Advance on August 14, 2002

STABLE ISOTOPES IN PLANT ECOLOGY

Todd E. Dawson[1], Stefania Mambelli[1], Agneta H. Plamboeck[1], Pamela H. Templer[2], and Kevin P. Tu[1]

[1]Center for Stable Isotope Biogeochemistry and the Department of Integrative Biology, University of California, Berkeley, California 94720; email: tdawson@socrates.berkeley.edu, mambelli@socrates.berkeley.edu, ktu@socrates.berkeley.edu, agneta@socrates.berkeley.edu

[2]Ecosystem Sciences Division, Department of Environmental Science, Policy and Management, University of California, Berkeley, California 94720; email: ptempler@nature.berkeley.edu

Key Words plant-environment interactions, resources, tracers, integrators, scaling, methods

■ **Abstract** The use of stable isotope techniques in plant ecological research has grown steadily during the past two decades. This trend will continue as investigators realize that stable isotopes can serve as valuable nonradioactive tracers and nondestructive integrators of how plants today and in the past have interacted with and responded to their abiotic and biotic environments. At the center of nearly all plant ecological research which has made use of stable isotope methods are the notions of interactions and the resources that mediate or influence them. Our review, therefore, highlights recent advances in plant ecology that have embraced these notions, particularly at different spatial and temporal scales. Specifically, we review how isotope measurements associated with the critical plant resources carbon, water, and nitrogen have helped deepen our understanding of plant-resource acquisition, plant interactions with other organisms, and the role of plants in ecosystem studies. Where possible we also introduce how stable isotope information has provided insights into plant ecological research being done in a paleontological context. Progress in our understanding of plants in natural environments has shown that the future of plant ecological research will continue to see some of its greatest advances when stable isotope methods are applied.

INTRODUCTION AND SCOPE

At the core of all plant ecological investigations is the notion of plant-environment interactions, be these with the physical environment or with other organisms. Investigations that seek to understand the nature of these interactions commonly focus on particular resources such as light, water, carbon dioxide, or nutrients and how the interaction is influenced or mediated by that resource. Understanding the importance of a particular resource in a plant ecological context requires the

acquisition of observational and experimental data; the collection of such data, in turn, requires suitable methods and measurements.

As with most areas of science our ability to obtain appropriate measurements that aid us with addressing the unanswered questions in plant ecology have often been limited or constrained by available tools. In this regard, stable isotope methods have recently emerged as one of the more powerful tools for advancing understanding of relationships between plants and their environment. Stable isotope techniques have permitted plant ecologists to address issues that have seemed intractable using other methods. They have therefore had a significant and positive impact on the science of plant ecology much like modern molecular techniques have for the fields of genetics, biochemistry, and evolutionary biology. Stable isotope information has provided insights across a range of spatial scales from the cell to the plant community, ecosystem, or region and over temporal scales from seconds to centuries. The elegance of stable isotope methods derives from the fact that it is generally easy to learn and the behavior of stable isotopes in ecological systems and biogeochemical cycles is reasonably well understood owing to the pioneering work of isotope chemists and geochemists. Areas in need of a deeper understanding seem well within our reach as stable isotope investigations and methods become more refined. Arguably, stable isotope methods are now among the most important empirical tools in modern plant ecological research, and the information they provide has yielded some of the newest and most important insights about plants in natural environments since the advent of the common garden experiment.

Our review highlights recent advances in plant ecology that have used stable isotope data to address questions at a variety of scales. We focus on carbon (C), water (H_2O), and nitrogen (N) because they are three of the most important resources influencing plant function, growth, distribution, and the biogeochemical cycles in which plants participate. We begin by briefly reviewing stable isotope terminology. Some essential principles for understanding how and why isotopes vary in nature and how isotope values alone or in mixtures are calculated are found in special topic boxes within the text. The sections that follow review studies that illustrate particular issues and identify where emerging trends or patterns exist, where areas of controversy and/or disagreement remain, and where promising areas of future research lie. For the newcomer, our hope is that this review enhances understanding of how stable isotopes might be used in plant ecological research. For the seasoned user, this review serves as a place to retrieve information on what we know, do not know, and need to know. Because space is limited, our review is not comprehensive but we hope that we have not been superficial and we apologize to scientists whose work we could not include. Wherever we feel it is helpful and possible we direct the reader toward other literature that provides more in-depth discussions of particularly important issues or areas of research. Last, we restrict our review to H, C, N, and O isotopes and terrestrial systems and attempt to show how both natural abundance and enrichment studies can be used.

STABLE ISOTOPES: CONCEPTS, TERMINOLOGY AND EXPRESSIONS

As noted previously (Peterson & Fry 1987), ecological studies have been informed by using stable isotopes at naturally occurring levels (called "natural abundance"; Table 1B) and at levels well outside the natural range of values (called "enriched" levels); enriched isotope studies therefore use "labeled" substances. Isotope abundance in any sample, enriched or not, is measured using a mass spectrometer. The details of how these measurements are made and how the mass spectrometer works

TABLE 1 The (*A*) isotope abundance ratios measured and their internationally accepted reference standards, and (*B*) the elements, their isotopes, their percent abundance, common form, relative molecular mass difference, and range (in ‰) measured in terrestrial environments of the principle stable isotopes discussed in this review

Isotope	Ratio measured	Standard	Abundance ratio of reference standard
A			
^{2}H (D)[a]	$^{2}H/^{1}H$ (D/H)	V-SMOW[b]	1.5575×10^{-4}
^{13}C	$^{13}C/^{12}C$	V-PDB[c]	1.1237×10^{-2}
^{15}N	$^{15}N/^{14}N$	N_2-atm.[d]	3.6764×10^{-3}
^{18}O	$^{18}O/^{16}O$	V-SMOW,	2.0052×10^{-3}
		V-PDB	2.0672×10^{-3}

Element	Isotope	Percent abundance	Form & relative molecular mass difference	Terrestrial[e] range
B				
Hydrogen	^{1}H	99.984	$^{1}HD/^{1}H^{1}H$	~700‰
	^{2}H (D)	0.0156	(3/2), 50%	
Carbon	^{12}C	98.982	$^{13}C^{16}O^{16}O/^{12}C^{16}O^{16}O$	~100‰
	^{13}C	1.108	(45/44), 2.3%	
Nitrogen	^{14}N	99.63	$^{15}N^{14}N/^{14}N^{14}N$	~50‰
	^{15}N	0.3663	(29/28), 3.6%	
Oxygen	^{16}O	99.759	$^{12}C^{16}O^{18}O/^{12}C^{16}O^{16}O$	~100‰
	^{17}O	0.037	(46/44), 4.5%	
	^{18}O	0.204		

[a]The hydrogen stable isotope with mass two is also called deuterium, D.

[b]The original standard was standard mean ocean water (SMOW) which is no longer available; however, Vienna-SMOW is available from the IAEA.

[c]The original standard was a belemnite from the PeeDee formation (PDB) which is no longer available; however, "Vienna"-PDB is available from the IAEA.

[d]atm. = atmospheric gas.

[e]Approximate range measured in all analyzed substances from Earth (gasses, solids, biological materials).

can be found in reviews by Criss (1999), Ehleringer et al. (2000b), and Dawson & Brooks (2001).

Natural abundance stable isotopes are used as both natural integrators and tracers of ecological processes. As integrators, they permit ecologists to evaluate the net outcome of many processes that vary both spatially and temporally, while not disrupting the natural activity or behavior of the element in that system (Handley & Raven 1992, Högberg 1997, Robinson 2001). As tracers, they allow ecologists to follow the fates and transformations of a resource. Using natural abundance isotopes as tracers requires that the different potential sources have repeatable and distinct δ values (Equation 1) that are broader than the natural range of plant δ values measured. Furthermore, for tracers to be most useful there must not be significant fractionation (Text Box 1) or mixing of sources during the steps that move the resource from its source to the plant. Because it can be very difficult to fulfill all these requirements, many plant ecological investigations cannot use natural abundance isotope data to determine sources or process rates (Handley & Scrimgeour 1997); these studies rely on enriched isotope approaches.

BOX 1 Natural Abundance Stable Isotope Fractionation

Changes in the partitioning of heavy and light isotopes between a source substrate and the product(s) is termed isotope fractionation. Fractionation occurs because physical and chemical processes that influence the representation of each isotope in a particular phase (e.g., liquid vs. vapor) are proportional to their mass. In plant ecological investigations, though these fractionations are typically quite small, they are nonetheless important and must be understood for proper data interpretation. Isotope fractionations are categorized as primarily of two types; equilibrium fractionation and kinetic fractionation. ***Equilibrium isotope fractionation*** occurs during isotope exchange reactions that convert one phase (e.g., liquid) to another phase (e.g., vapor). The forward and back reaction rates of the rare isotope that leads to isotope redistribution are identical to each other. These reactions are often incomplete or take place in an open system that result in unequal (or nonequilibrium) representation of all of the isotope species in the mixture in all of the phases. If the system in which the isotope exchange reaction is taking place is closed and/or the reaction is allowed to go to completion (full exchange has taken place), there will be no net fractionation. This can occur under natural conditions, for example, when all of a particular substrate is consumed, but under many circumstances these reactions are incomplete and therefore net fractionation does exist. ***Kinetic isotope fractionation*** occurs when the reaction is unidirectional and the reaction rates are mass-dependent. In biological systems, kinetic fractionations are often catalyzed by an enzyme that discriminates among the isotopes in the mixture such that the substrate and product end up isotopically distinct from one another. Biologically mediated isotope fractionation is also called isotope discrimination. Fractionations exist because the lighter isotope (with a lower atomic mass) forms bonds that are more easily broken. Therefore, the lighter isotope is more reactive and likely to be concentrated in the product faster and more easily than the heavier

isotope (Kendall & McDonnell 1998, Dawson & Brooks 2001). Many biochemical and biogeochemical processes discriminate against the heavier isotopic species in a mixture (e.g., against $^{13}CO_2$ more than $^{12}CO_2$ during C3 photosynthetic C fixation). This discrimination leads to marked variation in the isotopic ratios of source and product pools at different stages of a chemical reaction or biogeochemical cycle and of the different resources used by the organisms from these pools. Fractionations involved in biogeochemical reactions can provide information about processes. The resulting isotope ratio of any substance that is part of the reaction can act also as a fingerprint for that resource or transitional form. It can therefore be used as a tracer to follow the reaction products through complex cycles or into diets (e.g., you are what you eat ± 0.1 to 1‰ for δ^{13}C, and ± 3 to 4+‰ for δ^{15}N; see Griffiths 1998, Robinson 2001) or along an isotope gradient of continuum such as when water moves from soils through plants and into the atmosphere (Gat 1996, Dawson et al. 1998).

Enriched isotope methods involve applying trace amounts of a labeled substance. This procedure permits one to follow the flows and fates of an element without altering its natural behavior (Schimel 1993; go to Text Box 3). Because the substances are enriched, relative to the background, tracer studies remove or minimize problems of interpretation brought about by fractionation (Text Box 1) among pools that mix because the signal (the label) is amplified relative to the noise (variation caused by fractionation). Thus, the addition of an enriched substance acts as a powerful tracer for following a specific element's cohort through a system as well as for determining rates of biological process within the system (see Nadelhoffer & Fry 1994).

For natural abundance work we express the stable isotope composition of a particular material or substance as a ratio relative to an internationally accepted reference standard (Table 1A) as,

$$\delta^{XX}E = 1000 \cdot \left(\frac{R_{sample}}{R_{standard}} - 1 \right), ‰ \qquad 1.$$

where E is the element of interest (e.g., ^{2}H or D,^{13}C, ^{15}N or ^{18}O), "^{XX}" is the mass of the rarest (and heavier) isotope in the abundance ratio, and R is the abundance ratio of those isotopes (e.g., $^{18}O/^{16}O$). Absolute abundance ratios are often very small (on the order of a few parts per thousand; Table 1B), so expressing isotope values relative to a standard and multiplying these by 1000 simply expresses the very small fractional differences in convenient "per mil" (or ppt) notation shown as ‰. The final δ value is expressed as the amount of the rarest to commonest (heavy to light) isotope in the sample with higher values indicating greater amounts of the heavier isotope. By definition, standards have a δ value of 0‰. A positive δ value therefore indicates that the sample contains more of the heavy isotope than the standard whereas a negative δ value indicates that the sample contains less than the standard.

For studies using enriched materials, the labeled substance added (e.g., $^{15}NO_3$) has an isotopic composition that significantly differs (usually exceeds) from any natural occurring level. The expression of the isotopic composition of this type of material is referred to in "atom %" (A_b) which is defined as,

$$A_b = \frac{X_{heavy}}{X_{heavy} + X_{light}} = 100 \cdot \left(\frac{R_{sample}}{R_{sample} + 1} \right), \% \qquad 2.$$

where X_{heavy} and X_{light} are the numbers of heavy and light atoms present in the sample and R_{sample} is the isotope ratio (as above). Equation 2 is most commonly used when values of A_b exceed ~0.5 atom % (or 500‰). Atom % is thus the percentage contribution of the heavy isotope to the total number of atoms of that element in the sample.

STABLE ISOTOPES AND PLANT ECOLOGICAL RESEARCH

The sections that follow are arranged hierarchically. We begin with the individual plant and how it interacts with the environment to acquire the resources it needs. We then review examples of how isotopes have informed us about interactions that occur between plants and other organisms; this section therefore focuses on the population and community scales. The final section reviews ecosystem studies where plants play a central role. We conclude with our views on future directions in plant ecology where we believe stable isotopes can have a positive impact.

Plant Level Studies

The acquisition of resources is the dominant theme that encapsulates stable isotope research at the individual plant level. Stable isotope information has been most informative in studies focused on water, carbon, and nitrogen—three resources that influence and limit plant growth, survival, and distribution. The sections that follow are organized around these resources.

CARBON The utility of using C isotopes as an ecological index of plant function stems from the correlation between habitat quality and the biochemical discrimination (Text Box 1) against $^{13}CO_2$ during gas exchange, noted here as Δ. In C3 plants, discrimination (Δ) against ^{13}C by the carboxylating enzyme, Rubisco (~27‰), is linked to photosynthesis via c_i/c_a, the ratio of intercellular to atmospheric CO_2 concentrations (Farquhar et al. 1982, Brugnoli et al. 1988). This ratio reflects the relative magnitudes of net assimilation (A) and stomatal conductance (g) that relate to demand and supply of CO_2, respectively. Carbon-13 data are thus a useful index for assessing intrinsic water use efficiency (A/g; the ratio of carbon acquired to water vapor losses via stomatal conductance, g) and may even provide information on actual water use efficiency (the ratio of assimilation to transpiration) when the leaf-to-air vapor pressure difference is known (Farquhar et al. 1989). In C4

plants, variations in c_i/c_a and Δ are relatively small despite variation in A and g (Farquhar 1983, Henderson et al. 1992, Buchmann et al. 1996a). In CAM plants, Δ values generally lie between that for C3 ($\sim$15 to 25‰ or -20 to -35‰ using δ^{13}C notation) and C4 ($\sim$2.5 to 5‰ or -11 to -15‰ using δ^{13}C notation) plants (Griffiths 1992). Variation in Δ of nonvascular plants is similar to that in C3 plants (Rundel et al. 1979, Teeri 1981, Proctor et al. 1992).

In contrast to gas exchange techniques that provide measurements of photosynthetic rates at a single time, δ^{13}C integrates photosynthetic activity throughout the period the leaf tissue was synthesized. Moreover, leaf δ^{13}C values reflect the interplay among all aspects of plant carbon and water relations and are thereby more useful than plant gas exchange measurements as integrators of whole plant function (Figure 1). As such, the earliest observations of δ^{13}C values in plant tissues (Wickman 1952, Craig 1953, Baertschi 1953) quickly established that C-isotope analyses were an important tool for integrating photosynthetic performance across ecological gradients in both space and time. As reviewed by Ehleringer (1988, 1993a,b), C isotopes have also been instrumental in revealing how species adjust their gas exchange metabolism, strategies of resource acquisition and use, and life-history patterns to ensure competitiveness and survival in a given habitat. Variation in Δ is caused by genetic and environmental factors that combine to influence gas exchange through morphological and functional plant responses. Discrimination has been observed to vary in response to soil moisture (Ehleringer & Cooper 1988; Ehleringer 1993a, 1993b; Stewart et al. 1995; Korol et al. 1999), low humidity (Madhavan et al. 1991, Comstock & Ehleringer 1992, Panek & Waring 1997), irradiance (Ehleringer et al. 1986, Zimmerman & Ehleringer 1990), temperature (Welker et al. 1993, Panek & Waring 1995), nitrogen availability (Condon et al. 1992, Högberg et al. 1993, Guehl et al. 1995), salinity (Bowman et al. 1989, Sandquist & Ehleringer 1995, Poss et al. 2000), and atmospheric CO_2 concentration (Bettarini et al. 1995, Ehleringer & Cerling 1995, Williams et al. 2001). Furthermore, morphological features also impose constraints on the physiological response to these various conditions through their influence on such factors as leaf boundary layer resistance, hydraulic conductivity through xylem, and leaf internal resistance to CO_2 and H_2O. Accordingly, variation in Δ has been found in relation to leaf size (Geber & Dawson 1990) and thickness (Vitousek et al. 1990, Hanba et al. 1999, Hultine & Marshall 2000), stomatal density (Hultine & Marshall 2000), branch length (Waring & Silvester 1994, Panek & Waring 1995, Panek 1996, Walcroft et al. 1996, Warren & Adams 2000), and canopy height (Yoder et al. 1994, Martinelli et al. 1998). Finally, Δ is, to a large extent, genetically determined, as relative rankings within and among genotypes are maintained irrespective of variations in the environment or plant condition (Farquhar et al. 1989, Ehleringer 1990, Ehleringer et al. 1990, Geber & Dawson 1990, Johnson et al. 1990, Schuster et al. 1992a, Dawson & Ehleringer 1993, Zhang et al. 1993, Donovan & Ehleringer 1994, Johnsen & Flanagan 1995, Zhang & Marshall 1995, Damesin et al. 1998, Johnsen et al. 1999). In contrast to vascular plants, genetic variation among nonvascular plants appears to have little effect on Δ whereas environmental factors

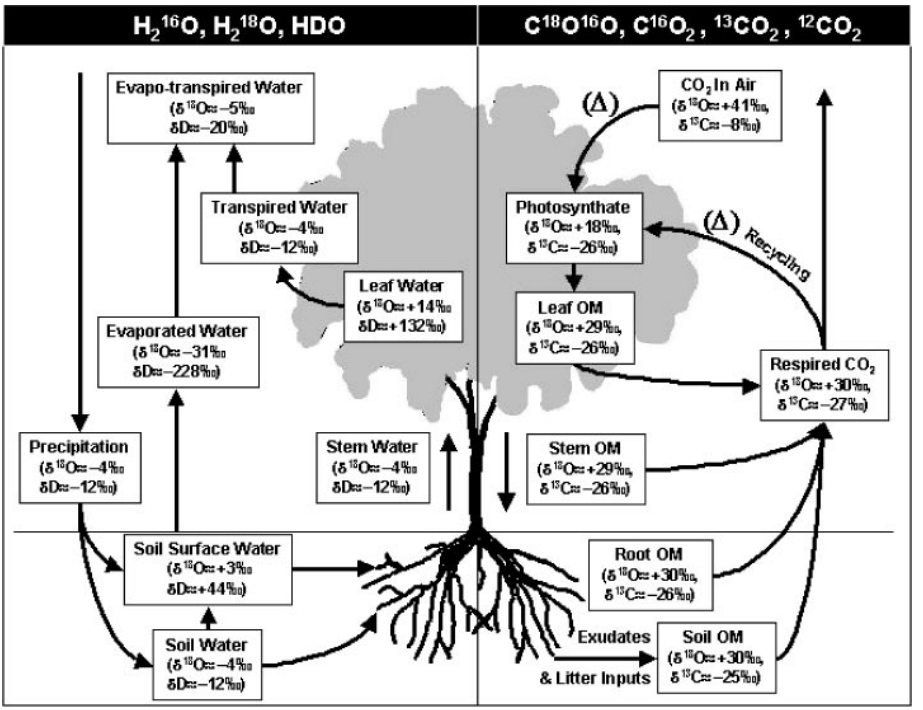

Figure 1 Isotopic composition of C, O, and H pools in the carbon and water cycles. Boxes represent pools and arrows represent processes. The values are rough approximations and can vary greatly with geographical location and environmental conditions. For demonstration purposes, we include data based on an example from Israel; δD values were estimated from δ^{18}O using the local meteoric water line for the same region following Gat & Carni (1970). The main advantages of the isotopic approach lie in the unique labeling of flux components; leaf transpiration and soil evaporation are isotopically very different; root and soil respiration can have distinct ^{13}C labeling; photosynthesis (depleted uptake) tends to enrich the atmosphere, while respiration (depleted release) tends to deplete the atmosphere in ^{18}O and ^{13}C. OM refers to organic matter. Δ indicates discrimination occurs during photosynthetic assimilation. Values are on the SMOW and PDB scales for δ^{18}O and δ^{13}C values, respectively. [Modified from Yakir & Sternberg (2000).]

such as moisture availability and water content are most important (Rice & Giles 1996, Williams & Flanagan 1996, Rice 2000). But unlike in vascular plants, Δ tends to increase with water limitation in nonvascular plant taxa (Williams & Flanagan 1996, 1998).

The factors cited above explain much of the variation in Δ observed with respect to phenology (Lowden & Dyck 1974, Smedley et al. 1991, Ehleringer et al. 1992, Damesin et al. 1998), development (Geber & Dawson 1990), age (Yoder

et al. 1994, Fessenden & Ehleringer 2002), and gender (Dawson & Ehleringer 1993, Kohorn et al. 1994, Retuerto et al. 2000, Ward et al. 2002). In addition, the aforementioned factors also explain spatial gradients in Δ found within canopies (Medina & Minchin 1980, Garten & Taylor 1992, Buchmann et al. 1997a, Hanba et al. 1997, Le Roux et al. 2001), across landscapes (Williams & Ehleringer 1996, Moore et al. 1999), and with altitude (Körner et al. 1991, Morecroft & Woodward 1990, Hultine & Marshall 2000). It should be noted that the causes of variation in Δ are clearly complex and are, at times, not straightforward. This complexity can make correlations between Δ and a single factor such as hydraulic conductivity (Cernusak & Marshall 2001), water availability (Warren et al. 2001), or rainfall (Miller et al. 2001) problematic. Further, variations in $\delta^{13}CO_2$ of source-air owing to recycling of respired CO_2 within canopies (Figure 1) may confound the ecological interpretation of $\delta^{13}C$ or Δ in leaf tissues (Schleser & Jayasekera 1985, Sternberg et al. 1989, Broadmeadow et al. 1992, Buchmann et al. 1997b, Yakir & Sternberg 2000).

Because of the integrative response of Δ to multiple eco-physiological constraints through time, C isotopes can be used to assess traits that co-vary with gas exchange, C gain, and water relations, including water use efficiency (WUE) (Farquhar & Richards 1984, Henderson et al. 1998), photosynthetic capacity (Virgona & Farquhar 1996), stomatal conductance (Condon et al. 1987, Ehleringer 1990, Ehleringer et al. 1990, Virgona et al. 1990, Meinzer et al. 1992), leaf nitrogen content (Sparks & Ehleringer 1997, Schulze et al. 1998), leaf mass per area (Vitousek et al. 1990, Hultine & Marshall 2000, Williams & Ehleringer 2000), longevity (DeLucia et al. 1988, Schuster et al. 1992b), and relative growth rate (Ehleringer 1993b, Poorter & Farquhar 1994). For example, working in boreal ecosystems, Brooks et al. (1997) used $\delta^{13}C$ as a surrogate for physiological characteristics and found that life form (deciduous or evergreen trees, shrubs, forbs, and mosses) can be a robust indicator of functional group membership related to carbon and water fluxes (see also Flanagan et al. 1997a). Whereas these data are consistent with those gathered by Marshall & Zhang (1994), Kelly & Woodward (1995) found that life form had no effect on Δ among three altitude catagories. In another example, Smedley et al. (1991) examined the seasonal time-course of $\delta^{13}C$ among grassland species and found lower WUE among the taxa active during the initial, less stressful months of the growing season. Further, WUE increased with evaporative demand as soil moisture declined. In a related fashion, Kloeppel et al. (1998) used $\delta^{13}C$ of leaf tissue to assess WUE and determined that, in general, larches (*Larix* spp.) use water less efficiently and maintain higher photosynthetic capacity (based on foliar N concentration) than co-occurring evergreen conifers from 20 locations in the northern hemisphere. Their results suggest that water is not the most limiting resource at these high elevation (3000–4000 m) sites. Finally, Flanagan et al. (1992) and Valentini et al. (1992) used $\delta^{13}C$ of leaves to assess WUE of species from different functional groups in a Pinyon-Juniper Woodland and the Mediterranean macchia, respectively. By concurrently measuring δD in xylem water to distinguish surface versus groundwater sources (see next section),

they found that species with more negative $\delta^{13}C$ values and therefore lower WUE had deeper rooting depths and a more reliable water supply than species that relied on rain water in the upper soil layers (also see Lajtha & Marshall 1994).

To separate the independent effects of photosynthetic capacity and stomatal conductance on c_i/c_a, Scheidegger et al. (2000) have recently proposed measuring both $\delta^{13}C$ and $\delta^{18}O$ in leaf organic matter (Figure 1). Whereas $\delta^{13}C$ reflects c_i/c_a, $\delta^{18}O$ generally varies with ambient humidity, which in turn reflects changes in water use [*g*] (Ball et al. 1987, Grantz 1990; but see also Mott & Parkhurst 1991, Monteith 1995). The $\delta^{18}O$ of leaf and tree ring cellulose are largely determined by the integrated leaf-to-air vapor pressure gradient during photosynthetic gas exchange (Farquhar et al. 1998). This leaf-air vapor pressure gradient changes with environmental conditions (atmospheric humidity, soil moisture, air temperature) and plant response to these environmental changes (e.g., *g*, leaf temperature, *A*). So measurement of the ^{18}O composition of plant tissues aids with the interpretation of differences in $\delta^{13}C$ among individual plants growing in the same location and among species in different environments. Moreover, the determination of WUE is greatly improved by the simultaneous use of $\delta^{13}C$ and $\delta^{18}O$ in plant tissues (Saurer et al. 1997). By considering concurrent variations $\delta^{13}C$ and $\delta^{18}O$, one can distinguish between biochemical and stomatal limitations to photosynthesis in response to a change in environmental conditions. Alternative methods to distinguish such effects rely on instantaneous gas exchange measurements (Farquhar & Sharkey 1982) that are more difficult to extend through time or to apply simultaneously on a large number of samples. Although further research is needed to develop a quantitative dual (C and O) isotope model, this approach should improve our ability to relate gas exchange characteristics to $\delta^{13}C$ and $\delta^{18}O$ signals in plant leaves and tree rings.

In fact, bulk wood or purified cellulose obtained from tree rings has provided some of the best samples for isotope analyses because the $\delta^{13}C$, δD, $\delta^{18}O$, and even $\delta^{15}N$ isotopes in the wood can record a great deal about the ecophysiology of the plants (Leavitt & Long 1986, 1988, 1989, 1991; Livingston & Spittehouse 1993; Bert et al. 1997; Saurer et al. 1997; Borella & Saurer 1999; Roden & Ehleringer 1999a,b), the resources they use (Roden et al. 2000, Ward et al. 2002), and the environments they inhabit, both now (Barbour et al. 2000, Roden et al. 2000) and in the past (Edwards et al. 1985; Leavitt 1993; Lipp et al. 1996; Switsur et al. 1996; Feng 1999; Hemming et al. 1998, 2000; Monserud & Marshall 2001). Recent modeling efforts that use $\delta^{13}C$ (Hemming et al. 2000) and δD and $\delta^{18}O$ (Roden & Ehleringer 2000; Barbour et al. 2000, 2001) have very much improved our interpretations of isotope variation in tree rings. In these models, fractionations are better understood and accounted for, allowing one to make more precise inferences about environmental conditions (temperature and humidity), plant resource status (water-use efficiency and/or sources of water and nitrogen), and environmental change (Epstein & Krishnamurthy 1990, Duquesnay et al. 1998).

In addition to the use of natural abundance $\delta^{13}C$ to deepen our understanding of plant gas exchange, stable isotope techniques based on 13-C labeling (see Text

Box 2) offer a means to trace and quantify the fate of C allocation to various plant organs, tissues, and even specific compounds or the surrounding soil that would have been difficult to study using other methods. For example, Simard et al. (1997a) used enriched ^{13}C-tracers (see Text Box 2) to examine the fate of C fixed by paper birch (*Betula papyrifera*) and Douglas fir (*Psuedotsuga menziesii*) seedlings and showed that half of the labeled ^{13}C that was assimilated was quickly lost via root and shoot respiration, root exudation, and tissue death. Interestingly, paper birch had higher assimilation rates and higher allocation of its remaining C to roots than Douglas fir, suggesting that it may have a competitive advantage when grown in mixed communities. In another study, the effect of seasonality on the temporal pattern of C partitioning to the root system was investigated (Mordacq et al. 1986). Here it was shown that very little C was allocated to roots during shoot and leaf elongation, whereas later in the season, the stem and root system were the major sinks. Working in grasslands, Niklaus et al. (2001) used labeled ^{13}C at elevated CO_2 concentrations to determine that an increased supply of CO_2 enhanced C assimilation but not root exudation and turnover.

BOX 2 Isotope additions: Tracer and Isotope Dilution Methods

The addition to a system (plant, soil, etc.) of a quantity of material with a δ value significantly different from any natural background level, followed by the observation of its fate, allows the study of its fluxes and/or transformations in undisturbed conditions. The amount of material required depends on detection limits for measurements, size of the pool to be labeled, rates of production or consumption, and duration of labeling. In tracer experiments, a known quantity of isotope is added to a pool and then recovered in a recipient pool after a known amount of time. The total amount of an element (tracer plus background isotope, M_{AB}) that moved from the labeled source pool (A) to the sink (B) can be calculated knowing the atom % excess (I_A) of pool A, and the mass (P_B) and the atom % excess (I_B) of pool B at the end of the experiment (from Stark 2000):

$$M_{AB} = \frac{P_B \cdot I_B}{I_A}. \qquad \text{B2.1.}$$

Dividing M_{AB} by the length of the experiment gives the flux rate from A to B. Calculation of % recovery of the label within a sink pool requires the measurement of the mass of the labeled source pool (P_A):

$$\%\,\text{recovery} = 100 \cdot \frac{P_B \cdot I_B}{P_A \cdot I_A}. \qquad \text{B2.2.}$$

This technique is usually applied in mass balance studies. The assumptions underlying the tracer method are: (*a*) Nonlabeled and labeled materials have the same chemical behavior (fractionations, except for small amounts caused by differences in heavy and light isotopes, do not occur), (*b*) the source pool is uniformly labeled by the isotope, (*c*) the addition of the isotope does not stimulate rates of transformations

and (d) material that is lost from sink pool(s) is accounted for (see Stark 2000, p. 224 for additional equation). The calculation of the rates of flow will be inaccurate if material flows into the source pool because of dilution or if there is outflow from the sink pool(s).

Isotope dilution techniques, in general, include the labeling of a pool that is the product of the transformation of interest (for example, labeling the soil ammonium pool to estimate the gross rate of mineralization) and the measuring of how rapidly the added isotope is diluted by influx of the natural isotope into the pool over time. This approach allows one to measure flux rates through different compartments that have simultaneous inputs and outputs. Some of the same requirements mentioned above, in particular a–c, must be met. In addition, the rates of transformation must be constant and unidirectional over the timescale of the experiment. When these assumptions are satisfied, the gross production rate (GPR) for a particular process can be calculated knowing the size (P) and atom % excess (I) of the labeled pool at the beginning (P_0 and I_0) and at the end (P_t and I_t) of the experiment (from Hart et al. 1994, modified by Stark 2000):

$$\mathrm{GPR} = \frac{P_0 - P_t}{t} \cdot \frac{\log(I_0/I_t)}{\log(P_0/P_t)}. \qquad \text{B2.3.}$$

Many different formulations for resolving specific applications of tracer and isotope dilution experiments exist and they are reviewed by Schimel (1993), Stark (2000), and Palta (2001).

WATER Stable isotope analyses of both H and O have significantly improved our understanding of water source acquisition by plants because the "pools" of water used by plants can easily be distinguished (Figure 1; Gat 1996). There are now examples from a wide range of ecosystems showing how different plant species use water resources in time and in space. Because much of this work has been reviewed recently (Ehleringer & Dawson 1992, Dawson 1993a, Dawson & Ehleringer 1998, Dawson et al. 1998, Ehleringer et al. 2000b, Walker et al. 2001), we mention only a few examples.

It is easy to apply δD and δ^{18}O data to water acquisition studies because there is no isotopic fractionation during water uptake by terrestrial plants (Wershaw et al. 1966), although Lin & Sternberg (1993) provide an example for a marine, salt-excluding plant species that does seem to fractionate H (but not O) during water uptake. For terrestrial plants, if samples of the different water sources can be obtained and the water within the plant's xylem sap is also extracted, it is possible to assess which sources of water are being used (Ehleringer et al. 2000b and Turner et al. 2001 provide detailed methods). Applying isotope mixing models (Text Box 3) coupled with other ecological or physiological measurements then becomes a particularly powerful way to link the water sources used by plants to other aspects of their water relations (Dawson 1993b, Flanagan et al. 1992, Jackson et al. 1995, Williams & Ehleringer 2000b).

BOX 3 Isotope Mixing Models

In situations where the isotope values of the sources can be determined, one can partition the use of each source using what have been called end-member mixing models. In the simplest case, proportional use of two known sources using a single isotope involves using a two-source mixing model that can be written as,

$$\delta_t = f_A\delta_A + (1 - f_A)\delta_B, \qquad \text{B3.1.}$$

where δ_t is the total δ value (e.g., plant xylem water $\delta^{18}O$), δ_A, and δ_B are the isotope values of sources A and B, and f_A is the fraction of the total contributed by source A. Rearranging for f_A gives

$$f_A = \frac{(\delta_t - \delta_B)}{(\delta_A - \delta_B)}. \qquad \text{B3.2.}$$

Brunel and co-workers (1995) proposed a variation on the model presented above that uses both the δD and $\delta^{18}O$ of source and plant water to determine proportional use of each source. This may be necessary when it is difficult to resolve the zone of uptake using only one isotope as reported in several plant water uptake studies in saline soils (Thorburn & Walker 1994, Thorburn et al. 1994, Mensforth et al. 1994, Mensforth & Walker 1996, Walker et al. 2001).

When more than two different sources are present, assessing the proportional use of each becomes much more challenging. However, a recent set of papers has provided guidelines for approaching this issue in a more robust fashion (see Phillips 2001, Ben-David & Schell 2001, Phillips & Gregg 2001, Phillips & Koch 2002, Zencich et al. 2002). The authors discuss sampling issues and develop significant improvements in the application of mixing models that involve de-convoluting the use of multiple-sources using stable isotope data. Moreover and perhaps more importantly, guidelines are provided for statistical error analysis associated with mixing model applications.

In our view, these are extremely important improvements over previous approaches because they not only provide a means to assess where, for example, the water being used by particular plants comes from when roots are found throughout a soil profile, but they standardize and improve upon the mathematical evaluation of the data obtained. Whereas these more complex models require additional information about the spatial and temporal variation of the resources within a system, they may be the only way to quantitatively access resource use and partitioning among multiple end-members and species, within an ecosystem. In some instances, there may be several different interpretations, and simple two- or even three-source models cannot and should not be applied. In these cases one may still be able to arrive at a best-case interpretation (as shown by Phillips & Gregg 2000).

Hydrogen and O isotope analyses have been used effectively to determine the reliance of a species on shallow versus deep soil water (White et al. 1985, White 1989, Dawson 1993b, Brunel et al. 1995), surface runoff or streamwater versus soil water (Dawson & Ehleringer 1991, Busch et al. 1992, Thorburn et al. 1994, Phillips & Ehleringer 1995, Kolb et al. 1997), and winter precipitation versus fog (Dawson

1998) or monsoonal rain (Lin et al. 1996, Williams & Ehleringer 2000b). Other studies have used δD or δ^{18}O to investigate differential water resource use among different species within a community (Ehleringer et al. 1991a; Flanagan et al. 1992; Dawson & Ehleringer 1991, 1998; Dawson 1993a,b; Jackson et al. 1995, 1999; Meinzer et al. 1999) and to examine the relationship between plant distribution along natural gradients of water availability and the depth at which plants obtain their water (Sternberg & Swart 1987; Thorburn et al. 1993a,b; Mensforth et al. 1994). Still others have used isotope analyses of source and plant waters to look at changes in the zone of water uptake over time when soil moisture at different depths varies with season (Ehleringer et al. 1991a, Dawson & Pate 1996, Lin et al. 1996, Dawson 1998) or in relation to life history stages (Feild & Dawson 1998), life form differences (Williams & Ehleringer 2000b), functional group classifications (Ehleringer et al. 1991a, Dawson 1993a), or changes in plant size (Dawson 1996, Meinzer et al. 1999).

Thorburn & Ehleringer (1995) provide an important caution regarding simple interpretations from isotope data used in tracing water source use. By measuring soil water isotope profiles, xylem water, and root water from three different systems they showed that plants may extract water from several zones simultaneously. Their data showed how the application of simple two-source (shallow versus deep) mixing models (Text Box 3) can lead to erroneous interpretations. Whereas this complication means that additional sampling is needed, this sampling can be done and adds additional power to the interpretation (also see Cramer et al. 1999).

The aforementioned examples highlight the importance of using the isotope data to determine the zones in soils where plant roots are actively extracting moisture (Ehleringer & Dawson 1992). This is critical information because roots can often be found throughout the soil profile. Therefore, isotope data show that the presence of roots does not always mean these roots are active in water uptake; we know no other method that can provide this perspective. Armed with this information, investigators may be better able to link species characteristics and species diversity to ecosystem functions (Dawson 1993b, 1996; Jackson et al. 2000; Meinzer et al. 2001). There may also be practical applications here such as the design of agroforestry systems (Pate & Dawson 1999).

At times, combining enriched and natural abundance tracers in water relations studies has helped in the interpretation of dynamic plant water uptake (Lin et al. 1996, Plamboeck et al. 1999) as well as water transfer behavior among ramets on the same plant (De Kroon et al. 1996). In these studies, pulses of D_2O-labeled water were added to individual plants or entire plots (see Plamboeck et al. 1999, Lin et al. 1996, Schwinning et al. 2002, for examples) in order to distinguish the precise zone in the soil (Moreira et al. 2000) or time of day or season that plants use their water in relation to a transition between conditions of low soil moisture availability and short episodes of high soil moisture availability (Plamboeck et al. 1999, Williams & Ehleringer 2000b). Pulse labeling has also helped reveal how different life forms within a community may partition water resources (Lin et al. 1996, Schwinning et al. 2002). In all these cases, whether using natural abundance

or enriched tracers of water, stable isotope methods have helped quantify the absolute and relative use of shallow versus deep soil water sources in different species. When it is difficult or impossible to use two- or three-source mixing models (Text Box 2), tracer-pulse methods, coupled with measurements of plant transpiration (T) and the exchangeable water volume (V) can provide a more precise quantification of water source utilization from different sources. Schwinning and coworkers (2002) developed a dynamic mixing model that uses measures of T and V as well as a labeled (f) and an unlabeled (1-f) water source to better understand water use behavior in a mixed shrub-grass community. In their study, the concentration of the D_2O-label, in a fixed V, depends on the relative contribution of f and T/V. However, because water uptake rates and ratios may not remain constant during or after a pulse, the pulse use must be estimated by integrating parameters over time. From these experimental and modeling efforts, Schwinning et al. (2002) suggested that relative pulse utilization by plants with contrasting life history strategies can be estimated with fair accuracy and the species-specific water use strategies estimated. This information in turn permitted Schwinning and her coworkers to better evaluate the validity of the assertion that plants partition water resources in desert communities (also see Schwinning & Ehleringer 2001).

NITROGEN Plant $\delta^{15}N$ values can vary as much as 10‰ in co-occurring species (Handley & Scrimgeour 1997). Early studies assumed that the $\delta^{15}N$ of whole plant or leaf tissues reflected the $\delta^{15}N$ of the form (source) of N most used by that plant. This assumption was the conceptual basis for predicting, for example, the ability of co-occurring plants to partition acquired N in time, space, and by form. It is now clear that such an interpretation is incorrect. Natural abundance $\delta^{15}N$ of plants we now know reflects the net effect of a range of processes (reviewed by Handley & Scrimgeour 1997, Robinson 2001, Evans 2001, Stewart 2001). The presence of multiple N-sources with distinct isotopic values (Figure 2), mycorrhizal associations, temporal and spatial variation in N availability, and changes in plant demand can all influence plant $\delta^{15}N$. To determine the importance of these effects, we must develop a more complete understanding of the controls over $\delta^{15}N$ in the plant-soil system (Handley et al. 1998). Even if the N source is the most important factor in determining plant $\delta^{15}N$, at the moment there is no easy technique for isolating and analyzing $\delta^{15}N$ in soil N pools that are available for plant uptake. Promising techniques that are currently being used, such as dual-isotope techniques (e.g., $\delta^{15}N$ and $\delta^{18}O$ in NO_3; Durka et al. 1994), need to be further explored so that we can more successfully distinguish the dominant N sources to plants. Better understanding of plant N sources will also be aided by the production of a mechanistic model demonstrating how ^{15}N behaves during N-acquisition by plants.

Recent investigations have begun to study the causal relationships between uptake, assimilation, and allocation of N and plant $\delta^{15}N$ values. To date, there is no evidence of fractionation of either ^{14}N or ^{15}N during its physical movement across living membranes (passive and active uptake; Handley & Raven 1992). Differences in $\delta^{15}N$ between the N source(*s*) and the plant are generally due to

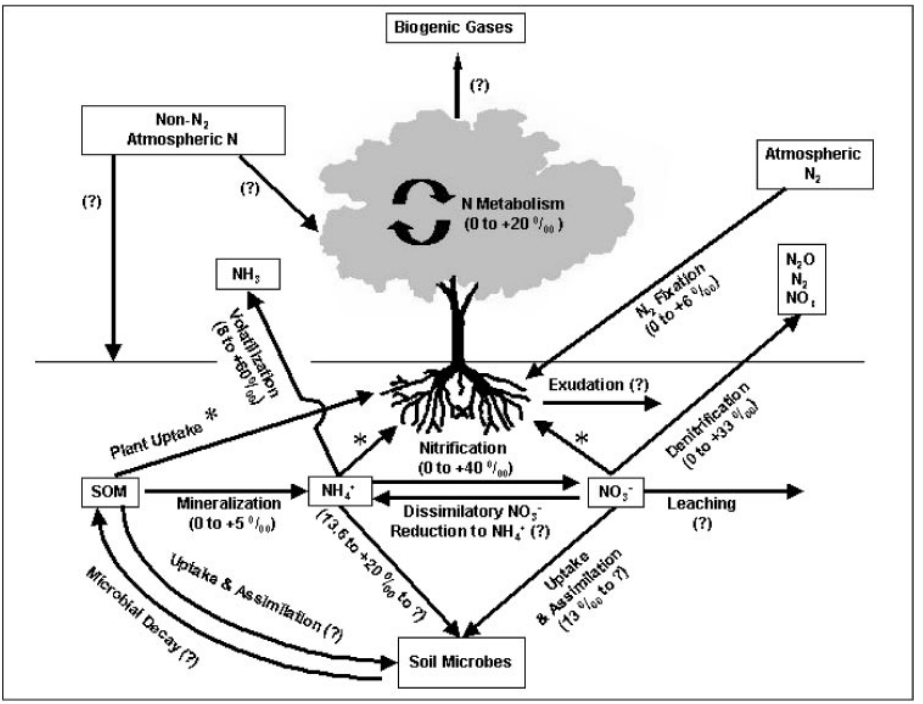

Figure 2 Major pathways and pools in the nitrogen cycle. Boxes represent pools and arrows represent processes. Figure illustrates that different N transformations lead to varying amounts of ^{15}N enrichment or depletion. Values in parentheses represent potential range of discriminations observed in controlled laboratory, greenhouse, and field experiments [values from Shearer & Kohl (1986) and Handley et al. (1999)]. Similar to the water and carbon cycle, these can vary greatly with geographical location and environmental conditions. The "*" indicates that plant N uptake could be via mycorrhizae and "?" indicates that the specific fractionation associated with that process is not fully characterized. SOM includes soil organic matter derived from plant, microbial, and faunal organic tissues. This figure does not include all of the possible N fractionations that occur within the N cycle (e.g., does not include NH_4^+ exchange in soils). [See Shearer & Kohl (1986) and Handley et al. (1999) for more details.]

enzyme-mediated reactions that commonly discriminate against the heavier ^{15}N (for example, assimilation of NH_4 mediated by glutamine synthetase or assimilation of NO_3 mediated by nitrate reductase) (Handley & Raven 1992). Whole plant $\delta^{15}N$ appears similar to the $\delta^{15}N$ value of the external source (implying no discrimination) only if the entire N pool is converted from source to product. But net isotope discrimination can occur if fractionated plant parts or fractionated N compounds are lost from roots (exudation) or leaves (loss of gaseous N; Figure 2).

New insights about the net discrimination that occurs during N-assimilation have been obtained by growing plants hydroponically in the presence of a single inorganic N-source. When NH_4 is the sole source of N there is little, if any, discrimination when the N concentration is limiting (Evans et al. 1996). But there may be large whole plant depletion in ^{15}N at high N concentrations (Yoneyama et al. 2001). The reasons why depletion occurs, including exudation of ^{15}N enriched NH_4 or organic N from roots, requires more explicit testing. External NO_3 concentrations, instead, appear to have a small effect on whole plant $\delta^{15}N$ (Mariotti et al. 1982, Kohl & Shearer 1980, Bergersen et al. 1988, Yoneyama & Kaneko 1989, Evans et al. 1996, Yoneyama et al. 2001). Plants can be either slightly enriched or slightly depleted in ^{15}N compared to the NO_3 source (Yoneyama et al. 2001). Release of ^{15}N fractionated compounds could account for this observation (Robinson et al. 1998). Very high external NO_3 concentrations, osmotic stress, or drought may induce N isotopic fractionation, although the mechanisms for this fractionation are still unknown (Handley et al. 1994, 1997). Remarkably little is known about whether fractionation occurs during the uptake and assimilation of organic forms of N.

Different plant parts, organs, and compounds can differ from the whole plant $\delta^{15}N$ values. Within-plant variation is typically small, between 2 and 3‰, but it can reach 7‰ in desert plants (Evans 2001). Understanding what causes this variation may help elucidate the metabolic events responsible for it because differences between plant parts or compounds are determined by differences in assimilation, reallocation, and/or N losses. If NO_3, for example, is the only source of N and is partially assimilated in the roots, there can be an isotopic difference between the root and shoot (Evans et al. 1996, Yoneyama et al. 2001). Kolb & Evans (in review) observed no discrimination during N resorption, but they did observe discrimination during re-allocation of N from storage.

Recently, it has been suggested that natural isotopic variation of phloem and xylem saps may provide insight into resource acquisition and use (Yoneyama et al. 1997). Further development of new technologies, such as a chromatographic separation of specific compounds coupled to the isotope ratio mass spectrometer, could provide powerful insights for resolving metabolic processes and making inferences about plants in relation to N.

Providing an enriched ^{15}N-label (Text Box 2) to plants and following its fate can be an effective way to differentiate between external and internal plant sources and to quantify the importance of the internal cycling of N to support new growth (Proe et al. 2000). Dual-isotope (^{13}C and ^{15}N) labeling may be the most powerful tool for demonstrating the relationship between internal N stores and recently fixed photosynthate (Dyckmans & Flessa 2001). Enriched N tracers can also be used to determine the interaction between N supply and atmospheric CO_2. For example, oak seedlings responded positively to elevated CO_2 concentration when N availability was high, whereas N deficiency created a growth imbalance, enhancing biomass accumulation and partitioning of newly assimilated C and N to the root system (Vivin et al. 1996, Maillard et al. 2001).

Population and Community Studies

Stable isotope methods have only very recently been featured in studies of plants at the population and community levels. These studies have employed H, C, O, and N isotope data to investigate competition, facilitation, parasitism, herbivory, and symbiotic relationships formed between fungi and N-fixing bacteria and their host plants. The sections below highlight some of this work and are organized by theme and then by resource.

Competition and Facilitation

Both positive (facilitation) and negative (competition) interactions among plants have been investigated using stable isotopes. We review some examples below, by resource.

CARBON A few recent studies are now using C isotope data to investigate competition. For example, based on the early work by Svejcar & Boutton (1985) that used $\delta^{13}C$ for investigating rooting patterns in mixed plant stands, Polley et al. (1992) provided some of the first C (and N) stable isotope evidence from root and shoot tissue analyses that competition structured mixed grass-shrubland communities. This approach was extended in two recent studies. Williams et al. (1991) used ^{13}C-analyses of two grasses in the presence and the absence of a co-occurring shrub. A second study (Rice et al. 1993) examined blue oak–grassland mixtures and used $\delta^{13}C$ values to infer the efficiency of water use in the presence or absence of either annual grass or perennial bunchgrass neighborhoods. In both studies, $\delta^{13}C$ values were useful in showing how the efficiency of resource use varied in the presence or absence of different neighbors. The work of Rice et al. (1993) on tree-grass interactions has recently been expanded in a study by Archer (1995). Working in savanna parklands in the southwestern United States, Archer (1995) used soil $\delta^{13}C$ data to show how this community, once dominated by C4 grasses, has been largely replaced by C3 shrubs during the past 100–200 years; these shifts appear to have been facilitated by changes in soil N.

WATER Our understanding of competition or facilitation among plants inhabiting the same population or community has been enhanced in a limited way through H and O isotope work (but see Schwinning et al. 2002 and above). Dawson (1993a) provided some of the first isotopic evidence that trees can have a positive influence (facilitation) on their neighbors via the process of hydraulic lift; the redistribution of water by plant root systems from deep moist layers in the soil to drier shallow layers (reviewed by Caldwell et al. 1998). Dawson (1993a) showed that water used by plants growing nearest sugar maple trees that showed hydraulic lift obtained a significant fraction of their water in summer from the trees that lifted and released this water into the soil and rhizosphere (see also Burgess et al. 2000). These same plants were less water-stressed, had greater water use, and grew more than plants inhabiting areas farther from trees. This study demonstrated that the long-held

assumption that plants living in close proximity will show negative, competitive, effects may not always be true. The δD data used in conjunction with measures of plant water use (Dawson 1996, 1998) and soil water transport (Emerman & Dawson 1996), showed that trees can have a positive influence on neighboring plants and on community diversity. This idea is supported by recent work of Caldeira et al. (2001) on positive biodiversity-production relationships; these workers used δ^{13}C data to establish a relationship between species richness and productivity. Their data indicated that there was higher water use and productivity when plants grew in species-rich mixtures compared to monocultures. Work by Ludwig (2001) and coworkers (in review) in *Acacia*-woodland/savannas in East Africa has shown how both competition between trees and grasses and facilitation brought about by hydraulic lift from the *Acacia* trees influences the interannual dynamics of tree-grass interactions. Using the δ^{18}O of plant and source waters coupled with trenching experiments and measures of productivity, Ludwig and his colleagues show that in dry years competition dominates and in wetter years facilitation dominates. Lastly, studies of the facilitation effects by plants on each other have now been discussed in the context of designing intercropping systems in agroforestry (Emerman & Dawson 1996) that in some cases mimic the natural ecosystems they are embedded within or replace (Pate & Dawson 1999). In this context, Smith et al. (1997, 1998) recently used isotope data to help design useful tree-crop systems in drought-prone Africa.

Parasitism

Plant parasites are important for shaping plant-plant interactions; here stable isotopes have been particularly powerful tools for understanding these interactions.

CARBON AND NITROGEN Variation in δ^{13}C, when combined with anatomical, morphological, and physiological information, has provided important insights into the complex physiological relationships between host plants and their associated plant parasites. Obligate parasites of higher plants have specialized absorptive organs called haustoria that penetrate the tissues of their hosts and acquire resources from them. Mistletoes, which are epiphytic parasites and root hemiparasites, are connected to the host via the xylem but are also photosynthetic. Estimates of WUE based on the δ^{13}C in host and mistletoe pairs have shown that not only do they differ but that mistletoes have lower WUE and higher overall water use, especially under conditions of N shortage (Schulze & Ehleringer 1984, Ehleringer et al. 1985). These findings strengthened the hypothesis that mistletoes regulate their transpiration (upwards) to obtain N from their hosts. Press et al. (1987) were the first to compare the δ^{13}C of a C4 host and its C3 root hemiparasites with predicted values based on foliar gas-exchange data; this information was used to demonstrate that substantial C transfer from host to parasite can occur even when the parasite can photosynthesize. The same approach was expanded by Marshall & Ehleringer (1990) to study host-mistletoe unions and subsequently formalized into a model

(Marshall et al. 1994) that calculated the C-contribution from heterotrophic carbon to the total C-budget of the parasite. The Marshall et al. (1994) model showed that the heterotrophic C contribution ranged from 15% to 60%. They also found a correlation between the total C gained by the mistletoe [via *A* plus heterotrophic C (acquisition) obtained in the transpiration stream] and the host's *A*, suggesting a convergence in parasite and host growth rates, which can provide a basis for the N-parasitism hypothesis. In contrast, Bannister & Strong (2001) recently found that the estimation of mistletoe heterotrophy calculated from $\delta^{13}C$ data can be confounded in moist temperate environments like New Zealand, where very small differences between host and parasite $\delta^{13}C$ were observed.

The movement of N from putative hosts to a woody root hemiparasite has been investigated in a coastand heathland in southwest Australia (Tennakoon et al. 1997). The similarity between the $\delta^{15}N$ values of the parasite and those of the N_2-fixing hosts was interpreted as a qualitative indicator of the parasite dependence on fixed N as opposed to soil inorganic N. These findings might explain why woody root hemiparasites can achieve such high biomass and become the dominant growth form in this ecosystem deficient in soil-available N.

Trophic Interactions—Herbivory/Grazing

The use of stable isotopes has recently helped inform research on trophic interactions. We review some important case studies below.

CARBON Several recent studies have illustrated that stable isotopes coupled with mixing models (Text Box 3) can inform us about the nature of trophic interactions. For example, using the $\delta^{13}C$ and $\delta^{15}N$ of ants in the genus *Philidris* and their host, the tropical epiphyte *Dischidia major*, Treseder et al. (1995) showed that ants provide C (as respired CO_2) and N in exchange for shelter. Because the epiphyte is an obligate CAM plant with higher $\delta^{13}C$ than a C3 tree, and the ants feed on Homoptera that ingest the phloem sap of C3 trees, unexpectedly low $\delta^{13}C$ values in the epiphyte showed the extent to which the plant was assimilating C derived from ant respiration. *D. major* leaves were also more enriched in ^{15}N than those of another epiphyte that grew close by but did not host ants, suggesting that *D. major* uses ant debris as an N source. Sagers et al. (2000) also documented that, within the specialized mutualism of *Azteca* ants and the plant *Cecropia peltata* there is exchange of resources between the ants and the trees, where the ants use some plant C products and provide N to their host. Earlier studies of carnivorous plants had used both the $\delta^{13}C$ and $\delta^{15}N$ of the predominant prey (ants or termites) to determine their contribution to the plants' resource requirements (Schulze et al. 1991, 1997; Moran et al. 2001). In these sorts of trophic investigations, the application of mixing models for determining proportional contributions of different sources is critical.

Approaches to isotope mixing have recently been critiqued (Phillips 2001, Phillips & Gregg 2001, Ben-David & Schell 2001, Phillips & Koch 2002). These

authors recommend measuring the isotopic composition of each component in the study system, its elemental concentration (Phillips & Koch 2002), and its variation, in order to achieve robust estimates of partitioning. Replication over time and space is critical for enhancing statistical power. Moreover, the interpretations should be based on good a priori knowledge of the system itself (Handley & Scrimgeour 1997).

Very few studies have used data on natural abundance $\delta^{13}C$ to assess herbivore impacts on plant performance. Fry et al. (1978) were among the first to use $\delta^{13}C$ data to look at effects of grasshopper feeding on plant C-balance. Recently, Alstad and coworkers (1999) showed that plant WUE improved in *Salix* with elk browsing, and Kielland & Bryant (1998) used $\delta^{13}C$ (and $\delta^{15}N$) of animals, vegetation, and soil to elucidate the important role of moose in shaping vegetation dynamics in a taiga forest (see additional examples in Lajtha & Michener 1994).

Tracer techniques have also proven useful in elucidating mechanisms of plant tolerance to herbivory, particularly when these mechanisms are based on patterns of C (or nutrient) allocation within the plant. For a group of C4 perennial prairie grasses, tolerance was associated with the capacity of the plant to reallocate C rapidly from roots to shoots in response to defoliation (Briske et al. 1996). Olson & Wallander (1999), however, showed that the amount of C allocated to the root system by the invasive leafy spurge (*Euphorbia esula*) was unaffected by defoliation, suggesting that the grazing tolerance of this species is instead linked to its ability to maintain an extensive root system that may store C and allow regrowth after tissue loss.

NITROGEN Despite the limitations in applying natural abundance $\delta^{15}N$ of plants to understanding N dynamics at the population and community levels (Handley & Scrimgeour 1997, Högberg 1997, Evans 2001, Robinson 2001, Stewart 2001), there is some consensus that under certain conditions N isotopes provide useful insights. This may be particularly true when pools within a system have distinct $\delta^{15}N$ values and these have been measured. Here, one may be able to use $\delta^{15}N$ to explore broad patterns of N use at the population and/or community level. For example, in sites that receive a high input of nitrogen from animals (animals are highly enriched compared to plants and soils; see Robinson 2001), tracing N inputs and movement within a plant community may be possible (Erskine et al. 1998, Stewart 2001). Under these conditions, $\delta^{15}N$ can serve as a nonenriched tracer, as recently demonstrated by Frank & Evans (1997) and Frank et al. (2000) in an elegant example of how N inputs by large herbivores (buffalo and elk) can alter both plant and soil $\delta^{15}N$ in the plant communities of Yellowstone National Park in the United States.

Under conditions where the study of natural abundance ^{15}N poses limitations, enriched ^{15}N-tracers can act as indispensable tools to evaluate the importance of N availability in shaping natural communities. Differences in uptake of N tracers, both spatially and temporally, have been used to infer what maintains species diversity (or niche diversification) in old-field (McKane et al. 1990) and desert

(Gebauer & Ehleringer 2000) plant communities. ^{15}N-tracers also have been used to show how plants can enhance rates of N uptake following defoliation (Wallace & Macko 1993). Tracers also showed that after simulated mammalian browsing the performance of several evergreen and deciduous tree saplings depended upon both the capacity to store N and the site of storage during the previous winter (Millard et al. 2001).

Symbioses with Plants—Mycorrhizal Fungi and N-Fixing Bacteria

The importance of plant symbioses have recently been studied using stable isotope methods. We review some important recent studies below.

CARBON Mycorrhizal fungi are known to influence plant acquisition of C, nutrients and water. Generally, in plant-mycorrhizal symbioses C moves from the plant to the fungus, whereas nutrients derived from the soil are passed from the fungus to the plant (Smith & Read 1997). Because the connection between plant roots and the fungus is not easily observed, and because many fungi are not host-specific, fungi might receive C from several hosts, whereas the plant in turn could receive N from many different fungal symbionts.

Several laboratory-based ^{13}C labeling studies indicate that C is transported between plants connected via ectomycorrhizal (ECM) and arbuscular-mycorrhizal (AM) networks (Simard et al. 1997b, Watkins et al. 1996, Fitter et al. 1998). This type of plant-to-plant C transport occurs via a mycorrhizal intermediate and may influence both plant C-balance and competition within a population or community. For example, this relationship may be of considerable ecological and physiological importance to the establishment of seedlings living in the shade of overstory trees where C-income of these very small plants may be severely limited. If the root system of the developing seedling were to be colonized by fungi that are connected to canopy trees then the shaded seedlings could potentially receive assimilates synthesized by large trees, thereby enhancing their growth and survival. Simard et al. (1997b) recently used both ^{13}C and radioactive ^{14}C to trace the movement of C through ectomycorrhizal *Betula papyrifera* and *Pseudotsuga menziesii*. The authors asserted that bidirectional transfer of C between plants through the fungi had occurred. However, when the fungal mycelia that linked the plants were severed, variation among replicates increased, making it difficult to demonstrate statistically the significance of the C-transfer between plants. Earlier, Watkins et al. (1996) used only natural abundance ^{13}C to quantify transfer of C between *Plantago lanceolata*, a C3 plant, connected by an AM network to *Cyndon dactylon*, a C4 plant. Their approach indicated that the gross, unidirectional transfer of C, via the mycorrhizae, from *P. lanceolata* into *C. dactylon* averaged 10% of the total C in the roots of *C. dactylon*. Fitter and coworkers (1998) used the same approach and showed that C transferred from the C3 plant to the C4 plant via the fungi remained in the roots and was never transferred to the plant shoots.

Because direct analysis of fungal mycelia is very difficult, most studies that have used isotopes to interpret the trophic status of fungi are based on measures of ^{13}C in the sporocarps. However, fungi may receive their C via hyphal connections to plants, decomposing organic matter, or both. Despite these potential limitations, $\delta^{13}C$ data have provided some general insights. For example, ECM fungi are generally more depleted in ^{13}C than saprotrophic fungi and both groups are enriched relative to the source they take up (Högberg et al. 1999b; Hobbie et al. 1999a, 2001; Kohzu et al. 1999). If there is net C-transport between a donor and recipient plant via mycorrhizae, it is critical to understand if fractionation occurs, otherwise estimates of the quantity of C-transferred made from isotope data may be in error. To date, uncertainties as to why and how $\delta^{13}C$ is altered when C is transported from the plant to the fungi remain. However, recent evidence presented by Henn & Chapela (2000) suggests there is an enrichment of ^{13}C in the fungal biomass that could occur because of selective uptake by the fungi of ^{13}C-enriched carbohydrates. They also suggest that the degree of enrichment caused by fractionation varies because of imbalances between respiratory physiology and fermentative physiology. This interpretation provides a challenge for previous interpretations, despite the fact that some investigators had used a dual-isotope ($\delta^{13}C$ and $\delta^{15}N$) approach. Clearly, more research is needed and compound-specific isotope analyses of plants, fungi, and the compounds they contain will be the method of choice.

WATER An early study that used the radioactive isotope, ^{3}H, reported that water could be transported through the mycorrhizal mycelium to plants (Duddridge et al. 1980). This investigation has stimulated three new studies (A. Plamboeck, E. Lilleskov, J. Querejeta, personal communication) using δD or $\delta^{18}O$ to look at water transport between mycorrhizae and plants. Having access to a greater soil water volume than plant roots and being able to literally act as a bridge among plant taxa in the same community means that these fungi have the potential to influence and/or mediate an array of individual- and community-level phenomena.

NITROGEN Because plants cannot directly access atmospheric N_2 and because soil N is not always available because of strong adsorption to soil particles, competition with soil microbes and processes that lead to N-losses, the majority of plants have evolved symbiotic relationships with mycorrhizal fungi and/or N-fixing bacteria (Figure 2). As stated already, these organisms supply the plant with N and in return receive C (Newman & Reddell 1987, Smith & Read 1997). Moreover, the mycorrhizae may enable host plants to use forms of N, such as labile organic N, that the host cannot assimilate directly. Abuzinadah & Read (1986a,b) and Finlay et al. (1992) demonstrated that many ECM fungi can use soluble peptides and proteins of animal and plant origin. The application of an enriched ^{15}N-tracer has been especially useful for demonstrating that ECM fungi are able to use, as N sources, amino acids and proteins that are not accessible for direct uptake by *Eucalyptus* species (Turnbull et al. 1995), and that the uptake of ^{15}N-labeled alanine and ammonium by *Pinus sylvestris* associated with a ECM fungi can be

much higher than the uptake of ^{15}N-labeled nitrate (Wallander et al. 1997). In a field study, Näsholm et al. (1998) showed for the first time that 91%, 64%, and 42% of the N added to the organic layer as the double-labeled (^{13}C, ^{15}N) amino acid glycine was taken up by dwarf shrubs, a grass, and the trees, respectively. They also showed that the plants, irrespective of their different types of mycorrhizal symbiosis, used organic N and thereby bypassed N mineralization. Michelsen et al. (1996) suggested that mycorrhizal species in the subarctic are specialized in using organic N from the litter and that this N source is depleted in ^{15}N relative to soil mineral N.

It is still unclear how, and under what conditions, fungi alter the $\delta^{15}N$ when N is taken up and transferred to the plant (Högberg 1997; Hobbie et al. 2000, 2001; Evans 2001). Data from Michelsen et al. (1998) and Emmerton et al. (2001) show that the ^{15}N abundance in plants is closely correlated with the presence and type of mycorrhizae. Sporocarps (Gebauer & Dietrich 1993, Taylor et al. 1997, Hobbie et al. 1999a) and sheaths of ECM fungi (Högberg et al. 1996) are enriched in ^{15}N compared to their host plants. Also, mycorrhizal fungi are generally more enriched in ^{15}N than saprotrophic fungi (Gebauer & Dietrich 1993, Taylor et al. 1997, Hobbie et al. 1999a, Kohzu et al. 1999).

The observed variation in $\delta^{15}N$ among plant species has led researchers to hypothesize that this could arise during the transfer of N from the fungus to the host (Högberg et al. 1999a, Hobbie et al. 1999a, Kohzu et al. 2000, Emmerton et al. 2001). Using N-sources with known $\delta^{15}N$ values, Högberg et al. (1999a) showed that plant uptake and assimilation of N discriminates against ^{15}N for both NH_4 and NO_3. The magnitude of the fractionation appeared to decrease with increased uptake of plant N and was largest when NH_4 was the N-source. Interestingly, these authors observed no apparent differences in fractionation between ECM and nonmycorrhizal plants. In field and modeling studies aimed at relating variation in the $\delta^{15}N$ of mineral N, plants, soils, and mycorrhizal fungi to N availability along a successional gradient in Glacier Bay, Alaska, the best fit model included net fractionation during mycorrhizal transfer (Hobbie et al. 1999b). The results for this study highlighted the importance of designing good experiments if we are to learn how different sources of N affect the ^{15}N value of plants associated with various mycorrhizae.

Studies using both enriched and natural abundance ^{15}N have advanced the measurement of biological N fixation (BNF) tremendously, as they avoid many of the problems associated with earlier methods based on acetylene reduction assay (Hardy et al. 1968) and plant and ecosystem N budgeting (see reviews by Boddey et al. 2000; Shearer & Kohl 1986, 1991; Unkovich & Pate 2001; Warembourg 1993). Isotopic measurements have been used to estimate the proportion of plant N derived from the atmosphere. Using labeled ^{15}N tracers, one creates an enriched $^{15}N_2$ gas atmosphere and follows the movement of the ^{15}N tracer into the plant (Warembourg 1993). Alternatively, one can add enriched ^{15}N to the soil and observe the plant as soil 15-N becomes diluted over time because of uptake of depleted-^{15}N from BNF sources. Using natural abundance ^{15}N takes advantage of the fact that soil

commonly has a $\delta^{15}N$ signature relatively distinct from the atmosphere, which has a $\delta^{15}N$ signature equal to zero. Thus, plant $\delta^{15}N$ can be used to determine whether the source of its N was predominantly atmosphere or the soil pool. Nitrogen derived from fixation is calculated by comparing the isotopic composition of an N_2-fixing plant with that of plant available soil N (usually not directly measured, but derived by the $\delta^{15}N$ of a nonfixing reference plant that relies solely on soil-derived N). Problems can arise if the N_2-fixing plant and the nonfixing reference plant differ in root distribution, temporal N uptake patterns, or preferences for soil N-forms (organic versus inorganic). Furthermore, this approach assumes that only two sources of N are available (N_2 and soil N) and that there is no movement of N from the N-fixing plant to the nonfixing reference plant (Shearer & Kohl 1991). Violation of these assumptions can cloud the interpretation of the observed variation in plant $\delta^{15}N$. Because all of these assumptions are often not met, the natural abundance ^{15}N method usually provides a qualitative, rather than completely quantitative measure of BNF. It is important to note though that each method for calculating BNF has its own advantages and disadvantages (Shearer & Kohl 1986, Warembourg 1993).

Isotopes, Plants and Ecosystem Studies

Stable isotopes have provided key insights into biogeochemical interactions between plants, soils, and the atmosphere. Through the exchange of gases and the uptake of water and nutrients by roots, plants mediate the influx of energy and the gain and loss of materials from ecosystems. The subsequent effects on the metabolism and resource status of the soil ultimately feed back to influence plant function via the dynamics of soil nutrient and water availability. The application of stable isotopes in the plant-ecosystem context is rapidly increasing as improved methods are developed to integrate plant function over large spatial scales and in response to recent changes in the global cycles of C, water, and N.

CARBON Spatially and temporally integrated values of ecosystem C-isotope discrimination (Δ) can be obtained from measurements of the $\delta^{13}C$ of whole ecosystem respiration (Figure 1). The so-called Keeling plot approach (Text Box 4) is used to obtain these data. This ecosystem Δ should convey analogous information to leaf level discrimination (see "Plant Level Studies" above). However, the comprehensive data sets needed to understand the biophysical processes that control its variation are only recently becoming available (Buchmann et al. 1998a, Pataki et al., in press). At present, ecosystem Δ is known to exhibit a high degree of spatial and temporal variability, with precipitation (Pataki et al., in press), water availability (Ometto et al., personal communication), vapor pressure deficit (Bowling et al. 2002), stand age (Fessenden & Ehleringer 2002), and species composition (Buchmann et al. 1997b) as the major drivers. These factors will affect canopy discrimination (Lloyd et al. 1996, Bowling et al. 2001) and the magnitude of leaf and root respiration, as well as respiration by rhizosphere organisms using carbon exudates from plant roots (Buchmann et al. 1998b; JPH Ometto et al.,

personal communication). As shifts in $\delta^{13}C$ of ecosystem respiration are likely to be dominated by fast-cycling carbon fixed from the atmosphere during the previous few days (Ekblad & Högberg 2001, Bowling et al. 2002), ecosystem discrimination should serve as an important tool for assessing the integrated response of the ecosystem to recent environmental changes (Pataki et al. 2002). A key issue in this approach is the distinction between whole ecosystem Δ and that of the plant and canopy, which will differ owing to the contribution of respiration from roots and soil organic matter decomposition, respectively. Over time, the $\delta^{13}C$ of the soil organic matter will approach that of leaf litter itself (Balesdent et al. 1993, Ehleringer et al. 2000a).

BOX 4 Keeling Plot Technique for Determining Source Signatures

Keeling (1958, 1961) developed a simple technique to determine the isotope ratio of respired CO_2 based on diurnal changes in the concentration and isotopic ratio of atmospheric CO_2 within a vegetation canopy. At night, the CO_2 concentration within the forest boundary layer increases owing to the input of respiratory CO_2. The CO_2 released from plant and soil respiration is depleted in ^{13}C and so causes a decline in $^{13}C/^{12}C$ ratio of atmospheric CO_2 within the forest boundary layer.

Keeling (1958, 1961) showed that by plotting the isotopic composition of the air (δ_{air}) against the inverse of its concentration ($1/[CO_2]_{air}$), a linear relationship was obtained and the intercept (b) of a linear regression provided an estimate of the isotope ratio of the ecosystem respiration (Flanagan & Ehleringer 1998, Yakir & Sternberg 2000),

$$\delta_{air} = m \cdot \frac{1}{[CO_2]_{air}} + b, \qquad \text{B4.1.}$$

where m and b are determined empirically as the slope and intercept of the regression. Conceptually, as the ecosystem respires, the CO_2 concentration approaches infinity ($1/[CO_2]_{air} \rightarrow 0$) and the isotopic composition of the air (δ_{air}) approaches that of the ecosystem itself ($\delta_{air} \rightarrow b$).

At the canopy scale, the intercept represents a spatially integrated measure of the $\delta^{13}C$ of respiration from aboveground vegetation and soil components. The spatial area integrated by the calculation depends on the height at which air samples are collected, or the footprint of the air sample mast. The intercept also represents a temporal integration because it includes contributions from different aged carbon pools in plants and soil that have different turnover times and different $\delta^{13}C$ values.

This approach has proven useful when applied to other gases (e.g., H_2O) and isotopes (e.g., ^{18}O; Flanagan et al. 1997b, Moreira et al. 1997). (Modified from Flanagan & Ehleringer 1998).

As tracers, C and O isotopes in CO_2 provide the means to trace the flow of CO_2 among plants, soil, and the atmosphere (Flanagan & Ehleringer 1991, 1998). However, this method requires contrasting isotopic signatures of the sources and sinks in question. As the largest difference in plant $\delta^{13}C$ exists between plants with the C3 ($\sim -27‰$) and C4 ($\sim -12‰$) photosynthetic pathways, the principle

application has been to distinguish the origin of respired CO_2 as being from either of these plant types (Miranda et al. 1997, Rochette & Flanagan 1997). This approach is limited to systems where both photosynthetic pathways are represented or that have experienced recent changes from C3 to C4 vegetation (or vice versa), as might occur after land use conversion (Trumbore et al. 1995) or agricultural cultivation (Robinson & Scrimgeour 1995, Schubler et al. 2000). Working in a mixed C3/C4 grassland, Still et al. (C. Still, submitted) used the Keeling plot approach (Text Box 4) and a two-source mixing model (Text Box 2) to determine the relative contribution of C3 and C4 sources to total ecosystem respiration by comparing $\delta^{13}C$ of ecosystem respiration to that of C3 ($\sim -28‰$) and C4 ($\sim -12‰$) plants. Rochette et al. (1999) used the $\delta^{13}C$ of C4 corn ($-12‰$) currently growing in a field where C3 wheat ($-26‰$) previously dominated to calculate the contribution of rhizosphere respiration (C4) to the total soil surface CO_2 flux (a mixture of respiration from both C3 and C4 sources). They found that it contributed up to 45% of total soil respiration and overall comprised 17% of crop net assimilation. Because these results were comparable to those made by root exclusion and ^{14}C labeling techniques, respectively, the natural abundance ^{13}C approach has the advantage of allowing for in situ measurements throughout the growing season. To date this approach has been limited to partitioning root from soil respiration. However, in any system where the isotopic difference between ecosystem components (roots, soils, stems, leaves, etc.) can be resolved, this approach can be applied to partition respiration sources (Tu & Dawson 2003 and unpublished manuscript). In a related approach, Hungate et al. (1997) and Andrews et al. (1999) separated root and microbial respiration from total soil surface CO_2 flux based on their different $\delta^{13}C$ values that resulted from exposing the vegetation to CO_2 depleted in ^{13}C ($\delta^{13}C$ of $-35‰$ versus $-8‰$ for CO_2 in air).

In a related approach, Still et al. (C. Still, submitted) determined the relative contribution of C3 and C4 vegetation to whole canopy photosynthesis by combining leaf-level C3 and C4 Δ measurements (see Evans et al. 1986) with estimates of canopy Δ derived from vertical gradients of $\delta^{13}CO_2$ (see Lloyd et al. 1996) and estimates of $\delta^{13}C$ in CO_2 respired during soil organic matter decomposition. By analyzing the isotopic composition of CO_2 rather than plant biomass, they could determine the relative flux-weighted physiological activity of C3 and C4 plants rather than simply their relative biomass abundance (e.g., Tieszen et al. 1997). Extending this approach further, Yakir & Wang (1996) used $\delta^{13}CO_2$ above crop canopies to partition measurements of net ecosystem CO_2 exchange between rates of photosynthesis and respiration. Bowling et al. (1999a, 1999b, 2001) provide a theoretical framework and experimental evidence to apply this approach in forests ecosystems. Combining isotope and micrometeorological measurements in this fashion will ultimately provide the continuous long-term observations necessary to understand the ecology and dynamics of both carbon production and storage in ecosystems. As noted by Bowling et al. (2001), the greatest uncertainty in this approach lies in the determination of canopy photosynthetic discrimination (Δ_{canopy}), which cannot presently be measured directly (see also Lloyd et al. 1996). As the collection of CO_2 without fractionation is technically demanding (Ehleringer &

Cook 1998, Bowling et al. 1999b, Tu et al. 2001), the development of sensors capable of fast response in situ measurements of isotope ratios or concentrations will greatly expand the application and potential of stable isotopes in the study of plant-atmosphere interactions.

It should be noted that in the above examples, O isotopes in CO_2 (Figure 1) provide a similar but alternative approach to trace the flow of CO_2 between plants, soils, and the atmosphere (Flanagan 1998, Flanagan et al. 1999). A major advantage of O isotopes is that large variations in $\delta^{18}O$ of CO_2 exchanged between these pools can occur even when the differences in the $\delta^{13}C$ signals are small (Yakir 1992, Flanagan & Varney 1995). Although substantial progress has been made in understanding the mechanistic basis for O isotope effects during plant-soil-atmosphere exchange (Farquhar et al. 1993, Farquhar & Lloyd 1993, Flanagan et al. 1994, Flanagan & Varney 1995, Tans 1998, Miller et al. 1999, Angert et al. 2001, Stern et al. 2001), the large variability and spatial heterogeneity in the $\delta^{18}O$ signal of CO_2 can at times make Keeling plot approaches or ecological interpretations difficult (Flanagan et al. 1997b, Bowling et al. 1999b).

The application of $\delta^{13}C$ as a tracer of CO_2 fluxes generally relies on the assumption that respired CO_2 has the same isotopic composition as the bulk organic C from which the CO_2 presumably originated. However, the results of several recent studies indicate that CO_2 evolved during dark respiration might be enriched relative to bulk leaf material by up to 6‰ (Duranceau et al. 1999, 2001; Ghashghaie et al. 2001). Earlier studies both support (Park & Epstein 1961, Troughton et al. 1974) and contradict (Troughton et al. 1974, Cheng 1996) these findings (see, also, O'Leary 1981). Some of this variation may be caused by differences between the C substrate for respiration and that of the bulk material (Duranceau et al. 1999, Cernusak et al. 2001). Further evidence suggests that apparent fractionation (Text Box 1) may occur when respired CO_2 reflects recent photosynthates whereas $\delta^{13}C$ of bulk tissues reflects C fixed earlier (Pate 2001). Discrimination during bark photosynthesis may also contribute to apparent differences between respired CO_2 and whole tissue samples (Cernusak et al. 2001). Whereas Lin & Ehleringer (1997) demonstrated that fractionation does not occur during dark respiration, fractionation can occur during synthesis of secondary metabolites (Park & Epstein 1961, Winkler et al. 1978, O'Leary 1981, Schmidt & Gleixner 1998). As noted by Park & Epstein (1961), any depletion (or enrichment) of ^{13}C in a compound must necessarily complement an enrichment (or depletion) of ^{13}C in some other compound such as respired CO_2. As there are isotopic differences among different plant tissues, such as leaves and roots (Gleixner et al. 1993), and among different compounds, such as starch and lipids (DeNiro & Epstein 1977, Ghashghaie et al. 2001), there may be differences in respired CO_2 during both biosynthesis and decomposition by soil microorganisms of these various tissues and metabolites. Further research is needed to develop a predictive understanding of the fractionations that occur during C metabolism in both plants and microbes and their effect on the ecological interpretation of isotopes in plants, soils, and air.

Lastly, research aimed at elucidating patterns of ecosystem (vegetation) and faunal change over hundreds to millions of years has also used stable C and O

isotope information preserved in fossilized materials (Cerling et al. 1993, 1998; Tu et al. 1999; Eshetu & Högberg 2000b; MacFadden 2000). The analysis of $\delta^{13}C$ in pedogenic carbonates (Quade et al. 1992) as well as the C and O isotope composition preserved in tooth enamel (see MacFadden 2000), fossil seeds, or bone collagen (DeNiro & Epstein 1979) has helped show when transitions occurred between vegetation dominated by C3 plants versus C4 plants (which were largely grasses), and how this timing may have had an impact on diet choice in animals. In addition, these data have been used to make arguments about the evolution of new photosynthetic pathways (e.g., C4; Ehleringer et al. 1991b), the rise and fall of atmospheric CO_2 (Cerling et al. 1998, Ehleringer et al. 1998, Arens et al. 2000) and other environmental changes (e.g., the origin and patterns of precipitation). In a related approach, Ehleringer & Cerling (1995) inferred c_i/c_a ratios from the $\delta^{13}C$ of current and fossil leaf material from glacial-interglacial periods to the present. Based on this isotopic evidence, they found strong regulation of c_i/c_a ratios over the range of conditions expected on evolutionary timescales (several million years) and predicted less control by plants exposed to current atmospheric CO_2 concentrations that are outside the range under which they evolved.

WATER Plants have an important influence on the magnitude and speed of water moving in ecosystems (Jackson et al. 2000, Yakir & Sternberg 2000, Feddes et al. 2001). In this context, δD and $\delta^{18}O$ analyses in soil, plant and water vapor have been used to explore the role of plants in catchment-scale processes (e.g., fluxes and runoff; Brunel et al. 1991; Busch et al. 1992; Thorburn et al. 1993a,b; Dawson & Ehleringer 1998; Harwood et al. 1998; Walker et al. 2001) and in the hydrological cycle itself (Gat 1996, 1998; Dawson et al. 1998; Figure 1). Much of this work involves understanding baseline hydrology and the isotope variation in water sources and precipitation within a region (Mazor 1991, Gat 1996, Ingraham 1998, Kendall & McDonnell 1998), how water vapor over the vegetation behaves (Bariac et al. 1989, Brunel et al. 1991, Harwood et al. 1998), and how isotope values in water change along the soil-plant-atmospheric continuum (Dawson et al. 1998). For example, Bariac and his coworkers (1983, 1987, 1989) established the utility of isotope analyses of leaf water to assess evapotranspirational flux from an alfalfa field (also see Wang & Yakir 1995). This work has been extended to forested ecosystems where a handful of investigations use direct measurements of water transpired from canopies (Harwood et al. 1998) plus other isotope data to link water-source uptake with ecosystem-level water loss; these data are used to make inferences about stand-level hydrologic processes (Walker & Brunel 1990, Brunel et al. 1991, Thorburn et al. 1993b) and to determine the role of the trees in these processes (Dawson 1996, Dawson & Ehleringer 1998).

Most recently, the information contained in the isotopic values of leaf water, the water vapor leaving leaf surfaces, atmospheric water vapor, and the sources of water taken up by plants has been used to estimate the proportion of water vapor flux leaving an ecosystem that comes from plant canopies versus from evaporation. Using the Keeling plot approach (Text Box 4), applied to the $\delta^{18}O$ of water vapor leaving an Amazonian forest (instead of CO_2), Moreira and coworkers

(1997) attempted to partition evapotranspiration between soil evaporation and plant transpiration (Figure 1). Because this approach has limitations (Mathieu & Bariac 1996a,b), the authors concluded that canopy transpiration was the dominant path for water vapor flux from this forested ecosystem (also, see Yakir & Sternberg 2000 for additional examples). A related approach was employed by Dawson (1996) to determine whether soil or ground water was being transpired by different age classes of sugar maple trees in a northeastern North American temperate forest ecosystem. Here, it was shown that small trees contribute water to the ecosystem flux from shallow layers in the soil, whereas larger trees transpire mostly deeper ground water (Dawson 1996). The findings from both of these investigations indicate that water vapor loss from forested ecosystems is dominated by transpiration and may vary with stand age and thus successional status, with season, and perhaps with tree species.

Related to the examples discussed above are ongoing efforts that use H or O isotope variation in leaf water either to determine the atmospheric conditions during plant transpiration or to directly estimate transpiration rate itself (Figure 1). As already critiqued in some detail elsewhere (Dawson et al. 1998, Yakir & Sternberg 2000) these types of investigation are still being refined and need further development before they can be used reliably. However, the incorporation of new empirical methods, such as relaxed eddy accumulation (REA; Pattey et al. 1993) and laser- or spectroscopic-based measurements of water vapor (and other gases) also need to be explored more fully. Such techniques allow the $\delta^{18}O$ of water vapor flux leaving an ecosystem to be directly measured (D. Hollinger, T. Dawson, K.P. Tu, unpublished manuscript). In addition, the development of predictive models that use these data is needed (W. Riley, C. Still, personal communication). Observations show that many assumptions in our current models may not be valid or may be valid only under certain circumstances (Wang & Yakir 1995, Yakir 1998, Dawson et al. 1998). If refined, this area of research holds a great deal of promise in allowing us to link plant ecophysiological behavior to local, regional, and perhaps even global hydrological processes.

NITROGEN Within the N-cycle, soil microbial processes fractionate ^{15}N leading to a large degree of variation in the $\delta^{15}N$ of N within soil pools (Figure 2). Therefore, understanding the processes that lead to changes in the soil $\delta^{15}N$ is imperative for determining the N sources used by plants because they obtain much of their N from the soil (Handley & Raven 1992). The major soil N transformations mediated by microbes, such as mineralization (conversion of organic to inorganic forms of N; Nadelhoffer & Fry 1994), nitrification (conversion of NH_4 to NO_3; Nadelhoffer & Fry 1994, Högberg 1997, Handley & Raven 1992), and denitrification (conversion of NO_3 to atmospheric NO, N_2O, or N_2 during microbial respiration; Piccolo et al. 1996) lead to N products that are depleted in ^{15}N relative to the substrates from which they were produced (Peterson & Fry 1987, Yoneyama 1996). For example, the residual organic matter pool may become increasingly ^{15}N enriched if the NO_3 produced during nitrification exceeds soil and plant demand and leaches out of a

forest (Piccolo et al. 1994, Nadelhoffer & Fry 1988). Further ^{15}N enrichment can occur during microbial decomposition of organic matter. A study in Wisconsin forests showed that the $\delta^{15}N$ of deeper soil reflected the presence of more enriched ^{15}N products from decomposition, whereas surface soils reflected leaf litter inputs that were depleted in ^{15}N (Nadelhoffer & Fry 1988). The pattern of ^{15}N enrichment with depth has been observed elsewhere (Rennie et al. 1976, Shearer et al. 1978, Shearer & Kohl 1986) and is important because it means that roots taking up the same form of N (e.g., NH_4) could have a different $\delta^{15}N$.

Nitrogen-15 pool dilution (Text Box 2) techniques can help determine what forms of N are available and what forms plants and soil microbes may compete for as shown in Alaska birch forests (Van Cleve & White 1980). The development of the pool dilution technique allows ecologists to examine gross rates of mineralization and nitrification in natural settings and to better understand the forms of inorganic N present in an ecosystem, rather than the net transformations over time. Davidson and coworkers (1992) employed this method to demonstrate that young and old forests of California have detectable rates of gross nitrification, a process previously thought not to occur in these mature forests. Schimel et al. (1989) used this method to compare plant and microbial competition for N in a California grassland.

There are many applications for adding enriched ^{15}N tracers to ecosystems and following the fate of N (Text Box 2). For example, Knowles (1975) showed that in many studies less than 30% of applied fertilizer N ended up in crop trees. Other research has used ^{15}N as a way to determine plant, microbial, and soil sinks within evergreen and deciduous forests of Europe (Koopmans et al. 1996, Buchmann et al. 1996b, Schleppi et al. 1999) and North America (Nadelhoffer et al. 1995, 1999; Groffman et al. 1993; Zak et al. 1990; Zogg et al. 2000; Templer 2001). Nitrogen-15 tracers have also been used in greenhouse experiments to determine if foliar uptake and assimilation of wet-deposited N takes place and to quantify its contribution to the N requirements of each plant species (Bowden et al. 1989, Garten & Hanson 1990, Wilson & Tiley 1998).

Measurements of natural abundance ^{15}N have been used increasingly as an indicator of change in the N cycling of forests. Humans have doubled the amount of N naturally fixed in the environment (Galloway et al. 1995, Vitousek et al. 1997). When the amount of N deposited exceeds biological demand, an ecosystem can reach N-saturation and increasing amounts of N may leave either through leaching or gas loss (Aber et al. 1989, Agren & Bosatta 1988, Peterjohn et al. 1996, Stoddard 1994). Elevated levels of N availability can lead to increased rates of N cycling. This increase in turn results in ^{15}N enrichment of each soil pool as the lighter ^{14}N isotopes are preferentially lost through leaching and denitrification (Figure 2). Plants accessing this soil N pool can then become relatively ^{15}N-enriched over time. Because plant biomass turns over at a faster rate than the total soil pool, plants themselves can also be used as indicators of anthropogenically caused environmental change (Johannisson & Högberg 1994). In this way, the measurement of foliar $\delta^{15}N$ has the potential to be used to indicate that

N cycling rates have increased. For example, several studies have found a strong correlation between enriched levels of ^{15}N in foliage and increased soil N (Emmett et al. 1998, Meints et al. 1975, Högberg 1990), increased rates of N-cycling (Garten 1993, Garten & Van Miegroet 1994), and increased loss of N (Högberg & Johannisson 1993). Other studies have used natural abundance ^{15}N and ^{18}O within NO_3^- simultaneously to examine whether N deposited onto a forest is cycled within plants and microbes or directly passes through the forest into nearby streams without biological processing, an indicator that the system may have reached N saturation (Durka et al. 1994). Other studies have linked land use change to a decline in N fixing cryptobiotic crusts in aridlands, which in turn has led to changes in N availability and subsequent enrichment in plant and soil $\delta^{15}N$ (Evans & Belnap 1999; Evans & Ehleringer 1993, 1994). Additionally, some studies have measured N pools and natural abundance ^{15}N simultaneously to indicate the relative degree of openness of the N-cycle, which relates how much N is lost from an ecosystem relative to its internal pool size N (Austin & Vitousek 1998, Chang & Handley 2000, Eshetu & Högberg 2000a, Brenner et al. 2001).

From a longer-term perspective, the analysis of ^{15}N in tree-ring cellulose and in peat deposits has been used as an indicator of ongoing environmental change. The work of Poulson et al. (1995) shows that ^{15}N in the wood of two eastern hemlock trees decreased from the early 1960s to 1992. The authors attribute this decrease to either a decrease in ^{15}N of available N over time or to isotope fractionation during translocation within the tree. Untangling which mechanism is responsible for these changes is the next step. In this same context, Bergstrom et al. (2002) examined the ^{15}N in fossil peat; this work allowed the authors to not only look at the long-term (8500 years) trend in N dynamics but also allowed them to show that some of this N-input is from animal sources.

FUTURE DIRECTIONS

This review has attempted to highlight how our knowledge of plant-environment interactions has been advanced by the application of stable isotope methods. We believe that the literature clearly shows that plant ecology has made very significant progress as a result of collecting and interpreting isotope data. Several important areas are in need of further research.

We believe that isotope methods, when merged with other information from modeling, molecular, and/or genetic data, have the potential to deepen our understanding of population- and community-level processes. For example, we need to determine if and how mycorrhizae may contribute to the plant water uptake in areas where water limits growth and survival. Additionally, further study is needed to determine what happens to C and N at the plant-mycorrhizae-interface. This study is important because it will enhance our understanding of what contributes to the overall variation in soil and plant $\delta^{15}N$ values. Finally, if we want to refine our estimates of the quantities of C transferred between plants via mycorrhizae, ^{13}C methods hold great promise.

The use of stable isotopes as integrators of plant C and water relations at spatial scales of individual leaves, whole plants, and entire ecosystems and temporal scales ranging from instantaneous gas exchange to paleontological tree-ring studies would be greatly enhanced by developing a quantitative linkage between C and O isotopes in leaf and stem tissues and physiological characteristics such as photosynthetic capacity and stomatal conductance. In this way, an improved measure of plant physiological status could be obtained from stable isotope signals recorded in tree rings under past environmental conditions and in plant tissues collected from remote locations or where gas exchange is not practical. Current single-isotope or single resource (e.g., isotopes in water) approaches rely on knowledge of ancillary climate or environmental data. In addition, further research is needed to develop a predictive understanding of C isotope fractionations during plant and microbial metabolism. The magnitude of such fractionations and their influence on the C isotope composition of respired CO_2 is not known, but they could have important implications for partitioning canopy photosynthesis, root respiration, and soil organic matter decomposition (see Tu & Dawson 2003). Then, for both C and N it is clear that further development of compound-specific $\delta^{13}C$ and $\delta^{15}N$ isotope analyses and dual-isotope approaches (e.g., Robinson et al. 2000) has the potential to enhance our understanding of plant ecological phenomena at all spatial and temporal scales.

Future advances in the use of ^{15}N isotopes in plant ecology will result from combining modeling and empirical studies that address the mechanisms underlying the variation in $\delta^{15}N$ of plant and ecosystem pools. A complete mechanistic model of ^{15}N behavior in plants is still lacking. Fractionations that may occur during direct uptake of inorganic N forms, during N uptake that is mediated by mycorrhizae, during N exudation, as well as within-plant transformations all need deeper understanding. Our current interpretation of plant-soil interactions is also constrained by the technical difficulties of measuring the $\delta^{15}N$ of soil N pools that is available for plant uptake. At the ecosystem scale, modeling may be the best tool for using $\delta^{15}N$ as an integrator of N cycling processes. For example, Hobbie et al. (1999b) developed the NIFTE model to predict the relationship between N cycling and natural abundance ^{15}N within ecosystem pools. Another model has been developed to examine the movement of enriched ^{15}N tracers throughout ecosystems (called TRACE; Currie et al. 1999, Currie & Nadelhoffer 1999). Future work needs to expand on these models and incorporate results from mechanistic studies.

ACKNOWLEDGMENTS

Foremost, we thank Jim Ehleringer; Jim has not only been a leading advocate for using stable isotopes in plant ecology but he has provided all of us, and many others, with the opportunity and inspiration to involve ourselves in using isotope methods in our own research. We thank Rick Harrison as well for initially encouraging this review and to our many colleagues who provided us with important feedback and

literature related to it. Finally, we thank Larry Flanagan, Thorsten Grams, Dave Evans, Murray Unkovich, Dave Williams, and John Roden for their comments and suggestions that improved the manuscript.

LITERATURE CITED

Aber JD, Nadelhoffer KJ, Steudler P, Melillo JM. 1989. Nitrogen saturation in northern forest ecosystems. *BioScience* 39:378–86

Abuzinadah RA, Finlay RD, Read DJ. 1986a. The role of proteins in the nitrogen nutrition of ectomycorrhizal plants. III. Protein utilisation by *Betula*, *Picea*, and *Pinus* in mycorrhizal association with *Hebeloma crustuliniforme*. *New Phytol.* 103:507–14

Abuzinadah RA, Finlay RD, Read DJ. 1986b. The role of proteins in the nitrogen nutrition of ectomycorrhizal plants. II. Utilisation of protein by mycorrhizal plants of Pinus contorta. *New Phytol.* 103:495–506

Ågren GI, Bosatta E. 1988. Nitrogen saturation of terrestrial ecosystems. *Environ. Pollut.* 54:185–98

Alstad KP, Welker JM, Williams SA, Trlica MJ. 1999. Carbon and water relations of *Salix monticola* in response to winter browsing and changes in surface water hydrology: an isotopic study using $\delta^{13}C$ and $\delta^{18}O$. *Oecologia* 120:375–85

Amundson R, Stern L, Baisden T, Wang Y. 1998. The isotopic composition of soil and soil-respired CO_2. *Geoderma* 82:83–114

Andrews JA, Harrison KG, Matamala R, Schlesinger WH. 1999. Separation of rot respiration from total soil respiration using carbon-13 labeling during free-air carbon dioxide enrichment (FACE). *Soil Sci. Soc. Am. J.* 63:1429–35

Angert A, Luz B, Yakir D. 2001. Fractionation of oxygen isotopes by respiration and diffusion in soils and its implications for the isotopic composition of atmospheric CO_2. *Glob. Biogeochem. Cycles* 15:871–80

Archer S. 1995. Tree-grass dynamics in a Prosopis-thornscrub savanna parkland: reconstructing the past and predicting the future. *Ecoscience* 2:83–99

Arens NC, Jahren AH, Amundson R. 2000. Can C3 plants faithfully record the carbon isotopic composition of atmospheric carbon dioxide? *Paleobiology* 26:137–64

Austin AT, Vitousek PM. 1998. Nutrient dynamics on a precipitation gradient in Hawai'i. *Oecologia* 113:519–29

Baertschi P. 1953. Die Fraktionierung der naturlichen kohlenstoffisotopen im kohlendioxydstoffenwechsel gruner pflanzen. *Helv. Chim. Acta* 36(4):773–81

Balesdent J, Girardin C, Mariotti A. 1993. Site-related ^{13}C of tree leaves and soil organic matter in a temperate forest. *Ecology* 74:1713–21

Ball JT, Woodrow IE, Berry JA. 1987. A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. In *Progress in Photosynthesis Research*, ed. I Biggins, pp. 221–24. Netherlands: Martinus Nijoff

Bannister P, Strong GL. 2001. Carbon and nitrogen isotope ratios, nitrogen content and heterotrophy in New Zealand mistletoes. *Oecologia* 126:10–20

Barbour MM, Andrews TJ, Farquhar GD. 2001. Correlations between oxygen isotope ratios of wood constituents of Quercus and Pinus samples from around the world. *Aust. J. Plant Physiol.* 28:335–48

Barbour MM, Fischer RA, Sayre KD, Farquhar GD. 2000. Oxygen isotope ratio of leaf and grain material correlates with stomatal conductance and grain yield in irrigated wheat. *Aust. J. Plant Physiol.* 27:625–37

Bariac T, Ferhi A, Jusserand C, Létolle R. 1983. Sol-plante-atmosphère: contribution à l'étude dé la composition isotopique de l'eau des differentes composantes de ce systeme. *Proc. Symp. Isotope Radiation Tech. Soil Phys. Irrig. Stud. IAEA, Vienna*, pp. 561–76

Bariac T, Klamecki S, Jusserand C, Létolle R. 1987. Evolution de la composition isotopique de l'eau (^{18}O) dans le continuum sol-plante-atmosphère (example d'une parcelle cultivée en blé, Versailles, France, Juin 1984). *Catena* 14:55–72

Bariac T, Rambal S, Jusserand C, Berger A. 1989. Evaluating water fluxes of field-grown alfalfa from diurnal observations of natural isotope concentrations, energy budget and ecophysiological parameters. *Agric. For. Meteorol.* 48:263–84

Ben-David M, Schell DM. 2001. Mixing models in analyses of diet using multiple stable isotopes: a response. *Oecologia* 127:180–84

Bergersen FJ, Peoples MB, Turner GL. 1988. Isotopic discriminations during the accumulation of nitrogen by soybeans. *Aust. J. Plant Physiol.* 15:407–20

Bergstrom DM, Stewart GR, Selkirk PM, Schmidt S. 2002. ^{15}N natural abundance of fossil peat reflects the influence of animal-derived nitrogen on vegetation. *Oecologia* 130:309–14

Bert D, Leavitt S, Dupouey J-L. 1997. Variations of wood $\delta^{13}C$ and water-use efficiency of *Abies alba* during the last century. *Ecology* 78:1588–96

Bettarini I, Calderoni G, Miglietta F, Raschi A, Ehleringer J. 1995. Isotopic carbon discrimination and leaf nitrogen content of *Erica arborea* L. along a CO_2 concentration gradient in a CO_2 spring in Italy. *Tree Physiol.* 15:327–32

Boddey RM, Peoples MB, Palmer B, Dart PJ. 2000. Use of the ^{15}N natural abundance technique to quantify biological nitrogen fixation by woody perennials. *Nutr. Cycl. Agroecosys.* 57:235–70

Borella S, Leuenberger M, Saurer M. 1999. Analysis of $\delta^{18}O$ in tree rings: wood-cellulose comparison and method dependent sensitivity. *J. Geophys. Res.* 104:19267–73

Bowden RD, Geballe GT, Bowden WB. 1989. Foliar uptake of ^{15}N from simulated cloud water by red spruce (*Picea rubens*) seedlings. *Can. J. For. Res.* 19:382–86

Bowling DR, Baldocchi DD, Monson RK. 1999a. Dynamics of isotopic exchange of carbon dioxide in a Tennessee deciduous forest. *Glob. Biogeochem. Cycles* 13:903–22

Bowling DR, Delany AC, Turnipseed AA, Baldocchi DD, Monson RK. 1999b. Modification of the relaxed eddy accumulation technique to maximize measured scalar mixing ratio differences in updrafts and downdrafts. *J. Geophys. Res.* 104:9121–33

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* 131:113–24

Bowling DR, Tans PP, Monson RK. 2001. Partitioning net ecosystem carbon exchange with isotopic fluxes of CO_2. *Glob. Change Biol.* 7(2):127–45

Bowman WD, Hubick KT, von Caemmerer S. 1989. Short-term changes in leaf carbon isotope discrimination in salt- and water-stressed C4 grasses. *Plant Physiol.* 90(1): 162–66

Brenner DL, Amundson R, Baisden WT, Kendall C, Harden J. 2001. Soil N and ^{15}N variation with time in a California annual grassland ecosystem. *Geochim. Cosmochim. Acta* 65:4171–86

Briske DD, Boutton TW, Wang Z. 1996. Contribution of flexible allocation priorities to herbivory tolerance in C4 perennial grasses: an evaluation with ^{13}C labeling. *Oecologia* 105:151–59

Broadmeadow MSJ, Griffiths H, Maxwell C, Borland AM. 1992. The carbon isotope ratio of plant organic material reflects temporal and spatial variations in CO_2 within tropical forest formations in Trinidad. *Oecologia* 89:435–41

Brooks JR, Flanagan LB, Buchmann N,

Ehleringer JR. 1997. Carbon isotope composition of boreal plants: functional grouping of life forms. *Oecologia* 110:301–11

Brugnoli E, Hubick KT, von Caemmerer S. 1988. Correlation between the carbon isotope discrimination in leaf starch and sugars of C3 plants and the ratio of intercellular and atmospheric partial pressures of carbon dioxide. *Plant Physiol.* 88:1418–24

Brunel J-P, Walker GR, Kennett-Smith AK. 1995. Field validation of isotopic procedures for determining sources of water used by plants in a semi-arid environment. *J. Hydrol.* 167:351–68

Brunel J-P, Walker GR, Walker CD, Dighton JC, Kennett-Smith A. 1991. Using stable isotopes of water to trace plant water uptake. In *Stable Isotopes in Plant Nutrition, Soil Fertility and Environmental Studies*, pp. 543–51. *Proc. Int. Symp., Oct. 1990.* Vienna: IAEA/FAO

Buchmann N, Brooks JR, Flanagan LB, Ehleringer JR. 1998a. Carbon isotope discrimination of terrestrial ecosystems. See Griffiths 1998, pp. 203–21

Buchmann N, Brooks JR, Rapp KD, Ehleringer JR. 1996a. Carbon isotope composition of C_4 grasses is influenced by light and water supply. *Plant Cell Environ.* 19:392–402

Buchmann N, Gebauer G, Schulze E-D. 1996b. Partitioning of ^{15}N-labeled ammonium and nitrate among soil, litter, below- and aboveground biomass of trees and understory in a 15-year-old *Picea abies* plantation. *Biogeochemistry* 33:1–23

Buchmann N, Guehl J-M, Barigah TS, Ehleringer JR. 1997a. Interseasonal comparison of CO_2 concentrations, isotopic composition, and carbon dynamics in an Amazonian rainforest (French Guiana). *Oecologia* 110:120–31

Buchmann N, Hinckely TM, Ehleringer JR. 1998b. Carbon isotope dynamics in *Abies amabils* stands in the Cascades. *Can. J. For. Res.* 28:808–19

Buchmann N, Kao W-Y, Ehleringer JR. 1997b. Influence of stand structure on carbon-13 of vegetation, soils, and canopy air within deciduous and evergreen forests in Utah, United States. *Oecologia* 110:109–19

Burgess SO, Pate JS, Adams MA, Dawson T. 2000. Seasonal water acquisition and redistribution in the Australian woody phreatophyte. *Banksia prionotes. Ann. Bot.* 85:215–24

Busch DE, Ingraham NL, Smith SD. 1992. Water uptake in woody riparian phreatophytes of the Southwestern United States a stable isotope study. *Ecol. Appl.* 2:450–59

Caldeira MC, Ryel RJ, Lawton JH, Pereira JS. 2001. Mechanisms of positive biodiversity-production relationships: insights provided by δ^{13}C analysis in experimental Mediterranean grassland plots. *Ecol. Lett.* 4:439–43

Caldwell MM, Dawson TE, Richards JH. 1998. Hydraulic lift: consequences of water efflux from the roots of plants. *Oecologia* 113:151–61

Cerling TE, Ehleringer JR, Harris JM. 1998. Carbon dioxide starvation, the development of the C4 ecosystem, and mammalian evolution. *Philos. Trans. R. Soc. London Ser. B* 353:159–71

Cerling TE, Wang Y, Quade J. 1993. Expansion of C4 ecosystems as an indicator of global ecological change in the late Miocene. *Nature* 361:344–45

Cernusak LA, Marshall JD. 2001. Responses of foliar δ^{13}C gas exchange and leaf morphology to reduced hydraulic conductivity in *Pinus monticola* branches. *Tree Physiol.* 21:1215–22

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

Chang SX, Handley LL. 2000. Site history affects soil and plant ^{15}N natural abundances (δ^{15}N) in forests of northern Vancouver Island, British Columbia. *Funct. Ecol.* 14:273–80

Cheng W. 1996. Measurement of rhizosphere respiration and organic matter decomposition using natural ^{13}C. *Plant Soil.* 183:263–68

Comstock JP, Ehleringer JR. 1992. Correlating

genetic variation in carbon isotopic composition with complex climatic gradients. *Proc. Natl. Acad. Sci. USA* 89:7747–51

Condon AG, Richards RA, Farquhar GD. 1987. Carbon isotope discrimination is positively correlated with grain yield and dry matter production in field-grown wheat. *Crop Sci.* 27:996–1001

Condon AG, Richards RA, Farquhar GD. 1992. The effect of variation in soil water availability, vapour pressure deficit and nitrogen nutrition on carbon isotope discrimination in wheat. *Aust. J. Agric. Res.* 43:935–48

Craig H. 1953. The geochemistry of the stable carbon isotopes. *Geochim. Cosmochim. Acta* 3:53–92

Cramer VA, Thorburn PJ, Fraser GW. 1999. Transpiration and groundwater uptake from farm forest plots of *Casuarina glauca* and *Eucalyptus camaldulensis* in saline areas of southeast Queensland, Australia. *Agric. Water Manag.* 39:187–204

Criss RE. 1999. *Principles of Stable Isotope Distribution*. New York: Oxford Univ. Press. 254 pp.

Currie WS, Nadelhoffer KJ. 1999. Dynamic redistribution of isotopically labeled cohorts of nitrogen inputs in two temperate forests. *Ecosystems* 2:4–18

Currie WS, Nadelhoffer KJ, Aber JD. 1999. Soil detrital processes controlling the movement of ^{15}N tracers to forest vegetation. *Ecol. Appl.* 9:87–102

Damesin C, Rambal S, Joffre R. 1998. Seasonal drought and annual changes in leaf $\delta^{13}C$ in two co-occurring Mediterranean oaks: relations to leaf growth and drought progression. *Funct. Ecol.* 12:778–85

Davidson EA, Hart SC, Firestone MK. 1992. Internal cycling of nitrate in soils of a mature coniferous forest. *Ecology* 73:1148–56

Dawson TE. 1993a. Hydraulic lift and water use by plants: implications for water balance, performance and plant-plant interactions. *Oecologia* 95:565–74

Dawson TE. 1993b. Water sources of plants as determined from xylem-water isotopic composition: perspectives on plant competition, distribution, and water relations. See Ehleringer et al. 1993, pp. 465–96

Dawson TE. 1996. Determining water use by trees and forests from isotopic, energy balance and transpiration analyses: the roles of tree size and hydraulic lift. *Tree Physiol.* 16:263–72

Dawson TE. 1998. Fog in the California redwood forest: ecosystem inputs and use by plants. *Oecologia* 117:476–85

Dawson TE, Brooks PD. 2001. Fundamentals of stable isotope chemistry and measurement. See Unkovich et al. 2001, pp. 1–18

Dawson TE, Ehleringer JR. 1991. Streamside trees that do not use stream water. *Nature* 350:335–37

Dawson TE, Ehleringer JR. 1993. Gender-specific physiology, carbon isotope discrimination, and habitat distribution in boxelder. *Acer negundo. Ecology* 74:798–815

Dawson TE, Ehleringer JR. 1998. Plants, isotopes, and water use: a catchment-level perspective. See Kendall & McDonnell 1998, pp. 165–202

Dawson TE, Pate JS. 1996. Seasonal water uptake and movement in root systems of Australian phraeatophytic plants of dimorphic root morphology: a stable isotope investigation. *Oecologia* 107:13–20

Dawson TE, Pausch RC, Parker HM. 1998. The role of H and O stable isotopes in understanding water movement along the soil-plant-atmospheric continuum. See Griffiths 1998, pp. 169–83

De Kroon H, Fransen B, Van Rheenen JWA, Van Dijk A, Kreulen R. 1996. High levels of inter-ramet water translocation in two rhizomatous Carex species, as quantified by deuterium labelling. *Oecologia* 106:73–84

DeLucia EH, Schlesinger WH, Billings WD. 1988. Water relations and the maintenance of Sierran conifers on hydrothermally altered rock. *Ecology* 69:303–11

DeNiro MJ, Epstein S. 1977. Mechanism of carbon isotope fractionation associated with lipid synthesis. *Science* 197:261–63

DeNiro MJ, Epstein S. 1979. Relationship between the oxygen isotope ratios of terrestrial

plant cellulose, carbon dioxide and water. *Science* 204:51–53

Donovan LA, Ehleringer JR. 1994. Carbon isotope discrimination, water-use efficiency, growth, and mortality in a natural shrub population. *Oecologia* 100:347–54

Duddridge JA, Malibari A, Read DJ. 1980. Structure and function of mycorrhizal rhizomorphs with special reference to their role in water transport. *Nature* 287:834–36

Duquesnay A, Breda N, Stievenard M, Dupouey JL. 1998. Changes of tree-ring $\delta^{13}C$ and water-use efficiency of beech (*Fagus sylvatica* L.) in north-eastern France during the past century. *Plant Cell Environ.* 21:565–72

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 Environ.* 22:515–23

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

Durka WE, Schultze DS, Gebauer G, Voerkelius S. 1994. Effects of forest decline on uptake and leaching of deposited nitrate determined from ^{15}N and ^{18}O measurements. *Nature* 372:765–69

Dyckmans J, Flessa H. 2001. Influence of tree internal N status on uptake and translocation of C and N in beech: a dual ^{13}C and ^{15}N labeling approach. *Tree Physiol.* 21:395–401

Edwards TWD, Aravena RO, Fritz P, Morgan AV. 1985. Interpreting paleoclimate from ^{18}O and ^{2}H in wood cellulose: paleoclimatic implications for southern Ontario. *Can. J. Earth Sci.* 22:1720–26

Ehleringer JR. 1989. Carbon isotope ratios and physiological processes in aridland plants. See Rundel et al.1989, pp. 41–54

Ehleringer JR. 1990. Correlations between carbon isotope discrimination and leaf conductance to water vapor in common beans. *Plant Physiol.* 93:1422–25

Ehleringer JR. 1993a. Carbon and water relations in desert plants: an isotopic perspective. See Ehleringer et al. 1993, pp. 155–72

Ehleringer JR. 1993b. Variation in leaf carbon isotope discrimination in *Encelia farinosa*: implications for growth, competition, and drought survival. *Oecologia* 95:340–46

Ehleringer JR, Buchmann N, Flanagan LB. 2000a. Carbon isotope ratios in belowground carbon cycle processes. *Ecol. Appl.* 10:412–22

Ehleringer JR, Cerling TE. 1995. Atmospheric CO_2 and the ratio of intercellular to ambient CO_2 levels in plants. *Tree Physiol.* 15:105–11

Ehleringer JR, Cook CS. 1998. Carbon and oxygen isotope ratios of ecosystem respiration along an Oregon conifer transect: preliminary observations based on small-flask sampling. *Tree Physiol.* 18:513–19

Ehleringer JR, Cooper TA. 1988. Correlations between carbon isotope ratio and microhabitat in desert plants. *Oecologia* 76:562–66

Ehleringer JR, Dawson TE. 1992. Water uptake by plants: perspectives from stable isotope composition. *Plant Cell Environ.* 15:1073–82

Ehleringer JR, Evans RD, Williams D. 1998. Assessing sensitivity to change in desert ecosystem—a stable isotope approach. See Griffiths 1998, pp. 223–37

Ehleringer JR, Field CB, Lin Z-F, Kuo C-Y. 1986. Leaf carbon isotope and mineral composition in subtropical plants along an irradiance cline. *Oecologia* 70:520–26

Ehleringer JR, Hall AE, Farquhar GD, eds. 1993. *Stable Isotopes and Plant Carbon-Water Relations*. San Diego, CA: Academic

Ehleringer JR, Phillips SL, Comstock JP. 1992. Seasonal variation in the carbon isotopic composition of desert plants. *Funct. Ecol.* 6:396–404

Ehleringer JR, Phillips SL, Schuster WSF, Sandquist DR. 1991a. Differential utilization of summer rains by desert plants. *Oecologia* 88:430–34

Ehleringer JR, Roden J, Dawson TE. 2000b. Assessing ecosystem-level water relations through stable isotope ratio analyses. See Sala et al. 2000, pp. 181–98

Ehleringer JR, Sage RF, Flanagan LB, Pearcy RW. 1991b. Climate change and the evolution of C4 photosynthesis. *Trends Ecol. Evol.* 6:95–99

Ehleringer JR, Schulze ED, Ziegler H, Lange OL, Farquhar GD, et al. 1985. Xylem-tapping mistletoes: water or nutrient parasites? *Science* 227:1479–81

Ehleringer JR, White JW, Johnson DA, Brick M. 1990. Carbon isotope discrimination, photosynthetic gas exchange, and water-use efficiency in common bean and range grasses. *Acta Oecol.* 11:611–25

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* 127:305–8

Emerman SH, Dawson TE. 1996. The role of macropores in the cultivation of bell pepper in salinized soil. *Plant Soil* 181:241–49

Emmerton KS, Callaghan TV, Jones HE, Leake JR, Michelsen A, et al. 2001. Assimilation and isotopic fractionation of nitrogen by mycorrhizal and nonmycorrhizal subarctic plants. *New Phytol.* 151:513–24

Emmett BA, Kjonaas OJ, Gundersen P, Koopmans C, Tietema A, et al. 1998. Natural abundance of ^{15}N in forests across a nitrogen deposition gradient. *For. Ecol. Manag.* 101:9–18

Epstein S, Krishnamurthy RV. 1990. Environmental information in the isotopic record in trees. *Philos. Trans. R. Soc. London Ser. B* 330:427–39

Erskine PD, Bergstrom DM, Schmidt S, Stewart GR, Tweedie CE, et al. 1998. Subantarctic Macquarie Island: a model ecosystem for studying animal-derived nitrogen sources using ^{15}N natural abundance. *Oecologia* 117:187–93

Eshetu Z, Högberg P. 2000a. Effects of land use on ^{15}N natural abundance of soils in Ethiopian highlands. *Plant Soil* 222:109–17

Eshetu Z, Högberg P. 2000b. Reconstruction of forest site history in Ethiopian highlands based on ^{13}C natural abundance of soils. *Ambio* 29:83–89

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. *Aust. J. Plant Physiol.* 13:281–92

Evans RD. 2001. Physiological mechanisms influencing plant nitrogen isotope composition. *Trends Plant Sci.* 6:121–26

Evans RD, Belnap J. 1999. Long-term consequences of disturbance on nitrogen dynamics in an arid grassland ecosystem. *Ecology* 80:150–60

Evans RD, Bloom AJ, Sukrapanna SS, Ehleringer JR. 1996. Nitrogen isotope composition of tomato (*Lycopersicon esculentum* Mill, cv. *T-5*) *grown under ammonium or nitrate nutrition. Plant Cell Environ.* 19:1317–23

Evans RD, Ehleringer JR. 1993. A break in the nitrogen cycle of aridlands: evidence from delta ^{15}N of soils. *Oecologia* 94:314–17

Evans RD, Ehleringer JR. 1994. Water and nitrogen dynamics in an arid woodland. *Oecologia* 99:233–42

Farquhar GD. 1983. On the nature of carbon isotope discrimination in C4 species. *Aust. J. Plant Physiol.* 10:205–26

Farquhar GD, Barbour MM, Henry BK. 1998. Interpretation of oxygen isotope composition of leaf material. See Griffiths 1998, pp. 27–62

Farquhar GD, Ehleringer JR, Hubick KT. 1989. Carbon isotope discrimination and photosynthesis. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 40:503–37

Farquhar GD, Lloyd J. 1993. Carbon and oxygen isotope effects in the exchange of carbon dioxide between terrestrial ecosystems and the atmosphere. See Ehleringer et al. 1993, pp. 47–70

Farquhar GD, Lloyd J, Taylor JA, Flanagan LB, Syvertsen JP, et al. 1993. Vegetation effects on the isotope composition of oxygen in atmospheric carbon dioxide. *Nature* 363:439–43

Farquhar GD, O'Leary MH, Berry JA. 1982. On the relationship between carbon isotope discrimination and intercellular carbon dioxide

concentration in leaves. *Aust. J. Plant Physiol.* 9:121–37

Farquhar GD, Richards RA. 1984. Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. *Aust. J. Plant Physiol.* 11:539–52

Farquhar GD, Sharkey TD. 1982. Stomatal conductance and photosynthesis. *Annu. Rev. Plant Physiol.* 33:317–45

Feddes RA, Hoff H, Bruen M, Dawson T, de Rosnay P, et al. 2001. Modeling root water uptake in hydrological and climate models. *B. Am. Meteorol. Soc.* 82:2797–810

Feild TS, Dawson TE. 1998. Water sources used by *Didymopanax pittieri* at different life stages in a tropical cloud forest. *Ecology* 79:1448–52

Feng X. 1999. Trends in intrinsic water-use efficiency of natural trees for past 100–200 years: a response to atmospheric CO_2 concentration. *Geochim. Cosmochim. Acta* 63: 1891–903

Fessenden JE, Ehleringer JR. 2002. Age-related variations in ^{13}C of ecosystem respiration across a coniferous forest chronosequence in the Pacific Northwest. *Tree Physiol.* 22:159–67

Finlay RD, Frostegard A, Sonnerfeldt A-M. 1992. Utilization of organic and inorganic nitrogen sources by ectomycorrhizal fungi in pure culture and in symbiosis with *Pinus contorta* Dougl. ex Loud. *New Phytol.* 120:105–15

Fitter AH, Graves JD, Watkins NK, Robinson D, Scrimgeour C. 1998. Carbon transfer between plants and its control in network of arbuscular mycorrhizas. *Funct. Ecol.* 12:406–12

Flanagan LB. 1998. Oxygen isotope effects during CO_2 exchange: from leaf to ecosystem processes. See Griffiths 1998, pp. 185–201

Flanagan LB, Brooks JR, Ehleringer JR. 1997a. Photosynthesis and carbon isotope discrimination in boreal forest ecosystems: a comparison of functional characteristics in plants from three mature forest types. *J. Geophys. Res.* 102:28861–69

Flanagan LB, Brooks JR, Varney GT, Ehleringer JR. 1997b. Discrimination against $C^{18}O^{16}O$ during photosynthesis and the oxygen isotope ratio of respired CO_2 in boreal forest ecosystems. *Global Biogeochem. Cycles* 11:83–98

Flanagan LB, Ehleringer JR. 1991. Stable isotope composition of stem and leaf water: applications to the study of plant water use. *Funct. Ecol.* 5:270–77

Flanagan LB, Ehleringer JR. 1998. Ecosystem-atmosphere CO_2 exchange: interpreting signals of change using stable isotope ratios. *Trends Ecol. Evol.* 13:10–14

Flanagan LB, Ehleringer JR, Marshall JD. 1992. Differential uptake of summer precipitation among co-occurring trees and shrubs in a pinyon-juniper woodland. *Plant Cell Environ.* 15:831–36

Flanagan LB, Kubien DS, Ehleringer JR. 1999. Spatial and temporal variation in the carbon and oxygen stable isotope ratio of respired CO_2 in a boreal forest ecosystem. *Tellus B* 51:367–84

Flanagan LB, Phillips SL, Ehleringer JR, Lloyd J, Farquhar GD. 1994. Effect of changes in leaf water oxygen isotopic composition on discrimination against C18O16O during photosynthetic gas exchange. *Aust. J. Plant Physiol.* 21:221–34

Flanagan LB, Varney GT. 1995. Influence of vegetation and soil CO_2 exchange on the concentration and stable oxygen isotope ratio of atmospheric CO_2 within a *Pinus resinosa* canopy. *Oecologia* 101:37–44

Frank DA, Evans RD. 1997. Effects of native grazers on grassland N cycling in Yellowstone National Park. *Ecology* 78:2238–48

Frank DA, Groffman PM, Evans RD, Tracy BF. 2000. Ungulate stimulation of nitrogen cycling and retention in Yellowstone Park grasslands. *Oecologia* 123:116–21

Fry B, Joern A, Parker PL. 1978. Grasshopper food web analysis: use of carbon isotope ratios to examine feeding relationships among terrestrial herbivores. *Ecology* 59:498–506

Galloway JN, Schlesinger WH, Levy H, Michaels A, Schnoor JL. 1995. Nitrogen

fixation: anthropogenic enhancement-environmental response. *Glob. Biogeochem. Cycles* 9:235–52

Garten CT. 1993. Variation in foliar ^{15}N abundance and the availability of soil nitrogen on Walker Branch Watershed. *Ecology* 74:2098–113

Garten CT Jr, Hanson PJ. 1990. Foliar retention of ^{15}N-nitrate and ^{15}N-ammonium by red maple (*Acer rubrum*) and white oak (*Quercus alba*) leaves from simulated rain. *Environ. Exp. Bot.* 30:333–42

Garten CT Jr, Taylor GE Jr. 1992. Foliar $\delta^{13}C$ within a temperate deciduous forest: spatial, temporal, and species sources of variation. *Oecologia* 90:1–7

Garten CT Jr, Van Miegroet H. 1994. Relationships between soil nitrogen dynamics and natural ^{15}N abundance in plant foliage from Great Smoky Mountains National Park. *Can. J. For. Res.* 24:1636–45

Gat JR. 1996. Oxygen and hydrogen stable isotopes in the hydrologic cycle. *Annu. Rev. Earth Plant. Sci.* 24:225–62

Gat JR. 1998. Stable isotopes, the hydrological cycle and the terrestrial biosphere. See Griffiths 1998, pp. 397–407

Gebauer G, Dietrich P. 1993. Nitrogen isotope ratios in different compartments of a mixed stand of spruce, larch and beech trees and of understorey vegetation including fungi. *Isotopenpraxis* 29:35–44

Gebauer G, Schulze ED. 1991. Carbon and nitrogen isotope ratios in different compartments of a healthy and a declining *Picea abies* forest in the Fichtelgebirge, northeastern Bavaria Germany. *Oecologia* 87:198–207

Gebauer RLE, Ehleringer JR. 2000. Water and nitrogen uptake patterns following moisture pulses in a cold desert community. *Ecology* 81:1415–24

Geber MA, Dawson TE. 1990. Genetic variation in and covariation between leaf gas exchange, morphology, and development in *Polygonum arenastrum*, an annual plant. *Oecologia.* 85:53–58

Ghashghaie J, Duranceau M, Badeck FW, Cornic G, Adeline MT, et al. 2001. ^{13}C of CO_2 respired in the dark in relation to ^{13}C of leaf metabolites: comparison between *Nicotiana sylvestris* and *Helianthus annuus* under drought. *Plant Cell Environ.* 24:505–15

Gleixner G, Danier H-J, Werner RA, Schmidt H-L. 1993. Correlation between the ^{13}C content of primary and secondary plant products in different cell compartments and that in decomposing basidiomycetes. *Plant Physiol.* 102:1287–90

Grantz DA. 1990. Plant responses to atmospheric humidity. *Plant Cell Environ.* 13: 667–79

Griffiths H. 1992. Carbon isotope discrimination and the integration of carbon assimilation pathways in terrestrial CAM plants: commissioned review. *Plant Cell Environ.* 15:1051–62

Griffiths H, ed. 1998. *Stable Isotopes: Integration of Biological, Ecological and Geochemical Processes*. Oxford: BIOS Sci.

Griffiths H, Smith J, eds. 1993. *Plant Responses to Water Deficits*. London, UK: BIOS Sci.

Groffman PM, Zak DR, Christensin S, Mosier A, Tiedje JM. 1993. Early spring nitrogen dynamics in a temperate forest landscape. *Ecology* 74:1579–85

Guehl J-M, Fort C, Ferhi A. 1995. Differential response of leaf conductance, carbon isotope discrimination and water-use efficiency to nitrogen deficiency in maritime pine and pedunculate oak plants. *New Phytol.* 131:149–57

Hanba YT, Miyazawa SI, Terashima I. 1999. The influence of leaf thickness on the CO_2 transfer conductance and leaf stable carbon isotope ratio for some evergreen tree species in Japanese warm–temperate forests. *Funct. Ecol.* 13:632–39

Hanba YT, Mori S, Lei TT, Koike T, Wada E. 1997. Variations in leaf $\delta^{13}C$ along a vertical profile of irradiance in a temperate Japanese forest. *Oecologia* 110:253–61

Handley LL, Austin AT, Robinson D, Scrimgeour CM, Raven JA, et al. 1999. The ^{15}N natural abundance ($\delta^{15}N$) of ecosystem samples reflects measures of water

availability. *Aust. J. Plant Physiol.* 26:185–99

Handley LL, Odee D, Scrimgeour CM. 1994. $\delta^{15}N$ and $\delta^{13}C$ patterns in savanna vegetation: dependence on water availability and disturbance. *Funct. Ecol.* 8:306–14

Handley LL, Raven JA. 1992. The use of natural abundance of nitrogen isotopes in plant physiology and ecology. *Plant Cell Environ.* 15:965–85

Handley LL, Robinson D, Forster BP, Ellis RP, Scrimgeour CM, et al. 1997. Shoot delta-^{15}N correlates with genotype and salt stress in barley. *Planta* 201:100–2

Handley LL, Scrimgeour CM. 1997. Terrestrial plant ecology and ^{15}N natural abundance: The present limits to interpretation for uncultivated systems with original data from a Scottish old field. *Adv. Ecol. Res.* 27:133–212

Handley LL, Scrimgeour CM, Raven JA. 1998. ^{15}N at natural abundance levels in terrestrial vascular plants: a precis. See Griffiths 1998, pp. 89–98

Hardy RWF, Holsten RD, Jackson EK, Burns RC. 1968. The acetylene-ethylene assay for N2 fixation: laboratory and field evaluation. *Plant Physiol.* 43:1185–207

Hart S, Stark JM, Davidson EA, Firestone MK. 1994. Nitrogen mineralization, immobilization, and nitrification. In *Methods of Soil Analysis. Part 2. Microbiological and Biochemicam Properties*; ed. RW Weaver, S Angle, P Bottomley, D Bedzicek, S Smith, et al., pp. 985–1018. Madison, WI: Soil Sci. Soc. Am.

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 Environ.* 21:269–83

Hemming D, Fritts HC, Leavitt SW, Wright WE, Long A, Shashkin A. 2001. Modelling tree-ring $\delta^{13}C$. *Dendrochronologia* 19:23–38

Hemming DL, Switsur VR, Waterhouse JS, Heaton THE, Carter AHC. 1998. Climate variation and the stable carbon isotope composition of tree ring cellulose: an intercomparison of Quercus robur, Fagus silvatica and Pinus silvestris. *Tellus B* 50:25–33

Henderson S, von Caemmerer S, Farquhar GD, Wade L, Hammer G. 1998. Correlation between carbon isotope discrimination and transpiration efficiency in lines of the C4 species *Sorghum bicolor* in the glasshouse and the field. *Aust. J. Plant Physiol.* 25:111–23

Henderson SA, von Caemmerer S, Farquhar GD. 1992. Short-term measurements of carbon isotope discrimination in several C4 species. *Aust. J. Plant Physiol.* 19:263–85

Henn RM, Chapela IH. 2000. Differential C isotope discrimination by fungi during decomposition of C3- and C4-derived sucrose. *Appl. Environ. Microbiol.* 66:4180–86

Hobbie EA, Macko SA, Shugart HH. 1999a. Insights into nitrogen and carbon dynamics of ectomycorrhizal and saprotrophic fungi from isotopic evidence. *Oecologia* 118:353–60

Hobbie EA, Macko SA, Shugart HH. 1999b. Interpretation of nitrogen isotope signatures using the NIFTE model. *Oecologia* 120:405–15

Hobbie EA, Macko SA, Williams M. 2000. Correlation between foliar $\delta^{15}N$ and nitrogen concentrations may indicate plant-mycorrhizal interactions. *Oecologia* 122: 273–83

Hobbie EA, Weber NS, Trappe NS. 2001. Mycorrhizal vs saprotrophic status of fungi: the isotopic evidence. *New Phytol.* 150:601–10

Högberg P. 1990. Forests losing large quantities of nitrogen have elevated nitrogen $^{15}N/^{14}N$ ratios. *Oecologia* 84:229–31

Högberg P. 1997. Tansley review no. *95* 15N natural abundance in soil-plant systems. *New Phytol.* 137:179–203

Högberg P, Högberg MN, Quist ME, Ekblad A, Näsholm T. 1999a. Nitrogen isotope fractionation during nitrogen uptake by ectomycorrhizal and non-mycorrhizal *Pinus sylvestris. New Phytol.* 142:569–76

Högberg P, Högbom L, Schinkel H, Högberg M, Johannison C, et al. 1996. ^{15}N abundance of surface soils, roots and mycorrhizas in

profiles of European forest soils. *Oecologia* 108:207–14

Högberg P, Johannisson C. 1993. ^{15}N abundance of forests is correlated with losses of nitrogen. *Plant Soil* 157:147–50

Högberg P, Johannisson C, Hällgren J-E. 1993. Studies of ^{13}C in the foliage reveal interactions between nutrients and water in fertilization experiments. *Plant Soil* 152:207–14

Högberg P, Plamboeck AH, Taylor AFS, Fransson PMA. 1999b. Natural ^{13}C abundance reveals trophic status of fungi and host-origin of carbon in mycorrhizal fungi in mixed forests. *Proc. Natl. Acad. Sci. USA* 96:8534–39

Hultine KR, Marshall JD. 2000. Altitude trends in conifer leaf morphology and stable carbon isotope composition. *Oecologia* 123:32–40

Hungate BA, Jackson RB, Chapin FS III, Mooney HA, Field CB. 1997. The fate of carbon in grasslands under carbon dioxide enrichment. *Nature* 388:576–79

Ingraham NL. 1998. Isotopic variations in precipitation. See Kendall & McDonell 1998, pp. 87–118

Jackson PC, Cavelier J, Goldstein G, Meinzer FC, Holbrook NM. 1995. Partitioning of water resources among plants of a lowland tropical forest. *Oecologia* 101:197–203

Jackson PC, Meinzer FC, Bustamante M, Goldstein G, Franco A, et al. 1999. Partitioning of soil water among tree species in a Brazilian Cerrado ecosystem. *Tree Physiol.* 19:717–24

Jackson RB, Sperry JS, Dawson TE. 2000. Root water uptake and transport: using physiological processes in global predictions. *Trends Plant Sci.* 5:482–88

Johannisson C, Högberg P. 1994. ^{15}N abundance of soils and plants along an experimentally induced forest nitrogen supply gradient. *Oecologia* 97:322–25

Johnsen KH, Flanagan LB. 1995. Genetic variation in carbon isotope discrimination and its relationship to growth under field conditions in full-sib families of *Picea mariana*. *Can. J. For. Res.* 25:39–47

Johnsen KH, Flanagan LB, Huber DA, Major JE. 1999. Genetic variation in growth, carbon isotope discrimination, and foliar N concentration in *Picea mariana*: analyses from a half-diallel mating design using field-grown trees. *Can. J. For. Res.* 29:1727–35

Johnson DA, Asay KH, Tieszen LL, Ehleringer JR, Jefferson PG. 1990. Carbon isotope discrimination—potential in screening cool-season grasses for water-limited environments. *Crop Sci.* 30:338–43

Keeling CD. 1958. The concentration and isotopic abundances of atmospheric carbon dioxide in rural areas. *Geochim. Cosmochim. Acta* 13:322–34

Keeling CD. 1961. The concentration and isotopic abundances of atmospheric carbon dioxide in rural and marine areas. *Geochim. Cosmochim. Acta* 24:277–98

Kelly FI, Woodward FI. 1995. Ecological correlates of carbon isotope composition of leaves: a comparative analysis testing for the effects of temperature, CO_2 and O_2 partial pressures and taxonomic relatedness on $\delta^{13}C$/C. *J. Ecol.* 83:509–15

Kendall C, McDonnell JJ, eds. 1998. *Isotope Tracers in Catchment Hydrology*. Amsterdam: Elsevier Science. 839 pp.

Kielland K, Bryant JP. 1998. Moose herbivory in taiga: effects on biogeochemistry and vegetation dynamics in primary succession. *Oikos* 82:377–83

Kloeppel BD, Gower ST, Treichel IW, Kharuk S. 1998. Foliar carbon isotope discrimination in Larix species and sympatric evergreen conifers: a global comparison. *Oecologia* 114:153–59

Knowles R. 1975. Interpretation of recent ^{15}N studies of nitrogen in forest systems. In *Forest Soils and Forest Land Management. Proc. 4th North Am. For. Soil Conf.*, ed. B Bernier, CH Winget, pp. 53–65. Quebec: Laval Univ. Press

Knowles R, Henry Blackburn T, eds. 1993. *Nitrogen Isotope Techniques*. San Diego, CA: Academic

Kohl DH, Shearer G. 1980. Isotope fractionation associated with symbiotic N_2 fixation and uptake of NO_3. *Plant Physiol.* 66:51–56

Kohorn LU, Goldstein G, Rundel PW. 1994.

Morphological and isotopic indicators of growth environment: variability in delta ^{13}C in *Simmondsia chinensis*, a dioecious desert shrub. *J. Exp. Bot.* 45:1817–22

Kohzu A, Tateishi T, Yamada K, Koba K, Wada E. 2000. Nitrogen isotope fractionation during nitrogen transport from ectomycorrhizal fungi. *Suillus granulatus*, to the host plant, *Pinus densiflora*. *Soil Sci. Plant Nutr.* 46:733–39

Kohzu A, Yoshioka T, Ando T, Takahashi M, Koba K, et al. 1999. Natural ^{13}C and ^{15}N abundance of field-collected fungi and their ecological implications. *New Phytol.* 144:323–30

Kolb TE, Hart SC, Amundson R. 1997. Boxelder water sources and physiology at perennial and ephemeral stream sites in Arizona. *Tree Physiol.* 17:151–60

Koopmans CJ, Tietema A, Boxman AW. 1996. The fate of ^{15}N enriched throughfall in two coniferous forest stands at different nitrogen deposition levels. *Biogeochemistry* 34:19–44

Körner C, Farquhar GD, Wong SC. 1991. Carbon isotope discrimination by follows latitudinal and altitudinal trends. *Oecologia* 88:30–40

Korol RL, Kirschbaum MUF, Farquhar GD, Jeffreys M. 1999. Effects of water status and soil fertility on the C-isotope signature in *Pinus radiata*. *Tree Physiol.* 19:551–62

Lajtha K, Marshall JD. 1994. Sources of variation in the stable isotopic composition of plants. See Lajtha & Michener 1994, pp. 1–21

Lajtha K, Michener RH, eds. 1994. *Stable Isotopes in Ecology and Environmental Science*. Oxford: Blackwell Sci.

Leavitt SW. 1993. Environmental information from 13C/12C ratios in wood. In *Climate Change in Continental Isotope Records*, ed. PK Swart, KC Lohmann, JA McKenzie, S Savin, 78:325–31. Am. Geophys. Union Monogr.

Leavitt SW, Long A. 1986. Stable-carbon isotope variability in tree foliage and wood. *Ecology* 67:1002–10

Leavitt SW, Long A. 1988. Stable carbon isotope chronologies from trees in the south western United States. *Glob. Biogeochem. Cycles* 2:189–98

Leavitt SW, Long A. 1989. Drought indicated in $^{13}C/^{12}C$ ratios of south western tree rings. *Water Resour. Bull.* 25:341–47

Leavitt SW, Long A. 1991. Seasonal stable carbon isotope variability in tree rings: possible paleoenvironmental signals. *Chem. Geol.* 87:59–70

Le Roux X, Bariac T, Sinoquet H, Genty B, Piel C, et al. 2001. Spatial distribution of leaf water-use efficiency and carbon isotope discrimination within an isolated tree crown. *Plant Cell Environ.* 24:1021–32

Lin G, Ehleringer JR. 1997. Carbon isotopic fractionation does not occur during dark respiration in C3 and C4 plants. *Plant Physiol.* 114:391–94

Lin G, Phillips SL, Ehleringer JR. 1996. Monsoonal precipitation responses of shrubs in a cold desert community on the Colorado Plateau. *Oecologia* 106:8–17

Lin G, Sternberg LDL. 1993. Hydrogen isotopic fractionation by plant roots during water uptake in coastal wetland plants. See Ehleringer et al. 1993, pp. 497–510

Lipp J, Timborn P, Edwards T, Waisel Y, Yakir D. 1996. Climatic effects on the $\delta^{18}O$ and $\delta^{13}C$ of cellulose in the desert tree *Tamarix jordanis*. *Geochim. Cosmochim. Acta* 60:3305–9

Livingston NJ, Spittlehouse DL. 1993. Carbon isotope fractionation in tree rings in relation to the growing season water balance. See Ehleringer et al. 1993, pp. 141–53

Lloyd J, Kruijt B, Hollinger DY, Grace J, Francey RJ, et al. 1996. Vegetation effects on the isotopic composition of atmospheric CO_2 at local and regional scales: theoretical aspects and a comparison between rain forest in Amazonia and a boreal forest in Siberia. *Aust. J. Plant Physiol.* 23:371–99

Lowden JA, Dyck W. 1974. Seasonal variations in the isotope ratios of carbon in maple leaves and other plants. *Can. J. Earth Sci.* 11:79–88

Ludwig F. 2001. *Tree-grass interactions on an*

east African savanna: the effects of competition, facilitation and hydraulic lift. PhD Diss., Wageningen Univ., The Netherlands

MacFadden BJ. 2000. Cenozoic mammalian herbivores from the Americas: reconstructing ancient diets and terrestrial communities. *Annu. Rev. Ecol. Syst.* 31:33–59

Madhavan S, Treichel I, O'Leary MH. 1991. Effects of relative humidity on carbon isotope fractionation in plants. *Bot. Acta* 104:292–94

Maillard P, Guehl JM, Muller JF, Gross P. 2001. Interactive effects of elevated CO_2 concentration and nitrogen supply on partitioning of newly fixed ^{13}C and ^{15}N between shoot and roots of pedunculate oak seedlings (*Quercus robur*). *Tree Physiol.* 21:163–72

Mariotti A, Mariotti F, Champigny ML, Amargar N, Moyse A. 1982. Nitrogen isotope fractionation associated with nitrate reductase activity and uptake of NO_3^- by pearl millet. *Plant Physiol.* 69:880–84

Marshall JD, Ehleringer JR. 1990. Are xylem-tapping mistletoes partially heterotrophic? *Oecologia* 84:244–48

Marshall JD, Ehleringer JR, Schulze ED, Farquhar G. 1994. Carbon isotope composition, gas exchange and heterotrophy in Australian mistletoes. *Funct. Ecol.* 8:237–41

Marshall JD, Zhang J. 1994. Carbon isotope discrimination and water-use efficiency in native plants of the north-central Rockies. *Ecology* 75:1887–95

Martinelli LA, Almeida S, Brown IF, Moreira MZ, Victoria RL, et al. 1998. Stable carbon isotope ratio of tree leaves, boles and fine litter in a tropical forest in Rondonia, Brazil. *Oecologia* 114:170–79

Mathieu R, Bariac T. 1996a. An isotopic study (2H and 18O) of water movements in clayey soils under a semi-arid climate. *Water Resour. Res.* 32:779–89

Mathieu R, Bariac T. 1996b. A numerical model for the simulation of stable isotope profiles in drying soils. *J. Geophys. Res.* 101:12585–696

Mazor E. 1991. Stable hydrogen and oxygen isotopes. *In Applied Chemical and Isotopic Groundwater Hydrology*, pp. 122–46. London: Halsted

McKane RB, Grigal DF, Russelle MP. 1990. Spatiotemporal differences in ^{15}N uptake and the organization of an old-field plant community. *Ecology* 71:1126–32

Medina E, Minchin P. 1980. Stratification of $\delta^{13}C$ values of leaves in Amazonian rain forests. *Oecologia* 45:377–78

Meints VW, Boone LV, Kurtz LT. 1975. Natural ^{15}N abundance in soil, leaves, and grain as influenced by long term additions of fertilizer N at several rates. *J. Environ. Qual.* 4:486–90

Meinzer FC, Andrade JL, Goldstein G, Holbrook NM, Cavelier J, et al. 1999. Partitioning of soil water among canopy trees in a seasonally dry tropical forest. *Oecologia* 121:293–301

Meinzer FC, Clearwater MJ, Goldstein G. 2001. Water transport in trees: current perspectives, new insights and some controversies. *Environ. Exp. Bot.* 45:239–62

Meinzer FC, Rundel PW, Goldstein G, Sharifi MR. 1992. Carbon isotope composition in relation to leaf gas exchange and environmental conditions in Hawaiian *Metrosideros polymorpha* populations. *Oecologia* 91:305–11

Mensforth LJ, Thorburn PJ, Tyerman SD, Walker GR. 1994. Sources of water used by riparian *Eucalyptus camaldulensis* overlying highly saline groundwater. *Oecologia* 100:21–28

Michelsen A, Quarmby C, Sleep D, Jonasson S. 1998. Vascular plant ^{15}N natural abundance in heath and forest tundra ecosystems is closely correlated with presence and type of mycorrhizal fungi in roots. *Oecologia* 115:406–18

Michelsen A, Schmidt IK, Jonasson S, Quarmby C, Sleep D. 1996. Leaf ^{15}N abundance of subarctic plants provides field evidence that ericoid, ectomycorrhizal and non- and arbuscular mycorrhizal species access different sources of soil nitrogen. *Oecologia* 105:53–63

Millard P, Hester A, Wendler R, Baillie G. 2001. Interspecific defoliation responses of trees

depend on sites of winter nitrogen storage. *Funct. Ecol.* 15:535–43

Miller JB, Yakir D, White JWC, Tans PP. 1999. Measurement of $^{18}O/^{16}O$ in the soil-atmosphere CO_2-flux. *Glob. Biogeochem. Cycles* 13:761–74

Miller JM, Williams RJ, Farquhar GD. 2001. Carbon isotope discrimination by a sequence of *Eucalyptus* species along a subcontinental rainfall gradient in Australia. *Funct. Ecol.* 15:222–32

Miranda AC, Miranda HS, Lloyd J, Grace J, Francey RJ, et al. 1997. Fluxes of carbon, water and energy over Brazilian cerrado: an analysis using eddy covariance and stable isotopes. *Plant Cell Environ.* 20:315–28

Monserud RA, Marshall JD. 2001. Time-series analysis of $\delta^{13}C$ from tree rings. I. Time trends and autocorrelation. *Tree Physiol.* 21:1087–102

Monteith JL. 1995. A reinterpretation of stomatal responses to humidity. *Plant Cell Environ.* 18:357–64

Moore DJ, Nowak RS, Tausch RJ. 1999. Gas exchange and carbon isotope discrimination of *Juniperus osteosperma* and *Juniperus occidentalis* across environmental gradients in the great Basin of western North America. *Tree Physiol.* 19:421–33

Moran JA, Merbach MA, Livingston NJ, Clarke CM, Booth WE. 2001. Termite prey specialization in the pitcher plant *Nepenthes albomarginata*: evidence from stable isotope analysis. *Ann. Bot.* 88:307–11

Mordacq L, Mousseau M, Deleens E. 1986. A ^{13}C method of estimation of carbon allocation to roots in a young chestnut coppice. *Plant Cell Environ.* 9:735–40

Morecroft MD, Woodward FI. 1990. Experimental investigation on the environmental determination of $\delta^{13}C$ at different altitudes. *J. Exp. Bot.* 31:1303–8

Moreira MZ, Sternberg LDL, Martinelli LA, Victoria RL, Barbosa EM, et al. 1997. Contribution of transpiration to forest ambient vapor based on isotopic measurements. *Glob. Change Biol.* 3:439–50

Moreira MZ, Sternberg LDL, Nepstad DC. 2000. Vertical patterns of soil water uptake by plants in a primary forest and an abandoned pasture in the eastern Amazon: an isotopic approach. *Plant Soil* 222:95–107

Mott KA, Parkhurst DF. 1991. Stomatal responses to humidity in air and helox. *Plant Cell Environ.* 14:509–15

Nadelhoffer K, Downs M, Fry B, Magill A, Aber J. 1999. Controls on N retention and exports in a forested watershed. *Environ. Monit. Assess.* 55:187–210

Nadelhoffer K, Fry B. 1994. Nitrogen isotope studies in forest ecosystems. See Lajtha & Michener 1994, pp. 22–44

Nadelhoffer KJ, Downs MR, Fry B, Aber JD, Magill AH, et al. 1995. The fate of ^{15}N-labelled nitrate additions to a northern hardwood forest in eastern Maine, USA. *Oecologia* 103:292–301

Nadelhoffer KJ, Fry B. 1988. Controls on natural ^{15}N and ^{13}C abundances in forest soil organic matter. *Soil Sci. Soc. Am. J.* 52:1633–40

Näsholm T, Ekblad A, Nordin A, Giesler R, Högberg M, et al. 1998. Boreal forest plants take up organic nitrogen. *Nature* 392:914–16

Newman EI, Reddell P. 1987. The distribution of mycorrhizas among families of vascular plants. *New Phytol.* 106:745–51

Niklaus PA, Glockler E, Siegwolf R, Korner C. 2001. Carbon allocation in calcareous grassland under elevated CO_2: a combined ^{13}C pulse-labelling/soil physical fractionation study. *Funct. Ecol.* 15:43–50

O'Leary MH. 1981. Carbon isotope fractionation in plants. *Phytochemistry* 20:553–67

Olson BE, Wallander RT. 1999. Carbon allocation in *Euphorbia esula* and neighbours after defoliation. *Can. J. Bot.* 77:1641–47

Palta JA. 2001. Source/sink interactions in crop plants. See Unkovich et al. 2001, pp. 145–65

Panek JA. 1996. Correlations between stable carbon-isotope abundance and hydraulic conductivity in Douglas-fir across a climate gradient in Oregon, USA. *Tree Physiol.* 16:747–55

Panek JA, Waring RH. 1995. Carbon isotope variation in Douglas-fir foliage: improving

the δ^{13}C-climate relationship. *Tree Physiol.* 15:657–63

Panek JA, Waring RH. 1997. Stable carbon isotopes as indicators of limitations to forest growth imposed by climate stress. *Ecol. Appl.* 7:854–63

Park R, Epstein S. 1961. Metabolic fractionation of ^{13}C and ^{12}C in plants. *Plant Physiol.* 36:133–38

Pataki DE, Ehleringer JR, Flanagan LB, Yakir D, Bowling DR, et al. 2002. The application and interpretation of Keeling plots in terrestrial carbon cycle research. *Glob. Biogeochem. Cycles.* In press

Pate J. 2001. Carbon isotope discrimination and plant water-use efficiency: case scenarios for C3 plants. See Unkovich et al. 2001, pp. 19–36

Pate JS, Dawson TE. 1999. Novel techniques for assessing the performance in uptake and utilisation of carbon, water and nutrients by woody plants: implications for designing agricultural mimics. *Agrofor. Syst.* 45:245–76

Pattey E, Desjardins RL, Rochette P. 1993. Accuracy of the relaxed eddy-accumulation technique, evaluated using CO_2 flux measurements. *Bound.-Lay. Meteorol.* 66:341–55

Peterjohn WT, Adams MB, Gilliam FS. 1996. Symptoms of nitrogen saturation in two central Appalachian hardwood forest ecosystems. *Biogeochemistry* 35:507–22

Peterson BJ, Fry B. 1987. Stable isotopes in ecosystem studies. *Annu. Rev. Ecol. Syst.* 18:293–320

Phillips DL. 2001. Mixing models in analyses of diet using multiple stable isotopes: a critique. *Oecologia* 127:166–70

Phillips DL, Gregg JW. 2001. Uncertainty in source partitioning using stable isotopes. *Oecologia* 127:171–79

Phillips DL, Koch PL. 2002. Incorporating concentration dependence in stable isotope mixing models. *Oecologia* 130:114–25

Phillips SL, Ehleringer JR. 1995. Limited uptake of summer precipitation by bigtooth maple (*Acer grandidentatum* Nutt) and Gambel's oak (*Quercus gambelii* Nutt). *Trees* 9:214–19

Piccolo MC, Neill C, Cerri CC. 1994. Natural abundance of ^{15}N in soils along forest-to-pasture chronosequences in the western Brazilian Amazon Basin. *Oecologia* 99: 112–17

Piccolo MC, Neill C, Melillo JM, Cerri CC, Steudler PA. 1996. ^{15}N natural abundance in forest and pasture soils of the Brazilian Amazon Basin. *Plant Soil* 182:249–58

Plamboeck AH, Grip H, Nygren U. 1999. A hydrological tracer study of water uptake depth in a Scots pine forest under two different water regimes. *Oecologia* 119:452–60

Polley HW, Johnson HB, Mayeux HS. 1992. Determination of root biomasses of three species grown in a mixture using stable isotopes of carbon and nitrogen. *Plant Soil* 142:97–106

Poorter H, Farquhar GD. 1994. Transpiration, intercellular carbon dioxide concentration and carbon-isotope discrimination of 24 wild species differing in relative growth rate. *Aust. J. Plant Physiol.* 21:507–17

Poss JA, Grattan SR, Suarez DL, Grieve CM. 2000. Stable carbon isotope discrimination: an indicator of cumulative salinity and boron stress in *Eucalyptus camaldulensis. Tree Physiol.* 20:1121–27

Poulson SR, Page Chamberlain C, Friedland AJ. 1995. Nitrogen isotope variation of tree rings as a potential indicator of environmental change. *Chem. Geol.* 125:307–15

Press MC, Shah N, Tuohy JM, Stewart GR. 1987. Carbon isotope ratios demonstrate carbon flux from C4 host to C3 parasite. *Plant Physiol.* 85:1143–45

Proctor MCF, Raven JA, Rice SK. 1992. Stable carbon isotope discrimination measurements in *Sphagnum* and other bryophytes: physiological and ecological implications. *J. Bryol.* 17:193–202

Proe MF, Midwood AJ, Craig J. 2000. Use of stable isotopes to quantify nitrogen, potassium and magnesium dynamics in young Scots pine (*Pinus sylvestris*). *New Phytol.* 146:461–69

Quade J, Cerling TE, Barry JC, Morgan ME, Pilbeam DR, et al. 1992. A 16 million year record of paleodiet from Pakistan using carbon isotopes in fossil teeth. *Chem. Geol.* 94:183–92

Rennie DA, Paul EA, Johns LE. 1976. Natural ^{15}N abundance of soil and plant samples. *Can. J. For. Res.* 56:43–50

Retuerto R, Lema BF, Roiloa SR, Obeso JR. 2000. Gender, light and water effects in carbon isotope discrimination, and growth rates in the dioecious tree *Ilex aquifolium*. *Funct. Ecol.* 14:529–37

Rice KJ, Gordon DR, Hardison JL, Welker JM. 1993. Phenotypic variation in seedlings of a "keystone" tree species (*Quercus douglasii*): The interactive effects of acorn source and competitive environment. *Oecologia* 96:537–47

Rice SK. 2000. Variation in carbon isotope discrimination within and among *Sphagnum* species in a temperate wetland. *Oecologia* 123:1–8

Rice SK, Giles L. 1996. The influence of water content and leaf anatomy on carbon isotope discrimination and photosynthesis in *Sphagnu*m. *Plant Cell Environ.* 19:118–24

Robinson D. 2001. $\delta^{15}N$ as an integrator of the nitrogen cycle. *Trends Ecol. Evol.* 16:153–62

Robinson D, Handley LL, Scrimgeour CM. 1998. A theory for $^{15}N/^{14}N$ fractionation in nitrate-grown vascular plants. *Planta* 205: 397–406

Robinson D, Handley LL, Scrimgeour CM, Gordon DC, Forster BP, et al. 2000. Using stable isotope natural abundances ($\delta^{15}N$ and $\delta^{13}C$) to integrate the stress responses of wild barley (*Hordeum spontaneum* C. *Koch.*) *genotypes*. *J. Exp. Bot.* 51:41–50

Robinson D, Scrimgeour CM. 1995. The contribution of plant C to soil CO_2 measured using $\delta^{13}C$. *Soil Biol. Biochem.* 27:1653–56

Rochette P, Flanagan LB. 1997. Quantifying rhizosphere respiration in a corn crop under field conditions. *Soil Sci. Soc. Am. J.* 61:466–74

Rochette P, Flanagan LB, Gregorich EG. 1999. Separating soil respiration into plant and soil components using analyses of the natural abundance of carbon-13. *Soil Sci. Soc. Am. J.* 63:1207–13

Roden JS, Ehleringer JR. 1999a. Observations of hydrogen and oxygen isotopes in leaf water confirm the Craig-Gordon model under wide-ranging environmental conditions. *Plant Physiol.* 120:1165–73

Roden JS, Ehleringer JR. 1999b. Hydrogen and oxygen isotope ratios of tree-ring cellulose for riparian trees grown long-term under hydroponically controlled environments. *Oecologia* 121:467–77

Roden JS, Ehleringer JR. 2000. Hydrogen and oxygen isotope ratios of tree-ring cellulose for field grown riparian trees. *Oecologia* 123:481–89

Roden JS, Lin G, Ehleringer JR. 2000. A mechanistic model for interpretation of hydrogen and oxygen isotope ratios in tree-ring cellulose. *Geochim. Cosmochim. Acta* 64:21–35

Rundel PW, Ehleringer JR, Nagy KA, eds. 1989. *Stable Isotopes in Ecological Research. Ecological Studies*, Vol. 68. Heidelberg: Springer-Verlag. 525 pp.

Rundel PW, Stichler W, Zander RH, Ziegler H. 1979. Carbon and hydrogen isotope ratios of bryophytes from arid and humid regions. *Oecologia* 44:91–94

Sagers CL, Ginger SM, Evans RD. 2000. Carbon and nitrogen isotopes trace nutrient exchange in an ant-plant mutualism. *Oecologia* 123:582–86

Sala O, Jackson R, Mooney HA, eds. 2000. *Methods in Ecosystem Science.* San Diego, CA: Academic

Sandquist DR, Ehleringer JR. 1995. Carbon isotope discrimination in the C4 shrub *Atriplex confertifolia* along a salinity gradient. *Great Basin Nat.* 55:135–41

Saurer M, Aellen K, Siegwolf R. 1997. Correlating delta^{13}C and delta^{18}O in cellulose of trees. *Plant Cell Environ.* 20:1543–50

Scheidegger Y, Saurer M, Bahn M, Siegwolf R. 2000. Linking stable oxygen and carbon isotopes with stomatal conductance and photosynthetic capacity: a conceptual model. *Oecologia* 125:350–57

Schimel DS. 1993. *Theory and Application of Tracers*. San Diego, CA: Academic

Schimel JP, Jackson LE, Firestone MK. 1989. Spatial and temporal effects of plant-microbial competition for inorganic nitrogen in a California annual grassland USA. *Soil Biol. Biochem.* 21:1059–66

Schleppi P, Bucher-Wallin I, Siegwolf R, Saurer M, Muller N, et al. 1999. Simulation of increased nitrogen deposition to a montane forest ecosystem: partitioning of the added ^{15}N. *Water Air Soil Pollut.* 116:129–34

Schleser GH, Jayasekera R. 1985. $\delta^{13}C$ variations of leaves in forests as an indication of reassimilated CO_2 from the soil. *Oecologia* 65:536–42

Schmidt H-L, Gleixner G. 1998. Carbon isotope effects on key reactions in plant metabolism and ^{13}C-patterns in natural compounds. See Griffiths 1998, pp. 13–25

Schubler W, Neubert R, Levin I, Fischer N, Sonntag C. 2000. Determination of microbial versus root-produced CO_2 in an agricultural ecosystem by means of $\delta^{13}CO_2$ measurements in soil air. *Tellus* B 52:909–18

Schulze ED, Ehleringer JR. 1984. The effect of nitrogen supply on growth and water-use efficiency of xylem-tapping mistletoes. *Planta* 162:268–75

Schulze ED, Gebauer G, Schulze W, Pate JS. 1991. The utilization of nitrogen from insect capture by different growth forms of *Drosera* from Southwest Australia. *Oecologia* 87:240–46

Schulze ED, Williams RJ, Farquhar GD, Schulze W, Langridge J, et al. 1998. Carbon and nitrogen isotope discrimination and nitrogen nutrition of trees along a rainfall gradient in northern Australia. *Aust. J. Plant Physiol.* 25:413–25

Schulze W, Schulze ED, Pate JS, Gillison AN. 1997. The nitrogen supply from soils and insects during growth of the pitcher plants *Nepenthes mirabilis*, *Cephalotus follicularis* and *Darlingtonia californica*. *Oecologia* 112:464–71

Schuster WSF, Sandquist DR, Phillips SL, Ehleringer JR. 1992a. Comparisons of carbon isotope discrimination in populations of arid land plant species differing in lifespan. *Oecologia* 91:332–37

Schuster WSF, Sandquist DR, Phillips SL, Ehleringer JR. 1992b. Heritability of carbon isotope discrimination in *Gutierrezia microcephala* (Asteraceae). *Am. J. Bot.* 79:216–21

Schwinning S, Davis K, Richardson L, Ehleringer JR. 2002. Deuterium enriched irrigation indicates different forms of rain use in shrub/grass species of the Colorado Plateau. *Oecologia* 130:345–55

Schwinning S, Ehleringer JR. 2001. Water use trade-offs and optimal adaptations to pulse-driven arid ecosystems. *J. Ecol.* 89:464–80

Shearer G, Kohl DH. 1986. Nitrogen fixation in field settings estimations based on natural ^{15}N abundance. *Aust. J. Plant Physiol.* 13:699–756

Shearer G, Kohl DH. 1991. The ^{15}N natural abundance method for measuring biological nitrogen fixation: practicalities and possibilities. In *Stable Isotopes in Plant Nutrition, Soil Fertility and Environmental Studies*, pp. 103–15. Vienna: IAEA

Shearer G, Kohl DH. 1993. Natural abundance of ^{15}N: fractional contribution of two sources to a common sink and use of isotope discrimination. See Knowles & Henry Blackburn 1993, pp. 89–125

Shearer G, Kohl DH, Chien S. 1978. The ^{15}N abundance in a wide variety of soils. *Soil Sci. Soc. Am. J.* 42:899–902

Simard SW, Durall DM, Jones MD. 1997a. Carbon allocation and carbon transfer between *Betula papyrifera* with *Pseudotsuga menziesii* seedlings using a ^{13}C pulse-labeling method. *Plant Soil* 191:41–55

Simard SW, Jones MD, Durall DM, Perry DA, Myrold DD, et al. 1997b. Reciprocal transfer of carbon isotopes between ectomycorrhizal *Betula papyrifera* and *Pseudotsuga menziesii*. *New Phytol.* 137:529–42

Smedley MP, Dawson TE, Comstock JP, Donovan LA, Sherril DE, et al. 1991. Seasonal carbon isotope discrimination in a grassland community. *Oecologia* 85:314–20

Smith DM, Jarvis PG, Odongo JCW. 1997.

Sources of water used by trees and millet in Sahelian windbreak systems. *J. Hydrol.* 198:140–53

Smith DM, Jarvis PG, Odongo JCW. 1998. Management of windbreaks in the Sahel: the strategic implications of tree water use. *Agrofor. Syst.* 40:83–96

Smith SE, Read DJ. 1997. *Mycorrhizal Symbiosis*. London, UK: Academic. 2nd ed.

Sparks J, Ehleringer JR. 1997. Leaf carbon isotope discrimination and nitrogen content for riparian trees along elevational transect. *Oecologia* 109:362–67

Stark JM. 2000. Nutrient transformations. See Sala et al. 2000, pp. 215–34

Stern LA, Amundson R, Baisden WT. 2001. Influence of soils on oxygen isotope ratio of atmospheric CO_2. *Glob. Biogeochem. Cycles* 15:753–60

Sternberg LDL. 1989. Oxygen and hydrogen isotope ratios in plant cellulose: Mechanisms and applications. See Rundel et al. 1989, pp. 124–41

Sternberg LDL, Mulkey SS, Wright SJ. 1989. Ecological interpretation of leaf carbon isotope ratios: influence of respired carbon dioxide. *Ecology* 70:1317–24

Sternberg LDL, Swart PK. 1987. Utilization of freshwater and ocean water by coastal plants of southern Florida USA. *Ecology* 68:1898–1905

Stewart GR. 2001. What do $\delta^{15}N$ signatures tell us about nitrogen relations in natural ecosystems? See Unkovich et al. 2001, pp. 91–101

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. *Aust. J. Plant Physiol.* 22:51–55

Stoddard JL. 1994. Long-term changes in watershed retention of nitrogen. In *Environmental Chemistry of Lakes and Reservoirs, Advances in Chemistry Series*, ed. LA Baker, 237:223–84. Washington, DC: Am. Chem. Soc.

Svejcar TJ, Boutton TW. 1985. The use of stable carbon isotope analysis in rooting studies. *Oecologia* 67:205–8

Switsur VR, Waterhouse JS, Field EM, Carter AHC. 1996. Climatic signals from stable isotopes in oak trees from East Anglia, Great Britain. In *Tree Rings, Environment and Humanity*, ed. JS Dean, DM Meko, TW Swetnam, *Radiocarbon*, pp. 637–45

Tans PP. 1998. Oxygen isotopic equilibrium between carbon dioxide and water in soils. *Tellus* B 50:162–78

Taylor AFS, Högbom L, Högberg M, Lyon AJE, Näsholm T, et al. 1997. Natural ^{15}N abundance in fruit bodies of ectomycorrhizal fungi from boreal forests. *New Phytol.* 136:713–20

Teeri JA. 1981. Stable carbon isotopes analysis of mosses and lichens growing in xeric and moist habitats. *Bryologist* 84:82

Templer P. 2001. *Direct and indirect effects of tree species on forest nitrogen retention in the Catskill Mountains, NY.* PhD Diss., Cornell Univ., Ithaca, NY

Tennakoon KU, Pate JS, Arthur D. 1997. Ecophysiological aspects of the woody root hemiparasite *Santalum acuminatum* (R. *Br.*) *A. DC and its common hosts in South Western Australia. Ann. Bot.* 80:245–56

Thorburn PJ, Ehleringer JR. 1995. Root water uptake of field-growing plants indicated by measurements of natural-abundance deuterium. *Plant Soil* 177:225–33

Thorburn PJ, Hatton TJ, Walker GR. 1993. Combining measurements of transpiration and stable isotopes of water to determine groundwater discharge from forests. *J. Hydrol.* 150:563–87

Thorburn PJ, Mensforth LJ, Walker GR. 1994. Reliance of creek-side river red gums on creek water. *Aust. J. Mar. Freshwater Res.* 45:1439–43

Thorburn PJ, Walker GR. 1993. The source of water transpired by *Eucalyptus camaldulensis*: soil, groundwater, or streams? See Ehleringer et al. 1993, pp. 511–27

Tieszen LL, Reed BC, Bliss NB, Wylie BK, DeJong DD. 1997. NDVI, C3 and C4 production and distribution in Great Plains grassland land cover classes. *Ecol. Appl.* 7:59–78

Treseder KK, Davidson DW, Ehleringer JR.

1995. Absorption of ant-provided carbon dioxide and nitrogen by a tropical epiphyte. *Nature* 375:137–39

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

Trumbore SE, Davidson EA, De Camargo PB, Nepstad DC, Martinelli LA. 1995. Belowground cycling of carbon in forests and pastures of Eastern Amazonia. *Glob. Biogeochem. Cycles* 9:515–28

Tu KP, Brooks PD, Dawson TE. 2001. Using septum-capped vials with continuous-flow isotope ratio mass spectrometric analysis of atmospheric CO_2 for Keeling plot applications. *Rapid Commun. Mass Spectrom.* 15:952–56

Tu KP, Dawson TE. 2003. Partitioning ecosystem respiration using stable carbon isotopes. In *Stable Isotopes and Biosphere-Atmosphere Interactions*, ed. LB Flanagan, JR Ehleringer. San Diego: Academic. In press

Tu TTN, Bocherens H, Mariotti A, Baudin F, Pons D, Broutin J, et al. 1999. Ecological distribution of Cenomanian terrestrial plants based on $^{13}C/^{12}C$ ratios. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 145:79–93

Turnbull MH, Goodall R, Stewart GR. 1995. The impact of mycorrhization on nitrogen source utilisation in *Eucalyptus grandis* and *Eucalyptus maculata*. *Plant Cell Environ.* 18:1386–94

Turner JV, Farrington P, Gailitis V. 2001. Extraction and analysis of plant water for deuterium isotope measurement and application to field experiments. See Unkovich et al. 2001, pp. 37–55

Unkovich M, Pate J. 2001. Assessing N_2 fixation in annual legumes using ^{15}N natural abundance. See Unkovich et al. 2001, pp. 103–18

Unkovich M, Pate J, McNeill A, Gibbs JD, eds. 2001. *Stable Isotope Techniques in the Study of Biological Processes and Functioning of Ecosystems*. Dordrecht: Kluwer Academic

Valentini R, Mugnozza GES, Ehleringer JR. 1992. Hydrogen and carbon isotope ratios of selected species of a mediterranean macchia ecosystem. *Funct. Ecol.* 6:627–31

Van Cleve K, White R. 1980. Forest-floor nitrogen dynamics in a 60-year old paper birch ecosystem in interior Alaska. *Plant Soil* 54:359–81

Virgona JM, Farquhar GD. 1996. Genotypic variation in relative growth rate and carbon isotope discrimination in sunflower is related to photosynthetic capacity. *Aust. J. Plant Physiol.* 23:227–44

Virgona JM, Hubick KT, Rawson HM. 1990. Genotypic variation in transpiration efficiency, carbon-isotope discrimination and carbon allocation during early growth in sunflower. *Aust. J. Plant Physiol.* 17:207–14

Vitousek PM, Aber JD, Howarth RH, Likens GE, Matson PA, et al. 1997. Human alteration of the global nitrogen cycle: source and consequences. *Ecol. Appl.* 7:737–50

Vitousek PM, Field CB, Matson PA. 1990. Variation in foliar $\delta^{13}C$ in Hawaiian *Metrosideros polymorpha*: a case of internal resistance? *Oecologia* 84:362–70

Vivin P, Martin F, Guehl JM. 1996. Acquisition and within-plant allocation of ^{13}C and ^{15}N in CO_2-enriched *Quercus robur* plants. *Physiol. Plant.* 98:89–96

Walcroft AS, Silvester WB, Grace JC, Carson SD, Waring RH. 1996. Effects of branch length on carbon isotope discrimination in *Pinus radiata*. *Tree Physiol.* 16:281–86

Walker CD, Brunel JP. 1990. Examining evapotranspiration in a semi-arid region using stable isotopes of hydrogen and oxygen. *J. Hydrol.* 118:55–76

Walker G, Brunel J-P, Dighton J, Holland K, Leaney F, et al. 2001. The use of stable isotopes of water for determining sources of water for plant transpiration. See Unkovich et al. 2001, pp. 57–89

Wallace LL, Macko SA. 1993. Nutrient acquisition by clipped plants as a measure of competitive success: the effects of compensation. *Funct. Ecol.* 7:326–31

Wallander H, Arnebrant K, Östrand F, Kårén O. 1997. Uptake of ^{15}N-labelled alanine,

ammonium and nitrate in *Pinus sylvestris* L. ectomycorrhiza growing in forest soil treated with nitrogen, sulphur or lime. *Plant Soil* 195:329–38

Wang XF, Yakir D. 1995. Temporal and spatial variations in the oxygen-18 content of leaf water in different plant species. *Plant Cell Environ.* 18:1377–85

Ward JK, Dawson TE, Ehleringer JR. 2002. Responses of *Acer negundo* genders to interannual differences in water availability determined from carbon isotope ratios of tree ring cellulose. *Tree Physiol.* 22:339–46

Warembourg FR. 1993. Nitrogen fixation in soil and plant systems. See Knowles & Henry Blackburn 1993, pp. 127–56

Waring RH, Silvester WB. 1994. Variation in foliar $\delta^{13}C$ values within the crowns of *Pinus radiata* trees. *Tree Physiol.* 14:1203–13

Warren CR, Adams MA. 2000. Water availability and branch length determine $\delta^{13}C$ in foliage of *Pinus pinaster*. *Tree Physiol.* 10:637–44

Warren CR, McGrath JF, Adams MA. 2001. Water availability and carbon isotope discrimination in conifers. *Oecologia* 127:426–86

Watkins NK, Fitter AH, Graves JD, Robinsson D. 1996. Carbon transfer between C3 and C4 plants linked by a common mycorrhizal network, quantified using stable carbon isotopes. *Soil Biol. Biochem.* 28:471–77

Welker JM, Wookey PA, Parsons AN. 1993. Leaf carbon isotope discrimination and vegatative responses of *Dryas octopetala* to temperature and water manipulations in a High Arctic polar semi-desert, Svalbard. *Oecologia* 95:463–69

Wershaw RL, Friedman I, Heller SJ. 1966. Hydrogen isotope fractionation of water passing through trees. In *Advances in Organic Geochemistry*, ed. F Hobson, M Speers, pp. 55–67. New York: Pergamon

White JWC. 1989. Stable hydrogen isotope ratios in plants: a review of current theory and some potential applications. See Rundel et al. 1989, pp. 142–62

White JWC, Cook ER, Lawrence JR, Broecker WS. 1985. The deuterium to hydrogen ratios of sap in trees: implications for water sources and tree ring deuterium to hydrogen ratios. *Geochim. Cosmochim. Acta* 49:237–46

Wickman FE. 1952. Variations in the relative abundance of the carbon isotopes in plants. *Geochim. Cosmochim. Acta* 2:243–54

Williams DG, Ehleringer JR. 1996. Carbon isotope discrimination in three semi-arid woodland species along a monsoon gradient. *Oecologia* 106:455–60

Williams DG, Ehleringer JR. 2000a. Carbon isotope discrimination and water relations of oak hybrid populations in southwestern Utah. *West. N. Am. Nat.* 60:121–29

Williams DG, Ehleringer JR. 2000b. Intra- and interspecific variation for summer precipitation use in pinyon-juniper woodlands. *Ecol. Monogr.* 70:517–37

Williams DG, Gempko V, Fravolini A, Leavitt SW, Wall GW, et al. 2001. Carbon isotope discrimination by *Sorghum bicolor* under CO_2 enrichment and drought. *New Phytol.* 150:285–93

Williams K, Richards JH, Caldwell MM. 1991. Effect of competition on stable carbon isotope ratios of two tussock grass species. *Oecologida* 88:148–51

Williams TG, Flanagan LB. 1996. Effect of changes in water content on photosynthesis, transpiration and discrimination against $^{13}CO_2$ and $C^{18}O^{16}O$ in *Pleurozium* and *Sphagnu*m. *Oecologia* 108:38–46

Williams TG, Flanagan LB. 1998. Measuring and modelling environmental influences on photosynthetic gas exchange in *Spagnum* and *Pleurozium*. *Plant Cell Environ.* 21:555–64

Wilson EJ, Tiley C. 1998. Foliar uptake of wet-deposited nitrogen by Norway spruce: an experiment using ^{15}N. *Atmos. Environ.* 32:513–18

Winkler FJ, Wirth E, Latzko E, Schmidt HL, Hoppe W, Wimmer P. 1978. Influence of growth conditions and development on ^{13}C values in different organs and constituents of wheat, oat, and maize. *Z. Pflanzenphysiol.* 87:255–63

Yakir D. 1992. Variations in the natural

abundance of oxygen-18 and deuterium in plant carbohydrates. *Plant Cell Environ.* 15: 1005–20

Yakir D. 1998. Oxygen-18 of leaf water: a crossroad for plant-associated isotopic signals. See Griffiths 1998, pp. 147–68

Yakir D, Sternberg LDL. 2000. The use of stable isotopes to study ecosystem gas exchange. *Oecologia* 123:297–311

Yakir D, Wang X-F. 1996. Fluxes of CO_2 and water between terrestrial vegetation and the atmosphere estimated from isotope measurements. *Nature* 380:515–17

Yoder BJ, Ryan MG, Waring RH, Schoettle AW, Kaufmann MR. 1994. Evidence of reduced photosynthetic rates in old trees. *For. Sci.* 40:513–27

Yoneyama T. 1996. Characterization of natural ^{15}N abundance of soils. In *Mass Spectrometry of Soils*, ed. TW Boutton, S Yamasaki, pp. 205–23. New York: Dekker

Yoneyama T, Handley LL, Scrimgeour CM, Fisher DB, Raven JA. 1997. Variations of the natural abundances of nitrogen and carbon isotopes in *Triticum aestivum*, with special reference to phloem and xylem exudates. *New Phytol.* 137:205–13

Yoneyama T, Kaneko A. 1989. Variations in the natural abundance of ^{15}N in nitrogenous fractions of Komatsuna plants supplied with nitrate. *Plant Cell Physiol.* 30:957–62

Yoneyama T, Matsumaru T, Usui K, Engelaar WMHG. 2001. Discrimination of nitrogen isotopes during absorption of ammonium and nitrate at different nitrogen concentrations by rice (*Oryza sativa* L.) plants. *Plant Cell Environ.* 24:133–39

Zak DR, Groffman PM, Pregitzer KS, Christensen S, Tiedje JM. 1990. The vernal dam: plant-microbe competition for nitrogen in northern Michigan, USA hardwood forests. *Ecology* 71:651–56

Zhang JW, Marshall JD. 1995. Variation in carbon isotope discrimination and photosynthetic gas exchange among populations of *Pseudotsuga mensiesii* and *Pinus ponderosa* in different environments. *Funct. Ecol.* 9:402–12

Zhang JW, Marshall JD, Jaquish BC. 1993. Genetic differentiation in carbon isotope discrimination and gas exchange in *Pseudotsuga mensiesii*: a common garden experiment. *Oecologia* 93:80–87

Zencich SJ, Froend RH, Turner JV, Gailitis. 2002. Influence of groundwater depth on the seasonal sources of water access by *Banksia* tree species on a shallow, sandy coastal aquifer. *Oecologia* 131:8–19

Zimmerman JK, Ehleringer JR. 1990. Carbon isotope ratios are correlated with irradiance levels in the Panamanian orchid *Catasetum viridiflavum. Oecologia* 83:247–49

Zogg GP, Zak DR, Pregitzer KS, Burton AJ. 2000. Microbial immobilization and the retention of anthropogenic nitrate in a northern hardwood forest. *Ecology* 81:1858–66