

Carbon isotope discrimination of terrestrial ecosystems

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13.1 Introduction

13.1.1 Use of ^{13}C at the ecosystem level

Detailed knowledge of the interactions between the atmosphere, biosphere and pedosphere is essential for an understanding of global carbon dynamics in terrestrial ecosystems. Understanding these linkages has become even more crucial as atmospheric carbon dioxide concentrations ($[\text{CO}_2]$) continue to increase (Conway *et al.*, 1988; Conway *et al.*, 1994; Komhyr *et al.*, 1985). In this context, stable isotopes have proved useful as indicators of the constraints on global carbon budgets (Tans *et al.*, 1996). Since tropospheric and respired CO_2 from terrestrial ecosystems have very different carbon isotope ratios (approximately -8‰ and -27‰ , respectively), these CO_2 sources can be differentiated, and the coupling of terrestrial and atmospheric carbon fluxes can be addressed (Keeling, 1958; Lloyd *et al.*, 1996; Sternberg, 1989; Tans *et al.*, 1990). Global circulation models have suggested a large carbon sink (either oceanic or terrestrial) in the Northern Hemisphere (Bender *et al.*, 1996; Ciais *et al.*, 1995; Denning *et al.*, 1995; Francey *et al.*, 1995; Keeling *et al.*, 1996; Tans *et al.*, 1990; see Chapter 24). Carbon isotope ratios ($\delta^{13}\text{C}$) of atmospheric carbon dioxide have been used in inverse global models (i.e. using a top-down approach) not only to determine the global distribution of carbon sinks, but also to quantify the relative contribution of oceans and terrestrial plants to the carbon removal from the atmosphere (Ciais *et al.*, 1995; Francey *et al.*, 1995; Keeling *et al.*, 1984; Mook *et al.*, 1983). However, lacking sufficient data from terrestrial ecosystems, important physiologically-based input parameters such as the ratio of internal to atmospheric $[\text{CO}_2]$ (C_i/C_a), and the carbon isotopic composition of respired CO_2 have been estimated using models for the dominant plant species within different biomes (but see Chapter 8). Further uncertainties

arise because of the regional and temporal variability of these estimates, and due to disequilibrium effects. Better quantification of ecophysiological parameters and an understanding of seasonal variation in these parameters could prove useful in identifying potential mechanisms constraining atmosphere/terrestrial ecosystem models.

13.1.2 Carbon isotope discrimination within ecosystems

Lloyd and Farquhar (1994) modelled the carbon isotope discrimination ($\Delta^{13}\text{C}^{16}\text{O}^{16}\text{O}$) of entire canopies (Δ_A), with the aim of integrating across plants present within an ecosystem. Separating biomes, they estimated Δ_A globally, using data sets for ecophysiological parameters from the dominant plant species (stomatal responses to leaf-to-air vapour pressure differences (VPD) mol fraction differences), and for climate (temperature, precipitation, and relative humidity), which was then scaled for the global distribution of vegetation. Lloyd and Farquhar (1994) then validated their model by calculating the difference between the $\delta^{13}\text{C}$ of atmospheric CO_2 within the nocturnal boundary layer and estimates of $\delta^{13}\text{C}$ of respired CO_2 : differences from the 1:1 line were less than 2.5 ‰. This modeling effort provided encouraging support for such a bottom-up approach, but some initial caution is necessary since the two terms compared integrate over very different temporal as well as spatial scales: Δ_A estimates integrate over periods of as long as a single growing season and represent values of a few dominant canopy forming (overstory) species only.

However, the estimates for $\delta^{13}\text{C}$ of respired CO_2 (Keeling, 1958; see Section 13.2.3) represent the carbon respired by all species (over- and understory vegetation), and also that respired by roots and microorganisms in the soil. In addition, the time scale represented by the respiration estimates is longer than a single growing season: turnover rates vary with mean annual temperature (Trumbore *et al.*, 1996), with relatively fast turnover in tropical forests (~5 years), but much slower turnover in temperal and boreal forests (as long as 100 years; Bird *et al.*, 1996). Thus, $\delta^{13}\text{C}$ of respired CO_2 will integrate carbon isotope composition of foliage and litter over much longer time spans than the Δ_A estimates. Additionally, land use changes account for the vast majority of the current global vegetation change (Houghton, 1995), and therefore $\delta^{13}\text{C}$ of soil organic carbon and soil respired CO_2 is more likely to be representative of the actual carbon released than is the current plant cover. Hence, in order to describe the impact that ecosystems have on the $\delta^{13}\text{C}$ of the atmosphere, one should consider not only the carbon isotope discrimination during current photosynthesis, but also the large historic signal recorded in the soil carbon stocks (Bird *et al.*, 1996; Trumbore *et al.*, 1996). Therefore, it seems appropriate to use a temporally and spatially integrated measure of ecosystem carbon isotope discrimination that includes soil carbon.

As a next step from the canopy discrimination Δ_A (Lloyd and Farquhar, 1994), we introduce Δ_c , a term that describes the carbon isotope discrimination of an entire ecosystem, including the soil compartment (Equation 13.1).

$$\Delta_c = \frac{\delta^{13}\text{C}_r - \delta^{13}\text{C}_R}{1 + \delta^{13}\text{C}_R} \quad (13.1)$$

where $\delta^{13}\text{C}_r$ is the carbon isotope ratio of the troposphere and $\delta^{13}\text{C}_R$ the carbon isotope ratio of CO_2 respired by soil microorganisms and vegetation (below- and above-ground). We use the $\delta^{13}\text{C}$ of respired CO_2 as an integrated value for the carbon isotopic

composition of all organic matter in an ecosystem, representing carbon both in soils and vegetation. Since there is no fractionation during mitochondrial respiration (Lin and Ehleringer, 1997), the $\delta^{13}\text{C}$ of ecosystem respiration best represents all organic carbon in this ecosystem. Thus, the familiar concept of carbon isotope discrimination at the leaf level is transferred to the ecosystem level (Figure 13.1). The individual terms of the equation for leaf level carbon isotope discrimination (Δ_l ; see Chapter 8) are substituted by the appropriate terms for the ecosystem level: $\delta^{13}\text{C}_a$ with $\delta^{13}\text{C}_T$ and $\delta^{13}\text{C}_l$ with $\delta^{13}\text{C}_R$. Δ_e is based on $\delta^{13}\text{C}$ of tropospheric CO_2 and on field measurements of canopy air to estimate $\delta^{13}\text{C}$ of ecosystem respired CO_2 . Thus, Δ_e integrates not only over Δ_l of all photosynthesising leaves but also includes information about the $\delta^{13}\text{C}$ of soil organic matter (for detailed information about how to calculate Δ_e see Section 13.3.3).

Recent studies have built on the pioneering work of Keeling (1958) to describe relationships between CO_2 concentration ($[\text{CO}_2]$) and $\delta^{13}\text{C}$ within and above canopies. The results of these studies can be used to estimate $\delta^{13}\text{C}$ of respired CO_2 for a wide range of different ecosystems, including tropical forests (Broadmeadow *et al.*, 1992; Buchmann *et al.*, 1997a; Francey *et al.*, 1985; Lancaster, 1990; Lloyd *et al.*, 1996; Quay *et al.*, 1989; Sternberg *et al.*, 1989), temperate forests (Buchmann *et al.*, 1997b,c; Keeling 1961a,b; Lancaster, 1990), boreal forests (Flanagan *et al.*, 1996), and agricultural ecosystems (Buchmann and Ehleringer, 1997; Yakir and Wang 1996). Models of turbulent mixing of canopy air with the convective boundary layer (CBL) or the free troposphere provided detailed insight into how canopy gradients of $[\text{CO}_2]$ and $\delta^{13}\text{C}$ develop (Grace *et al.*, 1995; Kruijt *et al.*, 1996; Lloyd *et al.*, 1996; Quay *et al.*, 1989; Yakir and Wang 1996). Thus, combining these datasets with an understanding of

Carbon isotope discrimination (Δ)

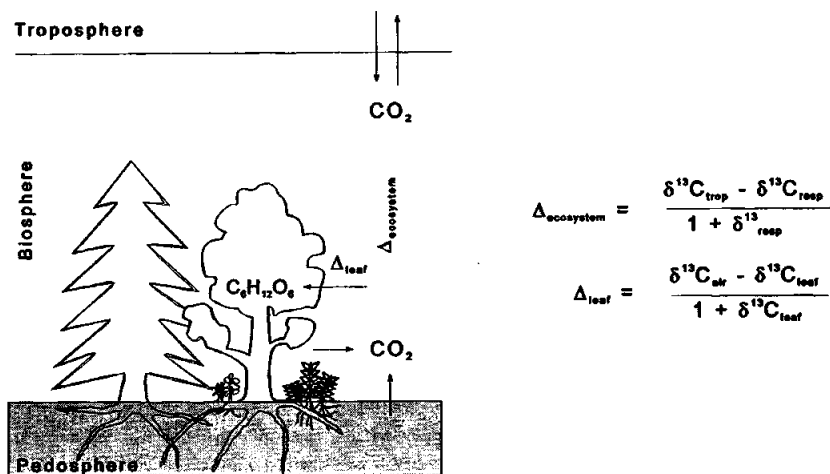


Figure 13.1. Conceptual model of carbon isotope discrimination within a terrestrial ecosystem.

canopy processes and their interactions with the atmosphere could be a valuable and promising approach to describe ecosystem functioning, especially with regard to climate change (Houghton *et al.*, 1996).

In this chapter, we will address ecosystem level variation of Δ_c , possible impacts of seasonality, of characteristic features of the dominant plant species within an ecosystem (life form, canopy structure, age) as well as the influence of climate and soil nutrient availability.

13.2 Methodology

This section introduces the methods needed to calculate ecosystem carbon isotope discrimination as described in Equation 13.1. We first focus on where to obtain tropospheric baseline data, and then discuss how to determine $\delta^{13}\text{C}$ of respired CO_2 . Potential sources of errors associated with Δ_c estimates will be addressed before we will give an overview about recent research about Δ_c in Section 13.3.

13.2.1 Isotope ratios

Carbon isotope ratios ($\delta^{13}\text{C}$) are calculated as

$$\delta^{13}\text{C} = 1000 \cdot \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \quad (13.2)$$

where R_{sample} and R_{standard} are the $^{13}\text{C}/^{12}\text{C}$ ratios of the sample and the standard (VPDB), respectively (Farquhar *et al.*, 1989). The overall precision of carbon isotope measurements with modern dual-inlet isotope ratio mass spectrometers is generally better than 0.03‰ for carbon in gas samples (with 100 μL CO_2 ; 10 μL CO_2 with a coldfinger). If a continuous flow mass spectrometer with a preconcentrator is available (conflow/precon), then precision for carbon isotope analysis is about 0.3‰ (with 0.2 μL CO_2).

13.2.2 Tropospheric baseline data for $[\text{CO}_2]$ and $\delta^{13}\text{C}$

Tropospheric baseline $[\text{CO}_2]_{\text{T}}$ have been measured on a regular basis since the International Geophysical Year (1958), and since then a steadily increasing number of land and oceanic stations have been established to monitor background levels of $[\text{CO}_2]$ globally. Keeling started $[\text{CO}_2]_{\text{T}}$ and $\delta^{13}\text{C}_{\text{T}}$ measurements at the South Pole in 1957 (Keeling *et al.*, 1976), and at Mauna Loa, Hawaii in 1958 (Pales and Keeling, 1965), which later became the SIO network (Scripps Institution of Oceanography). A second CO_2 flask sampling program, measuring first at Niwot Ridge, Colorado, and at Ocean Station 'Charlie' in the North Atlantic, followed in 1968. It was continuously expanded to become the present NOAA/CMDL Cooperative Flask Sampling Network (National Oceanic and Atmospheric Administration/Climate Monitoring and Diagnostics Laboratory), which today includes 43 stations and two cruise tracks in the South China Sea and the Pacific Ocean (Ciais *et al.*, 1995; Conway *et al.*, 1988; Conway *et al.*, 1994; Komhyr *et al.*, 1985). Since 1990, the INSTAAR (Stable Isotope Laboratory at the Institute of Arctic and Alpine Research) has been measuring tropospheric $\delta^{13}\text{C}_{\text{T}}$ ratios, complementing the concentration measurements of the

NOAA/CMDL network (Ciais *et al.*, 1995). Since 1982, $[\text{CO}_2]_{\text{T}}$ and $\delta^{13}\text{C}_{\text{T}}$ data have also been available from the CSIRO network (Commonwealth Scientific and Industrial Research Organization), including sites at high southern latitudes such as Cape Grim (Francey *et al.*, 1995). Recent efforts have expanded the existing sampling networks by creating a Global Carbon Cycle Observing System, which has the advantage of increasing spatial integration and achieving a better separation between natural variability and expected signals in response to increased atmospheric $[\text{CO}_2]$ (Tans *et al.*, 1996; see Chapter 24). All $[\text{CO}_2]$ data (unfortunately not $\delta^{13}\text{C}$) have been archived and summarized through the Carbon Dioxide Information Analysis Center at the Oak Ridge National Laboratory (e.g. Boden *et al.*, 1994). Data compilations are updated regularly, and also provide data from other national networks.

Within these networks, air samples are collected mainly in remote areas (oceanic or coastal sites, deserts, maintaintops) where $[\text{CO}_2]$ is not or least affected by local CO_2 sources and sinks. Thus, they represent almost free tropospheric air, although flasks are collected at 1 m height above the ground (SIO, at 7 and 27 m; NOAA/CMDL, some tall towers up to 500 m). Generally, replicate flasks are sampled weekly or biweekly during daytime hours (SIO, hourly), and analysed at one central laboratory for each network. We recommend using tropospheric $[\text{CO}_2]_{\text{T}}$ and $\delta^{13}\text{C}_{\text{T}}$ measured at a station as close as possible to the site under study (for discussion of errors, see Section 13.2.5).

13.2.3 Estimates of $\delta^{13}\text{C}$ of respired CO_2

For estimating ecosystem carbon isotope discrimination, the $\delta^{13}\text{C}$ of respired CO_2 should represent a weighted average of all respiration processes within the ecosystem. Because soil respiration chambers cover only a relatively small area and do not include foliage and branch/stem respiration, we discourage the use of such chambers to determine $\delta^{13}\text{C}_{\text{R}}$. Instead, to incorporate all respiratory processes within an ecosystem, we recommend using the so-called 'Keeling plot' method: canopy air samples are collected at times providing a wide range of $[\text{CO}_2]_{\text{a}}$, and their $[\text{CO}_2]$ and $\delta^{13}\text{C}$ ratios are analysed. Using a regression approach (see below), $\delta^{13}\text{C}_{\text{R}}$ of ecosystem respiration can be determined. Thus, all respiration fluxes are covered and weighted by their respective flux rates. In addition, this technique will average respiration over a larger ground area than is typically possible by using chamber or enclosure techniques.

Keeling (1958) observed that when measuring atmospheric air, the $[\text{CO}_2]_{\text{a}}$ and its $\delta^{13}\text{C}_{\text{a}}$ changed in concert in a predictable manner. If $1/[\text{CO}_2]_{\text{a}}$ is plotted against the corresponding $\delta^{13}\text{C}_{\text{a}}$ values (so-called 'Keeling plot'), a linear relationship is obtained (Figure 13.2). This relationship reflects the mixing of tropospheric CO_2 with an additional CO_2 source that is depleted in ^{13}C compared to the troposphere. The following linear equation describes the mixing model adequately (Keeling, 1961a,b):

$$\delta^{13}\text{C}_{\text{a}} = \frac{[\text{CO}_2]_{\text{T}}}{[\text{CO}_2]_{\text{a}}} \cdot (\delta^{13}\text{C}_{\text{T}} - \delta^{13}\text{C}_{\text{R}}) + \delta^{13}\text{C}_{\text{R}} \quad (13.3)$$

The intercept of this equation has been used to identify the carbon isotope ratio of the additional CO_2 source, for example, in forest canopies, of respired CO_2 ($\delta^{13}\text{C}_{\text{R}}$). The linear regression equation describes day and nighttime data very well, and r^2 are generally greater than 0.9.

Paracou, French Guiana

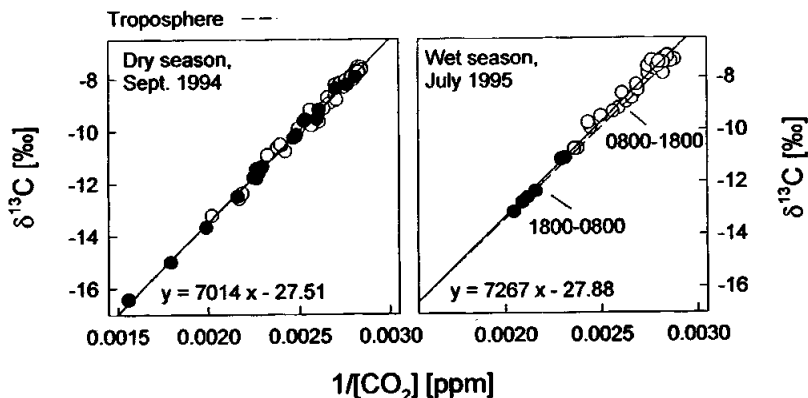


Figure 13.2. Relationship between $1/[\text{CO}_2]$ and $\delta^{13}\text{C}$ of canopy air in a primary tropical rainforest in French Guiana (after Buchmann *et al.*, 1997a).

13.2.4 Collection and analysis of canopy air

To determine the $\delta^{13}\text{C}$ of respired CO_2 accurately by using the 'Keeling plot' method, it is crucial to obtain very reliable estimates of the regression coefficients. Thus, canopy air must be sampled over a wide range of $[\text{CO}_2]$ (> 50 ppm), and both $[\text{CO}_2]$ and $\delta^{13}\text{C}$ need to be measured with high precision. How does one achieve a wide $[\text{CO}_2]$ range? $[\text{CO}_2]$ and $\delta^{13}\text{C}$ values change vertically and daily. Vertical CO_2 profiles are typically rather uniform during the day within the main canopy, except near to the soil surface, where $[\text{CO}_2]$ and $\delta^{13}\text{C}$ change, sometimes drastically (Brooks *et al.*, 1997a; Buchmann and Ehleringer, 1997; Buchmann *et al.*, 1996, 1997a-c; Flanagan *et al.*, 1996; Lloyd *et al.*, 1996). If understory vegetation is present, profiles can be strongly influenced by understory gas exchange (Buchmann *et al.*, 1997b). Six canopy air samples per height profile proved to be sufficient to characterise a canopy, with a sampling emphasis on lower heights where changes in $[\text{CO}_2]$ and $\delta^{13}\text{C}$ are more pronounced. If air is collected above the actual plant canopy, fetch size should be considered to identify potential additional sources of CO_2 (Gash 1986; Schuepp *et al.*, 1990). For example, fetch size for a 1.5 m tall crop canopy increases from 15 m to 125 m if the instrumental plane is moved from 1.5 m up to 2.5 m height; for a 10 m tall forest canopy, fetch size increases from 100 m to 613 m if the instrumental plane is moved from 10 m up to 15 m height (90% fetch, Gash 1986).

$[\text{CO}_2]$ and $\delta^{13}\text{C}$ ratios exhibit a distinct daily course, driven by turbulent mixing with the troposphere as well as by photosynthesis and respiration. $[\text{CO}_2]$ is typically high during times with high respiration and low turbulent mixing (at night). This nocturnal buildup dissipates in the morning when turbulent mixing (due to increasing temperatures) and active photosynthesis set in. $[\text{CO}_2]$ normally stays low during the day until the evening when temperatures, and therefore turbulent mixing, decrease

and respiration again prevails. We recommend collecting flasks during the nocturnal build-up, but also include some daytime samples to increase the coverage of a wide range of $[\text{CO}_2]$, and maybe even include flasks collected during a pronounced photosynthetic depletion in canopy $[\text{CO}_2]$ below tropospheric background concentrations. We have measured nighttime $[\text{CO}_2]$ gradients between 75 ppm and 140 ppm and daytime gradients between 6 ppm and 100 ppm in forest canopies, but for adequate accuracy to estimate $\delta^{13}\text{C}_\text{R}$, we recommend a range of 50 ppm or greater. Our experiences from several dozen forest stands showed that day and night data lie on the same regression line. Thus, increasing the range of the independent variable ($1/[\text{CO}_2]$) for the regression analysis by daytime samples will increase the precision of the regression technique and yield a more realistic estimate of the regression coefficients.

Canopy air should be collected dry, and stored in inert flasks that do not leak or exchange CO_2 (e.g. made of glass), with seals that do not exchange with CO_2 . We collected air for isotopic analyses by pumping dry air through pre-evacuated glass sampling flasks with two high-vacuum stopcocks. Care should be taken to flush the flask several times with canopy air, before the flask is closed, and returned to the lab for isotopic analysis. The size of the flask will depend on the method of CO_2 purification and carbon isotope analysis. For example, if the flasks are extracted manually using a vacuum extraction line (see below), and a modern mass spectrometer is used for isotope analysis, 1.7 to 2 l flasks filled with ambient $[\text{CO}_2]$ are sufficient for high precision carbon isotope determinations. Flask volumes might decrease if a cold finger or a preconcentrator is used. We generally collected 15–30 flasks to estimate Δ_c for a given ecosystem.

The concentration of CO_2 in the flask should be determined as precisely as possible, because the accuracy of this measurement will strongly affect the error associated with the intercept (see Section 13.2.5). We generally used an infra-red gas analyser (IRGA) to measure the $[\text{CO}_2]$ of the air being pumped out of the sampling flask while we were collecting samples in the field. These analysers are accurate to 0.1 ppm.

Before isotope ratios of CO_2 can be analysed, CO_2 is separated from other gases present in the canopy air sample. This can be done either on-line (e.g. using a gas chromatograph on-line with the mass spectrometer) or off-line. In the case of off-line preparation, CO_2 is extracted cryogenically using a three-trap vacuum line (each trap with a double loop), and transferred into a sampling tube (for more details, see Ehleringer, 1991). The first trap (ethanol-dry ice slurry at -86°C) is used to freeze water, the other two traps (liquid nitrogen) to collect CO_2 . This technique will also trap nitrous oxide (N_2O) which condenses with CO_2 at liquid nitrogen temperatures. CO_2 should be separated from N_2O prior to isotope analysis, either by combustion with copper oxide wire (not applicable if $\delta^{18}\text{O}$ is of interest as well) or by using a gas chromatograph. If $\delta^{18}\text{O}$ is of interest as well, but a gas chromatograph is unavailable, a correction factor can be applied after carbon and oxygen analyses of the $\text{CO}_2/\text{N}_2\text{O}$ gas mixture (Friedli and Siegenthaler, 1988; Mook and van der Hoek, 1983; Mook and Jongsma, 1987). A detailed discussion of the limitations to sampling and analysis of $\delta^{18}\text{O}$ in CO_2 is given in Chapter 24.

13.2.5 Expected errors associated with Δ_c estimates

Two major sources of error should to be considered for Δ_c estimates, these are errors associated with the $\delta^{13}\text{C}$ of tropospheric CO_2 and the $\delta^{13}\text{C}$ of respired CO_2 . The precision of the tropospheric background data, for example collected by NOAA/CMDL

is < 0.5 ppm for $[\text{CO}_2]$, and $\pm 0.03\text{‰}$ for $\delta^{13}\text{C}$. Natural temporal variability for baseline data, collected at the same station over a one month period is less than 0.2‰ (M. Trolier personal communication). Further isotopic shifts may occur as the air mass moves above continental areas before it reaches the study area. However, variability between stations at a similar latitude is between 0.5 and 1 ppm and around 0.25‰ (see Conway *et al.*, 1994; Ciais *et al.*, 1995 respectively; see Chapter 24).

The largest error for the Δ_c estimates is associated with the estimates of $\delta^{13}\text{C}_R$. Owing to the nature of regression analyses, the accuracy of the regression equation increases with sample number, and the spread of the data over the entire range of the independent variable (in our case, $1/[\text{CO}_2]$). This is of special importance, because the 'Keeling plot' method requires extrapolating an intercept that is far beyond the range of measured values. Furthermore, slopes and intercepts should be calculated by geometric mean regressions, because both x and y variables are associated with an error ($1/[\text{CO}_2]$ as well as $\delta^{13}\text{C}$) (Sokal and Rohlf, 1981). After using this approach for 49 different stands in ten different ecosystems, the standard error for $\delta^{13}\text{C}$ of respired CO_2 averaged ± 0.98 (SE ± 0.10) ‰ , with an absolute range from 0.2‰ to 4.0‰ .

13.3 Variation in Δ_c estimates

13.3.1 Evergreen versus deciduous forests

Natural landscapes comprise mosaics of evergreen and deciduous ecosystems, most pronounced in temperate and boreal regions. Information about the influence of different life forms on ecophysiological processes is therefore critical for our understanding what controls carbon dynamics in evergreen and deciduous forest ecosystems, and how to integrate over diverse regions.

Higher intrinsic water-use efficiencies (WUEs), lower stomatal conductance and lower photosynthetic rates have often been observed for evergreen compared with deciduous trees (e.g. Chabot and Hicks, 1982; Körner, 1994; Schulze, 1982), but this is not always the case (Sobrado and Ehleringer, 1997). Although evergreen forests may tend to support a larger leaf area index (LAI), a comparison of $[\text{CO}_2]$ and $\delta^{13}\text{C}$ profiles between deciduous and evergreen canopies has shown that $[\text{CO}_2]$ and $\delta^{13}\text{C}$ gradients are larger in deciduous than in evergreen forests, despite a similar overall shape of these profiles (Brooks *et al.*, 1997a; Buchmann *et al.*, 1997b,c). This observation was made for forest ecosystems in very different environments (for the boreal forest and for dry temperate mountain sites) as well as for non-average years with regard to precipitation and temperature.

However, Δ_c estimates for deciduous and evergreen forests growing within the same region tend to be similar, independent of biome (Table 13.1). Differences between deciduous and evergreen stands were smaller than the natural variability within a life form ($< 0.9\text{‰}$). These results illustrate a potential difficulty associated with scaling leaf-level patterns to the ecosystem level. At the leaf level, ecophysiological differences between deciduous and evergreen shrubs and trees might be reflected in different Δ_l values (Brooks *et al.*, 1997b; Marshall and Zhang, 1994). However, at the higher organisational level of the ecosystem, carbon isotope discrimination seemed to be dominated by different mechanisms and differences between deciduous and evergreen forests were smaller. This overall similarity of Δ_c might be a potential advantage to model carbon dynamics in highly diverse landscapes such as a mosaic of evergreen and deciduous forests.

Table 13.1. Comparison of Δ_c among deciduous and evergreen forest ecosystems, averaged over one growing season (mean \pm SE, $3 \leq n \leq 8$). From Flanagan et al., (1996); Buchmann et al., (1997b).

Life form	Species	Δ_c
Boreal (Man., Canada)		
Deciduous	<i>Populus tremuloides</i>	18.8 \pm 0.5‰
Evergreen	<i>Picea mariana</i>	19.0 \pm 0.2‰
	<i>Pinus banksiana</i>	18.9 \pm 0.2‰
Boreal (Sask., Canada)		
Deciduous	<i>Populus tremuloides</i>	19.3 \pm 0.6‰
Evergreen	<i>Picea mariana</i>	18.5 \pm 0.1‰
	<i>Pinus banksiana</i>	19.0 \pm 0.1‰
Temperate (UT, USA)		
Deciduous	<i>Populus tremuloides</i>	18.0 \pm 0.7‰
Evergreen	<i>Pinus contorta</i>	18.3 \pm 0.9‰

13.3.2. Stand structure

Forest architecture can be described by an array of different parameters such as the height of the dominant vegetation, the stand density, the LAI, the foliage distribution as well as the presence or absence of understorey vegetation. All of these parameters can be highly variable, spatially as well as temporally. We tested the effect of stand LAI on Δ_c by comparing stands ranging in LAI from 1.4 to 9.2, including evergreen and deciduous forests from boreal and temperate ecosystems (Figure 13.3). In boreal ecosystems, coniferous forests (either *Picea mariana* or *Pinus banksiana*) showed similar Δ_c estimates to deciduous forests (*Populus tremuloides*) (Figure 13.3), even though the LAI of the *Picea mariana* stands were about four times larger than those of the *Pinus banksiana* stands (Flanagan et al., 1996). Furthermore, these estimates were relatively stable at the regional scale. Stands at both southern and northern borders of the Canadian boreal forest showed similar Δ_c values: 18.9‰ (*Pinus banksiana*) and 19.0‰ (*Picea mariana*) at the northern border (Manitoba) versus 19.0‰ (*Pinus banksiana*) and 18.5‰ (*Picea mariana*) at the southern border (Saskatchewan). Differences between the two locations averaged about 0.4‰ throughout the growing season (recalculated from Flanagan et al., 1996).

Three *Abies amabilis* stands from the Pacific Northwest, differing in age (between 40 and >220 years old), height (between 8 and 42 m tall) as well as in stand and foliage density (D. G. Sprugel, unpublished data) were also included in this analysis (Buchmann et al., 1997c). [CO_2] and $\delta^{13}\text{C}$ profiles of canopy air were least pronounced in the tall old-growth stand that allowed for relatively free turbulent mixing with the air above the canopy (stand density: 488 trees per ha; LAI 6.4). However, the two younger stands showed lower daytime [CO_2] and more enriched canopy $\delta^{13}\text{C}$ values than the old-growth stand, clearly demonstrating less air turbulence and a large photosynthetic effect in these denser canopies (stand densities between 2241 and 70000 trees per ha, LAI around 9; Buchmann et al., 1997c). However, Δ_c estimates for these wet temperate ecosystems differed at maximum by 0.9‰ (Figure 13.3), although LAI were almost 3 m^2/m^2 larger for the younger stands than for the old-growth stand. Only a weak trend

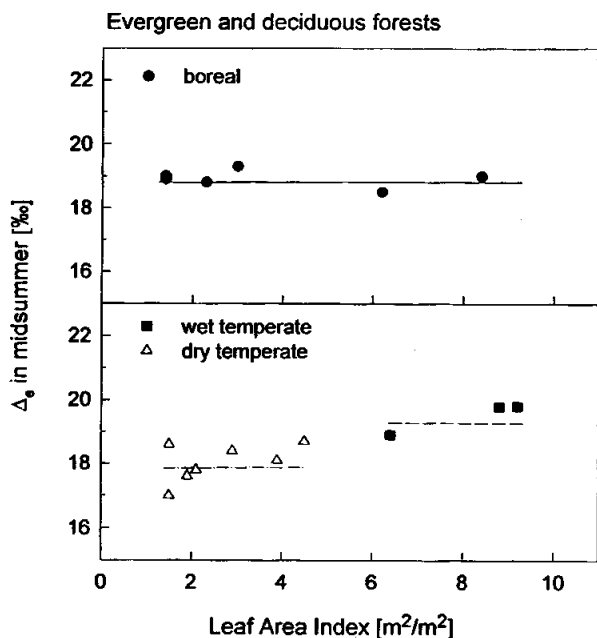


Figure 13.3. Midsummer Δ_c estimates for evergreen and deciduous forest ecosystems in relation to stand leaf area index. Data for boreal forests from Flanagan et al., (1996; *Populus tremuloides*, *Picea mariana*, *Pinus banksiana*), for wet temperate forests from Buchmann et al., (1997c; *Abies amabilis*), and for dry temperate forests from Buchmann et al., (1997b; *Acer ssp.*, *Populus tremuloides*, *Pinus contorta*).

was observed as Δ_c increased slightly with increasing foliage density: the old-growth *Abies amabilis* stand (LAI 6.4, foliage density <1 m³/m² throughout the canopy) had a Δ_c value of 18.9‰. The densest stand (LAI 8.8, peak foliage density of about 4 m³/m²) showed a Δ_c of 19.8‰.

Deciduous stands of *Acer ssp.* and *Populus tremuloides*, growing in the very different environment of dry temperate Utah, also exhibited rather constant Δ_c values as well (Buchmann et al., 1997b). Doubling the overstory LAI in relatively open canopies (LAI <4.5) did not affect upper canopy [CO₂] or $\delta^{13}\text{C}$ nor Δ_c estimates (Figure 13.3). This integrative measure for the entire ecosystem was very similar for open (LAI 2.1: 17.4‰) as well as for dense riparian *Acer ssp.* stands (LAI 4.5: 16.9‰), independent of the presence of a vigorous understory vegetation in the open stand. Thus, differences in forest architecture between stands growing in a similar abiotic environment did not have an effect on Δ_c estimates.

13.3.3. Seasonality

Seasonal effects in tropical forests might be expected to be minor because day length

varies little throughout the year, and temperatures also remain relatively constant. The Δ_e values estimated for a primary tropical rainforest in French Guiana (5° North) were very similar for the wet and the dry seasons (Buchmann *et al.*, 1997a). The seasonal difference between the dry season estimate (20.3‰) and the wet season estimate (20.5‰) was within the experimental error (see Section 13.2.5).

However, temperate and boreal regions are characterised by pronounced seasonal differences of incoming radiation, and temperature. Thus, differences in Δ_e values throughout the growing season were expected to be larger than in tropical forests. However, the seasonal course of Δ_e for three *Abies amabilis* forests in the Pacific Northwest (wet temperate) revealed only very weak patterns throughout the growing season (Figure 13.4;

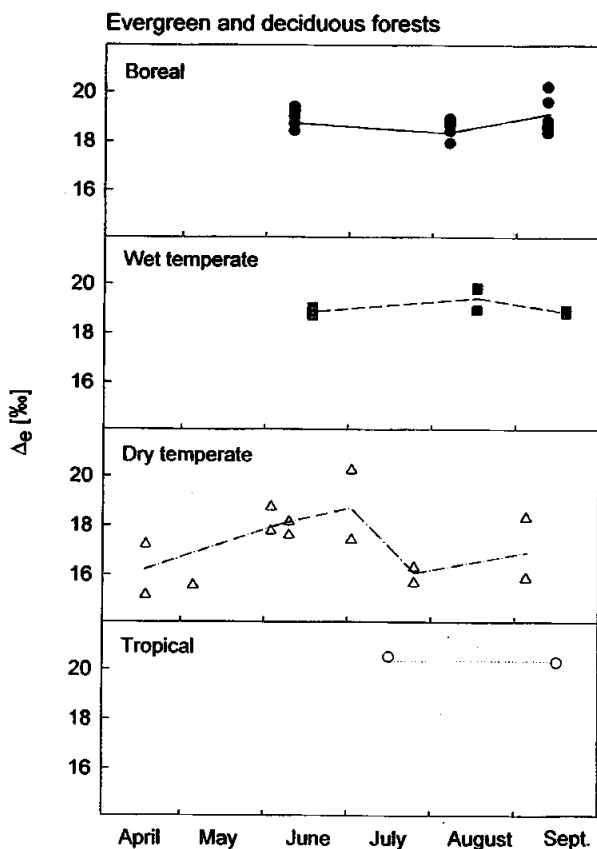


Figure 13.4. Seasonality of Δ_e for evergreen and deciduous forest ecosystems. Data for boreal forests from Flanagan *et al.*, (1996; *Populus tremuloides*, *Picea mariana*, *Pinus banksiana*), for wet temperate forests from Buchmann *et al.*, (1997c; *Abies amabilis*), for dry temperate forests from Buchmann *et al.*, (1997b; *Acer ssp.*), and for tropical forests from Buchmann *et al.*, (1997a).

Buchmann *et al.*, 1997c). Maximum differences between the stands were less than 1‰, well within the natural variability of $\delta^{13}\text{C}$ values of respired CO_2 . Although seasonal changes in Δ_c were small, they were consistent for both younger stands: August Δ_c values tended to be slightly higher than those of June or September. A similar trend with higher summertime Δ_c estimates was observed in a very different environment, in dry temperate Utah (Buchmann *et al.*, 1997b). We measured $[\text{CO}_2]$ and $\delta^{13}\text{C}$ of canopy air during two growing seasons in two riparian *Acer* spp. stands, differing in overstory LAI (LAI 2.1 and 4.5). Although the seasonal pattern of Δ_c within these deciduous multi-layered canopies as larger than in the tropical and the wet temperate forests, seasonal effects were not significant. A similar weak seasonal trend was seen in boreal forests. This common pattern for evergreen as well as deciduous forest ecosystems suggests either a strong regulation of canopy carbon and water fluxes, keeping Δ_c and therefore ecosystem intrinsic WUE constant, or the effects of changing leaf level carbon discrimination are swamped out by more constant soil biological processes.

13.3.4. Site history

Estimates of Δ_c are dependent on the $\delta^{13}\text{C}$ of ecosystem respiration (see Equation 13.1). Generally, one assumes that $\delta^{13}\text{C}$ of respired CO_2 is close to the carbon isotopic composition of the dominant vegetation, even if it represents a pooled value integrating over several decades. However, under certain circumstances, this might not be the case. Two examples illustrate this point: the agricultural practice of crop rotation, and land use changes such as the conversion of tropical forests to C_4 pastures.

Schönwitz *et al.*, (1986) measured the $\delta^{13}\text{C}$ values of CO_2 evolved during soil respiration on sites with C_3 and C_4 crops. A C_3 soil cropped with corn for about one year showed intermediate $\delta^{13}\text{C}$ values of soil respired CO_2 , indicating that about 30% of the respired carbon originated from C_4 residues. Other studies supported these results and have shown that soil organic carbon was a mixture of different crop generations (Table 13.2). Our study with C_4 and C_3 crop canopies also clearly demonstrated the importance of site history (Buchmann and Ehleringer, 1997). Although the recent plant cover had very distinct leaf $\delta^{13}\text{C}$ values (Table 13.2), the Δ_c estimates were not very different from each other, and averaged 13.2‰ for corn and 13.8‰ for alfalfa canopies. However, this implies that in spite of differences in the photosynthetic pathway of both crop species (C_4 vs. C_3), no differences existed in the $\delta^{13}\text{C}$ value of respired CO_2 . Why? The agricultural practice at these particular sites included crop rotation each 5 years. Thus, soil organic carbon (SOC) and CO_2 efflux were mixtures of litter from previous years of cropping and the current vegetation cover. Calculating the origin of respired carbon revealed that for both crop sites, about 35–40% originated from C_4 material and about 60% from C_3 material. These observations indicated a fast turnover rate for soil carbon and were within the range given in other studies (Table 13.2). The clearing of tropical forests and the subsequent conversion into C_4 pastures has a similar effect as crop rotation. Neill *et al.* (1996) measured $\delta^{13}\text{C}$ of soil organic matter and soil respired CO_2 on a sequence from C_3 forest to 81-year-old C_4 pastures. They found steadily increasing $\delta^{13}\text{C}$ ratios with pasture age, with values changing faster in the soil-respired CO_2 than those in SOC. However, how differences in decomposition rates, fractionation during decomposition and/or preferential decomposition of certain soil organic matter compounds might affect the $\delta^{13}\text{C}$ value of SOC and respired CO_2 is still unclear.

Table 13.2. Origin of C in soil organic matter (SOC) and of CO₂ released by soil respiration (resp)

History	$\delta^{13}\text{C}_{\text{leaf}}$		$\delta^{13}\text{C}_{\text{SOC}}$	$\delta^{13}\text{C}_{\text{resp}}$	% C ₄ origin	Reference
	C ₃	C ₄				
C ₃ → 1 yr C ₄	-26.0	-13.1		-19.1	30	Schönwitz <i>et al.</i> (1986)
C ₃ → 13 yr C ₄	-26.0	-12.0	-23.0		22	Balesdent <i>et al.</i> (1987)
C ₃ → 17 yr C ₄	-26.0	-12.5	-20.9		38	Balesdent <i>et al.</i> (1990)
C ₃ → 17 yr C ₄			-22.6		25	
C ₃ → 5 yr C ₄	-27.0	-12.0	-26.0		7	Arrouays <i>et al.</i> (1995)
C ₃ → 20 yr C ₄			-24.0		20	
C ₃ → 32 yr C ₄			-23.5		23	
C ₃ → 25 yr C ₄	-27.6	-13.4	-22.9		33	Gregorich <i>et al.</i> (1995)
C ₃ → 4 yr C ₄	-26.4	-12.0	-21.8		32	Wedin <i>et al.</i> (1995)
C ₃ → 4 yr C ₄			-22.3		28	
C ₄ → 5 yr C ₃	-28.2 ± 0.2	-12.8 ± 0.1	-23.6 ± 1.00	-22.3 ± 0.6	35	Buchmann and Ehleringer (1997)
C ₃ → 2 yr C ₄			-15.0 ± 0.73	-22.8 ± 0.5	38	
C ₃ → 3 yr C ₄	-28.0	-15.0	-25.5	-17.0	85	Neill <i>et al.</i> (1996)
C ₃ → 13 yr C ₄			-22.0	-17.0	85	
C ₃ → 81 yr C ₄			-17.0	-12.9	≈100	
C ₃ → 1 yr C ₄		-12.1	-25.8	-18.4	54	Rochette and Flanagan (1997)

13.4 Conclusions

Thus far, only a few studies have measured Δ_c or provide the necessary data to calculate Δ_c values (Table 13.3). However, the Δ_c estimates presented here proved to be less variable than previously expected, and therefore offer the great potential to be widely used in biosphere/atmosphere modeling since year-to-year fluctuations may be small (Buchmann *et al.*, 1997a,c). The Δ_c value is a temporal and spatial integration of foliage characteristics (past and current) within the entire ecosystem, and is influenced by litter and decomposition processes. A practical advantage of Δ_c estimates lies in the relatively simple data collection that can be easily performed in remote areas.

In Table 13.3, we compiled all of the Δ_c estimates available to the authors, spanning ecosystems from different biomes between 69° North and 42° South. We used the Lancaster (1990) dataset in combination with tropospheric data from Francey *et al.* (1995) to calculate Δ_c . However, uncertainties in the range 0.2–0.5‰ may arise because the Cape Grim data were used for all Lancaster sites. Δ_c estimates for boreal ecosystems ranged between 15.9‰ and 19.3‰, with an average value of 18.2‰. The most extensive boreal data set (Flanagan *et al.*, 1996), collected during one growing

Table 13.3. Estimates of Δ_c for evergreen (e) and deciduous (d) ecosystems

Latitude	Biome	Species	Life Form	Δ_c [‰] ^a	Reference
69°N	boreal	tussock tundra	d	15.9	from Lancaster (1990)
64°N		<i>Picea abies</i> / <i>Pinus sylvestris</i>	e	16.3	from Högberg and Ekblad (1996)
61°N		tundra	d	18.5	from Lancaster (1990)
56°N		<i>Picea mariana</i>	e	19.0 ± 0.2	Flanagan <i>et al.</i> (1996)
		<i>Pinus banksiana</i>	e	18.9 ± 0.2	Flanagan <i>et al.</i> (1996)
		<i>Populus tremuloides</i>	d	18.8 ± 0.5	Flanagan <i>et al.</i> (1996)
54°N		<i>Picea mariana</i>	e	18.5 ± 0.1	Flanagan <i>et al.</i> (1996)
		<i>Pinus banksiana</i>	e	19.0 ± 0.1	Flanagan <i>et al.</i> (1996)
		<i>Populus tremuloides</i>	d	19.3 ± 0.6	Flanagan <i>et al.</i> (1996)
		<i>Pinus ssp./Picea ssp.</i>	e	18.1	from Lancaster (1990)
48°N	temperate	<i>Pseudotsuga menziesii</i> / <i>Tsuga ssp.</i>	e	17.7 ^b	from Keeling (1961)
47°N		<i>Abies amabilis</i>	e	19.2 ± 0.2	Buchmann <i>et al.</i> (1997c)
46°N		<i>Pinus ssp.</i>	e	16.7 ± 0.2	from Lancaster (1990)
45°N		<i>Pinus resinosa</i>	e	17.7 ± 0.4	from Berry <i>et al.</i> (1997)
44°N		<i>Acer ssp./Alnus ssp.</i>	d	20.3 ± 0.1	from Lancaster (1990)
41°N		<i>Pinus contorta</i>	e	18.3 ± 0.9	Buchmann <i>et al.</i> (1997b)
		<i>Populus tremuloides</i>	d	18.0 ± 0.7	Buchmann <i>et al.</i> (1997b)
		<i>Acer ssp.</i>	d	17.1 ± 0.4	Buchmann <i>et al.</i> (1997b)
		deciduous forest	d	16.1	from Lancaster (1990)
38°N		<i>Pinus ssp.</i>	e	18.2	from Lancaster (1990)
		<i>Pinus ssp./Abies ssp.</i>	e	16.6 ± 0.2 ^b	from Keeling (1961)
36°N		<i>Sequoia sempervirens</i>	e	18.3 ± 0.5 ^b	from Keeling (1961)
		<i>Pinus ssp.</i>	e	18.5 ^b	from Keeling (1961)
33°N		scrub oak	d	19.4	from Lancaster (1990)
20°N	tropical	primary rainforest	d	20.2	from Lancaster (1990)
10°N		primary rainforest	d	17.3 ± 0.1	from Broadmeadow <i>et al.</i> (1992)
9°N		primary rainforest	d	21.1	from Sternberg <i>et al.</i> (1989)
		primary rainforest	d	20.7	from Lancaster (1990)
5°N		primary rainforest	d	20.4 ± 0.1	Buchmann <i>et al.</i> (1997a)
3°S		primary rainforest	d	20.3 ^b	from Quay <i>et al.</i> (1989)
10°S		primary rainforest	d	19.5	from Lloyd <i>et al.</i> (1996)
42°S		primary rainforest	d	16.2 ^b	from Francey <i>et al.</i> (1985)
Crop rotation, irrigated					
42°N	C ₃	<i>Medicago sativa</i>	d	13.8	Buchmann and Ehleringer (1997)
	C ₄	<i>Zea mays</i>	d	13.2	Buchmann and Ehleringer (1997)
Crops, irrigated					
32°N	C ₃	<i>Triticum aestivum</i>	d	21.6	from Yakir and Wang (1996)
	C ₃	<i>Gossypium hirsutum</i>	d	18.4	from Yakir and Wang (1996)
	C ₄	<i>Zea mays</i>	d	12.3	from Yakir and Wang (1996)

^a Original data or calculated from intercepts of the relationship of $1/[CO_2]$ versus $\delta^{13}C$ of canopy air given in the cited reference.

^b Samples analysed may have been contaminated by N_2O . Applying a N_2O correction factor of +0.2‰ would result in Δ_c 0.2‰ lower than the values given here.

season, provides Δ_c estimates that vary less, averaging 18.9‰ for both evergreen and deciduous boreal forests. The estimates for temperate forests were lower than those for boreal forests, averaging 18.0‰, and show a wide spread from 16.1‰ to 20.3‰. In contrast, the Δ_c estimates for tropical forests show generally a narrow range (19.5–21.1‰) and average 20.4‰, although two forests exhibited lower Δ_c estimates (Francey *et al.*, 1985 and Broadmeadow *et al.*, 1992). This may further indicate that most of these study sites were undisturbed by human impact such as historic or more recent land use changes (Bush and Colinvaux, 1994). Thus, the spread in the data for boreal and temperate forests is probably due to natural variations among sites. The most likely candidate may be climatic differences among sites, especially site moisture regime: wet coastal sites tended to have greater Δ_c than dry inland sites.

Results of studies where sites were sampled more than once indicated that the balance between photosynthesis and stomatal conductance (intrinsic WUE) also seems to influence carbon isotope discrimination of forest ecosystems. Δ_c of boreal *Picea mariana* and *Pinus banksiana* stands averaged 18.9‰ (54°–56° N; Flanagan *et al.*, 1996). Estimates for wet temperate *Abies amabilis* stands in the Pacific Northwest were on average 19.2‰ (47° N; Buchmann *et al.*, 1997c), while Δ_c estimates for dry temperate evergreen forests were lower: 16.7‰ for *Pinus* spp. stands in Montana (46° N; Lancaster, 1990), 18.3‰ for *P. contorta* stands in Utah (41° N; Buchmann *et al.*, 1997b), and 16.6‰ for *Pinus* spp./*Abies* spp. stands and 18.3‰ for *Sequoia sempervirens* in California (36°–38° N; Keeling, 1961). Deciduous forest ecosystems exhibited a similar trend with latitude. Boreal *Populus tremuloides* stands averaged 19.1‰ (54°–56° N; Flanagan *et al.*, 1996). Estimates for temperate deciduous forests decreased from 20.3‰ for *Acer* spp./*Alnus* spp. (44° N; Lancaster, 1990) to 17.1‰ for dry temperate *Acer* spp. stands in Utah (41° N; Buchmann *et al.*, 1997b). Thus, on a global scale, decreasing Δ_c might reflect increased ecosystem WUE, under conditions when precipitation decreases and/or the evaporative demand increases. However, further studies of Δ_c are required for a wide variety of terrestrial ecosystems throughout the globe to validate this trend.

How do Δ_A estimates compare with Δ_c estimates? Whereas the model from Lloyd and Farquhar (1994) implies pronounced differences between life forms, the field data do not yet support this separation between evergreen and deciduous forests. The modeled Δ_A estimates for cool/cold conifer forests averaged 15.4‰ (Lloyd and Farquhar, 1994). In contrast, all available Δ_c estimates for evergreen forests were higher, ranging from 16.3‰ to 19.2‰. The absolute differences between the modeled Δ_A and the calculated Δ_c values were between 0.1‰ and 4.0‰ for natural ecosystems of both evergreen and deciduous life forms, and up to 9.9‰ for agricultural stands. Differences of less than 1‰ for natural ecosystems are well within the analytical errors of the factors used to calculate Δ_c (see Section 13.2.5). Differences of 1–2‰ might be due to specific site conditions, and are within the expected variability of the modeled values (J. Lloyd personal communication). However, once these differences exceed the 2‰ range, they might either indicate the influence of the soil compartment or that the model does not adequately describe the stand ecophysiology at a certain site.

The largest discrepancy between modelled Δ_A and calculated Δ_c estimates were found for the agricultural sites (2.0‰ to 9.9‰), which may be associated with site history. The crop rotation study illustrated very nicely that Δ_c is not just the weighted average or integral of all Δ_{leaf} values, but that $\delta^{13}\text{C}$ of soil organic matter has a great

impact on ecosystem performance (Buchmann and Ehleringer, 1997). While Δ_{leaf} of corn plants ranged between 4‰ and 5‰, the estimate of Δ_c averaged 13.2‰ for two corn stands; Δ_{leaf} of alfalfa plants was about 20‰, whereas Δ_c was estimated as 13.8‰ for the alfalfa stand. Because Δ_c integrates not only over foliage carbon isotope discrimination, but also includes this 'memory effect' of past vegetation cover as reflected in soil organic matter, site history needs to be considered to estimate Δ_c values. This is not only true for systems that are currently heavily influenced by human activities such as agriculture or land use changes, but also for systems that are generally considered undisturbed mature forests as cautioned by Bush and Colinvaux (1994); they could demonstrate a 4000-year history of human disturbance in a so-called undisturbed remote tropical forest.

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