Can C3 Plants Faithfully Record the Carbon Isotopic Composition of Atmospheric Carbon Dioxide?

Nan Crystal Arens; A. Hope Jahren; Ronald Amundson

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Abstract.—Atmospheric carbon dioxide is the raw material for the biosphere. Therefore, changes in the carbon isotopic composition of the atmosphere will influence the terrestrial $\delta^{13}C$ signals we interpret. However, reconstructing the atmospheric $\delta^{13}C$ value in the geologic past has proven challenging. Land plants sample the isotopic composition of CO_2 during photosynthesis. We use a model of carbon isotopic fractionation during C3 photosynthesis, in combination with a meta–data set (519 measurements from 176 species), to show that the $\delta^{13}C$ value of atmospheric CO_2 can be reconstructed from the isotopic composition of plant tissue. Over a range of pCO_2 (198–1300 ppmv), the $\delta^{13}C$ value of plant tissue does not vary systematically with atmospheric carbon dioxide concentration. However, environmental factors, such as water stress, can influence the $\delta^{13}C$ value of leaf tissue. These factors explained a relatively small portion of variation in the $\delta^{13}C$ value of plant tissue in our data set and emerged strongly only when the carbon isotopic composition of the atmosphere was held constant. Members of the Poaceae differed in average $\delta^{13}C$ value, but we observed no other differences correlated with plant life form (herbs, trees, shrubs). In contrast, over 90% of the variation the carbon isotopic composition of plant tissue was explained by variation in the $\delta^{13}C$ value of the atmosphere under which it was fixed. We use a subset of our data spanning a geologically reasonable range of atmospheric $\delta^{13}C$ values (−6.4‰ to −9.6‰) and excluding C3 Poaceae to develop an equation to reconstruct the $\delta^{13}C$ value of atmospheric CO_2 based on plant values. Reconstructing the $\delta^{13}C$ value of atmospheric CO_2 in geologic time will facilitate chemostratigraphic correlation in terrestrial sediments, calibrate pCO_2 reconstructions based on soil carbonates, and offer a window into the physiology of ancient plants.

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Introduction

In terrestrial ecosystems, stable carbon isotopes have found a variety of applications. They have been used to reconstruct vertebrate paleodiets (reviewed in Koch 1998), major changes in plant community composition (e.g., global shift from C3 to C4 grasslands in the Miocene and Pliocene [Cerling 1992a; Cerling et al. 1993; MacFadden et al. 1994; Quade et al. 1994]), and the physiology, ecology, and taphonomy of individual plants (Nambudiri et al. 1978; Dupouey et al. 1993; Jones 1994; Nguyen Tu et al. 1999). Carbon isotopic measurements from paleosol organic matter calibrate paleo-pCO_2 reconstructions calculated from soil carbonates (Cerling 1992b). Carbon isotopic values in land plants have also been used to recognize quantitative shifts in the carbon isotopic composition of atmospheric CO_2 (Faure et al. 1995; Gröcke et al. 1999). Variation in the isotopic composition of atmospheric CO_2 mirrors changes in global carbon cycling and can be used for chemostratigraphic correlation between marine and terrestrial rocks and among terrestrial localities (Koch et al. 1992; Turney et al. 1997; Gröcke 1998).

These applications require a clear understanding of how faithfully land plants—the conduit for carbon into the terrestrial fossil record—reflect the isotopic composition of atmospheric CO_2. C4 plants precisely record the isotopic composition of atmospheric CO_2 (Marino and McElroy 1991); however, they became common only in the latest Miocene, are climatically restricted, and thus are of limited use. In contrast, C3 vascular land plants have been ubiquitous since the Devonian but display more variable carbon isotopic discrimination. Can ecological and atmospheric fac-

tors that generate variation in carbon isotopic composition of C3 plants be separated to produce a method for inferring the carbon isotopic composition of atmospheric CO_2? Such a method would fine-tune estimates of paleo-pCO_2 based on soil carbonates, provide confidence intervals for chemostratigraphic interpretations, and perhaps offer a way to apply carbon isotopic techniques to more subtle questions in the physiology of ancient plants (e.g., Dupouey et al. 1993).

During the 1980s, G. D. Farquhar and colleagues developed a now well-established conceptual model describing isotopic fractionation during carbon assimilation in C3 vascular land plants (Farquhar et al. 1980, 1989):

$$\delta^{13}C_p = \delta^{13}C_a - a - (b - a) C_p/C_a \quad (1)$$

where a is the isotopic discrimination due to the diffusion of $^{13}CO_2$ versus $^{12}CO_2$ through air; b is the isotopic discrimination imparted during carboxylation by ribulose-1,5-bisphosphate carboxylase-oxygenase (RuBisCO), the primary carbon-fixation enzyme in C3 plants; and C_p/C_a is the ratio of intercellular to atmospheric pCO_2 expressed in parts per million volume (ppmv). C_p/C_a is considered the metabolic set point relating the trade-off between carbon gain and water loss in photosynthesis (Ehleringer 1993); it summarizes ecophysiological variation in C3 carbon assimilation. $\delta^{13}C_p$ is the carbon isotopic composition of C3 plant tissue expressed in the δ notation

$$\delta^{13}C_{sample} = \left(\frac{[^{13}C/^{12}C]_{sample}}{[^{13}C/^{12}C]_{standard}} - 1 \right) \times 1000. \quad (2)$$

$\delta^{13}C_a$ is the carbon isotopic composition of atmospheric CO_2.

Equation (1) describes three important factors that influence the carbon isotopic composition of C3 vascular land plant tissue: (1) Physical and biochemical fractionation occurs both as CO_2 moves from the atmosphere to carboxylation sites within the leaf (summarized by a) and during carboxylation itself (b). (2) Ecological factors such as water and nutrient stress, light limitation, and thermal load (Table 1) influence the degree to which sto-

mata remain open and CO_2 can freely enter the leaf; these factors alter C_p/C_a and thus affect the $\delta^{13}C$ value of plant tissue. (3) Atmospheric CO_2 is the substrate for carbon fixation; therefore, the carbon isotopic composition of the atmosphere ($\delta^{13}C_a$) influences the composition of the resulting plant tissue. Over geologic time, changes in pCO_2 may also contribute to variation in the isotopic composition of C3 plants. Although not explicitly treated in equation one, changing atmospheric pCO_2 may affect C_p/C_a ratios and thus change carbon isotopic discrimination (Δ in eq. 3) in C3 plants:

$$\Delta = \frac{\delta^{13}C_a - \delta^{13}C_p}{1 + \delta^{13}C_p/1000}. \quad (3)$$

An array of environmental and physiological factors influence the $\delta^{13}C$ value of C3 plants (Table 1). The question remains: Are these effects small enough to allow an isotopic signal of the atmosphere to emerge from the $\delta^{13}C$ value of plant tissue? A large body of previously published research has addressed the effect of specific environmental factors on carbon isotopic discrimination. To address the more general question, we sampled this literature and compiled data from 44 studies. These studies encompassed a wide range of species that grew under varying pCO_2 and $\delta^{13}C_a$ values and varying environmental conditions (both natural and experimentally manipulated). The meta-analysis approach offers two advantages: amalgamating effects from a variety of sources to summarize natural range of variation more comprehensively and enhancing degrees of freedom for statistical analysis. Our goal was twofold: (1) to document and quantify the significant sources of variation in the $\delta^{13}C$ value of C3 vascular land plants across a range of pCO_2 values and environmental conditions and (2) to derive an empirical relationship between the $\delta^{13}C$ value of atmospheric CO_2 and the $\delta^{13}C$ value of plant tissue and discuss how it might be applied to the fossil record.

Data Set

We compiled a data set that included 519 measurements made on 176 C3 vascular land

TABLE 1. Factors that influence carbon isotopic discrimination in C3 plants. References: 1 (Broadmeadow et al. 1992); 2 (Brooks et al. 1997a); 3 (Medina et al. 1986); 4 (Ehleringer et al. 1986); 5 (Zimmermann and Ehleringer 1990); 6 (Tieszen 1991); 7 (Ehleringer et al. 1992); 8 (Ismail et al. 1994); 9 (Johnson and Tieszen 1993); 10 (Toft et al. 1989); 11 (Wright et al. 1994); 12 (Guy et al. 1980); 13 (Guy and Reid 1986); 14 (Neals et al. 1983); 15 (Körner et al. 1988); 16 (Friend et al. 1989); 17 (Körner et al. 1991); 18 (Smedley et al. 1991); 19 (Donovan and Ehleringer 1991); 20 (Donovan and Ehleringer 1992); 21 (Madhavan et al. 1991); 22 (Lockheart et al. 1997).

Factor	Effect on Cp/Ca	Effect on $\delta^{13}Cp$		Ecological conditions	Reference
		Range	Direction		
Recycled CO_2	little	1–5‰	negative	within closed canopies or in eco-systems where soil outgassing is high (boreal forest)	1, 2, 3
Low light	increase	5–6‰	negative	forest understory	4, 5
Water stress, low relative humidity	decrease	3–6‰	positive	arid and semiarid climate	6, 7, 8, 9, 10, 11, 20
Osmotic stress	decrease	3–10‰	positive	high-salinity soils, extreme at high pCO_2	12, 13, 14
Low nutrients	increase	4‰	negative	nutrient-poor soils	10
Low temperature	increase	3‰	negative	polar regions during ice house times, high altitude	6, 17
Reduced pCO_2 with altitude	decrease	3–7‰	positive	high mountains	15, 16, 17
Growth form and deciduousness	increase/decrease	1–3‰	negative/positive	variation between trees, forbs, and grasses, and between evergreen and deciduous species	2, 18, 20
Age (juvenile vs. adult)	increase in juvenile	2‰	negative in juvenile	seedling or sapling vs. reproductive individual	19, 20
Sun vs. shade leaves	increase in sun	1–3‰	negative in sun	variation due to position in the canopy relative to direction of sun	21
Seasonal variation	increase/decrease	1–2‰	negative/positive	strongest effect in semiarid and arid climate	7

plant species (Appendix). All δ¹³C values in our data set represent stable isotope mass spectrometer measurements of the ¹³C/¹²C in CO_2 produced by combustion of plant tissue, reported on the per-mil scale (eq. 2). Most $\delta^{13}C_p$ data came from whole-leaf tissue, although some reported $\delta^{13}C_p$ values for extracted xylem cellulose. To make cellulose and whole-leaf values commensurate, we applied a correction of δ¹³C value (whole-leaf carbon) = δ¹³C (cellulose) − 2‰ (Benner et al. 1987).

In published sources, data were reported as either δ¹³C value or carbon isotopic discrimination, calculated using equation (3) (Δ in eq. 3 of Farquhar et al. 1989) and a reported $\delta^{13}C_a$ value. In some cases, the δ¹³C value of the atmosphere and pCO_2 were measured directly (e.g., growth chamber and some field studies); in others, authors assumed the global average ambient value of −7.85‰ and 350 ppmv for plants growing in the open atmosphere and −8.0‰ and 390 ppmv for plants growing under a closed canopy or in dense stands, respectively (Broadmeadow et al. 1992). For his-

torical collections from herbaria and for late Pleistocene and Holocene fossils, δ¹³C value of the atmosphere and pCO_2 were inferred from high-resolution, time-correlated ice core records (Friedli et al. 1986; Neftel et al. 1988; Wahlen et al. 1991; Leuenberger et al. 1992).

Angiosperms dominated the data set, but conifers such as *Pinus radiata*, *Pinus flexilis*, *Pseudotsuga menziesii*, *Picea*, *Abies*, and *Larix* were also included. Carbon isotopic measurements of free-sporing vascular plants were not available. Although they are relatively minor players in most modern ecosystems, free-sporing lineages were ecosystem dominants during most of the Paleozoic. However, the Paleozoic was characterized by a dominantly C3 photosynthetic signal (Bocherens et al. 1993), indistinguishable from that of most modern C3 ecosystems. Consequently, there is no a priori reason why conclusions from our data set should not be generally applicable. To strengthen this analysis further, carbon isotopic measurements on free-sporing plants and additional nonangiosperm seed plants

TABLE 2. Summary statistics for 519 observations combined in this meta-analysis.

	$\delta^{13}C$ (atmos.) [‰]	pCO_2 (atmos.) [ppmv]	$\delta^{13}C$ (plant) [‰]	C_p/C_a
Mean	−9.21	367.65	−28.41	0.61
Standard error	0.09	4.87	0.26	0.00*
Median	−19.70	350.00	−27.05	0.61
Standard deviation	1.95	110.91	5.99	0.09
Minimum	−13.90	98.00	−70.00	0.38
Maximum	−32.19	1300.00	−21.45	0.89

* Actual standard error for C_p/C_a distribution is 0.0039.

(e.g., cycads, additional conifers, and *Gnetum*) should be made and added to the data set. Additional measurements were beyond the scope of this paper.

Observations included a pCO_2 range from 198 ppmv to 1300 ppmv (Table 2). This encompassed much of the variation since C3 vascular land plants became important players in the global carbon cycle in the Devonian (Berner 1998). Herbaria time-series collections (Peñuelas and Azcón-Bieto 1992; Woodward 1993), tree-ring data (Dupouey et al. 1993), and well-preserved late Pleistocene and Holocene fossil leaves (Van de Water et al. 1994; Beerling 1996b) tracked plants growing under natural conditions through time. These time series captured a range of postglacial and anthropogenic changes in pCO_2, atmospheric $\delta^{13}C$ values, and associated climate change. Growth-chamber studies extended the available range of pCO_2 conditions sampled from 225 ppmv to 1300 ppmv (Guy and Reid 1986; Beerling and Woodward 1995; Polley et al. 1995). Because these represent work from different laboratories, we do not have a continuous range of variation in pCO_2 between point clusters at 500, 700, and 1300 ppmv (e.g., Fig. 1).

The laboratory protocols for elevated-CO_2 studies preferentially enriched growth-chamber atmospheres in $^{12}CO_2$, making measured $\delta^{13}C_a$ values unnaturally low. By including these data we do not imply that the ancient atmosphere reached $\delta^{13}C_a$ values of −40‰. Rather, we wished to include plants that spanned the range of pCO_2 values reconstructed for most of the Phanerozoic (Berner 1998), so that paleoatmospheric $\delta^{13}C_a$ values based on our analysis can be interpolated (rather than extrapolated) across the range of realistic paleo-pCO_2 and $\delta^{13}C_a$ values. Note also that any relationship that predicts $\delta^{13}C_a$ from $\delta^{13}C_p$ will be driven by the plant's carbon isotope discrimination (Δ). Therefore, we must understand whether $\delta^{13}C_a$ and $\delta^{13}C_p$ vary linearly even at extreme values of $\delta^{13}C_a$.

Carbon isotopic composition of plant tissue also varies with water, nutrient, thermal, and edaphic stress, and with growth form, genotype, and competitive ability (Table 1). In assembling our data set, we have included studies that span a range of each of these conditions. We refer the reader to the original studies for details.

Data Analysis and Results

To separate the relative roles of the several parameters that contribute to variation in the carbon isotopic composition of C3 plant tissue, we performed a multiple linear regression upon $\delta^{13}C_p$ values using variables $\delta^{13}C_a$ value, pCO_2, and C_p/C_a. C_p/C_a values used in the multiple regression were calculated from gas-exchange measurements made on living plants. Because C_p/C_a is most commonly calculated from carbon isotopic measurements, only a subset ($n = 119$) of the entire data set was used for this analysis. Manipulations and analyses were performed in SYSTAT 5.2 and MS Excel 5.0a for Macintosh. Table 3 presents results of an *F*-test for homoscedasticity (equality of variances) among these variables.

The model including $\delta^{13}C_a$ value alone generated a coefficient of determination (r^2) of 0.98 and was statistically significant ($p < 0.001$). The model including C_p/C_a alone produced $r^2 = 0.02$ and was not significant ($p = 0.10$). A model including both $\delta^{13}C_a$ value and C_p/C_a was significant, and accounted for 98.2% of total variation. Thus, the observed variation in the isotopic composition of C3 plants in our data set was explained primarily by variation in the isotopic composition of atmospheric CO_2 and secondarily by ecological parameters that affect C_p/C_a. In the multivariate regression, pCO_2 was not a strongly significant variable ($p = 0.01$) and did not significantly change r^2 (0.983) when added to the model. We examined each of these parameters independently.

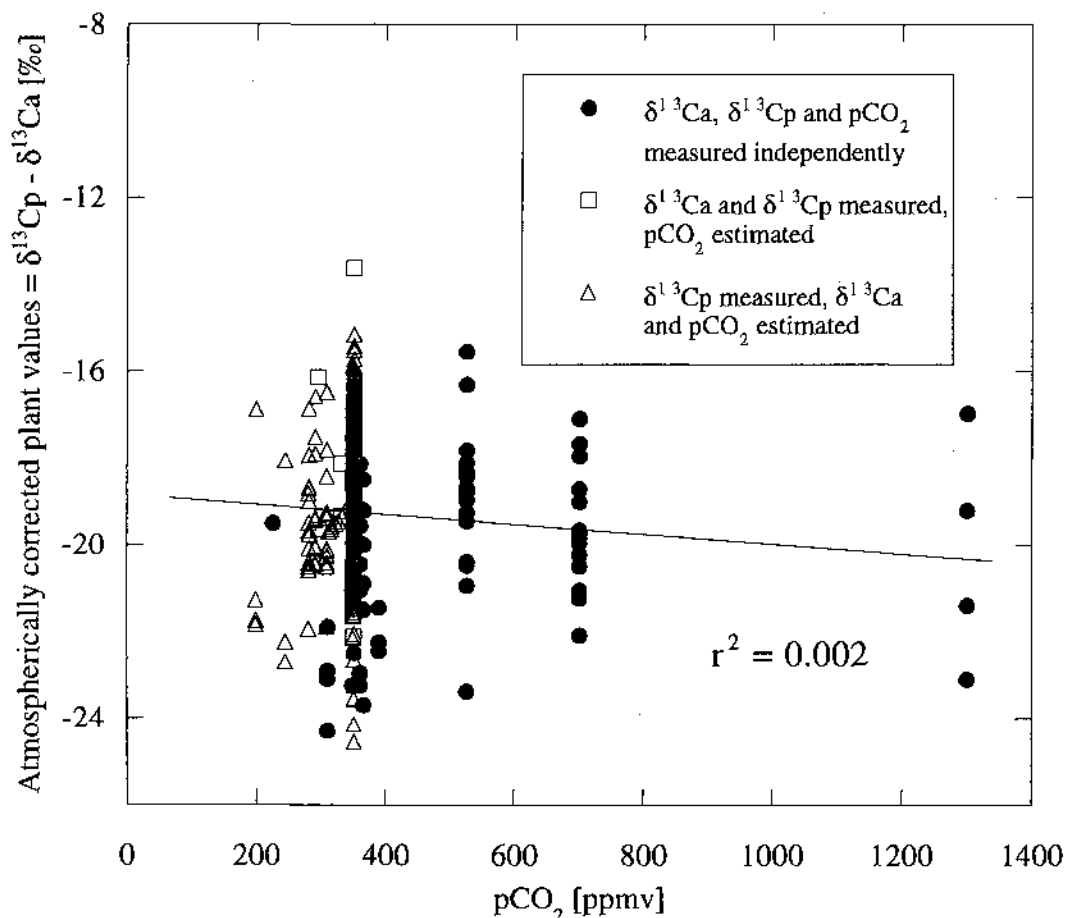*Variation in Atmospheric Carbon Dioxide Con-*

FIGURE 1. Regression of atmospherically corrected $\delta^{13}C_p$ value onto pCO_2. The full data set ($n = 519$) was used for this analysis to capture the range of pCO_2 that might be expected during the geologic history of C3 vascular land plants. This relationship was not significant ($p = 0.25$) and reflects a low correlation between the variables ($r = 0.05$). A small negative slope (slope $= -0.0008$) does not differ significantly from a slope of zero ($p = 0.25$), indicating no relationship between the isotopic composition of C3 plant tissue and pCO_2 under which the plant grew.

centration.—Although pCO_2 was not a strongly significant variable in the multivariate analysis, we explore this parameter in more detail because of the large changes in pCO_2 inferred for the Phanerozoic (Berner 1998). To further examine pCO_2 effects, we regressed atmospherically corrected $\delta^{13}C$ values of plant tissue on pCO_2 (Fig. 1). This correction (corrected $\delta^{13}C = \delta^{13}C_p - \delta^{13}C_a$) removed the atmospheric contribution to the $\delta^{13}C$ value of the plant by subtracting the isotopic composition of the atmosphere from the isotopic composition of plant tissue formed under that atmosphere (Feng and Epstein 1995). This correction is necessary because of the strong correlation ($r = 0.94$) between $\delta^{13}C_a$ and pCO_2 in

our data set. Because this covariance is ubiquitous, we cannot recognize the unique contribution of pCO_2 without removing the influence of the isotopic composition of that CO_2.

TABLE 3. F-test for equality of sample variances (homoscedasticity) among data-set parameters. Comparisons were not significant (N.S.) when we fail to reject the null hypothesis ($\sigma_1{}^2 = \sigma_2{}^2$). Results for Cp/Ca hold for the entire data set ($n = 519$), which includes values calculated from carbon isotopic and gas-exchange measurements, and for the subset ($n = 119$) of values calculated from gas-exchange measurements.

	$\delta^{13}Ca$	$\delta^{13}Cp$	Cp/Ca	pCO_2
$\delta^{13}Ca$	—			
$\delta^{13}Cp$	N.S.	—		
Cp/Ca	<0.001	<0.001	—	
pCO_2	N.S.	N.S.	<0.001	—

This correction does not induce circularity because the isotopic composition of plant and atmosphere were evaluated independently for each observation. We chose pCO_2 as the independent variable and atmospherically corrected $\delta^{13}C$ value of plant tissue as the dependent variable in order to test the hypothesis that pCO_2 systematically influences $\delta^{13}C_p$. Variances between these variables are not statistically different (Table 3), residuals have a mean of approximately zero (-8.7×10^{-15}) and are normally distributed (Lilliefors $p = 0.18$). This regression was not significant ($p = 0.31$), suggesting that pCO_2 does not systematically influence the carbon isotopic composition of C3 plant tissue.

However, large changes in pCO_2, such as those inferred to have occurred during the Phanerozoic, might influence C_p/C_a and, indirectly, the isotopic composition of C3 plant tissue. Because this pair of variables has unequal variance (Table 3), we compared them using the nonparametric Kendall tau coefficient, which produced a correlation of -0.01. This result agrees with those of other studies (Farquhar et al. 1982b; Polley et al. 1993; Ehleringer and Cerling 1995; Beerling 1996a), which reported near zero-slope relationships between C_p/C_a and pCO_2. Beerling (1996b) proposed that as pCO_2 changed, plants maintained a relatively constant ratio of intercellular to atmospheric carbon dioxide suitable for their environmental conditions (e.g., temperature, water, light, and nutrient availability). Beerling's (1996b) data spanned a pCO_2 range of only 198 ppmv to modern ambient. Our analysis expands his result to much higher pCO_2 values, making the conclusion applicable to the geologic past.

Variation in C_p/C_a.—In the Farquhar model (eq. 1), the term C_p/C_a encapsulates the ecophysiological control that C3 plants exert on carbon isotopic discrimination. This parameter has received extensive attention in modern systems and therefore must be considered here. In studies where $\delta^{13}C_a$ value remained constant, variation in C_p/C_a explained most of the observed variation in $\delta^{13}C_p$ value (summarized in Table 1; see also Farquhar et al. 1982b; Wullschleger 1993; Brodribb 1996). However, our larger data set produced a poor

correlation (Kendall tau $= -0.18$) between $\delta^{13}C_p$ value and C_p/C_a values calculated from gas-exchange measurements. When we corrected for the isotopic composition of the atmosphere under which plant tissue was fixed, the correlation became slightly stronger (Kendall tau $= -0.23$). This suggests that variation in plant carbon isotopic discrimination due to environmental factors emerges clearly only when atmospheric $\delta^{13}C$ value is held constant. Note that C_p/C_a values calculated from gas-exchange data generally do not represent the plant's environmentally mediated metabolism because they are instantaneous, rather than time-integrated, measurements (Ehleringer 1993; Beerling and Woodward 1995). We evaluated them here only to avoid circularity introduced by calculating intercellular-to-atmospheric pCO_2 ratios from carbon isotopic measurements with which we wish to compare C_p/C_a.

Variation Due to Plant Growth Form.—Brooks and colleagues (1997a) noted that in boreal systems, carbon isotopic composition of plant tissue was correlated with growth form. Evergreen trees had higher $\delta^{13}C$ values than deciduous trees. Deciduous trees, all shrubs, and evergreen herbs produced statistically indistinguishable carbon isotopic values, which were higher than those of deciduous herbs (including grasses). They attributed these differences to variation in C_p/C_a due to leaf longevity and light environment. Plant height was also a significant factor in explaining variation in carbon isotopic composition due to recycling of soil-respired CO_2 by ground-hugging plants (Brooks et al. 1997b).

To examine this variable in our data set, which includes more species and a wider sampling of ecosystems, we performed a Kolmogorov-Smirnov two-sample test on $\delta^{13}C_p$ value, using growth form as a grouping variable. The nonparametric Kolmogorov-Smirnov test compared growth form groups for mean, standard deviation, and shape of distribution, without assuming an underlying distribution. This test is appropriate because $\delta^{13}C_p$ value failed the Lilliefors test for normality of distribution ($p < 0.001$). Species in our data set included the following growth forms: forbs (annual or perennial herbs), grass (Poaceae),
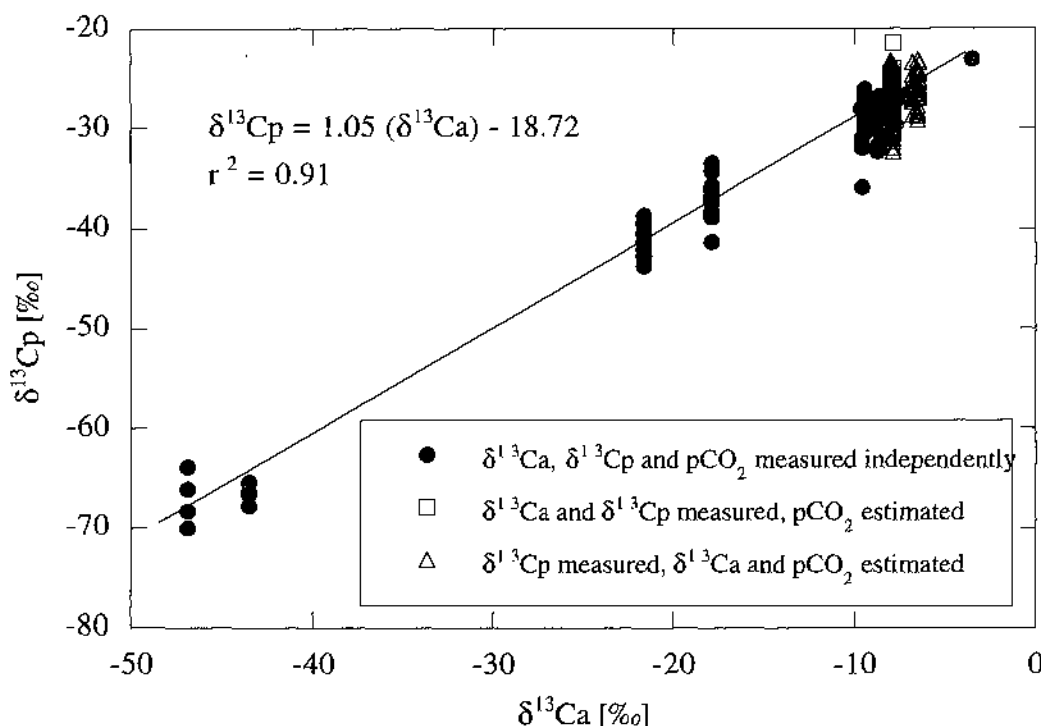
FIGURE 2. Regression of $\delta^{13}C_p$ value onto $\delta^{13}C_a$ value using the whole data set (n = 519). This relationship was statistically significant ($p < 0.001$, $r^2 = 0.91$).

shrubs (woody perennials that lack a distinct trunk-crown architecture), and trees (woody perennials with a distinct trunk-crown architecture at maturity) (Appendix). We segregated Poaceae as a distinct group because this lineage has evolved a wide range of unusual physiologies, many of which promote drought tolerance. Trees, shrubs, and forbs had statistically indistinguishable $\delta^{13}C_p$ value distributions at $p < 0.01$. C3 grasses, however, possessed average $\delta^{13}C$ values 1–2‰ higher than those of all other growth forms ($p < 0.001$). This is likely due to an average higher water-use efficiency in this lineage.

Variation Due to the Isotopic Composition of Atmospheric Carbon Dioxide.—In the multiple regression, $\delta^{13}C$ value of atmospheric CO_2 accounts for the bulk of variation in the $\delta^{13}C_p$ value. To evaluate this result in more detail, we regressed $\delta^{13}C_p$ value onto $\delta^{13}C_a$ value using the entire data set ($n = 519$), which included more species and plants from a wider range of environmental conditions. Variances of $\delta^{13}C_p$ value and $\delta^{13}C_a$ value were not statistically different (Table 3); regression residuals

have a mean of approximately zero (-2.7×10^{-14}) and are normally distributed (Lilliefors $p = 0.27$). The resulting regression (Fig. 2) was significant ($p < 0.001$), with high predictive power ($r^2 = 0.91$). Note that this coefficient of determination differs from that produced by the multiple regression because the former analysis used only a subset of the entire data. When we used only those observations in which $\delta^{13}C_a$ values were directly measured ($n = 169$), the relationship was also significant ($p < 0.001$, $r^2 = 0.97$) and the slope (1.05) and intercept (-18.84) were statistically indistinguishable from those generated from the full data set analysis. In addition to the strong influence of $\delta^{13}C_a$ value on the isotopic composition of plant tissue, this result showed that this relationship is linear even at extreme $\delta^{13}C_a$ values and high pCO_2.

The range of $\delta^{13}C_a$ values evaluated in Figure 2 exceeds that which might be reasonably expected during the Phanerozoic. Anthropogenic $\delta^{13}C_a$ variation of 2‰ occurred in the last 800 years (Friedli et al. 1986). Pleistocene glacial-interglacial cycling varied $\delta^{13}C_a$ value
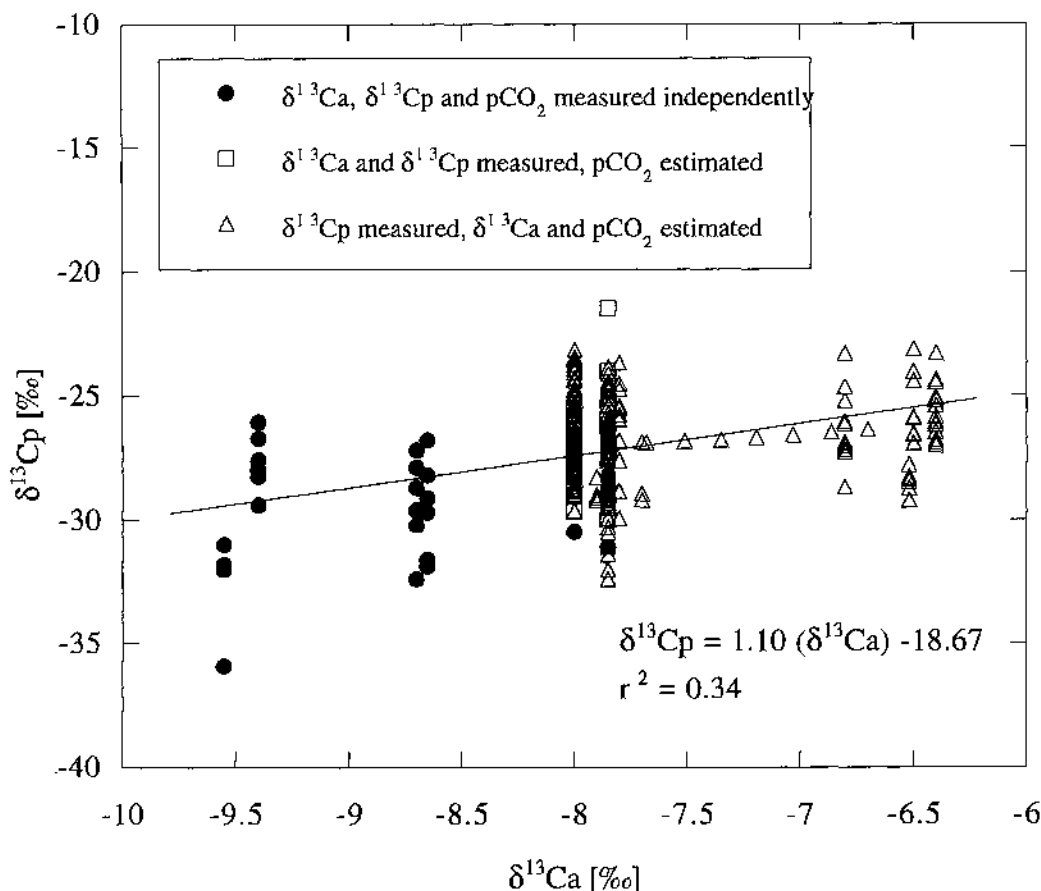
FIGURE 3. Regression of $\delta^{13}C_p$ value onto $\delta^{13}C_a$ value using a subset of the data ($n = 394$), excluding all measurements taken on members of the Poaceae and all $\delta^{13}C_a$ values that fall outside of a "geologically reasonable" range ($\delta^{13}C_a = -6.4‰$ to $-9.6‰$). The relationship was statistically significant ($p < 0.001$)

by 1.5‰ (Marino et al. 1992). Plio-Pleistocene variation of up to 3‰ was reported in marine sections (Shackleton and Hall 1984; Grazzini et al. 1990; Whitman and Berger 1994). A $-3‰$ excursion in $\delta^{13}C_a$ value was reported at the Paleocene/Eocene boundary (Koch et al. 1992; Corfield 1994), and a $-2‰$ excursion reported at the Cretaceous/Tertiary boundary (Zachos and Arthur 1986; Stott and Kennett 1989; D'Hondt et al. 1998). Up to 8‰ variation in the carbon isotopic composition of atmospheric CO_2 has been inferred during the Cenomanian–Turonian (Hasegawa 1997), and more than 3‰ reported for the Aptian (Menegatti et al. 1998; Gröcke et al. 1999). Variation of up to 8‰ has been reported in the Devonian and Carboniferous (Tajika 1998). To make our analysis more realistic, we selected a conservative subset of $\delta^{13}C_a$ values ranging

from $-3.5‰$ to $-9.6‰$. Regressing $\delta^{13}C_p$ value onto $\delta^{13}C_a$ value using this subset ($n = 477$) we recovered a significant relationship ($p < 0.001$, $r^2 = 0.33$).

To make our analysis still more general, we removed all observations made on members of the Poaceae. The carbon isotopic composition of Poaceae deviated from other growth forms in our analysis; the lineage has evolved a variety of physiologies (Schulze et al. 1996), and it became common in some ecosystems only during the Oligocene (Traverse 1988). Regressing $\delta^{13}C_p$ value onto $\delta^{13}C_a$ value using this subset ($n = 394$, $\delta^{13}C_a = -6.4$ to -9.6), we recovered a significant relationship ($p < 0.001$, $r^2 = 0.34$; Fig. 3). Both slope and intercept of this relationship were indistinguishable from those in Figure 2 ($p < 0.001$).

This result shows a significant relationship

between the carbon isotopic composition of C3 plant tissue and the carbon isotopic composition of the atmosphere under which it was fixed. Despite the strength of this relationship, it is important to note that ecological variation, manifested in C_p/C_a, adds noise to the $\delta^{13}C_a$ signal recorded in C3 plant tissue; hence the lower coefficient of determination in Figure 3.

Discussion

In light of this well-established mechanism of carbon isotopic fractionation during C3 photosynthesis, we expect our regression of $\delta^{13}C_p$ value onto $\delta^{13}C_a$ value to yield a slope equal to unity if C_p/C_a is constant. For a one-step chemical reaction, the isotopic composition of products (plant tissue) plotted as a function of isotopic compositions of reactants (atmospheric CO_2) should yield a slope equal to unity; in this case, the product directly reflects the reactant. If there is no isotope effect, the y-intercept will be zero. If isotopic discrimination yields product with less ^{13}C than the reactants (as is the case in C3 photosynthesis), the y-intercept will be negative. Our regression of $\delta^{13}C_p$ value on $\delta^{13}C_a$ value yields a slope (=1.05) close, but not equal, to unity and a negative intercept (=−18.72) of magnitude predicted by whole-ecosystem carbon isotopic discriminations (Lloyd and Farquhar 1994). For the data subset ($\delta^{13}C_p = -6.4$ to −9.6, without Poaceae) the slope remained close to unity (1.10) with a similar negative intercept (−18.67).

The Farquhar model for carbon isotopic discrimination in C3 plant photosynthesis (eq. 1) predicts that $\delta^{13}C_p$ value will be influenced by three factors: (1) kinetic discrimination associated with diffusion and carboxylation (a and b in eq. 1), (2) ecological factors (which influence C_p/C_a), and (3) the isotopic composition of atmospheric CO_2 ($\delta^{13}C_a$).

A value of a (=4.4‰) has been calculated from diffusivity comparisons of $^{13}CO_2$ versus $^{12}CO_2$ in air (Craig 1953). Carboxylation by RuBisCO further discriminates by the constant proportion $b = -29‰$ less than ±1‰ (Christeller et al. 1976; Schmidt et al. 1978; Wong et al. 1979). Therefore, these parameters

are considered constant for C3 vascular plants.

When the rate at which CO_2 enters the leaf is low relative to the rate of carbon fixation, C_p is small and $\delta^{13}C_p$ value tends to be high. A variety of ecological factors alter C_p/C_a in living plants (Table 1). In general, plants that experience water stress close their stomata to conserve water (increase water-use efficiency); closed stomata inhibit water loss but also retard CO_2 gain. The net result of drought stress—lower C_p/C_a—produces larger $\delta^{13}C_p$ values (Brodribb 1996). Soil salinity increases soil-water potential and causes the plant to close stomata, which results in larger $\delta^{13}C_p$ values (De Jong 1978; Guy et al. 1980; Farquhar et al. 1982a; Guy and Reid 1986; Flanagan and Jeffries 1989; Guy et al. 1989). Plants growing at low light levels also display high C_p/C_a values (Farquhar et al. 1982b). At very low and very high temperatures, C3 photosynthesis ceases and C_p/C_a approaches unity as assimilation rate declines (Smith et al. 1976). The mechanical resistance of soil to roots (Masler and Farquhar 1988) and relative humidity (Madhavan et al. 1991) have also been observed to raise C_p/C_a in C3 vascular land plants.

In an extensive review, Farquhar and colleagues (1982a) observed a range in C_p/C_a values of 0.30 to 0.85. Our analysis spanned much of this range of variation (Table 2) and showed that C_p/C_a influenced the isotopic composition of C3 plant tissue. However, this effect emerged clearly only when the isotopic composition of atmospheric CO_2 was held constant. Therefore, C_p/C_a gives useful information about carbon assimilation and plant water-use efficiency that is best interpreted for plants growing under a common atmosphere—past or present. However, comparison of plants across a geological time series—over which pCO_2 and $\delta^{13}C$ value of the atmosphere may have changed—will be confounded by variation in atmospheric $\delta^{13}C$ value.

Our analysis also showed that variation in pCO_2 does not significantly influence $\delta^{13}C$ value of plant tissue. This agrees with the conclusions of others (Beerling and Woodward 1995; Beerling 1996a,b) that individual plants maintain a C_p/C_a appropriate to environmental con-

ditions, regardless of atmospheric pCO_2. Several mechanisms have been proposed for maintaining consistent C_p/C_a with varying pCO_2. Ehleringer and Cerling (1995) proposed that plants maintained constant C_p/C_a by modulating C_p in response to changing C_a. In *Prosopis alba* from the Atacama Desert of Chile, increased water-use efficiency maintained C_p/C_a, while photosynthetic rate remained unchanged (Ehleringer and Cerling 1995). In *Salix herbacea*, C_p/C_a remained constant as $pCO2$ increased, because higher temperatures enabled increased photosynthetic capacity (Amthor 1995; Beerling 1996a,b). Changes in stomatal density may also help maintain consistent C_p/C_a. Stomatal density of *Salix herbacea* decreased by 60% with increasing pCO_2 during the last 200 years (Beerling 1996b). Similar reductions in stomatal density were reported for *Pinus flexilis* (Van de Water et al. 1994) and several other temperate angiosperm trees (Woodward 1987). Changes in stomatal density in response to changing pCO_2 appear to be acclimation effects that can occur over the lifetime of individual trees (Wagner et al. 1996). These results have been confirmed by other laboratory (Woodward and Bazzaz 1988; Woodward and Kelly 1995), field (Miglietta and Raschi 1993), and fossil observations (Beerling and Chaloner 1992; Beerling et al. 1993; Paoletti and Gellini 1993; McElwain et al. 1995; Kürschner et al. 1996). All of these mechanisms are likely to be important in the plant's response to changing environmental and atmospheric conditions over both ecological and evolutionary timescales.

Our analysis showed that the single most important parameter in explaining variation in carbon isotopic composition of C3 plant tissue was the $\delta^{13}C$ value of carbon dioxide fixed during photosynthesis. For comparisons in which the $\delta^{13}C$ value of the atmosphere is demonstrably invariant (e.g., modern studies or non-time-averaged fossil assemblages from open settings), variation in $\delta^{13}C_p$ value will be controlled primarily by environmental or growth-form variation in C_p/C_a. In contrast, for geological time series where $\delta^{13}C_a$ value has changed, variation in $\delta^{13}C_p$ value was likely to have been influenced most strongly by the isotopic composition of atmospheric CO_2.

In applying these results to the fossil record, however, it is essential to use other lines of evidence (e.g., sedimentological, paleontologic, paleopedologic, and paleoclimatic) to control for possible confounding environmental effects.

Reconstructing the Carbon Isotopic Composition of Atmospheric CO_2

We use the regression in Figure 3 to develop an inverse prediction solution that uses the $\delta^{13}C$ value of C3 land plant tissue to reconstruct the $\delta^{13}C$ value of the atmosphere under which it was fixed:

$$\delta^{13}C_a = \frac{\delta^{13}C_p + 18.67}{1.10}. \qquad (4)$$

We use an inverse prediction solution, rather than simply regressing $\delta^{13}C_p$ onto $\delta^{13}C_a$ values, to preserve the assumptions inherent in the choice of $\delta^{13}C_a$ value as the independent variable (Sokal and Rohlf 1981).

To test this predictive relationship, we used whole-ecosystem carbon isotopic discrimination data (Lloyd and Farquhar 1994) to calculate $\delta^{13}C$ values for the modern atmosphere using equation 4 (Table 4, Fig. 4). These data represented ecosystem averages for a variety of climates ranging from tropical ever-wet forests to semidesert, but we excluded agricultural systems because monoculture is rare in nature. Ninety-nine percent confidence intervals for predictions were calculated using the method outlined by Sokal and Rohlf (1981). We used ecosystem-average plant carbon isotopic composition for two reasons: (1) whole-ecosystem averages best represent the mixed assemblage of vascular land plant carbon most likely to be sampled from the sedimentary record, and (2) whole-ecosystem averages dilute the individual contribution of any species or individual plant. When individual plants—grown under a common atmosphere—were compared, ecophysiological effects emerged most strongly. Thus, we expect the most accurate predictions of atmospheric $\delta^{13}C$ value from a mixed assemblage like those presented by Lloyd and Farquhar (1994).

For most of the ecosystems evaluated, predicted $\delta^{13}C$ values of atmospheric CO_2 fell

TABLE 4. Predictions of δ¹³Ca value of the modern atmosphere using equation (4) and whole-ecosystem average δ¹³Cp values. Original data (Δ_A) from Lloyd and Farquhar 1994. Ecosystem types included several closely related vegetation and soil types that reflect specific climate conditions (Wilson and Henderson-Sellers 1985). Δ_A was defined by Lloyd and Farquhar (1994) as the summation of all discriminations associated with carbon assimilation, less fractionation resulting from photorespiratory and respiratory CO_2 releases. For this calculation, we have assumed that Δ_A was roughly equivalent to Δ (eq. 3) and from equation (3) calculated δ¹³Cp values using the global well-mixed average value of δ¹³Ca = −7.85‰. Measured δ¹³Cp and δ¹³Ca values for these ecosystems were not reported. Predicted δ¹³Ca values were calculated from equation (4), the inverse prediction solution based on the best-fit regression relationship between δ¹³Cp and δ¹³Ca values using the subset of data that includes only "geologically reasonable" δ¹³Ca values and excludes measurements made on members of the Poaceae (Fig. 3). Confidence intervals (see also Fig. 4) calculated for the inverse prediction solution following Sokal and Rohlf 1981.

Ecosystem type	Δ_A	δ¹³C (plant) [‰]	Predicted δ¹³C (atmos.) [‰]	99% confidence interval of prediction [‰]
Tropical ever-wet	18.4	−26.74	−7.34	−7.13 to −7.48
Tropical seasonal wet	18.9	−27.27	−7.81	−7.88 to −7.84
Tropical savanna	18.6	−26.95	−7.53	−7.43 to −7.63
Warm evergreen	19.0	−27.37	−7.91	−8.03 to −7.90
Cool deciduous	19.6	−28.00	−8.48	−8.93 to −8.33
Cool mixed hardwood and conifer	18.3	−26.64	−7.24	−6.98 to −7.41
C3 grassland/shrub	15.5	−22.99	−3.93	−1.78 to −4.97
C3 semidesert	14.2	−21.74	−2.79	0.01 to −4.13
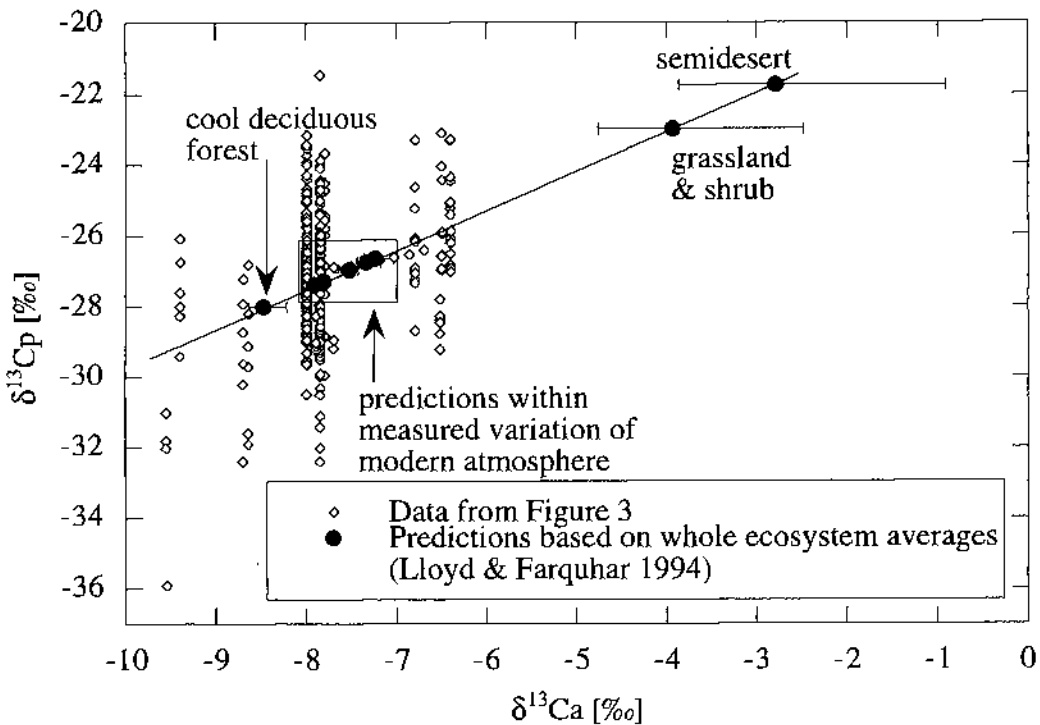
FIGURE 4. Data and regression line from Figure 3. Predicted δ¹³C$_a$ values generated from Lloyd and Farquhar (1994) and equation (4) (Table 4). Error bars on individual atmospheric δ¹³C$_a$ value predictions are 99% confidence intervals for the inverse prediction solution calculated according to Sokal and Rohlf (1981). Predictions within the box fall within the annual range of variation in measured atmospheric δ¹³C values in the Northern Hemisphere (approximately −8.4‰ to −7.4‰ [Ciais et al. 1995]). Note that confidence intervals are symmetrical around $\bar{X} + [b_{Y \cdot X}(Y_i - \bar{Y})/b^2_{Y \cdot X} - t^2_{0.01[n-2]} s^2_b]$ not $\hat{X}_i = (Y_i - a)/b_{Y \cdot X}$ as is required of the inverse solution (see Sokal and Rohlf 1981: pp. 496–498 for further discussion of this method).

within the seasonal range reported for the Northern Hemisphere (approximately -8.4‰ to -7.4‰, Ciais et al. 1995). Our reconstruction of modern atmospheric $\delta^{13}C$ value worked well for ever-wet and seasonally dry climates, suggesting that environmental factors did not significantly bias prediction in these environments. In semidesert and C3 grasslands, the reconstructed $\delta^{13}C_a$ values were larger than that of the actual atmosphere (Fig. 4). The deviation of semidesert and C3 grasslands from the general relationship might be due to generally low C_p/C_a induced by water stress, a predominance of grasses, C3/C4 intermediate physiologies, or a combination of these factors. The conclusion that our model did not work well in modern arid ecosystems does not pose a major problem for the application of this technique because this climate regime can be recognized on sedimentological criteria (e.g., paleosol carbonates).

Cool deciduous forests also did not conform to our model because they predicted a slightly low $\delta^{13}C_a$ value (Fig. 4). In this ecosystem, six Northern Hemisphere deciduous species were sampled: *Populus trichocarpa, Populus deltoides, Liriodendron tulipifera, Fagus sylvatica, Nyssa aquatica,* and *Fraxinus pennsylvanica* (Lloyd and Farquhar 1994). Most of the carbon used to build leaf tissue in these plants was fixed during the early spring flush, when the atmosphere had lowest $\delta^{13}C$ value (Ciais et al. 1995). Thus, when this leaf tissue was analyzed, we suspect that these plants generated erroneously low predictions for $\delta^{13}C$ value of atmospheric CO_2. This is consistent with the findings of Marshall and Zhang (1994), who reported that winter-deciduous C3 taxa had lower $\delta^{13}C_p$ values than evergreen taxa in the same community. In the fossil record, seasonally cold climates could be recognized using leaf margin analyses (Wolfe 1993; Wilf 1997). A more general caution might be made for geological time series in which paleobotanical evidence suggests major changes in plant composition, such as moving from forest to grassland.

To further test the predictive power of equation (4), we sought a geological time series over which atmospheric $\delta^{13}C$ value reconstructions could be compared with independent measurements of the isotopic composition of atmospheric CO_2. One such example compares carbon isotopic measurements from *Pinus flexilis* needles preserved in pack rat middens from Idaho, Nevada, Utah, and Arizona (Van de Water et al. 1994) with a $\delta^{13}C_a$ record from air bubbles trapped in the Byrd Glacier of Antarctica (Leuenberger et al. 1992) and an independent record from C4 plants (*Atriplex confertifolia,* also preserved in middens) from Wisconsin (Marino et al. 1992). C4 plants show little intraspecific ecophysiological variation in their carbon isotopic signatures and therefore have been used to reconstruct the $\delta^{13}C_a$ value (Marino and McElroy 1991). *P. flexilis* measurements used for this test were not included in the data set that produced equation (4).

In developing this test, several problems emerged. First, ice core and fossil samples were dated using different methods. Ice core ages were based on an unpublished depth-to-age scale (Leuenberger et al. 1992), while *P. flexilis* needles and *A. confertifolia* leaves were dated radiometrically, using ^{14}C (Marino et al. 1992; Van de Water et al. 1994). This raises the concern that reported ages are not commensurate. Second, assuming that age-dates for these records correspond, few individual samples were close enough in age to permit comparison. Table 5 presents data from the 11 most temporally correlative samples, which we use for this test. Third, fossil plants and the corresponding $\delta^{13}C_a$ values are geographically separated. Consequently, we must assume that Earth's atmosphere is homogeneous with respect to the $\delta^{13}C$ value of atmospheric CO_2, an assumption not valid in the modern atmosphere (Ciais et al. 1995).

Using a single species, rather than an ecosystem average, to reconstruct the carbon isotopic composition of atmospheric CO_2 also raises the possibility of error due to the specific physiology of the plant. Even among C4 plants, which vary less in their carbon isotopic discrimination than do C3 plants, interspecies variation in discrimination can be greater than 1‰ (Marino and McElroy 1991; Marino et al. 1992). This might pose a particular problem for our test, which uses data from the conifer *Pinus flexilis*. In general, conifers have lower

TABLE 5. Carbon isotropic measurements made on fossil *Pinus flexilis* needles preserved in pack rat middens from the Great Basin (Van de Water et al. 1994) were used to generate predictions of the carbon isotropic composition of atmospheric CO_2 based on equation (4). A correction of δ¹³C value (whole leaf carbon) = δ¹³C (cellulose) $-3‰$ was applied to make *P. flexilis* data commensurate with our model. A correction of $-2‰$ accounts for the difference between whole tissue and isolated cellulose carbon isotopic values (Benner et al. 1987). A $-1‰$ correction accounts for the systematic difference in carbon assimilation rate observed between conifers and angiosperms (Wullschleger 1993). Ninety-nine percent confidence intervals are calculated as in Table 4. Predictions are compared with approximately time-correlated measurements of the δ¹³C values of carbon dioxide trapped in Antarctic ice[1] (Leuenberger et al. 1992) and of C4 plants preserved in pack rat middens from Wisconsin[2] (Marino et al. 1992).

Age of atmospheric CO_2 [years B.P.]	Age of fossil [years B.P.]	δ¹³C (atmos.) [‰]	δ¹³C (plant) [‰]	Predicted δ¹³C (atmos.) [‰]	99% confidence interval of prediction [‰]
890[1]	1960	−6.44	−23.2	−6.8	−6.3 to −7.1
2635[2]	2760	−6.48	−22.6	−6.3	−5.4 to −6.7
5595[2]	5720	−6.54	−23.3	−6.9	−6.4 to −7.2
12,080[1]	12,190	−6.73	−23.4	−7.0	−6.5 to −7.3
14,720[1]	14,600	−6.72	−21.3	−5.1	−3.6 to −5.8
14,810[2]	14,810	−7.41	−23.8	−7.4	−7.1 to −7.5
20,200[2]	19,990	−7.09	−23.9	−7.5	−7.0 to −7.6
21,800[1]	21,740	−6.67	−23.4	−7.0	−6.5 to −7.3
22,640[1]	23,110	−7.02	−22.2	−5.9	−4.9 to −6.4
25,900[2]	26,170	−7.09	−22.5	−5.9	−4.9 to −6.5
27,920[1]	28,020	−6.93	−21.8	−5.6	−4.3 to −6.2

carboxylation rates than do angiosperm trees (Wullschleger 1993), a difference that might affect their carbon isotopic signature. In our meta–data set, conifers had an average δ¹³C value 1‰ greater ($-27.0‰$) than both angiosperm trees ($-27.9‰$) and forbs ($-28.0‰$).
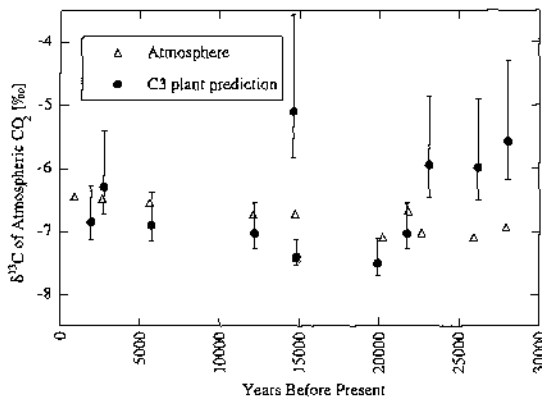
FIGURE 5. Time-series carbon isotopic measurements made on *Pinus flexilis* needles (Van de Water et al. 1994) were used to generate δ¹³C₂ predictions based on equation (4) (Table 5). Error bars on predictions are 99% confidence intervals calculated as in Figure 4. Atmospheric δ¹³C value predictions were compared with time-correlated measurements made on CO_2 trapped in Antarctic ice (Leuenberger et al. 1992) and reconstructed using a C4 plant (*Atriplex confertifolia*; Marino et al. 1992). Seven of 11 C3 plant-derived predictions accurately reconstruct δ¹³C₂ within an error of less than 0.4‰. The remaining four samples were collected from the desert of eastern Utah and show anomalously high δ¹³C values, probably due to water stress.

Since our predictive data set was derived primarily from angiosperm data, we applied a correction of $-1‰$ to *P. flexilis* data to compensate for this difference. This correction is only necessary because we use a single species rather than an ecosystem average. As discussed above, the atmospheric signal emerges more clearly when the ecophysiological signal of individual species is averaged across the community. This point is illustrated by the fact that the mixed conifer and hardwood ecosystem in the previous test (Table 4) returns an accurate reconstruction of atmospheric δ¹³C value, even though it included conifers (*Pinus radiata, Picea engelmanii, Picea rubens, Larix leptolepis,* and *Pseudotsuga menziesii*); thus, we generally prefer the whole-ecosystem approach.

Figure 5 and Table 5 show that 7 of 11 *Pinus flexilis* samples reconstructed the δ¹³C value of atmospheric CO_2 within the 99% confidence interval of prediction derived from equation (4). The actual difference between δ¹³C₂ measurements and predictions derived from equation 4 was less than 0.4‰. This precision was possible in spite of a 15% increase in water-use efficiency reported for *P. flexilis* during deglaciation (15,000–12,000 years B.P.; Van de Water et al. 1994). Four samples, collected from middens in the desert of eastern Utah

(Van de Water et al. 1994), produced anomalously high $\delta^{13}C_a$ value predictions (Table 5). In these samples, as in the semidesert example in Figure 4, unusually high $\delta^{13}C$ values likely resulted from water stress experienced by these trees. This further emphasizes the need for independent lines of climatological evidence supporting an analysis of this type. Nonetheless, despite the erroneously high predictions, these plant-derived values follow the same trend as atmospheric $\delta^{13}C$ values derived from ice core air and C4 plant data (Fig. 5), demonstrating that secular variation in the isotopic composition of atmospheric CO_2 emerges even when a strong ecophysiological signal is present.

Applying These Results to the Fossil Record

The stable carbon isotope composition of atmospheric CO_2 reflects changes in global carbon cycling. Throughout Earth's history, changes in CO_2 fluxes can be linked to carbon sources and sinks based upon differences in the isotope composition of specific carbon pools (Weissert 1989; Dickens et al. 1997; Algeo and Scheckler 1998). This may be particularly true when normal carbon cycling is disrupted (D'Hondt et al. 1998; Arinobu et al. 1999). Consequently, a quantitative estimate of the $\delta^{13}C$ value of atmospheric CO_2 that can be applied to geologic time will lend insight into carbon cycling in the Phanerozoic and the paleobiological factors that influence it. Such a measure may also extend ecophysiological models of carbon assimilation in plants to evolutionary timescale hypotheses (e.g., Gröcke 1998).

In applying our results to questions in earth history we must (1) identify and isolate a substrate that is uniquely derived from terrestrial vascular plants and (2) be confident that the isotopic composition of the isolated substrate reflects the isotopic composition of whole-plant tissue faithfully and with low variability. Whole-fossil carbon isotopic values may be difficult to interpret because early diagenetic changes alter the ratio of cellulose to lignin to polysaccharides in decomposing tissue. In the laboratory, decomposition changed the isotopic signature of leaf carbon by up to 4‰ (Ben-

ner et al. 1987). However, in both temperate (Vogel 1978) and tropical (Medina et al. 1986) forests, $\delta^{13}C$ value of undecomposed leaf litter equaled that of canopy leaves. The carbon isotopic composition of decomposing litter equaled that of soil organic matter, which was a consistent 2‰ greater than the $\delta^{13}C$ value of canopy leaves (Medina et al. 1986). This probably resulted from the preferential loss of ^{12}C due to bacterial activity and the enrichment of the remaining organic material in the lignin fraction (Benner et al. 1987).

Plant-derived macromolecules such as lignin, cellulose (a polymer of D-glucopyranose subunits), and a variety of plant lipids can also be isolated from sedimentary rock. Isolated cellulose is preferred by many workers studying Pleistocene and Holocene materials (e.g., Marino et al. 1992; Dupouey et al. 1993; Van de Water et al. 1994). Isolated cellulose values were 0.25‰ to 3‰ greater than whole-tissue $\delta^{13}C$ values (O'Leary 1988; Marino and McElroy 1991). Lignin ranged from 4.2‰ to 2.0‰ less than whole-plant tissue values (Benner et al. 1987). Lipids can be highly isotopically variable depending on the tissue and synthetic pathway from which they were derived. Values of bulk plant lipids range from 5‰ to 10‰ less than whole-plant tissue $\delta^{13}C$ values (Park and Epstein 1961). Individual lipids also vary. In *Fagus sylvatica*, the $\delta^{13}C$ value of n-C_{27} alkane was 2‰ less than that of whole-leaf tissue in south-facing leaves and 3‰ less in north-facing leaves (Lockheart et al. 1997). For sitosterol, the difference between north- and south-facing leaves was 3‰. In *Quercus robur* leaves growing in the sun, the $\delta^{13}C$ value of n-C_{27} alkane was consistently about 6‰ less than whole-leaf tissue values. However, values from leaves in the shade varied from 4‰ to 6‰ less than those of bulk tissue (Lockheart et al. 1997). Given the variability in all of these substrates, the best approach may be to look for confluence between two or more. Despite this variability, a n-C_{29} alkane has been used to reconstruct secular variation in the terrestrial $\delta^{13}C$ signal across the Cretaceous/Tertiary boundary (Arinobu et al. 1999).

Two land plant organs are common and easily isolated from sedimentary rock: plant cuti-

cle and palynomorphs (pollen and spores). Isolated pollen was "isotopically similar" to whole-tissue δ^{13}C values for several C3 and C4 grasses (Amundson et al. 1997). In the C3 grasses studied (*Lolium multiflorum*, *Hordeum murinum*, *Bromus corinatus*, and *Avena barbata*), pollen ranged from 6.3‰ greater than to 2.5‰ less than whole-plant δ^{13}C values (Amundson et al. 1997). This suggests that whereas pollen may be useful for distinguishing C3 from C4 carbon-fixation pathways, this organ may be too isotopically variable for questions that require finer resolution.

Plant cuticle, the waterproof coating on aerial surfaces, is composed primarily of cutin (esterified fatty acids, hydroxy fatty acids, and dicarboxylic acids) and cutan (*n*-alkyls linked by ether bonds), with lignin (a high molecular-weight polymer composed of aromatic alcohols) important in some species (De Leeuw et al. 1995). Epicuticular waxes (commonly *n*-alkanes) can also be preserved in association with plant cuticle. Cuticle can be easily removed from sedimentary rock by inorganic acid digestion and identified by the characteristic imprint of epidermal cells. Despite its complex composition, cuticle faithfully reflects the isotopic composition of whole-plant tissue. In a study of more than ten angiosperm and conifer species, including C3, C4, and CAM physiologies (G. Upchurch personal communication 1998), cuticle values were 3‰–3.5‰ less than whole-plant δ^{13}C values with an error of less than ±1‰ (Upchurch et al. 1997).

Our analyses showed that the δ^{13}C value of atmospheric CO_2 can be estimated using a relationship derived empirically from carbon isotopic measurements of C3 plant tissue. In a modern example, the predictive equation reconstructed the δ^{13}C value of CO_2 to within the annual range of atmospheric variation for most mesic climates. In a second, time-series test, our equation accurately reconstructed Holocene variation in the δ^{13}C value of atmospheric CO_2, except in samples from arid regions. Because most organic carbon preserved in the sedimentary record was buried under mesic or seasonally moist conditions, this method allows reconstruction of the isotopic history of atmospheric carbon dioxide throughout the 400-million-year history of C3 vascular plants on land.

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Appendix
Data Used in the Meta-Analysis

Data ($n = 519$) used in this meta-analysis. Growth-form categories are defined as follows: forbs are annual or perennial herbs, except grasses and sedges; grass includes Poaceae only; shrubs are woody perennials that lack a distinct trunk-crown architecture (includes subshrubs) as defined by Hickman 1993); trees are woody perennials with a distinct trunk-crown architecture. These parallel life-form classifications used in other studies of community-level carbon isotopic discrimination (Brooks et al. 1997a). $\delta^{13}Cp$ values reported here include a -2‰ correction to measurements made on extracted cellulose. This correction makes $\delta^{13}C$ measurements of extracted cellulose commensurate with whole-leaf measurements (Benner et al. 1987).

Species	Growth form	$\delta^{13}Ca$	$\delta^{13}Cp$	Source
Triticum aestivum	grass	-7.85	-25.20	(Araus et al. 1993)
Triticum aestivum	grass	-7.85	-25.20	(Araus et al. 1993)
Triticum aestivum	grass	-7.85	-24.91	(Araus et al. 1993)
Triticum aestivum	grass	-7.85	-25.49	(Araus et al. 1993)
Triticum aestivum	grass	-7.85	-24.53	(Araus et al. 1993)
Triticum aestivum	grass	-7.85	-25.87	(Araus et al. 1993)
Chamaenerion angustifolium	forb	-9.40	-28.25	(Beerling and Woodward 1995)
Digitalis purpurea	forb	-9.40	-26.72	(Beerling and Woodward 1995)
Epilobium hirsutum	forb	-9.40	-26.05	(Beerling and Woodward 1995)
Helianthus annuus	forb	-9.40	-29.39	(Beerling and Woodward 1995)
Plantago lanceolata	forb	-9.40	-27.97	(Beerling and Woodward 1995)
Urtica dioica	forb	-9.40	-27.58	(Beerling and Woodward 1995)
Agrostis capillaris	grass	-9.40	-29.58	(Beerling and Woodward 1995)
Anthoxanthum odoratum	grass	-9.40	-27.58	(Beerling and Woodward 1995)
Arrhenatherum elatius	grass	-9.40	-28.44	(Beerling and Woodward 1995)
Brachypodium pinnatum	grass	-9.40	-27.30	(Beerling and Woodward 1995)
Bromus erectus	grass	-9.40	-26.53	(Beerling and Woodward 1995)
Bromus sterilis	grass	-9.40	-27.11	(Beerling and Woodward 1995)
Dactylis glomerata	grass	-9.40	-28.44	(Beerling and Woodward 1995)
Holcus lanatus	grass	-9.40	-29.96	(Beerling and Woodward 1995)
Lolium perenne	grass	-9.40	-30.53	(Beerling and Woodward 1995)
Poa annua	grass	-9.40	-28.35	(Beerling and Woodward 1995)
Poa trivialis	grass	-9.40	-29.20	(Beerling and Woodward 1995)
Chamaenerion angustifolium	forb	-17.90	-36.68	(Beerling and Woodward 1995)
Digitalis purpurea	forb	-17.90	-36.02	(Beerling and Woodward 1995)
Epilobium hirsutum	forb	-17.90	-33.46	(Beerling and Woodward 1995)
Helianthus annuus	forb	-17.90	-36.59	(Beerling and Woodward 1995)
Plantago lanceolata	forb	-17.90	-38.29	(Beerling and Woodward 1995)
Urtica dioica	forb	-17.90	-36.59	(Beerling and Woodward 1995)
Agrostis capillaris	grass	-17.90	-37.16	(Beerling and Woodward 1995)
Anthoxanthum odoratum	grass	-17.90	-36.87	(Beerling and Woodward 1995)
Arrhenatherum elatius	grass	-17.90	-36.21	(Beerling and Woodward 1995)
Brachypodium pinnatum	grass	-17.90	-34.22	(Beerling and Woodward 1995)
Bromus erectus	grass	-17.90	-36.31	(Beerling and Woodward 1995)
Bromus sterilis	grass	-17.90	-37.16	(Beerling and Woodward 1995)
Dactylis glomerata	grass	-17.90	-35.74	(Beerling and Woodward 1995)
Holcus lanatus	grass	-17.90	-37.35	(Beerling and Woodward 1995)
Lolium perenne	grass	-17.90	-38.85	(Beerling and Woodward 1995)
Poa annua	grass	-17.90	-41.29	(Beerling and Woodward 1995)
Poa trivialis	grass	-17.90	-38.38	(Beerling and Woodward 1995)
Chamaenerion angustifolium	forb	-21.60	-41.25	(Beerling and Woodward 1995)
Digitalis purpurea	forb	-21.60	-38.71	(Beerling and Woodward 1995)
Epilobium hirsutum	forb	-21.60	-40.60	(Beerling and Woodward 1995)
Helianthus annuus	forb	-21.60	-41.82	(Beerling and Woodward 1995)
Plantago lanceolata	forb	-21.60	-43.69	(Beerling and Woodward 1995)
Urtica dioica	forb	-21.60	-39.56	(Beerling and Woodward 1995)

Appendix. Continued.

Species	Growth form	$\delta^{13}C_a$	$\delta^{13}C_p$	Source
Agrostis capillaris	grass	-21.60	-42.66	(Beerling and Woodward 1995)
Anthoxanthum odoratum	grass	-21.60	-42.10	(Beerling and Woodward 1995)
Arrhenatherum elatius	grass	-21.60	-41.25	(Beerling and Woodward 1995)
Brachypodium pinnatum	grass	-21.60	-39.28	(Beerling and Woodward 1995)
Bromus erectus	grass	-21.60	-41.54	(Beerling and Woodward 1995)
Bromus sterilis	grass	-21.60	-40.31	(Beerling and Woodward 1995)
Dactylis glomerata	grass	-21.60	-41.44	(Beerling and Woodward 1995)
Holcus lanatus	grass	-21.60	-41.35	(Beerling and Woodward 1995)
Lolium perenne	grass	-21.60	-42.85	(Beerling and Woodward 1995)
Poa annua	grass	-21.60	-42.85	(Beerling and Woodward 1995)
Poa trivialis	grass	-21.60	-42.10	(Beerling and Woodward 1995)
Salix herbacea	shrub	-6.52	-28.36	(Beerling 1996a)
Salix herbacea	shrub	-6.52	-27.79	(Beerling 1996a)
Salix herbacea	shrub	-6.52	-28.26	(Beerling 1996a)
Salix herbacea	shrub	-6.52	-29.21	(Beerling 1996a)
Salix herbacea	shrub	-6.52	-28.74	(Beerling 1996a)
Salix herbacea	shrub	-6.52	-28.45	(Beerling 1996a)
Aphelandra pulcherrima	tree	-7.85	-31.10	(Broadmeadow et al. 1992)
Brosimum alicastrum	tree	-7.85	-26.50	(Broadmeadow et al. 1992)
Cassearia guianensis	tree	-7.85	-28.30	(Broadmeadow et al. 1992)
Lundia corymbifera	tree	-7.85	-26.30	(Broadmeadow et al. 1992)
Philodendron krugii	tree	-7.85	-25.40	(Broadmeadow et al. 1992)
Swietenia macrophylla	tree	-7.85	-25.80	(Broadmeadow et al. 1992)
Tabernaemontanum attenuata	tree	-7.85	-28.90	(Broadmeadow et al. 1992)
Bactris cusea	tree	-8.65	-31.90	(Broadmeadow et al. 1992)
Calliandra guildingii	tree	-8.65	-29.70	(Broadmeadow et al. 1992)
Clathrotropis brachpetala	tree	-8.65	-28.20	(Broadmeadow et al. 1992)
Miconia affinis	tree	-8.65	-26.80	(Broadmeadow et al. 1992)
Philodendron lingulatum	tree	-8.65	-31.60	(Broadmeadow et al. 1992)
Ryania speciosa	tree	-8.65	-29.10	(Broadmeadow et al. 1992)
Aphelandra pulcherrima	tree	-8.70	-32.40	(Broadmeadow et al. 1992)
Brosimum alicastrum	tree	-8.70	-27.20	(Broadmeadow et al. 1992)
Cassearia guianensis	tree	-8.70	-29.60	(Broadmeadow et al. 1992)
Lundia corymbifera	tree	-8.70	-27.90	(Broadmeadow et al. 1992)
Philodendron krugii	tree	-8.70	-27.90	(Broadmeadow et al. 1992)
Swietenia macrophylla	tree	-8.70	-28.70	(Broadmeadow et al. 1992)
Tabernaemontanum attenuata	tree	-8.70	-30.20	(Broadmeadow et al. 1992)
Calliandra guildingii	tree	-9.55	-31.00	(Broadmeadow et al. 1992)
Clathrotropis brachpetala	tree	-9.55	-31.80	(Broadmeadow et al. 1992)
Miconia affinis	tree	-9.55	-31.80	(Broadmeadow et al. 1992)
Philodendron lingulatum	tree	-9.55	-35.90	(Broadmeadow et al. 1992)
Ryania speciosa	tree	-9.55	-32.00	(Broadmeadow et al. 1992)
Triticum aestivum	grass	-7.85	-25.01	(Condon et al. 1993)
Triticum aestivum	grass	-7.85	-24.91	(Condon et al. 1993)
Triticum aestivum	grass	-7.85	-24.63	(Condon et al. 1993)
Triticum aestivum	grass	-7.85	-24.24	(Condon et al. 1993)
Triticum aestivum	grass	-7.85	-23.76	(Condon et al. 1993)
Triticum aestivum	grass	-7.85	-24.63	(Condon et al. 1993)
Triticum durum	grass	-7.85	-25.30	(Condon et al. 1993)
Triticum durum	grass	-7.85	-24.82	(Condon et al. 1993)
Acer negundo	tree	-7.85	-26.05	(Dawson and Ehleringer 1993)
Acer negundo	tree	-7.85	-27.94	(Dawson and Ehleringer 1993)
Acer negundo	tree	-7.85	-25.34	(Dawson and Ehleringer 1993)
Acer negundo	tree	-7.85	-28.65	(Dawson and Ehleringer 1993)
Acer negundo	tree	-7.85	-24.63	(Dawson and Ehleringer 1993)
Acer negundo	tree	-7.85	-27.23	(Dawson and Ehleringer 1993)
Acer negundo	tree	-7.85	-24.63	(Dawson and Ehleringer 1993)
Acer negundo	tree	-7.85	-28.89	(Dawson and Ehleringer 1993)
Artemisia tridentata	shrub	-8.00	-27.87	(Donovan and Ehleringer 1991)
Artemisia tridentata	shrub	-8.00	-27.61	(Donovan and Ehleringer 1991)
Chrysothamnus nauseosus	shrub	-8.00	-28.01	(Donovan and Ehleringer 1991)
Chrysothamnus nauseosus	shrub	-8.00	-27.46	(Donovan and Ehleringer 1991)
Chrysothamnus nauseosus	shrub	-8.00	-26.02	(Donovan and Ehleringer 1992)
Chrysothamnus nauseosus	shrub	-8.00	-27.36	(Donovan and Ehleringer 1992)

Appendix. Continued.

Species	Growth form	$\delta^{13}C_a$	$\delta^{13}C_p$	Source
Chrysothamnus nauseosus	shrub	-8.00	-29.30	(Donovan and Ehleringer 1994)
Chrysothamnus nauseosus	shrub	-8.00	-27.74	(Donovan and Ehleringer 1994)
Fagus sylvatica	tree	-6.70	-26.40	(Dupouey et al. 1993)
Fagus sylvatica	tree	-6.86	-26.50	(Dupouey et al. 1993)
Fagus sylvatica	tree	-7.03	-26.60	(Dupouey et al. 1993)
Fagus sylvatica	tree	-7.19	-26.70	(Dupouey et al. 1993)
Fagus sylvatica	tree	-7.35	-26.80	(Dupouey et al. 1993)
Fagus sylvatica	tree	-7.51	-26.85	(Dupouey et al. 1993)
Fagus sylvatica	tree	-7.68	-26.90	(Dupouey et al. 1993)
Fagus sylvatica	tree	-7.84	-26.95	(Dupouey et al. 1993)
Fagus sylvatica	tree	-8.00	-27.00	(Dupouey et al. 1993)
Juniperus osteosperma	tree	-7.85	-23.86	(Ehleringer and Cerling 1995)
Pinus ponderosa	tree	-7.85	-25.39	(Ehleringer and Cerling 1995)
Psilostrophe cooperi	forb	-8.00	-27.83	(Ehleringer et al. 1992)
Psilostrophe cooperi	forb	-8.00	-24.87	(Ehleringer et al. 1992)
Sphaeralcea parvifolia	forb	-8.00	-27.64	(Ehleringer et al. 1992)
Sphaeralcea parvifolia	forb	-8.00	-24.77	(Ehleringer et al. 1992)
Stephanomeria pauciflora	forb	-8.00	-27.74	(Ehleringer et al. 1992)
Stephanomeria pauciflora	forb	-8.00	-25.06	(Ehleringer et al. 1992)
Acamptopappus sphaerocephalus	shrub	-8.00	-27.45	(Ehleringer et al. 1992)
Acamptopappus sphaerocephalus	shrub	-8.00	-26.97	(Ehleringer et al. 1992)
Ambrosia dumosa	shrub	-8.00	-26.59	(Ehleringer et al. 1992)
Ambrosia dumosa	shrub	-8.00	-24.39	(Ehleringer et al. 1992)
Ambrosia eriocentra	shrub	-8.00	-27.07	(Ehleringer et al. 1992)
Ambrosia eriocentra	shrub	-8.00	-25.73	(Ehleringer et al. 1992)
Bebbia juncea	shrub	-8.00	-26.02	(Ehleringer et al. 1992)
Bebbia juncea	shrub	-8.00	-23.91	(Ehleringer et al. 1992)
Chrysothamnus paniculatus	shrub	-8.00	-27.93	(Ehleringer et al. 1992)
Chrysothamnus paniculatus	shrub	-8.00	-24.68	(Ehleringer et al. 1992)
Encelia farinosa	shrub	-8.00	-25.35	(Ehleringer et al. 1992)
Encelia farinosa	shrub	-8.00	-24.29	(Ehleringer et al. 1992)
Gutierrezia sarothrae	shrub	-8.00	-26.78	(Ehleringer et al. 1992)
Gutierrezia sarothrae	shrub	-8.00	-24.01	(Ehleringer et al. 1992)
Hymenoclea monogyra	shrub	-8.00	-26.02	(Ehleringer et al. 1992)
Hymenoclea monogyra	shrub	-8.00	-23.14	(Ehleringer et al. 1992)
Hymenoclea salsola	shrub	-8.00	-26.59	(Ehleringer et al. 1992)
Hymenoclea salsola	shrub	-8.00	-23.72	(Ehleringer et al. 1992)
Porophyllum gracile	shrub	-8.00	-24.87	(Ehleringer et al. 1992)
Porphyllum gracile	shrub	-8.00	-27.26	(Ehleringer et al. 1992)
Salazaria mexicana	shrub	-8.00	-26.31	(Ehleringer et al. 1992)
Salazaria mexicana	shrub	-8.00	-23.53	(Ehleringer et al. 1992)
Senecio douglasii	shrub	-8.00	-23.43	(Ehleringer et al. 1992)
Senecio douglassi	shrub	-8.00	-26.11	(Ehleringer et al. 1992)
Phaseolus vulgaris	forb	-7.85	-21.45	(Ehleringer et al. 1991)
Phaseolus vulgaris	forb	-7.85	-25.39	(Ehleringer et al. 1991)
Phaseolus vulgaris	forb	-7.85	-27.30	(Ehleringer et al. 1991)
Phaseolus vulgaris	forb	-7.85	-29.97	(Ehleringer et al. 1991)
Encelia farinosa	shrub	-7.85	-24.43	(Ehleringer 1993)
Encelia farinosa	shrub	-7.85	-25.39	(Ehleringer 1993)
Encelia farinosa	shrub	-7.85	-26.35	(Ehleringer 1993)
Nardus stricta	shrub	-7.85	-24.00	(Friend et al. 1989)
Vaccinium myrtillus	shrub	-7.85	-27.50	(Friend et al. 1989)
Nardus stricta	shrub	-7.85	-26.00	(Friend et al. 1989)
Vaccinium myrtillus	shrub	-7.85	-27.20	(Friend et al. 1989)
Coffea arabica	shrub	-8.00	-27.11	(Gutiérrez and Meinzer 1994)
Coffea arabica	shrub	-8.00	-27.40	(Gutiérrez and Meinzer 1994)
Coffea arabica	shrub	-8.00	-27.40	(Gutiérrez and Meinzer 1994)
Coffea arabica	shrub	-8.00	-27.49	(Gutiérrez and Meinzer 1994)
Coffea arabica	shrub	-8.00	-27.49	(Gutiérrez and Meinzer 1994)
Coffea arabica	shrub	-8.00	-27.59	(Gutiérrez and Meinzer 1994)
Coffea arabica	shrub	-8.00	-27.88	(Gutiérrez and Meinzer 1994)
Coffea arabica	shrub	-8.00	-28.26	(Gutiérrez and Meinzer 1994)
Puccinellia nuttalliana	grass	-43.50	-67.80	(Guy and Reid 1986)
Puccinellia nuttalliana	grass	-43.50	-66.60	(Guy and Reid 1986)

Appendix. Continued.

Species	Growth form	$\delta^{13}C_a$	$\delta^{13}C_p$	Source
Puccinellia nuttalliana	grass	-43.50	-66.40	(Guy and Reid 1986)
Puccinellia nuttalliana	grass	-43.50	-65.40	(Guy and Reid 1986)
Puccinellia nuttalliana	grass	-46.90	-70.00	(Guy and Reid 1986)
Puccinellia nuttalliana	grass	-46.90	-68.30	(Guy and Reid 1986)
Puccinellia nuttalliana	grass	-46.90	-66.10	(Guy and Reid 1986)
Puccinellia nuttalliana	grass	-46.90	-63.90	(Guy and Reid 1986)
Vigna unguiculata	forb	-7.85	-29.49	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-29.40	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-29.30	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-29.21	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-29.21	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-29.11	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-29.11	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-29.11	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-29.11	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-29.11	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-29.11	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-29.11	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-29.11	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-29.02	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-29.02	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-28.92	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-28.92	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-28.92	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-28.92	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-28.92	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-28.92	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-28.83	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-28.83	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-28.83	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-28.73	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-28.73	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-28.73	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-28.64	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-28.64	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-28.64	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-28.64	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-28.64	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-28.54	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-28.54	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-28.54	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-28.54	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-28.54	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-28.54	(Hall et al. 1994)
Vigna unguiculata	forb	-7.85	-28.35	(Hall et al. 1994)
Acacia koa	tree	-8.00	-27.16	(Hansen and Steig 1993)
Acacia koa	tree	-8.00	-25.44	(Hansen and Steig 1993)
Carapa guianensis	tree	-8.00	-30.49	(Huc et al. 1994)
Dicorynia guianensis	tree	-8.00	-27.82	(Huc et al. 1994)
Eperua falcata	tree	-8.00	-26.81	(Huc et al. 1994)
Goupia glabra	tree	-8.00	-29.57	(Huc et al. 1994)
Jacaranda copaia	tree	-8.00	-29.52	(Huc et al. 1994)
Vigna unguiculata	forb	-8.00	-26.44	(Ismail and Hall 1993)
Vigna unguiculata	forb	-8.00	-26.54	(Ismail and Hall 1993)
Vigna unguiculata	forb	-8.00	-26.44	(Ismail and Hall 1993)
Vigna unguiculata	forb	-8.00	-26.64	(Ismail and Hall 1993)
Vigna unguiculata	forb	-8.00	-26.73	(Ismail and Hall 1993)
Vigna unguiculata	forb	-8.00	-27.30	(Ismail and Hall 1993)
Vigna unguiculata	forb	-8.00	-27.88	(Ismail and Hall 1993)
Vigna unguiculata	forb	-8.00	-26.73	(Ismail et al. 1994)
Vigna unguiculata	forb	-8.00	-26.92	(Ismail et al. 1994)
Vigna unguiculata	forb	-8.00	-26.83	(Ismail et al. 1994)

Appendix. Continued.

Species	Growth form	$\delta^{13}C_a$	$\delta^{13}C_p$	Source
Vigna unguiculata	forb	-8.00	-27.11	(Ismail et al. 1994)
Vigna unguiculata	forb	-8.00	-27.59	(Ismail et al. 1994)
Vigna unguiculata	forb	-8.00	-25.49	(Ismail et al. 1994)
Vigna unguiculata	forb	-8.00	-25.01	(Ismail et al. 1994)
Vigna unguiculata	forb	-8.00	-25.58	(Ismail et al. 1994)
Vigna unguiculata	forb	-8.00	-25.49	(Ismail et al. 1994)
Vigna unguiculata	forb	-8.00	-25.78	(Ismail et al. 1994)
Agropyron desertorum	grass	-7.85	-26.16	(Johnson and Tieszen 1993)
Dactylis glomerata	grass	-7.85	-24.53	(Johnson and Tieszen 1993)
Festuca arundinacea	grass	-7.85	-24.43	(Johnson and Tieszen 1993)
Lolium perenne	grass	-7.85	-24.72	(Johnson and Tieszen 1993)
Simmondsia chinensis	shrub	-7.70	-29.18	(Kohorn et al. 1994)
Simmondsia chinensis	shrub	-7.70	-28.93	(Kohorn et al. 1994)
Simmondsia chinensis	shrub	-7.70	-26.87	(Kohorn et al. 1994)
Lycopersicon esculentum	forb	-7.85	-27.90	(Martin and Thorstenson 1988)
Lycopersicon esculentum	forb	-7.85	-26.40	(Martin and Thorstenson 1988)
Lycopersicon esculentum	forb	-7.85	-25.10	(Martin and Thorstenson 1988)
L. esculentum x *pennellii*	forb	-7.85	-26.60	(Martin and Thorstenson 1988)
L. esculentum x *pennellii*	forb	-7.85	-25.40	(Martin and Thorstenson 1988)
L. esculentum x *pennellii*	forb	-7.85	-24.50	(Martin and Thorstenson 1988)
Lycopersicon pennellii	forb	-7.85	-26.10	(Martin and Thorstenson 1988)
Lycopersicon pennellii	forb	-7.85	-25.00	(Martin and Thorstenson 1988)
Lycopersicon pennellii	forb	-7.85	-24.70	(Martin and Thorstenson 1988)
Brassica oleracea	forb	-7.85	-28.97	(Martin et al. 1988)
Lactuca sativa	forb	-7.85	-25.91	(Martin et al. 1988)
Phaseolus vulgaris	forb	-7.85	-26.24	(Martin et al. 1988)
Triticum aestivum	grass	-7.85	-29.27	(Martin et al. 1988)
Abies alba	tree	-7.85	-26.91	(Martin et al. 1988)
Fagus sylvatica	tree	-7.85	-27.43	(Martin et al. 1988)
Picea abies	tree	-7.85	-26.59	(Martin et al. 1988)
Picea abies	tree	-7.85	-26.42	(Martin et al. 1988)
Pinus pinaster	tree	-7.85	-28.92	(Martin et al. 1988)
Pseudotsuga menziesii	tree	-7.85	-28.00	(Martin et al. 1988)
Agropyron desertorum	grass	-7.85	-26.83	(Mayland et al. 1993)
Agropyron desertorum	grass	-7.85	-23.95	(Mayland et al. 1993)
Agropyron desertorum	grass	-7.85	-26.83	(Mayland et al. 1993)
Agropyron smithii	grass	-8.00	-26.50	(Mole et al. 1994)
Stipa comata	grass	-8.00	-25.70	(Mole et al. 1994)
Carex heliophila	tree	-8.00	-25.70	(Mole et al. 1994)
Capsicum annuum	shrub	-7.85	-28.70	(Mooney et al. 1989)
Croton pseudoniveus	shrub	-7.85	-28.10	(Mooney et al. 1989)
Erythroxylum havanense	shrub	-7.85	-27.00	(Mooney et al. 1989)
Hamelia versicolor	shrub	-7.85	-27.40	(Mooney et al. 1989)
Jacquinia pungens	shrub	-7.85	-25.70	(Mooney et al. 1989)
Stemmadenia sp.	shrub	-7.85	-28.80	(Mooney et al. 1989)
Thevetia ovata	shrub	-7.85	-27.60	(Mooney et al. 1989)
Acacia angustissima	tree	-7.85	-26.90	(Mooney et al. 1989)
Apoplanesia paniculata	tree	-7.85	-27.30	(Mooney et al. 1989)
Bursera instabilis	tree	-7.85	-26.80	(Mooney et al. 1989)
Caesalpinia coriaria	tree	-7.85	-26.90	(Mooney et al. 1989)
Caesalpinia sclerocarpa	tree	-7.85	-26.50	(Mooney et al. 1989)
Capparis indica	tree	-7.85	-27.50	(Mooney et al. 1989)
Casearia corymbosa	tree	-7.85	-28.10	(Mooney et al. 1989)
Chlorophora tinctoria	tree	-7.85	-26.70	(Mooney et al. 1989)
Citharexylum sp.	tree	-7.85	-24.80	(Mooney et al. 1989)
Coccoloba liebmannii	tree	-7.85	-26.80	(Mooney et al. 1989)
Colubrina triflora	tree	-7.85	-27.60	(Mooney et al. 1989)
Cordia alliodora	tree	-7.85	-28.50	(Mooney et al. 1989)
Forchhammeria pallida	tree	-7.85	-24.10	(Mooney et al. 1989)
Triticum aestivum	grass	-8.00	-25.89	(Morgan et al. 1993)
Triticum aestivum	grass	-8.00	-25.79	(Morgan et al. 1993)
Triticum aestivum	grass	-8.00	-25.63	(Morgan et al. 1993)
Triticum aestivum	grass	-8.00	-25.86	(Morgan et al. 1993)
Triticum aestivum	grass	-8.00	-25.00	(Morgan et al. 1993)

Appendix. Continued.

Species	Growth form	δ¹³Ca	δ¹³Cp	Source
Triticum aestivum	grass	-8.00	-26.28	(Morgan et al. 1993)
Triticum aestivum	grass	-8.00	-24.92	(Morgan et al. 1993)
Triticum aestivum	grass	-8.00	-25.06	(Morgan et al. 1993)
Triticum aestivum	grass	-8.00	-24.62	(Morgan et al. 1993)
Triticum aestivum	grass	-8.00	-24.93	(Morgan et al. 1993)
Triticum aestivum	grass	-8.00	-24.84	(Morgan et al. 1993)
Triticum aestivum	grass	-8.00	-25.35	(Morgan et al. 1993)
Triticum aestivum	grass	-8.00	-24.37	(Morgan et al. 1993)
Triticum aestivum	grass	-8.00	-25.11	(Morgan et al. 1993)
Triticum aestivum	grass	-8.00	-25.01	(Morgan et al. 1993)
Triticum aestivum	grass	-8.00	-24.93	(Morgan et al. 1993)
Triticum aestivum	grass	-8.00	-24.42	(Morgan et al. 1993)
Triticum aestivum	grass	-8.00	-24.72	(Morgan et al. 1993)
Triticum aestivum	grass	-8.00	-24.40	(Morgan et al. 1993)
Triticum aestivum	grass	-8.00	-25.15	(Morgan et al. 1993)
Triticum aestivum	grass	-8.00	-23.93	(Morgan et al. 1993)
Triticum aestivum	grass	-8.00	-24.58	(Morgan et al. 1993)
Triticum aestivum	grass	-8.00	-24.45	(Morgan et al. 1993)
Triticum aestivum	grass	-8.00	-24.54	(Morgan et al. 1993)
Triticum aestivum	grass	-8.00	-25.04	(Morgan et al. 1993)
Triticum aestivum	grass	-8.00	-24.66	(Morgan et al. 1993)
Triticum aestivum	grass	-8.00	-24.37	(Morgan et al. 1993)
Triticum aestivum	grass	-8.00	-24.85	(Morgan et al. 1993)
Triticum aestivum	grass	-8.00	-24.13	(Morgan et al. 1993)
Triticum aestivum	grass	-8.00	-24.58	(Morgan et al. 1993)
Triticum aestivum	grass	-8.00	-24.52	(Morgan et al. 1993)
Triticum aestivum	grass	-8.00	-24.37	(Morgan et al. 1993)
Arachis hypogaea	forb	-7.85	-26.05	(Nageswara Roa et al. 1993)
Arachis hypogaea	forb	-7.85	-26.01	(Nageswara Roa et al. 1993)
Arachis hypogaea	forb	-7.85	-26.21	(Nageswara Roa et al. 1993)
Arachis hypogaea	forb	-7.85	-26.19	(Nageswara Roa et al. 1993)
Arachis hypogaea	forb	-7.85	-26.44	(Nageswara Roa et al. 1993)
Arachis hypogaea	forb	-7.85	-26.23	(Nageswara Roa et al. 1993)
Arachis hypogaea	forb	-7.85	-26.34	(Nageswara Roa et al. 1993)
Arachis hypogaea	forb	-7.85	-26.53	(Nageswara Roa et al. 1993)
Arachis hypogaea	forb	-7.85	-26.39	(Nageswara Roa et al. 1993)
Arachis hypogaea	forb	-7.85	-26.32	(Nageswara Roa et al. 1993)
Eucalyptus globulus	tree	-7.85	-27.40	(Osório and Pereira 1994)
Eucalyptus globulus	tree	-7.85	-26.80	(Osório and Pereira 1994)
Eucalyptus globulus	tree	-7.85	-26.80	(Osório and Pereira 1994)
Eucalyptus globulus	tree	-7.85	-26.80	(Osório and Pereira 1994)
Eucalyptus globulus	tree	-7.85	-26.80	(Osório and Pereira 1994)
Eucalyptus globulus	tree	-7.85	-25.70	(Osório and Pereira 1994)
Pseudotsuga menziesii	tree	-7.85	-25.00	(Panek 1996)
Gentiana alpina	forb	-6.40	-26.48	(Peñuelas and Azcón-Bieto 1992)
Helleborus foetidus	forb	-6.40	-25.39	(Peñuelas and Azcón-Bieto 1992)
Papaver alpinum	forb	-6.40	-25.06	(Peñuelas and Azcón-Bieto 1992)
Pistacia lentiscus	shrub	-6.40	-27.00	(Peñuelas and Azcón-Bieto 1992)
Rhododendron ferrugineum	shrub	-6.40	-25.87	(Peñuelas and Azcón-Bieto 1992)
Alnus glutinosa	tree	-6.40	-26.06	(Peñuelas and Azcón-Bieto 1992)
Betula pendula	tree	-6.40	-25.08	(Peñuelas and Azcón-Bieto 1992)
Buxus sempervirens	tree	-6.40	-24.34	(Peñuelas and Azcón-Bieto 1992)
Ceratonia siliqua	tree	-6.40	-26.18	(Peñuelas and Azcón-Bieto 1992)
Juniperus communis	tree	-6.40	-23.28	(Peñuelas and Azcón-Bieto 1992)
Pinus pinea	tree	-6.40	-26.81	(Peñuelas and Azcón-Bieto 1992)
Pinus uncinata	tree	-6.40	-26.91	(Peñuelas and Azcón-Bieto 1992)
Gentiana alpina	forb	-6.50	-25.88	(Peñuelas and Azcón-Bieto 1992)
Helleborus foetidus	forb	-6.50	-26.53	(Peñuelas and Azcón-Bieto 1992)
Papaver alpinum	forb	-6.50	-26.56	(Peñuelas and Azcón-Bieto 1992)
Pistacia lentiscus	shrub	-6.50	-26.55	(Peñuelas and Azcón-Bieto 1992)
Rhododendron ferrugineum	shrub	-6.50	-25.93	(Peñuelas and Azcón-Bieto 1992)
Alnus glutinosa	tree	-6.50	-26.56	(Peñuelas and Azcón-Bieto 1992)
Betula pendula	tree	-6.50	-26.95	(Peñuelas and Azcón-Bieto 1992)
Buxus sempervirens	tree	-6.50	-25.90	(Peñuelas and Azcón-Bieto 1992)

Appendix. Continued.

Species	Growth form	$\delta^{13}C_a$	$\delta^{13}C_p$	Source
Ceratonia siliqua	tree	-6.50	-24.41	(Peñuelas and Azcón-Bieto 1992)
Juniperus communis	tree	-6.50	-23.10	(Peñuelas and Azcón-Bieto 1992)
Pinus pinea	tree	-6.50	-26.92	(Peñuelas and Azcón-Bieto 1992)
Pinus uncinata	tree	-6.50	-24.02	(Peñuelas and Azcón-Bieto 1992)
Gentiana alpina	forb	-6.80	-24.62	(Peñuelas and Azcón-Bieto 1992)
Helleborus foetidus	forb	-6.80	-27.31	(Peñuelas and Azcón-Bieto 1992)
Papaver alpinum	forb	-6.80	-26.16	(Peñuelas and Azcón-Bieto 1992)
Pistacia lentiscus	shrub	-6.80	-27.05	(Peñuelas and Azcón-Bieto 1992)
Rhododendron ferrugineum	shrub	-6.80	-28.68	(Peñuelas and Azcón-Bieto 1992)
Alnus glutinosa	tree	-6.80	-27.21	(Peñuelas and Azcón-Bieto 1992)
Betula pendula	tree	-6.80	-25.22	(Peñuelas and Azcón-Bieto 1992)
Buxus sempervirens	tree	-6.80	-23.29	(Peñuelas and Azcón-Bieto 1992)
Ceratonia siliqua	tree	-6.80	-26.05	(Peñuelas and Azcón-Bieto 1992)
Juniperus communis	tree	-6.80	-26.07	(Peñuelas and Azcón-Bieto 1992)
Pinus pinea	tree	-6.80	-26.94	(Peñuelas and Azcón-Bieto 1992)
Pinus uncinata	tree	-6.80	-26.90	(Peñuelas and Azcón-Bieto 1992)
Gentiana alpina	forb	-7.80	-24.72	(Peñuelas and Azcón-Bieto 1992)
Helleborus foetidus	forb	-7.80	-24.50	(Peñuelas and Azcón-Bieto 1992)
Papaver alpinum	forb	-7.80	-29.94	(Peñuelas and Azcón-Bieto 1992)
Pistacia lentiscus	shrub	-7.80	-27.61	(Peñuelas and Azcón-Bieto 1992)
Rhododendron ferrugineum	shrub	-7.80	-25.54	(Peñuelas and Azcón-Bieto 1992)
Alnus glutinosa	tree	-7.80	-28.82	(Peñuelas and Azcón-Bieto 1992)
Betula pendula	tree	-7.80	-25.96	(Peñuelas and Azcón-Bieto 1992)
Buxus sempervirens	tree	-7.80	-23.67	(Peñuelas and Azcón-Bieto 1992)
Ceratonia siliqua	tree	-7.80	-26.84	(Peñuelas and Azcón-Bieto 1992)
Juniperus communis	tree	-7.80	-25.77	(Peñuelas and Azcón-Bieto 1992)
Pinus pinea	tree	-7.80	-27.61	(Peñuelas and Azcón-Bieto 1992)
Pinus uncinata	tree	-7.80	-25.43	(Peñuelas and Azcón-Bieto 1992)
Bromus tectorum	grass	-3.50	-23.00	(Polley et al. 1995)
Bromus tectorum	grass	-3.50	-23.00	(Polley et al. 1995)
Bromus tectorum	grass	-9.60	-28.00	(Polley et al. 1995)
Bromus tectorum	grass	-9.60	-28.00	(Polley et al. 1995)
Alyssum minus	forb	-8.00	-26.97	(Smedley et al. 1991)
Ambrosia psilostachya	forb	-8.00	-26.21	(Smedley et al. 1991)
Aster chilensis	forb	-8.00	-26.59	(Smedley et al. 1991)
Astragalus cibarius	forb	-8.00	-26.21	(Smedley et al. 1991)
Astragalus utahensis	forb	-8.00	-27.16	(Smedley et al. 1991)
Balsamorphiza macrophylla	forb	-8.00	-25.54	(Smedley et al. 1991)
Balsamorphiza sagittata	forb	-8.00	-26.40	(Smedley et al. 1991)
Camelina microcarpa	forb	-8.00	-27.93	(Smedley et al. 1991)
Cirsium undulatum	forb	-8.00	-25.92	(Smedley et al. 1991)
Comandra umbellata	forb	-8.00	-29.64	(Smedley et al. 1991)
Crepis occidentalis	forb	-8.00	-27.16	(Smedley et al. 1991)
Cryptantha torreyana	forb	-8.00	-28.40	(Smedley et al. 1991)
Cymopterus longipes	forb	-8.00	-26.78	(Smedley et al. 1991)
Erigeron divergens	forb	-8.00	-26.78	(Smedley et al. 1991)
Erodium cicutarium	forb	-8.00	-28.97	(Smedley et al. 1991)
Galium aparine	forb	-8.00	-28.78	(Smedley et al. 1991)
Grindelia squarrosa	forb	-8.00	-26.78	(Smedley et al. 1991)
Gutierrezia sarothrae	forb	-8.00	-26.02	(Smedley et al. 1991)
Hedysarum boreale	forb	-8.00	-26.50	(Smedley et al. 1991)
Lactuca serriola	forb	-8.00	-26.40	(Smedley et al. 1991)
Lepidium perfoliatum	forb	-8.00	-26.88	(Smedley et al. 1991)
Lindaria dalmatia	forb	-8.00	-26.11	(Smedley et al. 1991)
Lithospermum arvense	forb	-8.00	-27.74	(Smedley et al. 1991)
Lomatium triternatum	forb	-8.00	-27.45	(Smedley et al. 1991)
Lupinus argenteus	forb	-8.00	-26.88	(Smedley et al. 1991)
Lygodesmia grandiflora	forb	-8.00	-27.07	(Smedley et al. 1991)
Melica bulbosa	forb	-8.00	-26.59	(Smedley et al. 1991)
Microseris nutans	forb	-8.00	-27.55	(Smedley et al. 1991)
Phlox longifolia	forb	-8.00	-25.54	(Smedley et al. 1991)
Ranunculus testiculatus	forb	-8.00	-27.55	(Smedley et al. 1991)
Senecio integerrimus	forb	-8.00	-27.26	(Smedley et al. 1991)
Sisymbrium altissimum	forb	-8.00	-28.12	(Smedley et al. 1991)

Appendix. Continued.

Species	Growth form	$\delta^{13}C_a$	$\delta^{13}C_p$	Source
Sphaeralcea coccinea	forb	-8.00	-27.26	(Smedley et al. 1991)
Tragopogon dubius	forb	-8.00	-26.88	(Smedley et al. 1991)
Vicia americana	forb	-8.00	-26.21	(Smedley et al. 1991)
Wyethia amplexicaulis	forb	-8.00	-26.78	(Smedley et al. 1991)
Zigadenus paniculatus	forb	-8.00	-25.54	(Smedley et al. 1991)
Agropyron spicatum	grass	-8.00	-26.78	(Smedley et al. 1991)
Bromus tectorum	grass	-8.00	-26.97	(Smedley et al. 1991)
Poa bulbosa	grass	-8.00	-26.31	(Smedley et al. 1991)
Stipa comata	grass	-8.00	-25.54	(Smedley et al. 1991)
Artemisia ludoviciana	shrub	-8.00	-26.69	(Smedley et al. 1991)
Apeiba membranacea	tree	-7.85	-30.30	(Terwilliger 1997)
Apeiba membranacea	tree	-7.85	-30.50	(Terwilliger 1997)
Apeiba membranacea	tree	-7.85	-31.10	(Terwilliger 1997)
Apeiba membranacea	tree	-7.85	-32.00	(Terwilliger 1997)
Apeiba tibourbou	tree	-7.85	-30.50	(Terwilliger 1997)
Apeiba tibourbou	tree	-7.85	-29.50	(Terwilliger 1997)
Cecropia insignis	tree	-7.85	-30.50	(Terwilliger 1997)
Cecropia insignis	tree	-7.85	-30.50	(Terwilliger 1997)
Cecropia insignis	tree	-7.85	-31.40	(Terwilliger 1997)
Cecropia insignis	tree	-7.85	-32.40	(Terwilliger 1997)
Cecropia peltata	tree	-7.85	-29.90	(Terwilliger 1997)
Cecropia peltata	tree	-7.85	-29.20	(Terwilliger 1997)
Elymus elymoides	grass	-7.85	-25.00	(Toft et al. 1989)
Elymus elymoides	grass	-7.85	-25.40	(Toft et al. 1989)
Elymus elymoides	grass	-7.85	-25.80	(Toft et al. 1989)
Elymus elymoides	grass	-7.85	-26.40	(Toft et al. 1989)
Elymus lanceolatus	grass	-7.85	-24.20	(Toft et al. 1989)
Elymus lanceolatus	grass	-7.85	-25.20	(Toft et al. 1989)
Elymus lanceolatus	grass	-7.85	-26.00	(Toft et al. 1989)
Elymus lanceolatus	grass	-7.85	-26.60	(Toft et al. 1989)
Artemisia tridentata	shrub	-7.85	-25.80	(Toft et al. 1989)
Artemisia tridentata	shrub	-7.85	-25.90	(Toft et al. 1989)
Artemisia tridentata	shrub	-7.85	-26.00	(Toft et al. 1989)
Artemisia tridentata	shrub	-7.85	-26.30	(Toft et al. 1989)
Ceratoides lanata	shrub	-7.85	-27.60	(Toft et al. 1989)
Ceratoides lanata	shrub	-7.85	-28.80	(Toft et al. 1989)
Ceratoides lanata	shrub	-7.85	-28.90	(Toft et al. 1989)
Ceratoides lanata	shrub	-7.85	-28.90	(Toft et al. 1989)
Pinus flexilis	tree	-6.40	-23.30	(Van de Water et al. 1994)
Pinus flexilis	tree	-6.40	-24.45	(Van de Water et al. 1994)
Pinus flexilis	tree	-6.40	-25.21	(Van de Water et al. 1994)
Dryas octopetala	forb	-7.90	-28.26	(Welker et al. 1993)
Dryas octopetala	forb	-7.90	-29.21	(Welker et al. 1993)
Dryas octopetala	forb	-7.90	-29.11	(Welker et al. 1993)
Dryas octopetala	forb	-7.90	-29.02	(Welker et al. 1993)
Phaseolus vulgaris	forb	-8.00	-27.02	(White et al. 1994)
Phaseolus vulgaris	forb	-8.00	-27.37	(White et al. 1994)
Phaseolus vulgaris	forb	-8.00	-25.58	(White et al. 1994)
Phaseolus vulgaris	forb	-8.00	-27.16	(White et al. 1994)
Phaseolus vulgaris	forb	-8.00	-26.46	(White et al. 1994)
Phaseolus vulgaris	forb	-8.00	-27.88	(White et al. 1994)
Arachis hypogaea	forb	-7.85	-28.35	(Wright et al. 1994)
Arachis hypogaea	forb	-7.85	-27.97	(Wright et al. 1994)
Arachis hypogaea	forb	-7.85	-27.21	(Wright et al. 1994)
Arachis hypogaea	forb	-7.85	-26.73	(Wright et al. 1994)
Arachis hypogaea	forb	-7.85	-28.16	(Wright et al. 1994)
Arachis hypogaea	forb	-7.85	-26.73	(Wright et al. 1994)
Arachis hypogaea	forb	-7.85	-26.16	(Wright et al. 1994)
Arachis hypogaea	forb	-7.85	-25.97	(Wright et al. 1994)
Pseudotsuga menziesii	tree	-8.00	-27.89	(Zhang et al. 1993)
Pseudotsuga menziesii	tree	-8.00	-27.37	(Zhang et al. 1993)
Pseudotsuga menziesii	tree	-8.00	-28.79	(Zhang et al. 1993)
Pseudotsuga menziesii	tree	-8.00	-28.83	(Zhang et al. 1993)
Pseudotsuga menziesii	tree	-8.00	-27.61	(Zhang et al. 1993)

Appendix. Continued.

Species	Growth form	$\delta^{13}Ca$	$\delta^{13}Cp$	Source
Pseudotsuga menziesii	tree	-8.00	-27.40	(Zhang et al. 1993)
Pseudotsuga menziesii	tree	-8.00	-27.10	(Zhang et al. 1993)
Pseudotsuga menziesii	tree	-8.00	-27.25	(Zhang et al. 1993)
Pseudotsuga menziesii	tree	-8.00	-28.22	(Zhang et al. 1993)
Pseudotsuga menziesii	tree	-8.00	-28.99	(Zhang et al. 1993)
Pseudotsuga menziesii	tree	-8.00	-27.69	(Zhang et al. 1993)
Pseudotsuga menziesii	tree	-8.00	-27.51	(Zhang et al. 1993)
Pseudotsuga menziesii	tree	-8.00	-28.09	(Zhang et al. 1993)
Pseudotsuga menziesii	tree	-8.00	-27.02	(Zhang et al. 1993)
Pseudotsuga menziesii	tree	-8.00	-27.48	(Zhang et al. 1993)
Pseudotsuga menziesii	tree	-8.00	-27.25	(Zhang et al. 1993)
Pseudotsuga menziesii	tree	-8.00	-27.35	(Zhang et al. 1993)
Pseudotsuga menziesii	tree	-8.00	-28.53	(Zhang et al. 1993)
Pseudotsuga menziesii	tree	-8.00	-28.72	(Zhang et al. 1993)
Pseudotsuga menziesii	tree	-8.00	-29.62	(Zhang et al. 1993)
Pseudotsuga menziesii	tree	-8.00	-28.76	(Zhang et al. 1993)
Pseudotsuga menziesii	tree	-8.00	-28.81	(Zhang et al. 1993)
Pseudotsuga menziesii	tree	-8.00	-28.49	(Zhang et al. 1993)
Pseudotsuga menziesii	tree	-8.00	-28.24	(Zhang et al. 1993)
Pseudotsuga menziesii	tree	-8.00	-28.93	(Zhang et al. 1993)
Larix occidentalis	tree	-8.00	-26.33	(Zhang et al. 1994)
Larix occidentalis	tree	-8.00	-26.78	(Zhang et al. 1994)
Larix occidentalis	tree	-8.00	-27.15	(Zhang et al. 1994)
Larix occidentalis	tree	-8.00	-27.20	(Zhang et al. 1994)
Larix occidentalis	tree	-8.00	-28.63	(Zhang et al. 1994)