

STABLE-CARBON ISOTOPE VARIABILITY IN TREE FOLIAGE AND WOOD¹

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Abstract. This study documents variation of stable-carbon isotope ratios (¹³C/¹²C) in trees of genera *Juniperus* and *Pinus* under field conditions. Results are from cellulose analysis on leaves, twigs, and wood from a number of localities in the southwestern United States. Substantial variability, typically 1–3‰, exists among leaves, within wood (radially, vertically, circumferentially), and between individuals at a site. These results may help guide sampling in tracer-type studies with stable-carbon isotope ratios and aid in the interpretation of isotopic results from such studies.

Key words: carbon-13/carbon-12 ratios; carbon isotopes; isotopic variation; *Juniperus*; *Pinus edulis*; stable-carbon isotopes; tree rings.

INTRODUCTION

The natural abundance of stable-carbon isotopes in plants may be an indicator of environmental temperature (Grinsted et al. 1979, Leavitt and Long 1983*b*) and of changes in the ¹³C/¹²C ratio of atmospheric carbon dioxide, particularly as related to fossil-fuel combustion (Freyer and Belacy 1983, Leavitt and Long 1983*a*). Furthermore, pronounced ¹³C/¹²C differences exist among plants, which are related to different photosynthetic pathways (Calvin Cycle [C₃] or Hatch-Slack [C₄]). These differences allow us to infer herbivore diets (Teeri and Schoeller 1979, Sullivan and Krueger 1981) and the sources of carbon in food chains (Fry et al. 1978, Rau et al. 1983, Riggs 1984). However, among species within C₃ and C₄ groups, isotopic compositions may range over 10–20‰ (Lerman and Troughton 1975), and it is becoming increasingly apparent that individuals of the same species, even at the same site, can have distinct isotopic differences (Sternberg and DeNiro 1983, Leavitt and Long 1984).

Because the use of isotopic data will undoubtedly continue to grow, it is worthwhile to examine in some detail the variability of stable-carbon isotope ratios within and among individual plants. In this study we have measured ¹³C/¹²C ratios in a variety of trees (C₃ plants) primarily from the genera of *Juniperus* and *Pinus*. These original results are combined with scattered information from the literature to provide some insight into expected isotopic variation under field conditions. This information may be used in planning studies to ensure that sufficient and appropriate samples are taken to represent the relevant parts of the system. These

results refer primarily to measured isotopic variability in field situations, and the reader is referred to such studies as O'Leary (1981) and Francey and Farquhar (1982) for more details on the theoretical basis of the isotopic variability.

METHODS

The original data presented herein are stable-carbon isotopic analyses on tree leaf, twig, and wood materials collected at various locations (Table 1) in the southwestern United States between 1979 and 1983. In nearly all cases, the cellulose (holocellulose) component of the wood was isolated from solvent (toluene/ethanol)-extracted wood in an acidified sodium chlorite solution (Green 1963). Cellulose is preferred over whole tissue because it is a nonmobile wood component, whereas whole tissue consists of varying proportions of organic constituents, each with a distinct isotopic composition (Park and Epstein 1961). In our experience cellulose is usually isotopically lighter than whole tissue by ≈ 1–2‰.

Cellulose samples were combusted to CO₂ in a recirculating oxygen atmosphere and the CO₂ was analyzed mass spectrometrically to determine ¹³C/¹²C ratios. The ¹³C/¹²C ratios are expressed as delta (δ) values in thousandths (‰) with respect to the internationally accepted Pee Dee belemnite (PDB) carbonate standard from the Pee Dee Formation, South Carolina (Craig 1957):

$$\delta^{13}\text{C} = \frac{(^{13}\text{C}/^{12}\text{C})_{\text{sample}} - (^{13}\text{C}/^{12}\text{C})_{\text{PDB}}}{(^{13}\text{C}/^{12}\text{C})_{\text{PDB}}} \times 1000.$$

Overall reproducibility, including cellulose preparation, combustion, and mass-spectrometric analysis, is estimated to be ±0.1‰ based on replicate analyses of a wood cellulose standard.

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TABLE 1. Samples analyzed in this study. The figures containing data from each of these samples are indicated in the right column.

Site	State	Latitude/longitude	Elev. (m)	Species	Fig.
Red Mountain	AZ	35°01'10" N/112°49'10" W	1635	<i>Pinus edulis</i> (pinyon)	1, 4
Walnut Canyon	AZ	35°10'50" N/111°29'15" W	2005	<i>Pinus edulis</i>	1, 4
Stoneman	AZ	35°45'50" N/111°38'40" W	1660	<i>Pinus edulis</i>	1, 4, 5
Hackberry	AZ	34°27'10" N/111°41'50" W	1195	<i>Pinus edulis</i>	1, 4
Nutrioso	AZ	34°02'10" N/109°09'55" W	2395	<i>Pinus edulis</i>	1, 4
Hay Hollow	AZ	34°30'50" N/109°58'15" W	1785	<i>Pinus edulis</i>	1, 4
Defiance	AZ	35°43'15" N/109°21'45" W	2180	<i>Pinus edulis</i>	1, 4
Reserve	NM	33°36'35" N/108°45'00" W	2020	<i>Pinus edulis</i>	1, 3, 4
Dry Creek	AZ	34°53'45" N/111°49'30" W	1380	<i>Pinus edulis</i>	1, 4
Prescott	AZ	34°35' N/112°34' W	1705	<i>Juniperus monosperma</i>	*
Tucson	AZ	32°15' N/110°56' W	750	<i>Juniperus monosperma</i>	2
Cerro Colorado	NM	35°16'50" N/107°43'10" W	2500	<i>Pinus edulis</i>	4
Lower Colonias	NM	35°33'25" N/105°33'20" W	2375	<i>Pinus edulis</i>	4
Bears Ears	UT	37°37' N/109°51' W	2575	<i>Pinus edulis</i>	4
Alton	UT	37°26'30" N/112°29'00" W	2245	<i>Pinus edulis</i>	4
Kane Spring	UT	37°31'30" N/109°54'00" W	1965	<i>Pinus edulis</i>	4
Dry Canyon	CO	37°35'05" N/108°32'40" W	2150	<i>Pinus edulis</i>	4
Aztec	NM	36°59'50" N/107°48'45" W	2080	<i>Pinus edulis</i>	4
Bat Cave	NM	33°46' N/108°12' W	2400	<i>Pinus edulis</i>	4
Ozena	CA	34°43'20" N/119°14'00" W	1370	<i>Pinus monophylla</i> (pinyon)	4
Santa Ynez	CA	34°30'50" N/119°48'10" W	815	<i>Pinus coulterii</i>	*
Figueroa Mt.	CA	34°44'30" N/119°59'20" W	1280	<i>Pinus ponderosa</i>	*
Santa Cruz Is.	CA	34°00'40" N/119°48'30" W	365	<i>Pinus muricata</i>	*

* In Results and Discussion: Longitudinal Variability of $\delta^{13}\text{C}$.

RESULTS AND DISCUSSION

Longitudinal variability of $\delta^{13}\text{C}$

The longitudinal variability may be expressed as differences between $\delta^{13}\text{C}$ of cellulose in leaves and wood, and as the changes in $\delta^{13}\text{C}$ of wood cellulose at various vertical levels along the same annual growth ring (cylinder). Few data on leaf/wood values exist (summary in Leavitt and Long 1982a), particularly for cellulose. Careful isotopic analysis of leaves and corresponding growth rings within and among juniper trees (*Juniperus* spp.) from Arizona (Leavitt and Long 1982a) revealed a typical difference of 2–3‰ for cellulose, with the ring wood being isotopically heavier (having a less negative $\delta^{13}\text{C}$ value).

The $\delta^{13}\text{C}$ of pinyon (*Pinus edulis* Engelm.) leaf cellulose, twig cellulose from the branchlets to which the needles were directly attached, and wood cellulose from the outer two growth rings (1980–1981) that correspond roughly to the age of the leaves, are given in Fig. 1. Pooled leaves and twigs were sampled at four cardinal directions around the crown circumference at ≈ 1.5 –2.5 m. The rings were milled from the full circumference to avoid effects of any circumferential isotopic variation in the wood (see Circumferential $\delta^{13}\text{C}$ Variability), except for one tree where the growth ring sequence was not datable. In most cases, the pinyon rings are also heavier in isotopic composition by ≈ 1 –2‰ than the leaves. However, the twigs are not intermediate in composition relative to the leaves and rings as might be expected in a gradient, but are isotopically lighter than the leaves. A closer correspondence emerges between the $\delta^{13}\text{C}$ values in the rings and twigs ($r = 0.82$, $P < .01$) with a fairly constant 2–3‰ offset, than

between rings and leaves ($r = 0.24$, NS) or between twigs and leaves ($r = 0.17$, NS). The sites in Fig. 1 are discretely ordered in decreasing elevation (approximately increasing temperature) from left to right on the x axis. Relationships between pinyon leaf $\delta^{13}\text{C}$ and temperatures in these samples have previously been explored in Leavitt and Long (1983b).

Francey (1986) reports cellulose $\delta^{13}\text{C}$ from some growing tips and branches (20–30 cm from the tips) of Tasmanian Huon pine (*Dacrydium franklinii*). The isotopic composition of the branch wood is heavier than the growing tips by 2–3‰. He proposes a high internal-to-external CO_2 concentration ratio in these immature leaves due to their limited carbon-fixing capability, and therefore a low $\delta^{13}\text{C}$ value, according to the model of Francey and Farquhar (1982):

$$\delta_p^{13}\text{C} = \delta_a^{13}\text{C} - a - (b - a)C_i/C_a$$

where $\delta_p^{13}\text{C}$, $\delta_a^{13}\text{C}$ are plant and atmospheric values, respectively, a , b are fractionation by diffusion through stomata and by the carbon-fixing enzyme, respectively, and C_a , C_i are the atmospheric and the plant's internal CO_2 concentrations, respectively.

All of the pinyon samples, however, were collected at the end of the 1981 growing season and should include a full complement of mature leaves retained by the trees from the previous growing seasons. If these pinyon results do not reflect a direct internal fractionation effect, then they may represent some complex interaction of differential photosynthetic efficiency of young and old needles, different relative amounts of wood laid down in the twigs each year, the photosynthetic contributions from chlorenchyma in the young

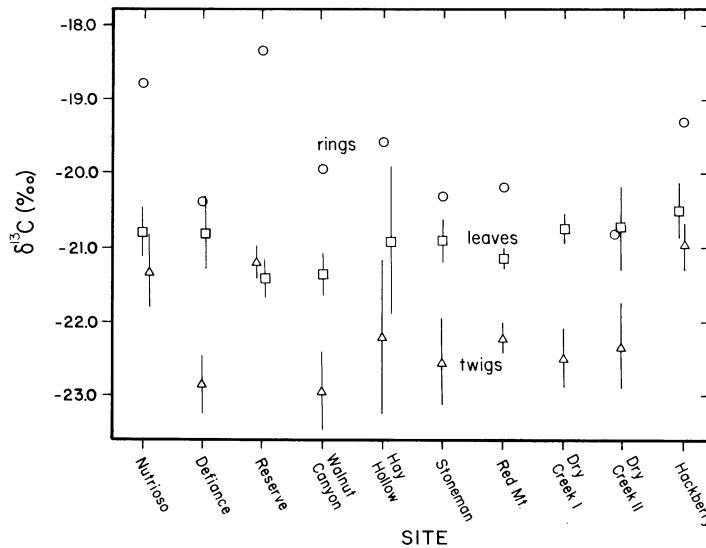


FIG. 1. The $\delta^{13}\text{C}$ values ($\bar{X} \pm 1 \text{ SD}$) of cellulose from *Pinus edulis* leaves, twigs, and growth rings of age equivalent to the leaves, from trees at sites in Arizona and New Mexico. The leaf results have been reported previously (Leavitt and Long 1983b).

twigs, changing environmental effects on fractionation from year to year, and other factors.

Leaf-twig $\delta^{13}\text{C}$ differences may also depend on species. For example, we have found the $\delta^{13}\text{C}$ values for cellulose of twigs from California *Pinus ponderosa* (Figueroa Mountain) and *P. muricata* (Santa Cruz Island) individuals to be isotopically heavier than the associated leaves by $\approx 1\text{‰}$, i.e., the opposite of the result in Fig. 1. Individuals from species *P. monophylla* (Ozema) and *P. coulterii* (Santa Ynez) conform to the results in Fig. 1, with leaves 1–2‰ heavier than twigs.

A second major question is whether a longitudinal isotopic gradient exists within the rings. If this is the case, then the $\delta^{13}\text{C}$ results in a tree-ring study will be dependent on the height from which the samples are taken. Such a gradient might also indicate direct or indirect fractionation during glucose assimilation into cellulose. Freyer and Wiesberg (1974) measured $\delta^{13}\text{C}$ of a 7-yr ring group of *Quercus robur* from seven cross-sections at 2-m intervals. They noted a slight but non-significant gradient for the wood cellulose of $0.01\text{‰}/\text{m}$ as measured from the base upward. de Silva (1978) measured $\delta^{13}\text{C}$ of cellulose in a 25-yr ring group of *Pinus silvestris* for three levels at 1-m intervals, but found no statistical difference in their means. Tans and Mook (1980) analyzed $\delta^{13}\text{C}$ of acid-alkali-acid treated *Quercus rubra* rings at various positions over a 40-cm vertical distance. They found up to a 1‰ variation when measured directly along the vertical, but a nearly constant $\delta^{13}\text{C}$ when measured along the fiber direction at an angle to the vertical. Finally, Leavitt (1982) analyzed $\delta^{13}\text{C}$ of cellulose from the 1979 ring of a *Juniperus monosperma* from different sides of several wood slices representing a vertical distance of $\approx 15 \text{ cm}$. On the north, east, and southwest sides $\delta^{13}\text{C}$ decreased 0.1–

0.3‰ overall with height, but the trend on the south side was irregular. Although a negative gradient would be consistent with the leaf-ring $\delta^{13}\text{C}$ differences observed in pinyon (Fig. 1) and juniper (Leavitt and Long 1982a), results that follow suggest the longitudinal pattern in one ring (year) may not reflect that of others.

In a previous study of stable-carbon isotope differences between leaves and wood (Leavitt and Long 1982a), we reported on sample cores from different levels along the trunk and branch of a juniper individual (*Juniperus monosperma*) in which the rings could not be reliably age-dated. Following subsequent resurfacing of those cores, we found the 1981 ring at several levels to be distinct enough to test for a gradient. Fig. 2 contains the $\delta^{13}\text{C}$ results for cellulose from six equal subdivisions ($\approx 1 \text{ mm}$ each) of the 1981 growth ring sampled at five levels over a distance of $\approx 2.5 \text{ m}$ in the same trunk (level 2 was reported in Leavitt and Long 1982a). The $\delta^{13}\text{C}$ pattern is remarkably consistent, and the $\delta^{13}\text{C}$ range at each subdivision (assuming age equivalency) is $\approx 1\text{--}1.5\text{‰}$. A gradient is not evidenced because the highest (5) and the lowest (1) level of the 1981 growth ring have $\delta^{13}\text{C}$ differences of only 0.1–0.5‰, whereas the intermediate levels 3 and 4 are consistently heavier in isotopic composition than levels 1 and 5 by 0.5–1.0‰. Analysis of variance indicates no difference in population ($n = \text{six subdivisions}$) $\delta^{13}\text{C}$ means among levels ($\alpha = .05$).

Interestingly, another core from about the same height but from the most northerly of several trunks that branched from the base of the tree (marked by "N" in Fig. 2) yielded quite a different $\delta^{13}\text{C}$ trend in the 1981 ring. Thus, under essentially equal conditions of soil moisture, ambient air temperature, and heredity, differences may exist in $\delta^{13}\text{C}$ of the cellulose laid down

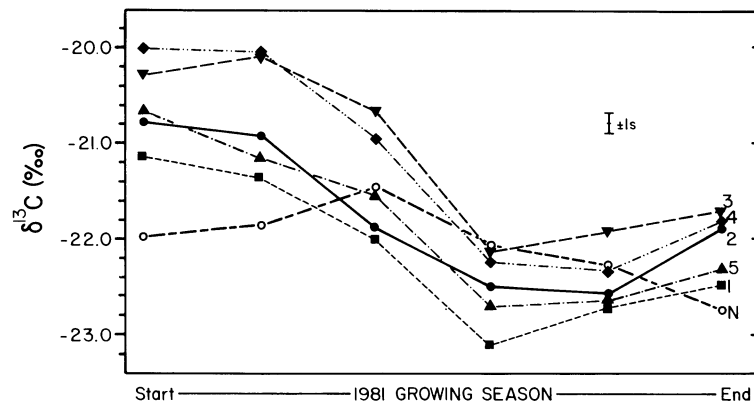


FIG. 2. The $\delta^{13}\text{C}$ values of cellulose from equal subdivisions of the 1981 growth ring of a *Juniperus monosperma* sampled at 70 cm (level 1), 77.5 cm (2), 216 cm (3), 229 cm (4), and 250 cm (5) above the ground along the southernmost of several trunks branching from near the ground. The curve at level 2 has been reported previously (Leavitt and Long 1982a). The trend marked "N" is the 1981 growth ring from a northern trunk of the same tree at a height of 51 cm.

in different major branches of the same individual. The growth chamber experiments of Smith et al. (1976) demonstrated influence of light levels on plant $\delta^{13}\text{C}$. Francey (1986) suggests that the contribution of sunlight and shading effects may be very important in accounting for some of the observed $\delta^{13}\text{C}$ differences among leaves within an individual; these differences may subsequently propagate to the rings. By the Francey and Farquhar (1982) model, the trend in the south trunk may reflect greater sun exposure of its leaves (high rate of photosynthesis, low internal-to-external CO_2 ratio, high $\delta^{13}\text{C}$) in the early portions of the growing season, whereas the north branch will not receive high exposure until the middle of the growing season.

In another longitudinal test we analyzed cellulose from seven rings of a pinyon pine sampled at Reserve, New Mexico. The samples were wedges from five levels over a 3-m vertical distance (Fig. 3). The 1980 and 1981 rings show a generally decreasing $\delta^{13}\text{C}$ trend with height with a slight trend dislocation in those samples below the lowest living branch. The rings of the branch did not cross-date, but assuming the outer two rings are the 1980 and 1981 rings, the $\delta^{13}\text{C}$ value shows their cellulose to be isotopically much lighter than that from the main trunk. In some closed-canopy forests lower leaves are isotopically lighter than those at canopy top, a phenomenon attributed to high concentrations of isotopically light respired CO_2 near the ground (Medina and Minchin 1980) or to effects of shading on rates of carbon assimilation (Francey 1986). For the 1980 and 1981 rings, the first level below this branch appears to have a deflection of $\delta^{13}\text{C}$ values, perhaps reflecting input of isotopically light carbon from this branch.

An examination of all seven years in Fig. 3, however, shows no evidence for a longitudinal isotopic gradient. Linear regression reveals negative slopes for 1977, 1980, and 1981, with positive slopes for the other years, but only the slope for the 1981 ring (-0.15‰ per metre)

is significant at $P < .05$. For a given year the $\delta^{13}\text{C}$ values ranged from 0.5 to 1‰ among levels. A comparison of $\delta^{13}\text{C}$ time series from each level (not shown) revealed similar trends; analysis of variance indicates no difference in the population ($n = 7$ yr) $\delta^{13}\text{C}$ means of each level.

Most studies testing for a longitudinal $\delta^{13}\text{C}$ gradient, including these data from juniper and pinyon, use single radii at different levels. It will become apparent in the next section that single radii are probably not highly accurate representations of either the trend or the absolute values of $\delta^{13}\text{C}$ contained in a ring series representing all radii at a specific level aboveground. The $\delta^{13}\text{C}$ range among levels for each year is similar in magnitude to circumferential variability observed in rings from a single level. The results in Fig. 3 and from the other studies to date, therefore, cannot absolutely preclude the presence of some longitudinal isotopic gradient in tree rings.

Circumferential $\delta^{13}\text{C}$ variability

Any circumferential $\delta^{13}\text{C}$ variability found in tree rings may largely reflect variations in isotopic fractionation where the carbon is fixed, i.e., the leaves. Francey (1986) has reported up to a 4‰ difference in leaf composition of *D. franklinii*, which he attributed to canopy shading. In a study of leaves taken from four directions around the crown of >20 juniper trees (*Juniperus* spp.) from Arizona, Arnold (1979) found the mean intratree variance in $\delta^{13}\text{C}$ of the cellulose to be $\approx 0.38\text{‰}$. Likewise, Leavitt (1982) found the mean intratree $\delta^{13}\text{C}$ variance of cellulose from leaves of 10 juniper trees (four crown directions per sample) to be 0.46‰. We have found a similar mean variance for leaves of nine *P. edulis* trees of $\approx 0.38\text{‰}$ (Fig. 1). The actual $\delta^{13}\text{C}$ values of leaf and twig cellulose from each of the four crown directions for the 10 pinyon in Fig. 1 as well as nine additional pinyon sites from around

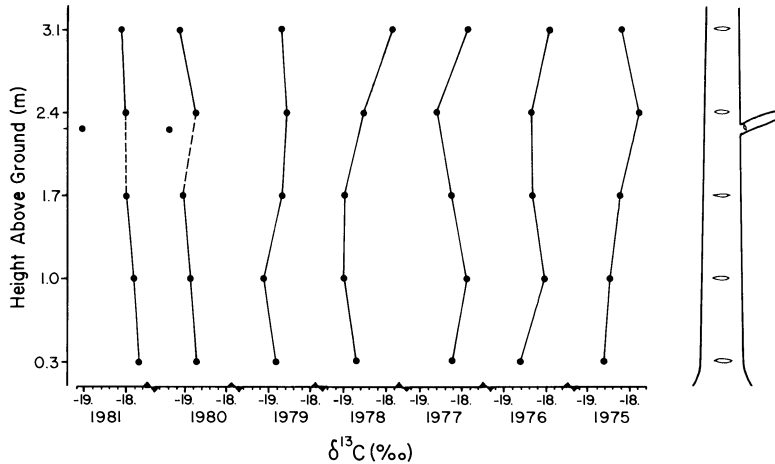


FIG. 3. The $\delta^{13}\text{C}$ of cellulose from seven annual growth rings at five positions along the trunk of a *Pinus edulis* individual from Reserve, New Mexico. A sixth position was sampled from the lowest living branch just below the position of the main trunk sample at 2.4 m (see drawing at right).

the American Southwest are depicted in Fig. 4. As discussed previously under Longitudinal Variability of $\delta^{13}\text{C}$, the pinyon leaves are nearly always isotopically heavier than the branchlets. For the most part, the pattern in the leaves roughly parallels that in the twigs, but both leaves and twigs generally have substantial isotopic differences around the circumference. For the individuals in Fig. 4, the range in isotopic values for both leaves and twigs around the canopy is 0.3–2.5‰.

Previous findings on circumferential $\delta^{13}\text{C}$ variations in tree rings generally conform to this 0.5–2.5‰ variation observed in leaves about the crown. Table 2 summarizes the circumferential results from eight studies representing seven species. The results of Freyer and Belacy (1983) and Francey (1981) further indicate that in the earliest several decades of tree growth there is

very little circumferential variation. After this period, circumferential isotopic variation becomes significant as the crown enlarges and associated microenvironmental heterogeneities develop.

In a detailed recent study, Leavitt and Long (1984) analyzed ring series (subdivided into 5-yr ring groups) from eight equally spaced cores (5 mm diameter) around the circumference of the pinyon tree from the Stoneman, Arizona site. Although the trends of each series were broadly similar, the $\delta^{13}\text{C}$ differences among radii for any 5-yr group ranged from ≈ 0.5 to 1.2‰, similar to the isotopic differences among leaves and among twigs from the Stoneman site in Fig. 1. We concluded that to ensure accurate representation of $\delta^{13}\text{C}$ values of all wood around the full circumference for any 5-yr ring group, pooling of rings from four orthogonal cores

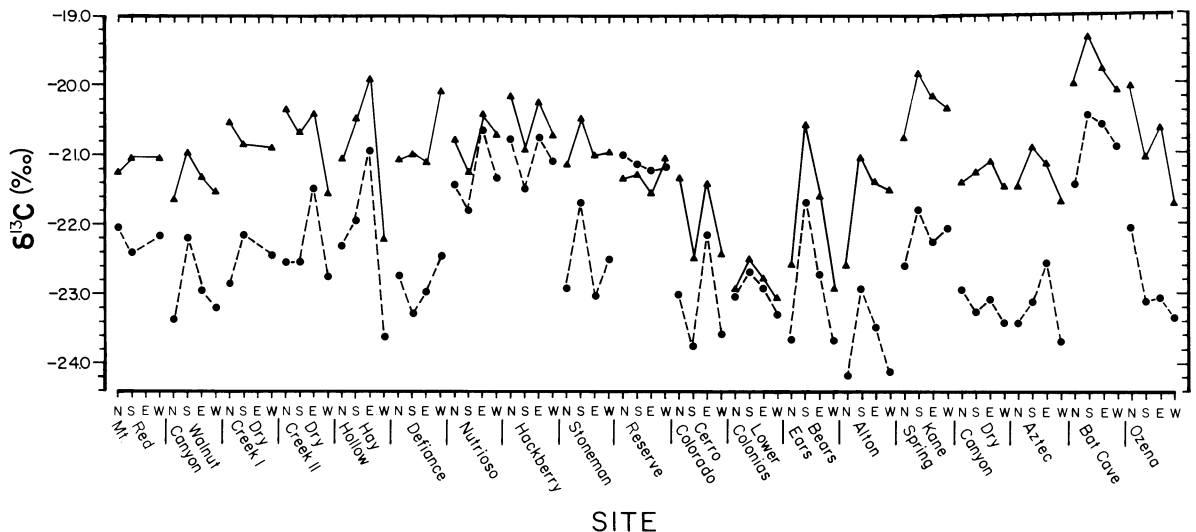


FIG. 4. The $\delta^{13}\text{C}$ values of cellulose from (●) pinyon branchlets and (▲) attached leaves on different sides of canopy (North, South, East, West).

TABLE 2. Reported circumferential variation in tree rings.

Species	No. of radii	Ring group	No. of groups	Variation	Study
<i>Quercus lusitanica</i>	2	5-yr	series	1‰	Freyer and Wiesberg (1974)
<i>Q. rubra</i>	7	2-yr	5	0.2–0.4‰	de Silva (1978)
<i>Q. rubra</i>	2	single-yr	series	up to 4‰	Tans and Mook (1980)
<i>Q. robur</i>	8	single-yr	1	1.5‰	" "
<i>Pinus ponderosa</i>	5	10-yr	3	1‰	Mazany et al. (1980)
<i>Phyllocladus osplenifolius</i>	4	5-yr	series	1‰	Francey (1981)
<i>Juniperus deppeana</i>	4	single-yr	1 (3 heights)	0.7–0.9‰	Leavitt (1982)
<i>Q. macrocarpa</i>	2	single-yr	series	0–1.5‰	Bender and Berge (1982)
<i>Pinus silvestris</i>	3	10-yr	series	0.5–0.8‰	Freyer and Belacy (1983)

would be necessary. Stuiver et al. (1984) also found, on average, a range of ≈ 1 –1.5‰ among four radii in each of two trees (*Picea sitchensis*, *Nothofagus pumillio*), but they had analyzed each ring in a 100-yr sequence.

Intrasite $\delta^{13}\text{C}$ variability

Adequate representation of $\delta^{13}\text{C}$ values from a given locality requires a knowledge of $\delta^{13}\text{C}$ variability among individuals. In the study of juniper leaves in Arizona, Arnold (1979) analyzed leaves from 2–4 trees per site (four directions per tree) and found the variance among trees at a site to be 0.38‰, i.e., similar to the circum-canopy variance. For tree-ring series, Freyer (1979) found deviations among five trees representing several species at each of two sites near Eifel, Germany, to be ≈ 0.5 –2‰. However, his site means and confidence intervals were calculated after first normalizing the individual trends to their respective 1930–1950 $\delta^{13}\text{C}$ means. Among similarly normalized $\delta^{13}\text{C}$ trends from seven trees representing five species from North Carolina, de Silva (1978) found variations of the same magnitude. For means of unnormalized trends, the variability among the absolute $\delta^{13}\text{C}$ values should generally be larger. Francey (1981) examined ring series of seven Tasmanian trees (two species) and found a range of ≈ 2 –3‰ among their absolute $\delta^{13}\text{C}$ values for any time interval. Among three oaks from a locality in Wisconsin, Bender and Berge (1982) measured an absolute $\delta^{13}\text{C}$ range for all intervals of ≈ 0.5 –2‰. Finally Freyer and Belacy (1983) found variations in the means of normalized $\delta^{13}\text{C}$ trends of 0.5–2‰ among five *Q. robur* from Spessart, Germany and 0.5–1‰ among five *Pinus silvestris* from Muddus National Park, Sweden. Unfortunately, in these intralocality $\delta^{13}\text{C}$ comparisons single radii represent most trees, thus introducing the attendant uncertainties associated with circumferential variability.

The study of Leavitt and Long (1984) countered this problem by comparing $\delta^{13}\text{C}$ values in ring series from eight pinyon trees from a single site (Stoneman, Arizona) in which each tree was represented by a pooled sample of four orthogonal cores. The results indicate $\delta^{13}\text{C}$ differences of 2–3‰ among the eight trees for each of the 17 5-yr ring groups in the ring series. Further-

more, the sampling of any four trees from the site was found to produce a $\delta^{13}\text{C}$ time series that was representative of both the absolute value and trend of the mean curve for all eight trees.

Year-to-year isotopic variability in tree rings

Most of the isotopic studies with tree ring series have been used to attempt to develop chronologies for climate (Farmer 1979) or for $\delta^{13}\text{C}$ of atmospheric CO_2 (Freyer and Belacy 1983). The majority of these studies have analyzed $\delta^{13}\text{C}$ in 5-yr and 10-yr ring groups, although some studies have developed isotopic time series from year-by-year analyses (Farmer 1979, Tans and Mook 1980, Bender and Berge 1982, Stuiver et al. 1984). Some of the year-to-year (or group-to-group) isotopic variability in these series could be random or the result of environmental influences. Regardless of source, this "scatter" usually amounts to ≈ 1 –2‰ fluctuation superimposed on the overall trend.

Fig. 5 contains a typical example of annual $\delta^{13}\text{C}$ variability for the period 1895 to 1914 in the rings of the pinyon from the Stoneman site. Over this period, the absolute $\delta^{13}\text{C}$ values range from ≈ -19.5 to -17 ‰. Plotted below the $\delta^{13}\text{C}$ curve are curves representing individual tree growth (ring widths and ring areas) and the normalized average growth indices of all trees at the site (STRI). The latter indices are used in dendroclimatological reconstructions of temperature and precipitation (Fritts 1976). These various growth measures are broadly inverse to the $\delta^{13}\text{C}$ curve, suggesting that environmental factors affecting growth may contribute to the "scatter" in tree-ring $\delta^{13}\text{C}$ time series.

The overall trend is believed to contain a drop in $\delta^{13}\text{C}$ values from 1800 to the present of at least ≈ 1.1 ‰, owing to combustion of fossil fuels and consequent input of isotopically light CO_2 into the atmosphere (Stuiver 1978). The $\delta^{13}\text{C}$ drop may be larger or smaller due to net effects of an expanding or diminishing global biosphere, and the study of $\delta^{13}\text{C}$ in tree-ring sequences may help to quantify the net biospheric activity (Stuiver 1978, Peng et al. 1983). However, Francey and Farquhar (1982) have suggested mechanisms whereby environmental influences may override the expected trend, e.g., shading, nutrient depletion, pollution.

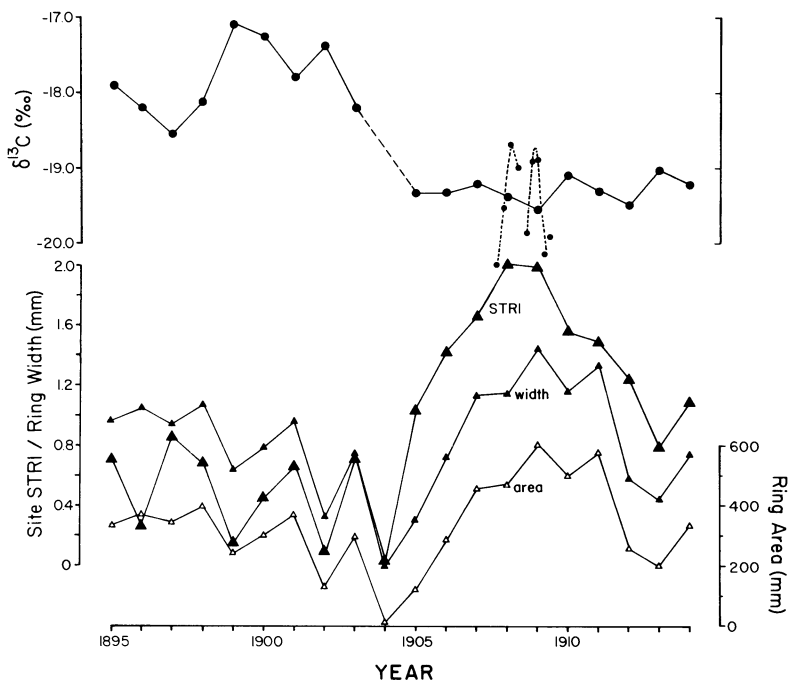


FIG. 5. The single-year $\delta^{13}\text{C}$ values (●) of cellulose from one radius of the Stoneman *P. edulis* from 1895–1914, with the seasonal $\delta^{13}\text{C}$ variation (● ··· ●) shown within the 1908 and 1909 rings. This 20-yr period is characterized by large variations not only in the $\delta^{13}\text{C}$ values, but also in the tree-ring widths (▲) and areas (△) and the site's standardized tree-ring indices (▲, STRI). (The 1904 ring was missing in this radius.)

Seasonal intra-ring $\delta^{13}\text{C}$ variability

Variations in the stable-carbon isotope ratios in plant tissues exist on scales much finer than those discussed heretofore. Growth rings and leaves exhibit a radial or seasonal variation in $\delta^{13}\text{C}$. Fig. 2 illustrates this variation, and several other studies have reported these intra-annual isotopic changes in rings (Wilson and Grinsted 1977, Leavitt and Long 1982a, b) and leaves (Lowden and Dyck 1974, Leavitt and Long 1982b). These trends appear to repeat from one year to the next, suggesting mechanisms related to variations in temperature, light, atmospheric CO_2 concentration or

atmospheric $\delta^{13}\text{C}$ over the growing season. The magnitude of this variation may be as large as the year-to-year $\delta^{13}\text{C}$ variation in whole tree rings. The years 1908 and 1909 in Fig. 5 were subdivided into 4 and 5 equal subdivisions, respectively, and analyzed separately. The results are plotted in Fig. 5 and exhibit a seasonal range of $\delta^{13}\text{C}$ values of $\approx 1.5\text{‰}$ (from ≈ -20.0 to -18.5‰). The patterns of both years are concave downward. Because whole rings or ring groups are used in most tree-ring isotopic reconstruction studies, no special precaution need to be taken in field sampling. However, in interpreting the change in $\delta^{13}\text{C}$ values from one year to the next, changing patterns of this intra-ring variation may contribute to differences.

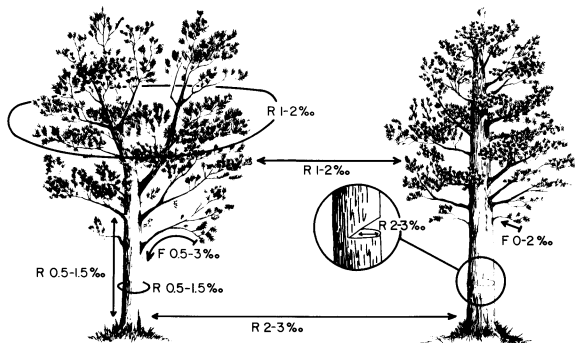


FIG. 6. Summary of the $\delta^{13}\text{C}$ variation within and among trees as determined in this study. The expected range of isotopic composition (R) and apparent fractionation effects (F) are denoted in the figure.

SUMMARY AND CONCLUSIONS

This report describes the state of knowledge on the isotopic variability in tree leaves and wood, with evidence taken primarily from the genera *Pinus* and *Juniperus*. The results may be relevant to tree-ring isotopic reconstructions, to terrestrial ecosystem studies where food chains may be identified or quantified with carbon isotopes, and even to growth chamber experiments where environmental parameters (light, temperature, CO_2 concentration) may be varied in order to influence plant $\delta^{13}\text{C}$.

The stable-carbon composition within and among trees at a site is not a precise value. Although the field variability is complex, the maximum observed ranges

of isotopic variation may serve as "confidence limits." Fig. 6 summarizes the expected ranges of isotopic composition determined in this study. Circumferentially, the ranges of $\delta^{13}\text{C}$ of cellulose in leaves about the crown and in wood of equivalent age about the trunk are approximately equal. From pinyon and juniper leaf data this amounts to a variation of 1–2‰, and for pinyon tree-ring data in 5-yr groups in a range of ≈ 0.5 –1.5‰ is typical. In a series of rings, year-to-year variability may amount to 2–3‰. Actual seasonal isotopic variation within tree rings may also be quite substantial, amounting to ≈ 1 –2‰.

Longitudinally, isotopic differences exist between equivalent-age tree leaves and growth rings in the trunk. For juniper, leaves are isotopically lighter than equivalent-age wood by 1–3‰ (Leavitt and Long 1982a). Pinyon also has leaves isotopically lighter than the trunk wood by 0.5–3‰, but in one case leaf and wood compositions (Fig. 1) were virtually identical. Although twigs (branchlets) are intermediate in position between leaves and trunk wood, they are not intermediate in isotopic composition. For pinyon, the leaves are isotopically heavier than the twigs by 1–2‰, although in two instances (Fig. 4) their $\delta^{13}\text{C}$ values are nearly identical. We find no evidence for a longitudinal gradient in tree rings (Fig. 3), although variability with height amounts to ≈ 0.5 –1.5‰ in juniper and pinyon (Fig. 2).

Variation among individuals within a site amounts to 1–2‰ as seen in juniper leaves (Arnold 1979), and 2–3‰ in pinyon tree rings of equivalent age (Leavitt and Long 1984). This 2–3‰ range apparently also characterizes $\delta^{13}\text{C}$ differences among C_3 trees of different species at the same site (de Silva 1978, Freyer 1979, Francey 1981), although these studies measured $\delta^{13}\text{C}$ on rings from a single radius without accounting for circumferential variability.

We suggest some caution in extrapolating the results from a few species of *Pinus* and *Juniperus* to other species, physiognomies, and environments. However, studies cited in support of our results represent a variety of species and localities, and conform well with results presented. Furthermore, although this study deals with a single wood constituent (cellulose), studies involving $\delta^{13}\text{C}$ analysis of both cellulose and whole tissue (Leavitt and Long 1982a, Francey 1986) indicate that although they are distinctly different isotopically, the relative isotopic changes in each from one sample to the next are broadly similar.

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