

Seasonal stable-carbon isotope variability in tree rings: possible paleoenvironmental signals

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ABSTRACT

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Plant stable-carbon isotope fractionation models indicate that $\delta^{13}\text{C}$ of atmospheric CO_2 , CO_2 concentration, light and moisture stress, among other factors, may potentially affect the $\delta^{13}\text{C}$ of fixed carbon. Seasonal $\delta^{13}\text{C}$ variations in tree rings may therefore represent a new tool for paleoenvironmental reconstruction. The seasonal $\delta^{13}\text{C}$ patterns in growth rings exist in trees (conifer and hardwood) from tropical and temperate localities, and isotopic variation is even seen in trees which are lacking or have poorly-defined rings. The patterns in different rings from a single tree are usually similar, although differences in amplitude and timing of maxima and/or minima are common. Some of the differences may be attributable to radial variation of the $\delta^{13}\text{C}$ patterns which was found to be substantial in a severely water-stressed tree. Correlations of $\delta^{13}\text{C}$ patterns and corresponding seasonal environmental variation for one well-monitored tree showed greater response of the $\delta^{13}\text{C}$ change to measured soil moisture and precipitation than to temperature, calculated soil moisture, solar radiation, or net photosynthesis (as estimated from CO_2 release).

1. Introduction and background

A number of studies have found distinct seasonal variations of $\delta^{13}\text{C}$ in tree foliage and growth rings. Lowden and Dyck (1974) first observed such seasonal changes in leaves (whole tissue) of maple trees (*Acer rubrum*) growing in Canada, and found a decrease of 2–3‰ during the growing season. A study of two growth rings (cellulose and lignin components) from a *Pinus radiata* tree in New Zealand by Wilson and Grinstead (1977) revealed seasonal $\delta^{13}\text{C}$ first decreasing 1.5‰ then increasing 1.5‰, and they calculated a temperature coefficient of $+0.2\text{‰}^\circ\text{C}^{-1}$. Freyer (1980) examined $\delta^{13}\text{C}$ in earlywood and late-

wood of 50 individual tree rings (cellulose?) and found that in the mean, $\delta^{13}\text{C}$ of the earlywood was isotopically “lighter” (more negative) than the latewood. Research on fir tree rings (cellulose) by Moser (1984) also found earlywood isotopically lighter than latewood. Moser (1983) additionally subdivided 11 consecutive growth rings (cellulose) of spruce and found widely varying patterns of isotopic change among rings.

Leavitt and Long (1982a) studied the leaves and corresponding growth ring (cellulose and whole tissue) of a *Juniperus monosperma* tree growing at a well-irrigated site in Tucson, Arizona, finding the seasonal trends to be nearly identical, and consistent with a temperature coefficient of $-0.27\text{‰}^\circ\text{C}^{-1}$. Further analysis of core samples from the same tree, but different locations around the trunk (Leavitt and

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Long, 1986) verified the trend of the previous study with the exception of a single core from the north side, suggesting lighting and shading effects (seasonally dependent) are also important influences on the $\delta^{13}\text{C}$ seasonal pattern. Analysis of two rings (cellulose and whole tissue) from two rings from a *Juniperus deppeana* growing at Prescott, Arizona, showed a variation consistent with a temperature trend of $+0.13\text{‰}^\circ\text{C}^{-1}$ (Leavitt and Long, 1982b). Finally, a study of leaves and the related growth ring (cellulose and whole tissue) from an *Acer grandidentatum* tree in southern Arizona (Leavitt and Long, 1985) showed comparable seasonal patterns.

Models of plant carbon-isotope fractionation have been developed to explain the $\delta^{13}\text{C}$ composition of leaves (Farquhar et al., 1982) and growth rings (Francey and Farquhar, 1982). Not only is $\delta^{13}\text{C}$ of atmospheric CO_2 an important factor, but so are any conditions which affect the ratio of internal plant CO_2 to external CO_2 concentrations (C_i/C_a). When the ratio is low, the plant does not discriminate as effectively against ^{13}C . This ratio is in turn, affected by the rates of CO_2 fixation and sto-

matal conductance. For example, drought could reduce C_i/C_a by decreasing stomatal conductance, whereas light could reduce C_i/C_a by increasing CO_2 fixation. The seasonal $\delta^{13}\text{C}$ variation reflects these changes in C_i/C_a , and therefore contain some combination of these environmental influences.

If these patterns are universal and if they can be related to a single factor or well-constrained combination of factors, it might be possible to analyze these patterns in old wood to reconstruct seasonal aspects of past environments. In this study we report on the ubiquity of these seasonal isotopic patterns as observed in a number of different species at sites thousands of kilometers apart, in both temperate and tropical environments. The representativeness of isotopic patterns from a single radial direction versus the full circumference is addressed with results from two trees. Finally, we analyze further the influence of environmental factors on these patterns through use of some detailed micrometeorological measurements made in close proximity to one of these trees.

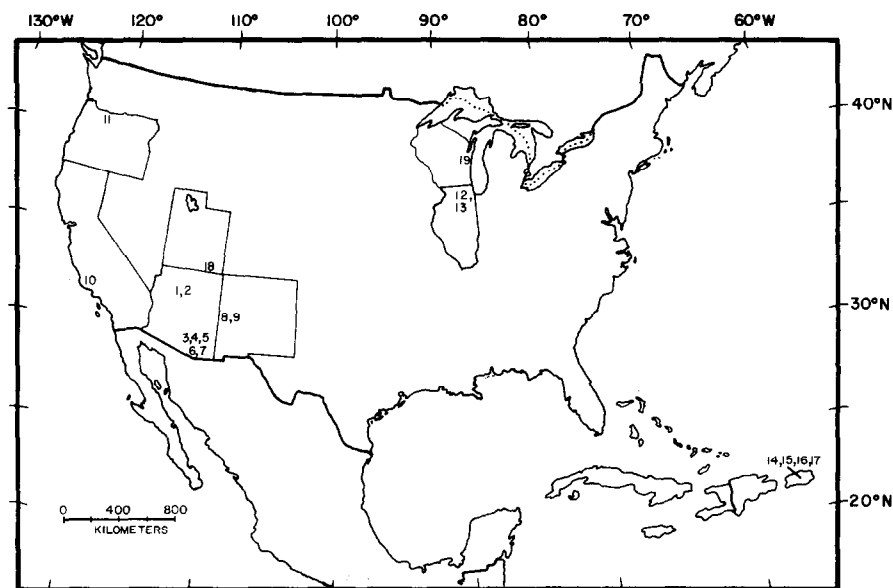


Fig. 1. Location map showing where samples were collected.

2. Methods

We obtained samples of tree rings as cores or cross-sections from several localities throughout North America (Fig. 1, Table I). Because a number of these samples were provided to us

by others, we frequently lack information about individual tree sizes and stand density. The samples were surfaced and most were dendrochronologically dated, but several could be only approximately dated by ring counting and a few would be considered non-datable (some not

TABLE I

Site, species and tree rings analyzed in this study

Site	Location	Elevation	Species	Ring width
1 Prescott* ¹	34°36'N, 112°31'W	1705 m	<i>Juniperus deppeana</i>	1978–1.9 mm; 1979–3.0
2 Stoneman* ¹	35°45'50"N, 111°38'40"W	1660 m	<i>Pinus edulis</i>	1980–1.14 mm; 1909–1.44
3 Radio Ridge* ¹	32°26'N, 110°47'W	2740 m	<i>Pseudotsuga menziesii</i>	1970–1.8 mm; 1908–2.0; 1909–2.0; 1910–2.0; 1911–2.7; 1912–2.8; 1913–2.5; 1914–3.2; 1915–2.4; 1916–2.9; 1917–3.2
4 Hitchcock* ¹	33°23'N, 110°41'W	1830 m	<i>P. menziesii</i>	1908–1.7 mm; 1909–1.8
5 Bigelow* ¹	32°25'16"N, 110°42'40"W	2590 m	<i>Pinus ponderosa</i>	1963–0.87 ± .23 mm; 1964– 1.01 ± .50; 1965– 1.33 ± .23; 1966– 1.38 ± .64; 1967– 1.18 ± .34
6 Kellogg* ¹	35°25'20"N, 110°42'30"W	2590 m	<i>P. ponderosa</i>	1909–3.2 mm (I); 2.8 (II); 3.3 (III); 4.3 (IV)
7 San Pedro* ³	32°08'N, 110°18'W	975 m	<i>Prosopis juliflora</i>	7.4 mm
8 Gila* ¹	33°14'N, 108°26'W	2380 m	<i>P. ponderosa</i>	1908–1.0 mm; 1909–1.0
9 Gila* ¹	33°14'N, 108°28'W	2365 m	<i>P. ponderosa</i>	1908–4.0 mm; 1909–2.7
10 Santa Ynez* ²	34°30'50"N, 119°48'10"W	815 m	<i>Pinus coulteri</i>	1978–22.5 mm; 1979–23.0
11 Oregon* ¹	44°50'N, 120°25'W	760 m	<i>Juniperus occidentalis</i>	1977; 1978–1.8 mm
12 Chicago* ²	41°31'30"N, 87°40'W	198 m	<i>Juniperus virginiana</i> (or <i>J. communis</i>)	1978–4.0 mm; 1979–2.0
13 Chicago* ²	41°31'30"N, 87°40'W	198 m	<i>Acer saccharinum</i>	1980–5.5 mm; 1981–7.5
14 Rio Abajo* ³	18°21'N, 66°42'W	250–425 m	<i>Ocotea leucoxydon</i>	25.4 mm
15 Rio Abajo* ³	18°21'N, 66°42'W	250–425 m	<i>Tectona grandis</i>	2.1 mm; 2.0
16 Rio Abajo* ³	18°21'N, 66°42'W	250–425 m	<i>Montezuma</i> <i>speciosissima</i>	2.1 mm; 2.0
17 Rio Abajo* ³	18°21'N, 66°42'W	250–425 m	<i>Pinus caribea</i>	3.0 mm; 2.6
18 Bears Ears	37°37'N, 109°51'W	2575 m	<i>P. edulis</i>	1983 (twig and leaves)
19 Two Creeks* ³	44°17'N, 87°27'W	180 m	spruce	2.6 mm

*¹Dendrochronologically-dated.*²Ring-counted date.*³Undated or non-datable.

even showing distinct rings). For samples that were datable, the rings chosen for analysis were in many cases the years 1908 and 1909, or 1978 and 1979. This selection was based on some initial sampling in the Southwest in which we commonly found wide rings in these years and they were thus easier to work with. Regardless of the years chosen from each sample, we separated the rings under a binocular microscope into a number of subdivisions using a razor knife. Generally, the larger the ring width the more subdivisions into which the rings could be accurately and conveniently subdivided. Ring widths as small as ~ 1 mm could be divided into up to 4 segments.

In some cases, isotopic analysis was performed on both original whole tissue and on cellulose isolated in a procedure after Green (1963). The samples were combusted to CO_2 in an oxygenated atmosphere at 800°C in a recirculating microcombustion line. The CO_2 was analyzed mass-spectrometrically and $\delta^{13}\text{C}$ (‰ units) was computed relative to the PDB standard (Craig, 1957). Historically, our precision (± 1 s) for replicate analysis of large, well-mixed samples is ± 0.1 ‰. We estimate precision for these intra-annual samples to be about ± 0.2 ‰ because of difficulties in exact replication of subdivision boundaries, and because there is apparently sufficient heterogeneity even within each subdivision to cause isotopic differences in splits from the same subdivision.

3. Results and discussion

3.1. $\delta^{13}\text{C}$ seasonal variations in dated leaves and twigs

A direct correspondence of seasonal patterns in $\delta^{13}\text{C}$ of leaves and corresponding tree rings has already been demonstrated (Leavitt and Long, 1982a, 1985). Samples were obtained from a *Pinus edulis* tree in Utah to determine if the same relationship exists between seasonal $\delta^{13}\text{C}$ patterns in the 1983 leaves and corresponding branch. The branch was di-

vided into 5 equal segments and the needles on each of those segments were detached and collected. The analysis of cellulose from each of these samples is depicted in Fig. 2. Except for the outside (youngest) leaf and branch segments labeled "A", the seasonal variation observed in the foliage is mirrored in the branch.

3.2. $\delta^{13}\text{C}$ seasonal variations in dated tree rings

The isotopic patterns of cellulose and whole wood for the 1908 and 1909 growth rings of 4 trees are represented in Figs. 3 and 4. In all cases, the whole-wood values are isotopically lighter than those of the cellulose by about 1.5 to 2‰. The patterns of all 4 trees show increasing $\delta^{13}\text{C}$ values at the beginning of the growing season and decreasing values toward the end. The location of latewood in this and subsequent figures is denoted by the shaded pattern just above the x-axis, and although it is isotopically light in most cases, the $\delta^{13}\text{C}$ values had already been declining in segments previous to those containing the latewood. Within the same tree, the 1908 and 1909 patterns are similar but not identical.

Two of the trees are Douglas fir (Figs. 3a and 4) from the Santa Catalina Mts., separated by about 11.6 km distance and 910 m elevation.

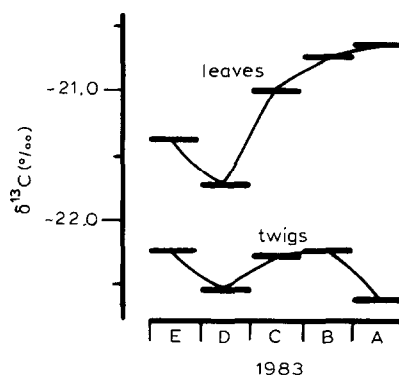


Fig. 2. $\delta^{13}\text{C}$ patterns in cellulose of a pinyon twig and its leaves (site 18).

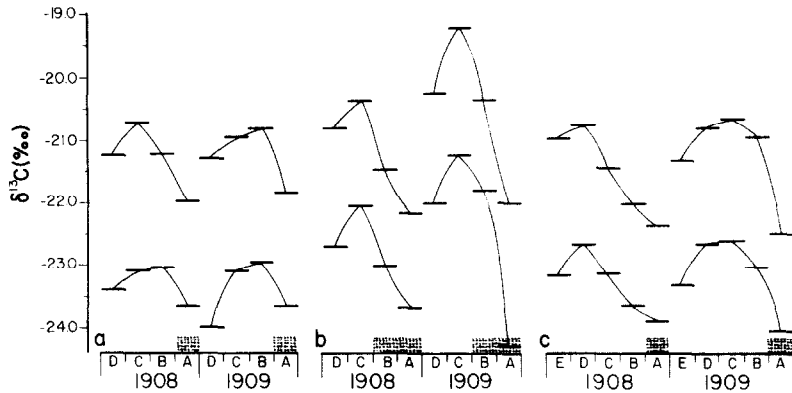


Fig. 3. $\delta^{13}\text{C}$ patterns in cellulose (top curves) and whole wood (lower curves) of rings from the: (a) Hitchcock Douglas fir (site 4); (b) Gila Douglas fir (site 8); and (c) Gila ponderosa pine (site 9).

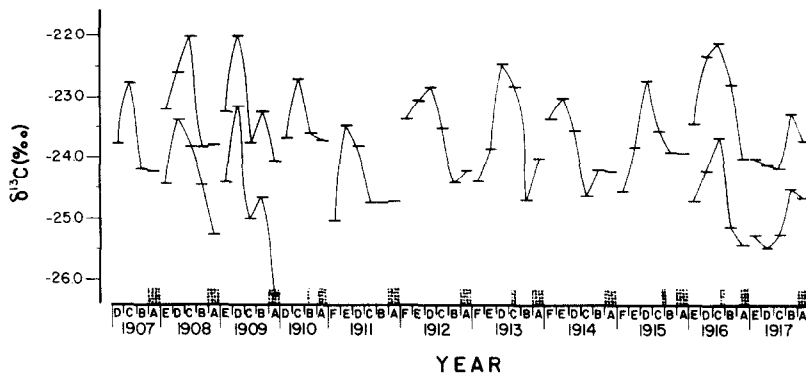


Fig. 4. $\delta^{13}\text{C}$ patterns in cellulose from rings of the Radio Ridge Douglas fir (site 3). The lower curves for 1908, 1909, 1916 and 1917 are patterns in whole wood.

The amplitude of variation is much greater for the Radio Ridge sample (Fig. 4) than for the lower elevation Hitchcock sample (Fig. 3a). From the Gila region of New Mexico, a Douglas fir and ponderosa pine (Fig. 3b and c) separated by about 2 km distance and 10 m elevation show similar seasonal patterns, but with greater amplitude in the Douglas fir. In both trees $\delta^{13}\text{C}$ values decline and begin to flatten out in the 1908 ring but decline sharply in the 1909 ring. The close proximity of these latter two trees suggests the minor differences may be species-related, but differences in microclimate cannot be excluded.

Although the 1908 and 1909 rings have similar patterns in all four trees, an examination of a series of rings from 1907 through 1917 of

the Radio Ridge Douglas fir shows a variety of patterns (Fig. 4), most of which could be characterized as initially increasing then decreasing. By the fractionation models, this pattern would be produced by C_i/C_a ratios decreasing to a minimum near the middle of the growing season. Such a decline could be associated with moisture stress and/or increase CO_2 fixation associated with higher light levels. The complexity of these patterns, however, is enhanced by the fact that each has starting and ending $\delta^{13}\text{C}$ values different from the others, and in about half of the cases the beginning $\delta^{13}\text{C}$ value of one ring is quite distinct from the ending $\delta^{13}\text{C}$ value of the previous ring.

Fig. 5 displays seasonal isotopic patterns in more recent rings of trees from other localities,

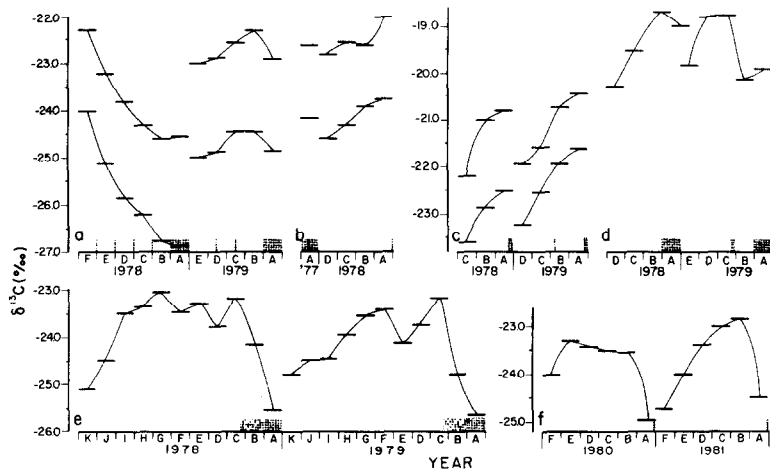


Fig. 5. $\delta^{13}\text{C}$ patterns from rings of the: (a) Chicago juniper (site 12); (b) Oregon juniper (site 11); (c) Prescott juniper (site 1); (d) Stoneman pinyon pine (site 2); (3) Santa Ynez Coulter pine (site 10); and (f) Chicago silver maple (site 13). Where two patterns are shown for the same year, the upper is for cellulose and the lower is for whole wood.

primarily 1978 and 1979, but in one case 1980 and 1981. Three of the trees represent different juniper species (Fig. 5a–c) from distinctly different climates. The Oregon juniper (Fig. 5b) and Prescott juniper (Fig. 5c) have similar patterns, but the Chicago juniper (Fig. 5a) is different from the others and its own 1978 and 1979 patterns are dissimilar. A pinyon pine about 90 km from the Prescott juniper (Fig. 5d) shows a $\delta^{13}\text{C}$ pattern more similar to those of the Douglas firs and ponderosa pine.

Fig. 5e is the isotopic pattern from a Coulter pine tree which had very large rings, allowing more subdivisions to be made. The 1978 and 1979 patterns are quite similar down to the starting and ending $\delta^{13}\text{C}$ values. This tree is from a coastal California site, and the similarity may be related to climate-moderating effects of the Pacific Ocean. Fig. 5f contains the 1980 and 1981 patterns of the only angiosperm analyzed, a maple tree from the same location as the juniper in Fig. 5a. Despite major genetic differences from the other trees, this pattern is again similar to patterns in many of the previous figures. This suggests environmental rather than genetic factors are a key to interpretation of the patterns.

3.3. $\delta^{13}\text{C}$ patterns in “undatable” tree rings

Among dendrochronologists, tree species gain the reputation of being “non-datable” if there is no correspondence of width of rings of the same age between adjacent trees, or if there are no distinct ring boundaries. The rings depicted in Fig. 6d and e would probably represent the former case, while those in Fig. 6a–c have no well-defined ring structure. The rings in Fig. 6a, c, d and e are tropical woods from Puerto Rico harvested in 1982 and the rings in Fig. 6b are from a mesquite tree from Arizona cut in 1981.

The patterns in Fig. 6d and e (clear ring boundaries) repeat in a fashion similar to that seen in some of the temperate dated trees, showing substantial seasonal variation in spite of the limited seasonal climatic variation at this latitude. For the ring in Fig. 6a (~9 mm radial length), there were no boundaries, but the pattern suggests there may be ~2 years represented. The sample in Fig. 6b (~8 mm radial length) showed some evidence of ring boundaries between segments B and C and between segments E and D, and the isotopic patterns suggest 3 years may be represented. The sam-

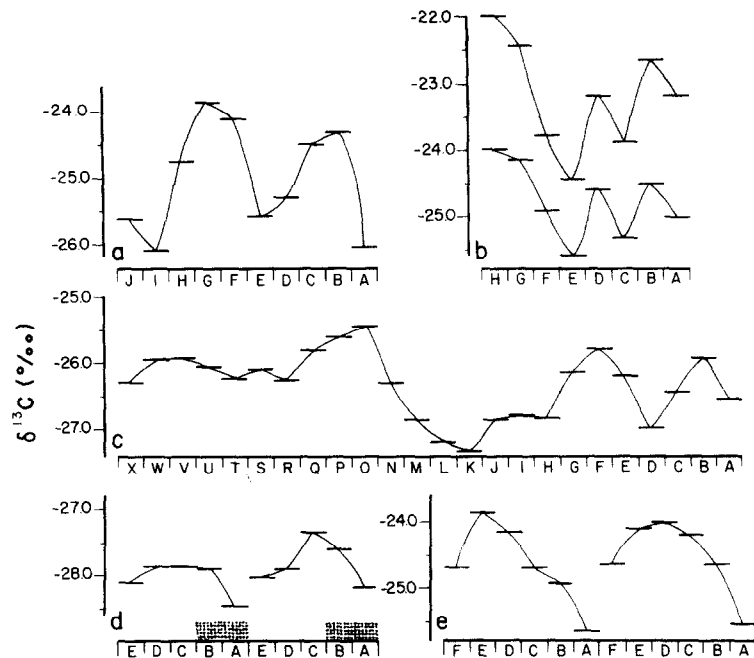


Fig. 6. $\delta^{13}\text{C}$ patterns in cellulose from undated rings of the: (a) Rio Abajo maga (site 16); (b) San Pedro mesquite (site 7); (c) Rio Abajo laurel (site 14); (d) Rio Abajo Caribbean pine (site 17); and (e) Rio Abajo teca (site 15). The lower curve in b represents the pattern in whole wood. The rings in a, b and c showed poor or no ring boundaries.

ple in Fig. 6c (~ 25.4 mm radial length) had several possible ring boundaries between segments D and E, G and H, J and K, N and O, and R and S. Simply from the isotopic patterns, at least 3 or 4 years are suggested but the patterns are much less constant with time.

3.4. $\delta^{13}\text{C}$ patterns in ancient wood

These $\delta^{13}\text{C}$ patterns are not restricted to modern trees. Fig. 7 displays the pattern in one ring of a specimen of spruce collected from the Two Creeks buried forest site in Wisconsin. The age of this forest has been radiocarbon

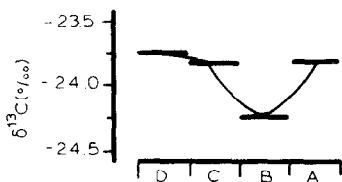


Fig. 7. $\delta^{13}\text{C}$ pattern in cellulose of spruce from a ring from spruce from the Two Creeks buried forest, ca. 11,000–12,000 years old (site 19).

dated as 11,000 to 12,000 year B.P. (Black and Rubin, 1968). The isotopic pattern is inverted relative to most of the others, indicating the C_i/C_a ratio was highest in the middle of the growing season.

3.5. Radial variation in $\delta^{13}\text{C}$ patterns

The question arises as to whether some of the differences among patterns discussed in 3.2. are attributable to variation of the pattern among different radial directions in the same tree (all of the results presented thus far are from single radial directions). The absolute isotopic value of the complete ring has been shown to vary circumferentially by up to 2‰ among radial directions (Tans and Mook, 1980; Leavitt and Long, 1984). To test this variation with respect to the seasonal patterns, a cross-section of a ponderosa pine tree growing several km from the Radio Ridge and Hitchcock sites was obtained. The cardinal directions were not marked on the cross-section so we simply took

samples of the 1909 ring along 4 orthogonal directions and subdivided each into 5 segments. The curves in Fig. 8 show the variation among radii and the mean pattern. Except for the oldest segment "E", the patterns are quite similar. This tree (harvested in 1977) is about 150 years old so the 1909 ring occurs about midway through its life, i.e. at a time of mature growth. In principle, in the youthful stage of growth the circumferential isotopic differences may be small, but with growth to maturity and beyond, the differences will increase as the diversity of canopy microenvironments also increases. Comparatively, we may thus find less radial variability in pre-1909 rings but increasing variability in post-1909 rings.

Rings from the north, south, east and west directions of another ponderosa pine at a more xeric site near the Hitchcock and Radio Ridge localities were subdivided and analyzed. The patterns of each radial direction are not displayed, but rather the mean curves for the years 1963 through 1967 of the Bigelow tree are depicted in Fig. 9 with vertical bars signifying ± 2 standard errors. The length of these error bars demonstrates that there is substantially more variation of these seasonal patterns among radii from this tree than that of the Kellog tree. The greater radial variability of the Bigelow patterns may in part be a consequence of the rings being 25–50% of the width of the Kellog rings, making accurate, uniform subdivision more difficult, complicated by substantial ring width variation (ring widths in one direction

may be up to twice those in other directions). Additionally, the Bigelow tree was about 110 years old when cut in 1969, so the rings represented in Fig. 9 are during mature growth when canopy microenvironmental variation may have been greater.

3.6. Environmental factors influencing $\delta^{13}\text{C}$ patterns

The Bigelow tree described in section 3.5. had been the subject of intensive study over the period 1963 through 1967 in regard to factors influencing tree-ring growth throughout the tree (Brown, 1968; Fritts, 1976). A number of parameters were collected at the Bigelow site throughout the 5-year period including temperature, precipitation, measured soil moisture, calculated soil moisture, solar radiation and net photosynthesis (by CO_2 released). These values were tabulated from Fritts (1976) and compared to the $\delta^{13}\text{C}$ variation displayed in Fig. 9.

Ring subdivision was made into approximately equal segments, but because the growth rate of the rings were likely not constant, each segment probably does not represent equal amounts of time. Fritts (1976), however, did present the average cell size of each row of tracheids from the beginning to the end of each growing season. From this, we could estimate the number of cells radially contained in each of our equal subdivisions: for example, in the 1963 ring there were 5 cells in the inside sub-

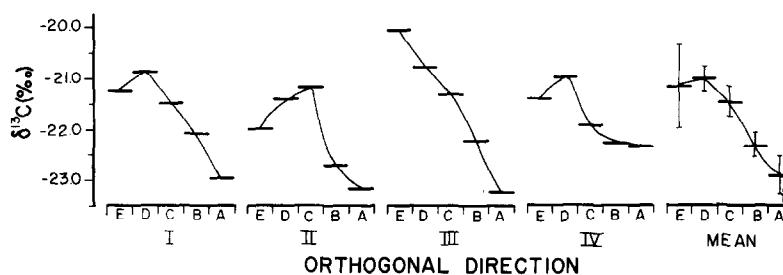


Fig. 8. $\delta^{13}\text{C}$ patterns in cellulose from the 1909 ring sampled at 4 orthogonal directions from the Kellog ponderosa pine (site 6). The vertical bars in the mean curve represent ± 2 standard errors.

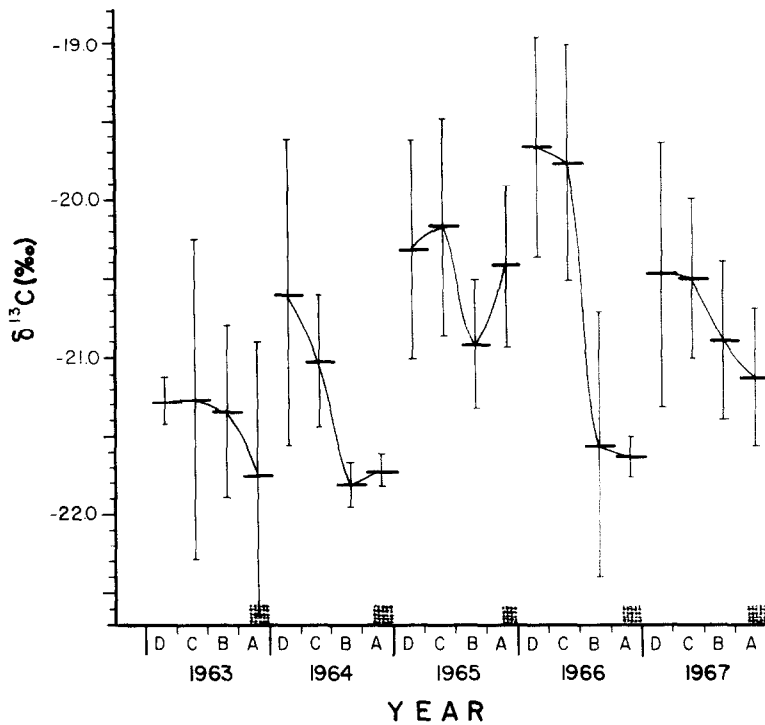


Fig. 9. $\delta^{13}\text{C}$ patterns in cellulose from 5 years of the Bigelow ponderosa pine (site 5). Patterns from 4 orthogonal directions of each ring were first analyzed separately and the means of these patterns (± 2 standard errors) are represented here.

division, 5 cells in the next, 7 cells in the next, and 13 cells in the outside subdivision, indicating very large inside cells and small cells toward the outside. The best estimate of the actual time represented in each subdivision was made for the 1966 ring because Fritts (1976) presented a very precise plot of cell formation with time. This plot was actually for a tree adjacent to that monitored, but we inferred from it that 1/3 of our first subdivision (D) of the 1966 ring grew in April and 2/3 grew in May. For the second 1966 subdivision, 2/3 grew in May and 1/3 in June, the third subdivision grew in July, and the fourth subdivision experienced 2/9 growth in July, 5/9 in August and 2/9 in September.

With these proportions, we weighted our environmental data and correlated them with the corresponding $\delta^{13}\text{C}$ of each subdivision. Table II summarizes the results of these correlations. For the 1966 ring using the weighting de-

scribed above with the mean monthly average of the various parameters, we found significant correlations with solar radiation and with measured soil moisture. For the other years, the weighting could not be determined as precisely as for 1966 because growth development graphs had not been constructed, but were estimated from the narrative seasonal growth descriptions of Fritts (1976). The strongest correlations for the years 1964, 1965 and 1966 were measured soil moisture or precipitation. For each year, the correlations with measured soil moisture and precipitation were negative, consistent with a link between stomatal closure (low available moisture) and elevated $\delta^{13}\text{C}$ values. Correlation coefficients were also calculated with all the Bigelow data for temperature ($r = -0.47$, $n = 16$), precipitation ($r = -0.85$, $n = 16$), measured soil moisture ($r = -0.75$, $n = 16$), calculated soil moisture ($r = +0.27$, $n = 16$), solar radiation ($r = +0.75$,

TABLE II

 $\delta^{13}\text{C}$ -environment correlations in Bigelow tree rings

Year	Subdivision	Weighting	Correlation coefficients (<i>r</i>)					
			Temp.	Precip.	Measured soil moisture	Calculated soil moisture	Solar radiation	CO ₂
1964	D	0.17Ap, 0.83 Ma	-0.84	-0.97* ²	-0.89	+0.37	-	-
	C	0.22Ma, 0.56Jn, 0.22Jl						
	B	0.83Jl, 0.17Au						
	A	0.45Au, 0.55Se						
1965	D	0.25Ap, 0.75Ma	-0.45	-0.88	-0.95* ²	+0.31	+0.83	-0.36
	C	0.3Ma, 0.7Jn						
	B	0.18Jn, 0.82Jl						
	A	0.38Jl, 0.31Au, 0.31Se						
1966* ¹	D	0.33Ap, 0.67Ma	-0.86	-0.92	-0.98* ²	+0.68	+0.99* ³	+0.64
	C	0.67Ma, 0.33Jn						
	B	1.0Jl						
	A	0.22Jl, 0.56Au, 0.22Se						
1966	D	0.22Ap, 0.78Ma	-0.59	-0.89	-0.97* ²	+0.15	+0.98* ²	+0.74
	C	0.23Ma, 0.77Ju						
	B	0.91Jl, 0.09Ap						
	A	0.5Au, 0.5Se						
1967	D	0.22Ap, 0.78Ma	-0.59	-0.76	-0.87	+0.70	-	-
	C	0.64Jn, 0.36Jl						
	B	0.44Jl, 0.56Au						
	A	0.35Au, 0.65Se						

*¹Weighting derived from precise cell formation-time plots; for all other weighting was estimated from narrative descriptions of Fritts (1976).

*² $P < 0.05$; *³ $P < 0.01$.

$n=8$) and CO₂ ($r = +0.58$, $n=8$). The correlations of $\delta^{13}\text{C}$ with precipitation and with measured soil moisture are significant at $P < 0.01$, and $\delta^{13}\text{C}$ with solar radiation is significant at $P < 0.05$.

It should be noted that weighting of environmental data was done with monthly averages (or totals in the case of precipitation). For example, subdivision "D" of the 1966 ring had 17% of its growth in April and 83% in May, so the climate value to which it was compared was computed by adding 17% of the April average (or total) to 83% of the May average (or total) of the particular environmental parameter. This is not as precise as weighting the 83% to the average of only that part of May during which the subdivision grew. However, given uncertainties in estimating the weighting, the

use of monthly averages should provide a satisfactory first approximation.

Similar regression tests with the other patterns are not easily done because of lack of the cell development timing constraints that the Bigelow rings have. Future environment calibration experiments with the $\delta^{13}\text{C}$ patterns in tree rings will need records of ring development with time for more precise analysis.

4. Conclusions

Plant carbon isotope fractionation is a complex process with a number of environmental factors capable of influencing the $\delta^{13}\text{C}$ of tree rings. The patterns of seasonal $\delta^{13}\text{C}$ changes in tree rings likely contain the record of seasonal environmental changes as they affect C_i/C_a ,

and this preliminary study suggests the patterns may be dominated by one or two parameters and may therefore be useful in paleoclimatic reconstructions.

These $\delta^{13}\text{C}$ patterns are widespread: they are present in many species (conifer and hardwood) in a number of different climatic types at different latitudes. Most samples for which $\delta^{13}\text{C}$ patterns in a sequence of rings were determined show generally similar pattern shapes, with differences in absolute values, timing of maxima and minima, and in initial and final $\delta^{13}\text{C}$ values in each pattern.

Correlations suggest precipitation and/or soil moisture are the most important environmental factors influencing the $\delta^{13}\text{C}$ patterns in tree rings at the Bigelow site. As predicted in plant fractionation models, moisture deficiency favors elevated $\delta^{13}\text{C}$ values as stomatal conductance is decreased. However, it would be reasonable to expect that in locations where moisture is less limiting that the patterns may be dominated by some other factor.

Some studies have attempted to use $\delta^{13}\text{C}$ measurements in tree rings to reconstruct the $\delta^{13}\text{C}$ of atmospheric CO_2 (e.g., Leavitt and Long, 1988) and to reconstruct climate (temperature) (e.g., Libby et al., 1976), and one might suppose the results of this study could provide insight into greater validity of one application over the other. The $\delta^{13}\text{C}$ of atmospheric CO_2 of these sites should reach an annual maximum in late summer with the peak value 0.4 to 0.6‰ higher than the annual minimum for these latitudes (Mook et al., 1983). Atmospheric CO_2 does not seem to be the primary influence in seasonal tree-ring variation because (a) some tree-ring seasonal patterns show highest $\delta^{13}\text{C}$ only in the first or last subdivision of the ring, (b) many show a maximum much earlier in the growing season than would be expected, and (c) the magnitude of the seasonal $\delta^{13}\text{C}$ variation within these tree rings is commonly 1–2‰, i.e., far in excess of atmospheric changes. Therefore, on this short seasonal timescale it is more likely that the rel-

atively large changes in microclimate during the growing season dominates the patterns, although a long sequence of these patterns (e.g., 100 years) should likely effect both seasonal variability and a long-term change in mean $\delta^{13}\text{C}$ as a consequence of the changing atmospheric CO_2 composition.

Further studies (laboratory and field) are needed to test the influence of individual environmental parameters and to demonstrate how representative the $\delta^{13}\text{C}$ patterns from one tree are of trees at a site. If results are favorable, these patterns may ultimately be measured in Pleistocene and Holocene subfossil wood samples to reconstruct seasonal aspects of ancient climates.

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