POSSIBLE CLIMATIC RESPONSE OF δ^{13} C IN LEAF CELLULOSE OF PINYON PINE IN ARIZONA, U.S.A.

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ABSTRACT

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Leaves of pinyon pine (*Pinus edulis*) were collected from ten living trees at nine sites in Arizona and New Mexico, representing elevations from 1200 to 2200 m. Stable-carbon isotopic analysis was performed on cellulose isolated from the whole leaf material. In spite of the range of conditions, the δ^{13} C response only varies over $\sim 1^{0}/_{00}$ with an average δ^{13} C variance among leaves of the same tree of $0.4^{0}/_{00}$. The δ^{13} C-values were regressed with elevation and with monthly, seasonal and annual climate data obtained from nearby climatological stations. Linear relations of δ with temperature, T, and δ with precipitation, T0, yield mostly positive correlations, not significant at 95%. Because of high δ^{13} C-values of the two highest elevation sites, the regressions improve greatly for second-order polynomials of elevation and temperature (T0,05). The mechanism for higher δ^{13} C at higher elevations is not clear, but perhaps related to length of growing season. There may be some potential for reconstructions based on strong linear relations derived for the lower elevation trees.

INTRODUCTION AND BACKGROUND

Trees have already provided much information on past climates from the variability of growth-ring thicknesses in dendroclimatological studies (Fritts, 1976). The application of isotopic measurements on natural materials to paleothermometry was first proposed by Urey (1947), and several studies have since attempted to calibrate the hydrogen, carbon and oxygen stable-isotope compositions in tree rings to climate variables (e.g., Libby and Pandolfi, 1974; Epstein and Yapp, 1976; Gray and Thompson, 1976; Pearman et al., 1976; Farmer, 1979).

In this study, we examine the stable-carbon isotopic ratio (13 C/ 12 C) in cellulose of pinyon pine (*Pinus edulis* Engelm.) leaves in relation to the influence of climate. This particular pinyon species grows over a wide variety of site conditions in the southwestern U.S.A. from ~ 1000 to ~ 2500 m elevation. Because of this range, we were able to obtain leaves from in-

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dividuals representing a variety of temperature and precipitation exposures. The calibration of the isotopic composition of these leaves to climate parameters may eventually be applicable to future climatic research with pinyon tree rings. More immediately, the results may be useful as an aid in climate reconstruction from "fossil" pinyon leaves. These fossil pinyon leaves are part of a large assemblage of plant and animal materials conveniently available through the labors of the packrat (g. Neotoma) and preserved in packrat middens of the Late Pleistocene in the western U.S.A. (Van Devender, 1973; Lanner and Van Devender, 1974; Wells, 1976; Cole, 1981). An isotopic paleothermometer would be valuable as an independent test of conclusions of these previous studies which relate climate to species abundances in the middens.

Some work has already been done with stable carbon isotopes in cellulose of juniper (g. Juniperus) leaves and their relation to climate (Arnold, 1979). Despite the pinyon remnants of these middens being less ubiquitous than the juniper remains, a variety of pinyon species, Pinus edulis, P. monophylla and P. cembroides, have been reported in fossil packrat middens. Although this study examines only P. edulis, the results may perhaps be extended to P. monophylla as well because there is evidence of their genetic similarity to the extent that natural hybridization occurs between these species where their ranges overlap (Lanner, 1974). Evidence of the similarity in carbon isotopic composition of different juniper species at the same site (Arnold, 1979) may portend similar environmental response for the various pinyon species.

MATERIALS AND METHODS

Sampling and analysis

Pinus edulis leaves were collected from eight sites in Arizona and one in New Mexico (Fig. 1) at the end of the 1981 growing season. At the Dry Creek site, leaf samples from two different trees were obtained. We endeavored to sample leaves on several branchlets from each of the four cardinal directions at a height of 1—2 m. In a few cases, leaves could only be obtained from greater heights, and in the extreme there were two cases where leaves did not grow on one side of the trees.

In the laboratory, the leaves were separated from the branchlets, airdried, and ground in a Wiley® mill. All analyses were ultimately performed on the cellulose component of the leaves in order to avoid the case of isotopic variation due solely to varying proportions of organic constituents, each of a distinct isotopic composition (Park and Epstein, 1961). In a method modified after Green (1963), the initial chemical step removes oils and resins from the ground leaves with a 2:1 mixture of toluene—ethanol in a Soxhlet extraction apparatus. The second step employs a hot (70°C), acidified sodium chlorite solution to oxidize the remaining materials with the exception of the residual cellulose (holocellulose).

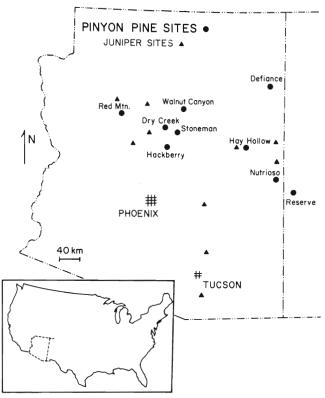


Fig. 1. Pinyon sampling sites in Arizona and New Mexico. Location of juniper trees from study of Leavitt (1982) are also indicated.

The cellulose samples were burned to CO_2 and H_2O in the presence of CuO and O_2 in a recirculating microcombustion system. Cold ethanol traps (-80°C) effectively removed the H_2O and liquid nitrogen trapped the CO_2 sample for mass-spectrometric analysis. Following analytical and computational procedures outlined by Craig (1957), the following relation expresses the isotopic composition (δ) of the sample with respect to the international PDB standard in per mil units:

$$\delta^{13}C (^{0}/_{00}) = \left[\frac{(^{13}C/^{12}C)_{sample}}{(^{13}C/^{12}C)_{PDB}} - 1 \right] \times 1000$$

Based on 30 repeats of combustion and analysis for a cellulose standard over the past year, reproducibility is $\pm 0.05^{\circ}/_{00}$ (1 std. dev.).

Weather data

Fortunately, the network of climatological stations in Arizona (and New Mexico) is sufficiently extensive that representative climate data were

TABLE I

Pinyon sites, their associated weather stations and long-term climate means

Pinyon site	Elevation (m)	Weather station designation	Elevation (m)	Distance (km), direction	Site long-term mean annual	
				from site	tempera- ture (°C)	precipi- tation (cm)
Red Mountain	1,635	Seligman 13SSW	1,597	8, N	10.9	32.3
Walnut Canyon	2,005	Flagstaff WSO (temperature, T)	2,135	11, wsw	8.2	44.9
		Walnut Canyon N.M. (precipitation, R)	2,038	1, WSW		
Dry Creek I	1,390	Sedona R.S.	1,317	8, ESE	15.2	43.6
Dry Creek II	1,380	Sedona R.S.	1,317	8. ESE	15,2	43.6
Hay Hollow	1,785	Snowflake	1,720	13, W	10.4	28.9
Defiance	2,180	Window Rock	2,059	30, E	7.7	30.7
	,	Ganado (annual temperature	1,932	15, W		
		Tannual)	•			
Nutrioso	2,395	Alpine	2,454	16, S	6.8	49.0
Hackberry	1,195	Childs (temperature, T)	808	11, S	15.7	47.1
		Irving (precipitation, R)	1,157	9, SE		
Stoneman	1,660	Sedona R.S.	1,317	15, NW	13.4	43.6
Reserve	2,020	Reserve R.S.	1,782	7, N	8.7	35.6

available for all sampling sites. Table I lists the sampling sites together with their spatial relationship to the respective weather stations supplying the climate data. For all but two sites, the weather stations were within 15 km of the sampling sites. Data from two weather stations were used in representing the climate of three of the sampling sites. In two of these cases, the closest weather stations in distance and elevation (Walnut Canyon N.M. and Irving) only record precipitation so that a more distant station was required for temperature data. In the other case, we used long-term temperature data for the Ganado weather station in conjunction with the Window Rock data to estimate the Defiance sampling site temperature.

The long-term climate data for the weather stations in Table I were compiled from the climate summaries in Sellers and Hill (1974). These averages constitute 10–30 years depending on the length of station operation. The precipitation value is that of the nearest weather stations, whereas the temperature is adjusted for the elevational difference between sampling site and weather station at an average lapse rate of –6.5°C per 1000 m (Battan, 1979). Of course, slope, aspect, neighboring vegetation type and distribution, topography and other factors will all influence the actual site microclimate.

Because pinyons typically begin to lose leaves in the third year (Sargent, 1933), weather data of the most recent two growth years (1980 and 1981) were also obtained from N.O.A.A. (1979—1981a, b) as potentially more representative of the climate during actual leaf growth. For the 1980 and 1981 data, we calculated monthly, seasonal and annual temperature and

precipitation. The few cases of missing data were estimated from data of other stations. The growing "year" was considered as the months prior to and including the growing season, i.e. October of the prior year through September of growing season. Thus, weather data from October—December of 1979 and 1980 were included in the 1980 and 1981 growth-years, respectively. When months were combined as seasons, rainfall of the three-month groups was taken as the sum whereas temperature is the average of the three months.

RESULTS AND DISCUSSION

For each of the trees, Table II lists the cellulose δ^{13} C from leaves of each direction and the overall mean. Despite a range of 1200 m in elevation among sites, the average δ^{13} C-value range over only $\sim 1^0/_{00}$, from -21.41 to $-20.51^0/_{00}$. The standard deviation for the mean of each tree represents the scatter associated with the different sides of the tree. With the notable exception of the Hay Hollow tree, this scatter is generally less than $0.5^0/_{00}$. The mean of these intra-individual variances is $\sim 0.38^0/_{00}$, quite similar to the mean δ^{13} C variance of $\sim 0.37^0/_{00}$ found in 23 juniper trees of Arnold's (1979) study. The mean intra-tree variance for leaves of ten juniper trees (see Fig. 1) in the study of Leavitt (1982) was $0.46^0/_{00}$. The range of elevations in that study was also ~ 1200 m and the δ^{13} C-values varied over $\sim 1.5^0/_{00}$ (see Table IV).

In an effort to determine $\delta^{13}\mathrm{C}$ —climate relationships, the mean $\delta^{13}\mathrm{C}$ -values were regressed against elevation (ELEV), temperature (T), precipitation (R) and temperature/precipitation (T/R). Table III summarizes representative correlation coefficients of these relationships. For the linear regressions, only one correlation was found at a significance of P < 0.05. The correlations of $\delta^{13}\mathrm{C}$ with T tend to be of uniform strength, nearly al-

TABLE II δ^{13} C results for pinyon leaves

Site	North (°/ ₀₀)	South (?/ ₀₀)	East (°/00)	West (°/ ₀₀)	$\bar{x} \pm 1s$ (°/00)
Red Mountain	-21.27	-21.06	_	-21.07	-21.13 ± 0.12
Walnut Canyon	-21.65	-20.97	-21.34	-21.52	-21.37 ± 0.30
Dry Creek I	-20.53	-20.84	_	-20.88	-20.75 ± 0.19
Dry Creek II	-20.35	-20.67	-20.42	-21.57	-20.75 ± 0.56
Hay Hollow	-21.05	-20.47	-19.90	-22.21	-20.91 ± 0.99
Defiance	-21.06	-20.99	-21.11	-20.09	-20.81 ± 0.48
Nutrioso	-20.79	-21.24	-20.41	-20.70	-20.79 ± 0.34
Hackberry	-20.17	-20.94	-20.23	-20.71	-20.51 ± 0.37
Stoneman	-21.14	-20.48	-21.00	-20.96	-20.90 ± 0.29
Reserve	-21.46	-21.37	-21.72	-21.10	-21.41 ± 0.26

TABLE III Correlation coefficients for various linear and multiple regressions with pinyon leaves

(A)	Ele	vation

	δ vs.:	ELEV	ELEV, ELEV ²			
Sterner w		-0.45	0.79*1			
(B) Climate						
	δ vs.:	T	T , T^2 R	R, R^2	T/R	T/R , $(T/R)^2$
Long-term annual means		0.56*2	0.75*2 0.31	0.52	0.37	0.52
1980 + 1981 individual month	s:					
Jan.		0.45	0.83^{*1} 0.49	0.69	0.00	0.00
Feb.		0.49	0.83^{*1} 0.54	0.72^{*2}	0.02	0.18
Mar.		0.47	0.83^{*1} 0.27	0.56	0.36	0.79^{*1}
Apr.		0.48	0.81^{*1} 0.46	0.55	0.19	0.23
May		0.50	0.80*1 0.66*1	0.66	0.48	0.49
Jun.		0.52	0.77^{*1} 0.23	0.25	0.02	0.02
Jul.		0.50	0.78^{*1} -0.15	0.34	0.42	0.50
Aug.		0.47	0.79^{*1} -0.04	0.08	0.20	0.20
Sep.		0.48	0.80*1 0.30	0.30	0.05	0.06
Oct.		0.53	0.79^{*1} -0.28	0.41	0.46	0.53
Nov.		0.48	0.82^{*1} -0.07	0.15	0.57	0.70
Dec.		0.45	0.82^{*1} -0.21	0.57	0.25	0.30
1980 + 1981 month combinat	ions:					
Winter (Nov.—Dec.—Jan.)		0.47	0.83^{*1} 0.39	0.52	0.10	0.20
Winter (DecJanFeb.)		0.47	0.83^{*1} 0.48	0.72	0.08	0.20
Spring (Mar.—Apr.—May)		0.48	0.82^{*1} 0.42	0.60	0.09	0.10
Summer (JunJulAug.)		0.50	0.78^{*1} 0.07	0.25	0.37	0.41
Fall (Sep.—Oct.—Nov.)		0.50	0.80^{*1} 0.10	0.11	0.20	0.21
Annual (Oct.—Sep.)		0.49	0.80^{*1} 0.38	0.81*1	0.06	0.06

TABLE IV Arizona juniper trees and δ¹³C of leaf cellulose (from Leavitt, 1982)

Juniper site	Elevation (m)	1970—1	979 mean temperature*1 (°C)	$\delta \pm 1s^{*2}$	
		annual	Mar.—Apr.—May	(°/ ₀₀)	
Globe	1,195	16.6	14.4	-21.64 ± 0.25	
Jerome	1,845	13.1	11.3	-22.85 ± 0.47	
Oracle	1,450	16.4	14.7	-22.36 ± 0.33	
Prescott	1,705	11.4	9.4	-22.18 ± 0.30	
Santa Rita	1,370	16.9	15.7	-22.29 ± 0.31	
Seligman	1,605	11.3	9.3	-23.04 ± 0.76	
Snowflake	1,735	11.0	9.6	-22.78 ± 0.65	
Springerville	2,315	7.5	6.1	-22.93 ± 0.50	
St. Johns	1,790	11.6	10.8	-21.66 ± 0.72	
Williams	2,055	10.1	7.5	-22.78 ± 0.28	

^{*1} Corrected for elevation difference between site and weather station.
*2 Standard deviation associated with δ -values of leaves from the north, east, south, and west sides of the tree.

ways stronger than δ with T/R but less frequently stronger than δ with R. For the most part, both the δ vs. T and δ vs. R relationships have positive coefficients.

For comparison, the δ^{13} C of leaf cellulose from juniper trees growing at ten sites around Arizona (Leavitt, 1982) was linearly regressed with elevation and selected temperature measures (Table IV). These include three different species of *Juniperus* (Leavitt and Long, 1982). Because the juniper leaves are retained for ~10 years (Arnold, 1979) and the leaf samples were collected at the end of the 1979 growing season, the temperature data represent the years 1970–1979. The pinyon pine regressions below are with temperature for the years 1980 and 1981:

$$\delta^{13}C = \begin{cases} -3.32 \cdot 10^{-4} \text{ELEV} - 20.35, & r = 0.45 \\ -8.64 \cdot 10^{-4} \text{ELEV} - 20.98, & r = 0.56 \end{cases} \text{ (pinyon)}$$

$$\delta^{13}C = \begin{cases} 4.70 \cdot 10^{-2} T_{\text{annual}} - 21.46, & r = 0.56 \\ 8.54 \cdot 10^{-2} T_{\text{annual}} - 23.53, & r = 0.52 \end{cases} \text{ (pinyon)}$$

$$\delta^{13}C = \begin{cases} 4.13 \cdot 10^{-2} T_{\text{Mar-Apr-May}} - 21.33, & r = 0.48 \\ 8.90 \cdot 10^{-2} T_{\text{Mar-Apr-May}} - 23.42, & r = 0.55 \end{cases} \text{ (pinyon)}$$

$$\delta^{13}C = \begin{cases} 4.13 \cdot 10^{-2} T_{\text{Mar-Apr-May}} - 21.33, & r = 0.48 \\ 8.90 \cdot 10^{-2} T_{\text{Mar-Apr-May}} - 23.42, & r = 0.55 \end{cases} \text{ (pinyon)}$$

The coefficients are all of the same sign and magnitude, but none of these relationships is significant at 95%. With the juniper trees, however, there is some evidence that the most southerly trees (Globe, Oracle and Santa Rita) may be biased by local pollution related to mining activities (Leavitt, 1982).

For the pinyon pine, regression of δ vs. second-order polynomials of T and T^2 and ELEV and ELEV² greatly improves the fit as reflected in the statistically significant correlation coefficients in Table III. The linear and second-order regression for δ vs. ELEV and δ vs. spring temperature (March—April—May) are plotted in Figs. 2 and 3, respectively. It is apparent that the two highest elevation sites, Nutrioso and Defiance, are very influential in the regressions. In fact, if these two sites are removed (n=8) and only the high-temperature (low-elevation) "limb" of the parabolas in Figs. 2 and 3 are considered, highly significant linear regressions result:

$$\delta^{13}C = -9.87 \cdot 10^{-4}ELEV - 19.35,$$
 $r = 0.94;$ $(P < 0.001)$
 $\delta^{13}C = 0.11T - 22.16,$ $r = 0.95;$ $(P < 0.001)$

With all ten sites, the parabolic trends of δ vs. T, T^2 and δ vs. ELEV, ELEV² are stronger than the linear relationships. The fact that two and not just one of the highest elevation sites have the high δ^{13} C-values which make second-order polynomials a better fit make it less likely that those values are anomalies in what should be a linear relationship. This parabolic trend is suggestive of those processes such as net photosynthesis where increased activity is promoted over one range of stimulation but inhibition occurs above some threshold. Francey and Farquhar (1982) have recently reported

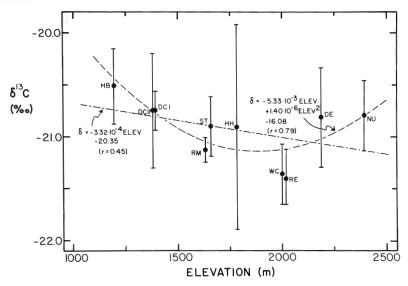


Fig. 2. Plot of δ^{13} C vs. site elevation. Vertical bars represent leaf δ^{13} C variability within each tree (± 1 std. dev. from Table II). Best-fit linear and multiple regressions with second-order polynomials are shown.

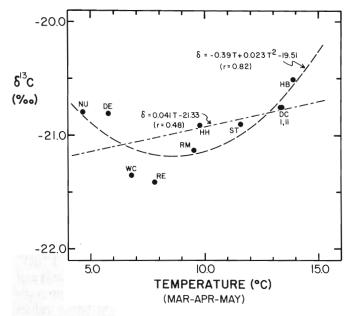


Fig. 3. Plot of $\delta^{13}C$ vs. average spring (March—April—May) temperature of the 1980 and 1981 growing seasons. Best-fit linear and second-order multiple regressions are shown. The $\delta^{13}C$ scatter would be the same as vertical bars in Fig. 2.

a model to explain the δ^{13} C-value of plants as strongly dependent on the ratio of internal (plant) to external (atmospheric) CO2 concentrations. This ratio is in turn controlled by stomatal conductance and the rate of CO₂ assimilation. In their model, increased assimilation below the photosynthetic maximum would generally favor increasing δ ¹³C-values, perhaps corresponding to the positive limb of the parabola in Fig. 3. The negative slope at lower temperatures (higher elevations) would require an increasing assimilation/ stomatal conductance ratio as temperature decreases by this model. However, at higher elevations, lower assimilation and higher conductance (i.e. lower δ^{13} C) would actually be promoted due to lower barometric pressure and higher CO2 diffusivity (Gale, 1972). An alternative hypothesis is that shorter growing seasons at higher elevations result in plants sampling a more ¹³C-enriched atmosphere due to the hemispheric, vegetational CO₂ (and preferentially ¹²CO₂) uptake during the spring and summer (Keeling, 1958). The high-elevation juniper sites do not show a similar upswing in δ^{13} C-values. However, these are two distinct genera with different physiologies and ecological ranges so that responses may differ as well.

Based on this sample size of n = 10, the linear regressions of δ vs. T and δ vs. ELEV would only provide fair predictors for climate reconstruction from pinyon leaves. There is a statistically significant fit for δ vs. polynomial elevation or temperature functions, but these present the potential for non-unique solutions for a measured pinyon leaf δ^{13} C. Expanded sampling will be required to determine whether the negatively-sloping limb of the δ vs. T-, T²-curves, apparently forced by the Defiance and Nutrioso sites, is indeed real. However, the highly significant linear relationships for δ vs. T and δ vs. ELEV for the other eight sites are encouraging. For example, a reconstruction may be possible if middens from lower elevations are selected for reconstruction such that the Late Pleistocene temperature changes they represent would correspond to the range used to derive linear regressions for n = 8. Likely candidates would be the middens from the lower elevations of the Mojave Desert (Wells and Berger, 1967), the Chihuahuan Desert (Wells, 1966), and western Arizona and the Sonoran Desert (Van Devender and King, 1971; Van Devender, 1973). Middens from some of these sites are at the lowest part of the modern pinyon range and some are in locations where pinyon presently does not grow. Again, this application assumes that the relations derived here for Pinus edulis would also apply to P. monophylla and P. cembroides as the dominant pinyon pines of the above studies. At these lower elevations, extrapolation of δ vs. T linear curves to higher temperature may also be necessary, bringing attendant uncertainties associated with operating beyond the range of values which have defined the regression. P. edulis remains are found in packrat middens from the Grand Canyon (Cole, 1981), but the high- and mid-elevation sites may be nearing the inflection in the polynomial regression equations and the correct of two solutions may not be distinguishable.

CONCLUSIONS

Stable-carbon isotopic analysis of old vegetation, such as in tree rings or the organic material preserved in fossil packrat middens, offers the potential for independent climate reconstruction. In this study, the carbon isotopic composition of cellulose in modern Pinus edulis leaves sampled from a variety of locations shows a weak linear response to elevation and climate, although the coefficients are similar to those found for juniper leaves. Several second-order polynomial relationships of δ with elevation and temperature, however, emerged statistically significant at P < 0.05. This result includes long-term temperature at the site, as well as monthly, seasonal and annual temperatures of the two most recent years corresponding to the age of the bulk of leaves carried by the trees. The better second-order polynomial fit may relate to greater δ¹³C of the highest elevation sites due to shorter growing seasons and CO₂ uptake from a ¹³C-enriched atmosphere. Relationships of δ with precipitation were not statistically significant, perhaps related to the reliability of using precipitation data from weather stations up to 30 km distant as representative of the sampling site, given the scattered, shower-type precipitation common in the southwestern U.S.A. Relationships of δ with T/R are generally poor, even though elevation increases are commonly associated with decreased temperatures and increased precipitation.

A promising result is that the δ vs. elevation and temperature relationships appear strongly linear (P < 0.001) over the warmest (lowest elevation) eight cases in this study. If the δ vs. T relationship is linear over these warmer sites, it may be possible to use pinyon remains in packrat middens for climate reconstruction when care is taken to ensure the middens are selected from those locations where temperatures would likely only fluctuate over a range representing the "warm" limb of the δ vs. T-, T^2 -parabola. Such reconstructions, however, should only be considered tentative until more sites are added to fully define the curves.

Because leaf cellulose δ^{13} C variations within pinyon trees averaged ~ 0.4 $^{0}/_{00}$ (1 std. dev.), middens containing a large quantity of pinyon needles would increase the probability of obtaining a truly representative isotopic sample of the nearby pinyon growth at the time of midden formation. Although many of the middens examined thus far are dominated by the pinyons P. monophylla and P. cembroides, evidence of natural hybridization between pinyons and isotopic similarity found among juniper species suggest that these results may be applicable to all of the pinyon species.

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REFERENCES

- Arnold, L.D., 1979. The climatic response in the partitioning of the stable isotopes of carbon in juniper trees from Arizona. Ph.D. Dissertation, University of Arizona, Tucson, Ariz.
- Battan, L.J., 1979. Fundamentals of Meteorology. Prentice-Hall, Englewood Cliffs, N.J. Cole, K.L., 1981. Late Quaternary environments in the eastern Grand Canyon: vegetational gradients over the last 25,000 years. Ph.D. Dissertation, University of Arizona, Tucson, Ariz.
- Craig, H., 1957. Isotopic standards for carbon and oxygen and correction factors for mass-spectrometric analysis of CO₂. Geochim. Cosmochim. Acta, 27: 133-149.
- Epstein, S. and Yapp, C.J., 1976. Climatic implications of the D/H ratio of hydrogen in C-H groups in tree cellulose, Earth Planet. Sci. Lett., 30: 252-261.
- Farmer, J.G., 1979. Problems in interpreting tree-ring δ¹³C records. Nature (London), 279: 229-231.
- Francey, R.J. and Farquhar, G.D., 1982. An explanation of ¹³C/¹²C variations in tree rings. Nature (London), 297: 28-31.
- Fritts, H.C., 1976. Tree Rings and Climate. Academic Press, London,
- Gale, J., 1972. Availability of carbon dioxide for photosynthesis at high altitudes: theoretical considerations. Ecology, 53: 494-497.
- Gray, J. and Thompson, P., 1976. Climatic information from ¹⁸O/¹⁶O ratios of cellulose in tree rings. Nature (London), 262: 481-482.
- Green, J.W., 1963. Wood cellulose. In: R.L. Whistler (Editor), Methods of Carbohydrate Chemistry, Vol. III. Academic Press, New York, N.Y., pp. 9-21.
- Keeling, C.D., 1958. The concentration and isotopic abundances of atmospheric carbon dioxide in rural areas. Geochim. Cosmochim. Acta, 13: 322-324.
- Lanner, R.M., 1974. Natural hybridization between Pinus edulis and Pinus monophylla in the American Southwest. Silvae Genet., 23: 108-116.
- Lanner, R.M. and Van Devender, T.R., 1974. Morphology of pinyon pine needles from fossil packrat middens in Arizona. For. Sci., 20: 207-211.
- Leavitt, S.W., 1982. Inference of past atmospheric δ^{13} C and P_{CO} , from 13 C/ 12 C measurements in tree rings. Ph.D. Dissertation, University of Arizona, Tucson, Ariz.
- Leavitt, S.W. and Long, A., 1982. Evidence for ¹³C/¹²C fractionation between tree leaves and wood. Nature (London), 298: 742-744.
- Libby, L.M. and Pandolfi, L.J., 1974. Temperature dependence of isotope ratios in tree rings. Proc. Natl. Acad. Sci., 71: 2482-2486.
- N.O.A.A. (National Oceanic and Atmospheric Administration), 1979—1981a. Climatological data, Arizona. Natl. Ocean. Atmos Adm. Environ. Data Ser., Natl. Climat. Cent., Asheville, N.C.
- N.O.A.A. (National Oceanic and Atmospheric Administration), 1979—1981b. Climatological Data, New Mexico. Natl. Ocean. Atmos. Adm., Environ. Data Serv., Natl. Climat. Cent., Asheville, N.C.
- Park, R. and Epstein, S., 1961. Metabolic fractionation of ¹³C and ¹²C in plants. Plant Physiol., 36: 133-138.
- Pearman, G.I., Francey, R.J. and Fraser, P.J., 1976. Climatic implications of stable carbon isotopes in tree rings. Nature (London), 260: 771-772.
- Sargent, C.S., 1933. Manual of the Trees of North America. Houghton-Mifflin, Boston, Mass.
- Sellers, W.D. and Hill, R.H., 1974. Arizona Climate, 1931—1972. University of Arizona Press. Tucson. Ariz.
- Urey, H.C., 1947. The thermodynamic properties of isotopic substances. J. Chem. Soc., pp. 562-581.
- Van Devender, T.R., 1973. Late Pleistocene plants and animals of the Sonoran Desert: a survey of ancient packrat middens in southwestern Arizona. Ph.D. Dissertation, University of Arizona, Tucson, Ariz.

- Van Devender, T.R. and King, J.E., 1971. Late Pleistocene vegetational records in western Arizona. J. Ariz. Acad. Sci., 6: 240-244.
- Wells, P.V., 1966. Late Pleistocene vegetation and degree of pluvial climatic change in the Chihuahuan Desert. Science, 153: 970-975.
- Wells, P.V., 1976. Macrofossil analysis of woodrat (Neotoma) middens as a key to the Quaternary vegetational history of arid America. Quat. Res., 6: 223-248.
- Wells, P.V. and Berger, R., 1967. Late Pleistocene history of coniferous woodland in the Mohave Desert. Science, 155: 1640—1647.