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Carbon Isotope Compositions of Terrestrial C3 Plants as Indicators of (Paleo)Ecology and (Paleo)Climate

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Carbon isotope compositions of terrestrial C3 plants as indicators of (paleo)ecology and (paleo)climate

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A broad compilation of modern carbon isotope compositions in all C3 plant types shows a monotonic increase in δ13C with decreasing mean annual precipitation (MAP) that differs from previous models. Corrections for temperature, altitude, or latitude are smaller than previously estimated. As corrected for altitude, latitude, and the δ13C of atmospheric CO2, these data permit refined interpretation of MAP, paleodiet, and paleoecology of ecosystems dominated by C3 plants, either prior to 7–8 million years ago (Ma), or more recently at mid- to high latitudes. Twenty-nine published paleoecological studies suggest preservational or scientific (Ma), or more recently at mid- to high latitudes. Twenty-nine published paleoecological studies suggest preservational or scientific bias toward dry ecosystems, although wet ecosystems are also represented. Unambiguous isotopic evidence for C4 plants is lacking paleontological studies suggest preservational or scientific bias toward dry ecosystems, although wet ecosystems are also represented. Unambiguous isotopic evidence for C4 plants is lacking.

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Discussion

Average C3 Composition and Isotopic Bounds on C3 δ13C. A commonly quoted "average" C3 composition (δ13C_{C3,ave}) is −26 to −27‰ (e.g., 2, 13–15) similar to or slightly higher than compilation means (Fig. 1). Such high values, however, are strongly biased toward dry ecosystems (Fig. 1A). For example, the global δ13C_{C3,ave} as estimated from Eq. 3 and distributions of plant biomass and precipitation, is approximately −28.5‰, or approximately 2‰ lower than commonly assumed. This low δ13C_{C3,ave} mainly reflects the importance of equatorial and midlatitude northern hemisphere C3 biomass, which is less well represented in the literature. The δ13C_{C3,ave} value is important for models of carbon fluxes, atmospheric CO2 compositions, and soil organic matter (e.g., 7, 15).

Paleoprecipitation Reconstructions. The regressed curve allows prediction of MAP from the average modern equivalent of diet composition (δ13C_{diet,meq}), which can be estimated from fossil tooth or collagen δ13C values and δ13C_{atm} (see SI Text). Most studies that inferred mixed C3-C4 ecosystems were omitted from consideration because obvious C4 consumption (δ13C_{diet,meq} values for individual species well above −22‰) would otherwise imply low or negative MAP. Corrections for δ13C_{atm} are key for predicting accurate C3 composition and MAP. For example, two high values for tooth enamel δ13C at approximately 15.5 Ma in East Africa (c. −8‰; 18) were interpreted as approximately 2‰ higher than the range of C3 compositions, requiring a C4 dietary component. A high δ13C_{atm} at that time (c. −5.25, or a 2.75‰ downward correction), however, implies δ13C_{diet,meq} of −24.8‰, well within the range of a pure C3 diet in dry ecosystems (Fig. 1B and Fig. 3, “−m”). Similarly large corrections apply to several other studies (19–21) and indicate wetter conditions than suggested by corrections for modern fossil fuel burning alone (c. −1.5‰ correction).

Results correlate generally with previous interpretations regarding “dry” vs. “wet” environments and with the possibility of alternative food sources. Few independent measures of MAP are available, but include estimates of 300–700 mm/yr for late Cenozoic Spain (22) vs. 500 mm/yr (Fig. 3, “v”), approximately 1,200 mm/yr for Paleocene-Eocene strata in Wyoming (23) vs. 1,000 mm/yr (Fig. 3, “k”), and 740 ± 280 mm/yr for Eocene-Oligocene strata in Nebraska (24) vs. approximately 200 mm/yr (Fig. 3, “z”). In the latter case, only a few taxa were analyzed, probably compromising estimates of average compositions. Several

![Image of diagram](https://example.com/diagram.png)

**Fig. 1. (A)** Histogram of MAP values for isotopically characterized C3 plants, showing emphasis on relatively arid ecosystems (MAP ≤ 500 mm/yr) and tropical rainforests (spikes at MAP > 2,000, 3,000 mm/yr). (B) Histogram of δ13C values of modern C3 plants. Data compiled in this study. Average δ13C is smaller by a factor of 3 to 5,000 than indicated in other studies. (C) δ13C values vs. MAP showing increasing δ13C with aridity. Data sources are listed in SI Text. White dots are average compositions of data from a large collection made in a single month during a wet year.

\[
\Delta(\text{‰, VPDB}) = 2.01 - 1.98 \times 10^{-4} \text{ Altitude (m)} + 5.88 \log_{10}(\text{MAP + 300, mm/yr}) + 0.0129 \text{ Abs (latitude,°)} \tag{2}
\]

where:

\[
\Delta = \delta^{13}\text{C}_{\text{atm}} - \delta^{13}\text{C}_{\text{leaf}} \left/ 1 + \delta^{13}\text{C}_{\text{leaf}} / 1000 \right. \tag{3}
\]

(3) Both regressions have an \(R^2\) of 0.59, a significant improvement over the functional form used by Diefendorf et al. (8; \(R^2 = 0.34\), including their altitude and latitude coefficients). These equations allow evaluation of the effects of MAP, altitude, and latitude on δ13C values or \(\Delta\), or alternatively estimation of MAP from altitude, latitude, and δ13C or \(\Delta\). Note that the altitude coefficient is smaller by a factor of 3 to 5,000 than indicated in other studies (8, 12). Latitudinal effects have not been estimated for data that simultaneously account for altitude and MAP. Uncertainties of ±0.5‰ in mean δ13C or \(\Delta\) propagate to uncertainties in MAP of as little as ±100 mm/yr at MAP = 100–500 mm/yr, to ±500 mm/yr at MAP ~ 2,000 mm/yr.
other palaeo-environments were viewed as particularly wet, either from palaeobotanical and palaeofaunal observations or because of geographic location (20, 21, 25, 26). For three of these studies, estimates of average MAP for these localities exceed 2,000 mm yr⁻¹. For data from the Eocene Arctic (21), the relatively high δ¹³C value results from the latitude correction, and a smaller correction would result in a higher estimated MAP. Only two studies have reported sufficiently low δ¹³C for any fossil species to indicate closed-canopy conditions (20, 27). Taxonomically extensive isotopic data do not directly support the conclusion that the early hominin Ardipithecus ramidus occupied a closed forest (28); the lowest inferred δ¹³Cdiet,meq is approximately −30.5‰ (for a colobine monkey), and the assumed isotopic boundary for closed-canopy forests δ¹³Cdiet,meq = −27.8‰ was unrealistically high. Overall most data from most studies appear to support low MAP, typically <800 mm yr⁻¹, below mean global MAP between 60°S and 75°N (~850 mm yr⁻¹). This probably reflects overall preservation or research bias toward drier ecosystems.

Two studies indicated average δ¹³Cdiet,meq above the range of average C3 δ¹³C. Wang et al. (29) inferred consumption of high δ¹³C C4 plants, which is consistent with the new compilation (Fig. 3, “w”) and with individual δCdiet,meq values for several taxa above ~22‰ (i.e., generally inaccessible to C3 plants). Pleistocene Irish deer data imply either dietary specialization on high δ¹³C C3 plants (Fig. 3, point “e1”; 30), or lichen consumption (31).

Several qualifications apply to estimating MAP. First, environments with C4 plants cannot be interpreted because high δ¹³Cdiet,meq may reflect C4 consumption rather than aridity, although closed-canopy occupancy or C4 consumption can be evaluated. Second, C3 plant isotope compositions within a single locality show significant variation (e.g., Fig. 1B), and different taxa prefer different microhabitats and foods. Robust estimates of MAP require averaging over multiple taxa in a single locality, just as strong correlations between global plant δ¹³C and MAP require averaging (4; this study). Some studies analyze numerous taxa (27, 32) and are well suited for estimating MAP, whereas others focus on specific ecological or climatic questions with only a few taxa or even just one taxon (19, 30, 33, 34), and MAP estimates are more tentative. Dry environments may contain wet microhabitats, e.g., along rivers or at springs, and flora may exhibit relatively low δ¹³C values either seasonally or in an unusually wet year. For example, δ¹³C of plants from the dry environments in one study (35) might be interpreted as higher MAP. In the most arid environments, plants may preferentially grow in cracks or declivities where precipitation accumulates, effectively increasing MAP (36), and other sources of precipitation, such as fog, may contribute significantly to total moisture (37, 38). These processes provide greater moisture than implied by MAP alone, and in these cases paleo-MAP estimates will be
relative to \(\delta^{13}C\) of -8‰.

![Fig. 3. Paleodepositional compositions corrected for altitude and latitude tuned for MAP; this plot permits interpretation of paleo-environments from carbon isotope compositions of fossil tooth enamel or collagen. Tooth enamel and collagen compositions are averaged across species and corrected for \(\delta^{13}C\) of atmospheric CO2, physiological fractionalations, altitude, and latitude. Most data plot at MAP < 600 mm yr\(^{-1}\), i.e., relatively dry environments, although wetter environments are also represented. \(\delta^{13}C\) values for C3 plants, with a dependence of approximately 2‰/100 ppm \((e.g., 39)\). Eocene pCO\(_2\) estimates of 1,000–1,500 ppm \((50)\), \(\delta^{13}C_{atm}\) of 5.5 to -6 (41) and fossil tooth enamel \(\delta^{13}C\) (19, 21, 25, 33) would then imply \(\delta^{13}C_{diss,\text{meq}}\) of -5 to -10‰. Such high values exceed the range of even C4 plants today \((e.g., 11, 42)\), further supporting a negligible pCO\(_2\) correction \((43)\).

Conclusions

Carbon isotope compositions show a distinct but nonlinear increase in \(\delta^{13}C\) values with decreasing MAP. A regressed expression provides a new basis for estimating MAP from carbon isotope compositions of fossil tooth enamel or collagen, after first correcting for changes to \(\delta^{13}C_{atm}\), altitude, latitude, and physiological fractionalations. Research bias toward dry ecosystems appears in analysis of paleoecologies. A downward revision in modern \(\delta^{13}C_{pe}\) for C3 plants may improve models of carbon fluxes and soil \(\delta^{13}C\) values.

Methods

Data and methods are described in further detail in SI Text. In brief, data were taken from the literature, preferring large national datasets that included date of collection, location, MAP, and mean annual temperature. In some instances, specific locations were not provided, and an estimated or average location was assigned based on descriptions in the primary source. Compositions were corrected for secular changes to the composition of atmospheric CO2 \((\delta^{13}C_{atm}\) to a common \(\delta^{13}C_{diss,\text{meq}}\) of -8.0‰ based on modern secular trends \((0.023‰/\text{yr}, 44)\). If not reported, the date of collection was assumed to be 2 yr prior to the date of publication. Nearly all climate data were taken directly from the original publications, and gaps in climate data were obtained from online and published local meteorological tabulations, or, in the few instances where local data were unavailable, from models. Most data are for whole leaves, and for nonleaf data, isotopic offsets were applied as recommended by the authors. Where no recommendation was made, offsets of -2‰ and -0.5‰ were assumed for soil organic matter and leaf litter, respectively \((15, 45)\). It may be argued that environmental parameters other than MAP correlate better with leaf \(\delta^{13}C\), such as potential evapotranspiration, water deficit, or growing season precipitation. Although such parameters may be calibrated in modern settings, they involve additional variables (e.g., seasonal temperature or precipitation) that may be difficult to constrain in paleoenvironments. Modern data show sufficiently strong correlations with MAP to allow MAP inferences.

Prior to regressions, data were averaged over all C3 plant species at an individual site. This averaging approach differs markedly from all other studies except Stewart et al. \((4)\), whose dataset was over 40 times smaller. Assignment of sites was based on how authors reported their data, i.e., if authors distinguished one set of analyses from another, they were treated as separate sites. Understory, midlevel canopy, and upper-level canopy compositions were distinguished in tropical forests, and analyses from different years were considered as different sites. The total dataset has approximately 570 sites \((95\) usable sites from ref. 8\)) and is especially dense at low MAP \((\text{Fig. 1C})\). Many different regression approaches were tested to relate carbon isotope composition to MAP. Averaging data over small MAP ranges \((e.g., <100, 100–200, 250–300 \text{ mm yr}^{-1})\) resulted in the highest correlation coefficients \((R^2 > 0.95)\), but this approach is compromised by requiring a priori corrections for altitude and latitude. Instead, the preferred and simpler approach involved regressing \(\delta^{13}C\) vs. altitude, latitude, and log\(_{10}\)(MAP + meq), where \(m_0\) is an offset that is determined iteratively and ensures that the intercept of the regression is finite. An alternative regression with \(\Delta\) as the dependent variable was also calculated. Outliers at \(\pm 3\)σ from local means were removed iteratively and represent approximately 4% of sites. Understory compositions from dense forests were also omitted \((-2% of sites)\). Data from Schulze et al. \((35)\) for MAP = 130–250 mm yr\(^{-1}\) deviate significantly from global data trends. These data represent >50% of data in that precipitation range and were collected in a single month during a wet year. To avoid bias compared to other datasets, the Schulze et al. data for <200 and for 200–250 mm yr\(^{-1}\) were averaged to separate values.

Global distributions of precipitation between 60°S and 75°N latitudes were estimated from 2.5° grids obtained from the Global Precipitation Climatology Center (GPCC) and averaged over 20 yr \((1986\) to 2005) \(\text{http://gpcp.dwd.de}\). Global plant biomass was either assumed to increase linearly with precipitation or taken from compilations of C3 plant biomass vs. latitude \((46)\), with precipitation vs. latitude for vegetated areas determined from GPCC. The global average \(\Delta\) value was then predicted by using the fitted curve to model \(\delta^{13}C\) vs. MAP, ignoring low \(\delta^{13}C\) understory, which represents a negligible fraction of total leaf biomass in the tropics \((47, 48)\). Both coefficients from different forests were also omitted \((-2% of sites)\). Note that these calculations ignore corrections for altitude but include a latitude correction of approximately -0.3‰.

For comparison to herbivore tooth enamel and collagen compositions, correction for changes to \(\delta^{13}C_{atm}\) over geologic time was made based on the \(\delta^{13}C\) of benthic foraminifera as adjusted for calcification temperature \((41)\;\text{see also ref.s}\, 25\;\text{and}\; 49\). No dependence of plant \(\delta^{13}C\) on atmospheric CO2 concentrations was considered because experimental data show no consistent resolvable relationship for pCO2 between 200 and 1,300 ppm \((43)\). The effect of this assumption is further discussed. Compositions of fossil teeth and collagen were converted to paleoecological plant composition by subtracting 14% \((42)\) and 5% \((50)\), respectively, except for three studies that focused exclusively on tooth enamel from bovids younger than 10 Ma \((30, 51, 52)\); for these a larger tooth-diet offset of 14.5‰ was used \((53)\). All paleoecological compositions were converted to \(\Delta\), and modern equivalent compositions \((\delta^{13}C_{diss,\text{meq}})\) were calculated for \(\delta^{13}C_{atm} = -8.00‰.\)

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42. Arens NC, Jahren AH, Amundson RG Can C3 plants faithfully record the carbon isotope composition of atmospheric carbon dioxide? Paleobiology 26:137–164.


