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

Matthew J. Kohn

Department of Geosciences, Boise State University, Boise, ID 83725

Edited by Mark H. Thiemens, University of California, San Diego, La Jolla, CA, and approved September 24, 2010 (received for review April 11, 2010)

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 paleontological studies suggest preservational or scientific bias toward dry ecosystems, although wet ecosystems are also represented. Unambiguous isotopic evidence for C4 plants is lacking prior to 7–8 Ma, and hominid ecosystems at 4.4 Ma show no isotopic evidence for dense forests. Consideration of global plant biomass indicates that average δ13C of C3 plants is commonly overestimated by approximately 2‰.

Results

Data. The dataset, provided in Dataset S1, encompasses all types of C3 plants, including trees, shrubs, herbs, and grasses from approximately 570 individual sites, and spans ranges of MAP, mean annual temperature (MAT), altitude, and latitude of 1 to 3,700 mm/yr, −13.5 to 28.4°C, −391 to 4,900 m, and 54.9°S to 69.5°N. This dataset is ca. six times larger than any previous analysis of C3 isotopic systematics and covers more types of C3 plants.

C3 Data Distributions. For the global C3 δ13C dataset, a histogram of corresponding MAP values (Fig. 1A) demonstrates research bias toward dry ecosystems (high δ13C) and tropical rain forests (low δ13C). Thus the histogram of δ13C values, which shows the well-known range from −20 to −37‰ (Fig. 1B), is broader than expected for global C3 biomass. Values above −23‰ are almost completely restricted to the Atacama Desert (9), the driest desert on Earth, and to Pinus in dry settings (10). Values below −31.5‰ reflect canopy effects in low-light tropical forests. The compilation from O’Leary (11; downward corrected by −0.25‰ for fossil fuel burning) and from this study average about −27.25‰ and −27.0‰, respectively, omitting understory analyses below −31.5‰.

Correlation of MAP with δ13C. Carbon isotope compositions exhibit a systematic change over the range of MAP, excepting low δ13C values associated with the understory of dense forests (Figs. 1 and 2). High δ13C values (above −25.5‰) are essentially restricted to environments with MAP < 500 mm/yr. The trend noticeably “flattens” at high MAP, indicating nearly constant isotopic discrimination in wet environments. Other attempts to quantify this correlation have resulted in widely disparate results (Fig. 2), largely because they were based on limited datasets. The results of Stewart et al. (4) and Diefendorf et al. (8) most closely match the new compilation, but the Stewart et al. model deviates from observations at MAP > 1,000 mm/yr, whereas the Diefendorf et al. model predicts unusually high δ13C values at low MAP (Fig. 2). The preferred equation for MAP as a function of δ13C is:

Δδ13C(%ε, VPDB) = −10.29 + 1.90 \times 10^{-4} \text{ Altitude (m)} + 5.61 \log_{10}(\text{MAP} + 300, \text{ mm/yr}) − 0.0124 \text{ Abs (latitude,°)}

or alternatively for Δ:

Author contributions: M.J.K. designed research, performed research, contributed new reagents/analytic tools, analyzed data, and wrote the paper.

The author declares no conflict of interest.

This article is a PNAS Direct Submission.

PLOS ECOLOGY

www.pnas.org/cgi/doi/10.1073/pnas.1004933107

PNAS | November 16, 2010 | vol. 107 | no. 46 | 19691–19695
Discussion

Average C3 Composition and Isotopic Bounds on C3 δ13C. A commonly quoted "average" C3 composition (δ13CC3,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 δ13CC3,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 δ13CC3,ave mainly reflects the importance of equatorial and midlatitude northern hemisphere C3 biomass, which is less well represented in the literature. The δ13CC3,ave value is important for models of carbon fluxes, atmospheric CO2 compositions, and soil organic matter (e.g., 7, 15–17). Seasonal changes to δ13Camm depend on C3–C4 biomass ratios and their compositions, and differences in modeled C3 biomass discrimination perturb predicted δ13C of atmospheric CO2 most strongly (16). The dataset and equations developed here could be used to test and calibrate these models. Considering that δ13C > +23‰ is restricted to MAP < 10 mm/yr, non-C3 vegetation (e.g., C4 plants, lichen, or CAM plants) or the genus Pinus in some settings, this value is recommended as a likely maximum for typical C3 plants. Likewise, δ13C < −3.15‰ is recommended as a cutoff indicating the understory of closed-canopy forests.

Paleoprecipitation Reconstructions. The regressed curve allows prediction of MAP from the average modern equivalent of diet composition (δ13Cdiet,meq), which can be estimated from fossil tooth or collagen δ13C values and δ13Camm (see SI Text). Most studies that inferred mixed C3-C4 ecosystems were omitted from consideration because obvious C4 consumption (δ13Cdiet,meq values for individual species well above −22‰) would otherwise imply low or negative MAP. Corrections for δ13Camm 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 δ13Camm at that time (c. −5.25, or a 2.75‰ downward correction), however, implies δ13Cdiet,meq of −24.8‰, well within the range of a pure C3 diet in dry ecosystems (Fig. 1B and Fig. 3, “mI”). 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
other paleoenvironments were viewed as particularly wet, either from paleobotanical and paleofaunal 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. 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 δ13C_{diet,meq} is approximately ~30‰ (for a colobine monkey), and the assumed isotopic boundary for closed-canopy forests δ13C_{diet,meq} = ~27.8‰) was unrealistically high. Overall most data from most studies appear to support low MAP, typically <800 mm/yr, below mean global MAP between 60°S and 75°N (~850 mm/yr). This probably reflects overall preservation or research bias toward drier ecosystems.

Two studies indicated average δ13C_{diet,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 δ13C_{diet,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_{diet,meq} C3 plants (Fig. 3, point “c1”; 30), or lichen consumption (31).

Several qualifications apply to estimating MAP. First, environments with C4 plants cannot be interpreted because high δ13C_{diet,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 thus 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
Carbon isotope compositions show a distinct but nonlinear variation with latitude and altitude. A downward revision in δ13C values for C3 plants may improve interpretations of 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 then 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 (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 mm/yr, etc.) resulted in the highest correlation coefficients (r, 0.95), but this approach is compromised by requiring prior corrections for altitude and latitude. Instead, the preferred and simpler approach involved regressing δ13C vs. altitude, latitude, and log10(MAP + m0), where m0 is an offset that is determined iteratively and ensures that the intercept of the regression is finite. An alternative regression with Δ as the dependent variable was also calculated. Outliers at ±3σ from local means were removed iteratively and represent approximately 4% of sites. Underscores indicate datasets that were omitted (−2% of sites). Data from Schulze et al. (35) for MAP = 130–250 mm/yr 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 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) (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 C3 value was then predicted by using the fitted curve to model δ13C vs. MAP, ignoring low δ13C underruns, which represents a negligible fraction of total leaf biomass in the tropics (47, 48). Both coefficients from dense forests were also omitted (−2% of sites). Data from Schulze et al. (35) for MAP = 130–250 mm/yr 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 were averaged to separate values.

Carbon isotope compositions show a distinct but nonlinear increase in δ13C 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 altitude and latitude, latitude, and physiological fractionations, altitude, latitude, and log10(MAP + m0), where m0 is an offset that is determined iteratively and ensures that the intercept of the regression is finite. An alternative regression with Δ as the dependent variable was also calculated. Outliers at ±3σ from local means were removed iteratively and represent approximately 4% of sites. Underscores indicate datasets that were omitted (−2% of sites). Data from Schulze et al. (35) for MAP = 130–250 mm/yr 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 were averaged to separate values.

Comparison to herbivore tooth enamel and collagen compositions, correction for changes to δ13C in fossil tooth enamel from bovids younger than 10 Ma

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 (δ13C CO2) to a common δ13C CO2 of −8.0‰ based on modern secular trends (0.02‰/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 any gaps in climate data were obtained from online and published local meteorological tabulations, or, if no recommendations were 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 δ13C, such as potential evapotranspiration, water deficit, or growing season precipitation. Although such parameters may be calculated 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 then 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 (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 mm/yr, etc.) resulted in the highest correlation coefficients (r, 0.95), but this approach is compromised by requiring prior corrections for altitude and latitude. Instead, the preferred and simpler approach involved regressing δ13C vs. altitude, latitude, and log10(MAP + m0), where m0 is an offset that is determined iteratively and ensures that the intercept of the regression is finite. An alternative regression with Δ as the dependent variable was also calculated. Outliers at ±3σ from local means were removed iteratively and represent approximately 4% of sites. Underscores indicate datasets that were omitted (−2% of sites). Data from Schulze et al. (35) for MAP = 130–250 mm/yr 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 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) (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 C3 value was then predicted by using the fitted curve to model δ13C vs. MAP, ignoring low δ13C underruns, which represents a negligible fraction of total leaf biomass in the tropics (47, 48). Both coefficients from dense forests were also omitted (−2% of sites). Data from Schulze et al. (35) for MAP = 130–250 mm/yr 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 were averaged to separate values.