Carbon isotope discrimination in C3 land plants is independent of natural variations in $p_{\text{CO}_2}$

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Abstract

The $\delta^{13}C$ of terrestrial C3 plant tissues and soil organic matter is important for understanding the carbon cycle, inferring past climatic and ecological conditions, and predicting responses of vegetation to future climate change. Plant $\delta^{13}C$ depends on the $\delta^{13}C$ of atmospheric $\text{CO}_2$ and mean annual precipitation (MAP), but an unresolved decades-long debate centres on whether terrestrial C3 plant $\delta^{13}C$ responds to $p_{\text{CO}_2}$. In this study, the $p_{\text{CO}_2}$-dependence of C3 land plant $\delta^{13}C$ was tested using isotopic records from low- and high-$p_{\text{CO}_2}$ times spanning historical through Eocene data. Historical data do not resolve a clear $p_{\text{CO}_2}$-effect ($-1.2 \pm 1.0$ to $0.6 \pm 1.0$ ‰/100 ppmv). Organic carbon records across the Pleistocene-Holocene transition are too affected by changes in MAP, carbon sources, and potential differential degradation to quantify $p_{\text{CO}_2}$-effects directly, but limits of $-0.03 \pm 0.13$ and $-0.03 \pm 0.24$ ‰/100 ppmv between 200 and 700 ppmv. Combining all constraints yields a preferred value of $0.0 \pm 0.3$ ‰/100 ppmv (2 s.e.). Recent models of $p_{\text{CO}_2}$-dependence imply unrealistic MAP for Cenozoic records.

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Introduction

C3 plants (trees, shrubs, herbs and cool-climate grasses) constitute c. 95 % of terrestrial plant biomass (Still et al., 2003), so understanding C3 plant response to changes in the partial pressure of atmospheric $\text{CO}_2$ ($p_{\text{CO}_2}$) is key for modelling Earth’s carbon cycle (e.g., Cao et al., 2010; Shevliakova et al., 2013). Carbon isotope compositions ($\delta^{13}C$) of C3 plants are a principal means of inferring water use efficiency (Farquhar et al., 1989), which is important to models of future C3 biomass, and have been proposed to allow estimation of mean annual precipitation (MAP) in the geologic past (Kohn, 2010). Plant $\delta^{13}C$ depends on the $\delta^{13}C$ of atmospheric $\text{CO}_2$ (Freyer and Wiesberg, 1973), but an unresolved decades-long debate centres on whether terrestrial C3 plant $\delta^{13}C$ responds to $p_{\text{CO}_2}$. Many studies have argued that increasing $p_{\text{CO}_2}$ increases carbon isotope discrimination (e.g., Feng and Epstein, 1995; Schubert and Jahren, 2012); others have argued for no $p_{\text{CO}_2}$-effect (e.g., Arens et al., 2000; Saurer et al., 2004; Frank et al., 2015). Recent work (Schubert and Jahren, 2012) integrated natural and experimental data to infer that C3 plant $\delta^{13}C$ depends hyperbolically on $p_{\text{CO}_2}$ (Fig. 1a) and that changes to carbon isotope compositions in leaves and sediment organic matter over the last 30 ka parallel and predict $p_{\text{CO}_2}$ (Schubert and Jahren, 2015). In this study, carbon isotope records ranging from the last several decades through the early Cenozoic are critically evaluated to identify which records indeed provide quantitative constraints on $p_{\text{CO}_2}$-dependencies, and to provide a robust estimate of that dependence.

Multiple factors besides atmospheric $\text{CO}_2$ can affect C3 plant $\delta^{13}C$, including MAP, ontogeny, light levels, genetics and fertilisation (e.g., through atmospheric nitrogen deposition; Farquhar et al., 1989; Stewart et al., 1995; McCauley and Loader, 2004; Diefendorf et al., 2010; Kohn, 2010; Fig. 1b). Other physical factors, including latitude and altitude, have a minor impact on C3 plant $\delta^{13}C$ (Diefendorf et al., 2010; Kohn, 2010), but high variability both within and among trees must reflect individual responses to other, less easily identified, environmental or physiological factors (McCauley and Loader, 2004). Thus, records of natural $\delta^{13}C$ through time, e.g., from tree rings, sediment records, etc. must account for changes to MAP and other environmental changes, most recently from anthropogenic activities, before any $p_{\text{CO}_2}$-dependence can be quantified.

“Modern” conditions anchor many quantitative estimates of palaeoclimate, e.g., $\delta^{13}C$-based estimates of MAP are normalised to AD 2000 data ($p_{\text{CO}_2} = 370$ ppmv, $\delta^{13}C_{\text{CO}_2} = -8.0$ ‰). If C3 plant $\delta^{13}C$ does depend on $p_{\text{CO}_2}$, $\delta^{13}C$ values from periods of low $p_{\text{CO}_2}$ (e.g., late Pleistocene) are anomalously high, and must be downward corrected for any calculations ($\Delta^{13}C$ increases); conversely, $\delta^{13}C$ values from periods of high $p_{\text{CO}_2}$ (e.g., Eocene) must be upward corrected ($\Delta^{13}C$ decreases; Fig. 1a). In comparison with the modern dependence of C3 plant $\delta^{13}C$ on MAP (Fig. 1b), uncorrected estimates of MAP must be too dry for the Pleistocene and too wet for the Eocene. Fortunately, estimates of MAP for many times are known from independent proxies (e.g., floral analysis) and general circulation models, and $p_{\text{CO}_2}$ is known either from measurements in ice cores or from geochemical proxies. Thus, $p_{\text{CO}_2}$-effects on C3 $\delta^{13}C$ values can now be evaluated from ancient sediments and fossils, albeit with careful consideration of sometimes substantial errors in proxy estimates of $p_{\text{CO}_2}$ and MAP (see Supplementary Information).

This study evaluates $p_{\text{CO}_2}$-dependencies in the context of two endmember models – a null hypothesis of no dependence vs. a hyperbolic dependence that integrates numerous other studies (Schubert and Jahren, 2012). Ultimately four datasets are considered: modern leaves (1970 through 2007; Kohn, 2010), tropical rainforest tree rings (least susceptible to changes in MAP; Fig. 2a;
van der Sleen et al., 2015), sediment organic matter (SOM) from three representative studies of the Pleistocene–Holocene transition (Fig. 2b,c; Hatté et al., 1998; Sinninghe Damsté et al., 2011; Barker et al., 2013), and herbivore collagen and tooth enamel for especially low-pCO2 (<250 ppmv) and high-pCO2 (>500 ppmv) periods of the geologic past (Fig. 3; Supplementary Information). The overall intent of these comparisons is to correct first for factors that we know influence δ13C (especially MAP, carbon sources) and ascribe any residual effect to pCO2.

The combined isotopic effects of changes to MAP and organic C content (c. 2 ‰) correlate with changes in δ13C independent of pCO2, H1, H3 = Heinrich events 1 and 3; DO2 = Dansgaard-Oeschger event 2; B-A = Bolling-Allered; YD = Younger Dryas. (c) An abrupt shift at c. 15.8 ka could reflect an abrupt threshold response of C4 biomass in the local ecosystem or variable contributions of diatoms to SOM (Fig. S-1).

Modern/Historical records. Linear regression of modern leaf Δ13C (Kohn, 2010), treating pCO2 as an independent variable (Table S-1), results in a pCO2 coefficient for Δ13C of -1.2 ± 1.0 ‰/100 ppmv (2σ). These data do not generally support a positive pCO2-dependence for Δ13C but are quite imprecise. Historical cellulose data from tropical rainforests (Fig. 2a; van der Sleen et al., 2015; Table S-1) suggest a positive slope with respect to pCO2 (0.62 ± 1.05 ‰/100 ppmv, 2 s.e.; Supplementary Information), but are also strongly influenced by an up-tick in Δ13C between 2000 and 2010 AD (Fig. 2a; Toona, Chukrasia, which might reflect other factors. For example, 10-20 yr, 1-2 ‰ oscillations at all sites (e.g., Melia, Afzelia, Fig. 2a) probably reflect susceptibility to environmental factors besides precipitation and pCO2, and such an effect might explain specific slopes. Tree ring isotope data across Europe, corrected for climate variables, suggest a negative pCO2-dependence (-0.55 ± 0.67 ‰/100 ppmv; data from Frank et al., 2015).

Overall, modern/historical data are too imprecise and idiosyncratic to either require or preclude a pCO2-effect.

Pleistocene-Holocene sediment records. Mid-latitude sediments from the Rhine River valley in France and Germany present one of the better cases for a pCO2-effect: a gradual 2 % increase in Δ13C between 20 and 10 ka parallels pCO2 (Fig. 2b). A near doubling of MAP across the Pleistocene–Holocene transition (Bartlein et al., 2011; Alder and Hostetler, 2015), however, predicts c. 1.25 % of the observed ~2 % increase (Fig. 2b), so any pCO2-effect must be ≤-1.0 %/100 ppmv. In addition, organic C content in these records increases by a factor of 9 across the Pleistocene-Holocene boundary (Hatté et al., 1998). Numerous studies show a linear correlation between Δ13C and the logarithm of soil organic C content, (e.g., Poage and Feng, 2004) with a minimum slope of c. 0.7 % per log10[OC] (Balesdent et al., 1993). If the striking increase in organic C content in the European records represents differential degradation, Δ13C should increase by at least c. 0.65 %. The combined isotopic effects of changes to MAP and organic C content (c. 2 %) can explain the data without resort to any pCO2-effects.

Because plants track the δ13C of atmospheric CO2, which has changed through time, data are presented in terms of isotope discrimination (Δ13C):

\[
\Delta^{13}C(CO_2) - \delta^{13}C = \frac{\delta^{13}C_{CO_2} - \delta^{13}C_i}{1 + \delta^{13}C_i/1000}
\]

Eq. 1

By correcting for secular changes to atmospheric δ13C from recent direct measurements, ice core measurements, and foraminiferal data (Supplementary Information), Equation 1 allows comparisons of data from different times.

Supplementary Information explains materials and methods, including error propagation.

Results and Discussion
Alternatively, an estimate of ecosystem impacts on $\Delta^{13}C$ can be made for the French record in reference to the Dansgaard-Oeschger 2 (DO2) and the Belling-Allerød (B-A) warming events, which caused brief 2-2.5‰ spikes in $\Delta^{13}C$ without obvious changes to $p_{CO_2}$. Subtracting this ($p_{CO_2}$-independent) effect from the Pleistocene-Holocene transition yields a residual $p_{CO_2}$-effect of ~0‰/100 ppmv.

A large, abrupt increase in $\Delta^{13}C$ in low-latitude Kenyan lake data (Fig. 2c) likely reflects decreasing abundances of C4 vegetation (Sinninghe Damsté et al., 2011), rather than increasing $p_{CO_2}$. Increasing $p_{CO_2}$ tends to destabilize C4 plants (Ehleringer et al., 1997), so an abrupt decrease in C4 abundance (Prentice et al., 2011) during the Pleistocene-Holocene rise in $p_{CO_2}$ logically explains the observations. Changes to lake diatom abundance and preservation may also play a role (Fig. S-1).

Overall, for the Pleistocene-Holocene transition, widespread increases in MAP across much of Earth (Bartlein et al., 2011) and concomitant changes to floral ecosystems (CLIMAP, 1976; Prentice et al., 2011), especially changes in C3/C4 abundances at low latitudes, generally predict an increase in $\Delta^{13}C$, compromising any quantitative retrieval or validation of $p_{CO_2}$-dependencies using these records. At present, the best constrained data imply a maximum value of ≤1.0‰/100 ppmv (MAP-correction alone) or possibly ~0‰/100 ppmv (DO-event analog, France; MAP plus organic C degradation) between 180 and 270 ppmv.

Fossil herbivore records. Pleistocene and Tertiary herbivore data place the most stringent constraints on a $p_{CO_2}$-dependence: -0.03 ± 0.13‰/100 ppmv between 180 and 370 ppmv, and -0.03 ± 0.24‰/100 ppmv between 370 and 715 ppmv. The $p_{CO_2}$-dependent model strongly overestimates $\Delta^{13}C$ for the Pleistocene and underestimates $\Delta^{13}C$ for the Tertiary (Fig. S-2). Similarly, isotopically-based estimates of MAP without correction of $p_{CO_2}$ reproduce independent estimates within uncertainties (Fig. S-3), whereas estimates from the $p_{CO_2}$-dependent model strongly overestimate MAP for Pleistocene data, and strongly underestimate MAP for Tertiary data (Fig. 3d). Uncertainties in estimates of MAP, $p_{CO_2}$, or the $\delta^{13}C$ of atmospheric $CO_2$ do not likely bias interpretation of Pleistocene data because $p_{CO_2}$ and $\delta^{13}C$ are directly determined from ice cores, and MAP is based on large numbers of floral observations coupled to GCM’s with especially well constrained boundary conditions. Large errors for Tertiary $p_{CO_2}$ cause the $p_{CO_2}$-dependent model errors to overlap independent estimates of $\Delta^{13}C$ and MAP. The point of overlap, however, occurs only at quasi-modern $p_{CO_2}$ levels, which is generally inconsistent with Eocene and middle Miocene proxies (Beerling and Royer, 2011). Note that a systematic error for Pleistocene calculations operates in the opposite direction for Tertiary data, so the internal consistency of both sets of calculations (the same $p_{CO_2}$ coefficient) suggests that systematic errors are small.

Considering calculated MAP throughout the Cenozoic, a U-shaped distribution (Fig. 4a) highlights unusually dry conditions [low $\Delta^{13}C$($CO_2$)-plant], high $\delta^{13}C$(plant)] during the late Eocene and early/middle Oligocene. Aggregating Cenozoic MAP estimates, the $p_{CO_2}$-independent model exhibits a predominance of values between 0 and 1.0 m/yr (>80%; Fig. 4b) with a distribution that mimics modern Earth’s area distribution of MAP (dashed line, Fig. 4b). In contrast, the $p_{CO_2}$-dependent model implies widespread rainforests during the Pleistocene (Fig. 4a), which contrasts starkly with global climate and vegetation syntheses that have long indicated greater aridity across much of the globe (e.g., CLIMAP, 1976; Prentice et al., 2011), especially in Europe where many of the Pleistocene fossils were collected. The $p_{CO_2}$-dependent model also implies negative MAP during the Eocene-Old Oligocene (Fig. 4a). A histogram of $p_{CO_2}$-dependent predictions (Fig. 4e) yields unrealistically abundant hyperarid deserts (MAP < 0) and rainforests (>2.5 m/yr).

Figure 3 Cenozoic herbivore data. (a-d) Calculated vs. measured $\Delta^{13}C$, and calculated vs. independently estimated MAP, showing good correspondence with $p_{CO_2}$-independent model. Representative error bars (2σ) reflect propagated uncertainties in isotope compositions and tissue-diet fractionations, the dependence of $\delta^{13}C$ on MAP, and proxy estimates of MAP and $p_{CO_2}$ (Table S-2).

Figure 4 (a) Estimates of MAP for the Cenozoic based on fossil herbivore isotope compositions show a U-shaped distribution, $p_{CO_2}$-corrections imply widespread rainforests in the Pleistocene and hyper-deserts in mid-Cenozoic. $p_{CO_2}$ curve simplified from Beerling and Royer (2011). (b-c) Histograms of Cenozoic MAP estimates show a better match between the global distribution (by area) of MAP (Kohn, 2010) vs. MAP estimated using the $p_{CO_2}$-independent model. The $p_{CO_2}$-dependent model predicts unusually high proportions of deserts (MAP < 0.1 m/yr) and rainforests (MAP > 2.5 m/yr) in the geologic record.
As discussed elsewhere (Schubert and Jahren, 2012), studies investigating $pCO_2$-effects rarely account for other factors that may influence δ$^13$C, making cross-study comparisons difficult. One recent study that did attempt to account for such factors (Frank et al., 2015) concluded that $pCO_2$ has no effect on tree δ$^13$C (-0.55 ± 0.67 ‰/100 ppmv; Supplementary Information), in good agreement with results here. Although susceptible to individual idiosyncrasies, cellulose records from individual trees from the Borneo rainforest (Lauer et al., 2011; MAP c. 3 m/yr) also imply a $pCO_2$-effect indistinguishable from zero (0.0 ± 0.2 ‰/100 ppmv; Supplementary Information). Early Eocene isotopees of angiosperms further support $pCO_2$-independence (Diefendorf et al., 2015). At present, the most discrepant study (Schubert and Jahren, 2012) represents short-term experiments on two orbs (Arabidopsis and radish). As discussed recently (Diefendorf et al., 2015; Voelker et al., 2015), plants may exhibit short-term phenotypic and isotopic changes in response to abrupt changes to $pCO_2$, but on evolutionary timescales (decades to centuries) may evolve towards an optimal physiology whose isotopic fractionation is $pCO_2$-independent. Short-term experiments might have relevance for modern rapid changes to $pCO_2$, but not for ancient isotope records.

Overall, natural data either do not resolve a $pCO_2$-dependence or indicate an effect far smaller than recent models. On geologic timescales, a best estimate for a $pCO_2$-dependence between c. 200 and c. 700 ppmv averages -0.04 ± 0.02 ‰/100 ppmv (2 s.e.; Table S-3), i.e. $pCO_2$-dependencies are negligible. Because no correction for $pCO_2$ is needed, this result vastly simplifies interpretations of past climates and carbon use by C3 land plants.

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**Additional Information**

Supplementary information accompanies this letter at www.geochemicalperspectivesletters.org/article1604

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**References**


