

Carbon isotope discrimination in C3 land plants is independent of natural variations in p_{CO_2}

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Abstract

The $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ depends on the $\delta^{13}\text{C}$ of atmospheric CO_2 and mean annual precipitation (MAP), but an unresolved decades-long debate centres on whether terrestrial C3 plant $\delta^{13}\text{C}$ responds to p_{CO_2} . In this study, the p_{CO_2} -dependence of C3 land plant $\delta^{13}\text{C}$ was tested using isotopic records from low- and high- p_{CO_2} times spanning historical through Eocene data. Historical data do not resolve a clear p_{CO_2} -effect (-1.2 ± 1.0 to 0.6 ± 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_{CO_2} -effects directly, but limits of ≤ 1.0 ‰/100 ppmv or ~ 0 ‰/100 ppmv are permissible. Fossil collagen and tooth enamel data constrain p_{CO_2} -effects most tightly to -0.03 ± 0.13 and -0.03 ± 0.24 ‰/100 ppmv between 200 and 700 ppmv. Combining all constraints yields a preferred value of 0.0 ± 0.3 ‰/100 ppmv (2 s.e.). Recent models of p_{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 CO_2 (p_{CO_2}) is key for modelling Earth's carbon cycle (*e.g.*, Cao *et al.*, 2010; Shevliakova *et al.*, 2013). Carbon isotope compositions ($\delta^{13}\text{C}$) 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 $\delta^{13}\text{C}$ depends on the $\delta^{13}\text{C}$ of

atmospheric CO_2 (Freyer and Wiesberg, 1973), but an unresolved decades-long debate centres on whether terrestrial C3 plant $\delta^{13}\text{C}$ responds to p_{CO_2} . Many studies have argued that increasing p_{CO_2} increases carbon isotope discrimination (*e.g.*, Feng and Epstein, 1995; Schubert and Jahren, 2012); others have argued for no p_{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 $\delta^{13}\text{C}$ depends hyperbolically on p_{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_{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_{CO_2} -dependencies, and to provide a robust estimate of that dependence.

Multiple factors besides atmospheric CO_2 can affect C3 plant $\delta^{13}\text{C}$, including MAP, ontogeny, light levels, genetics and fertilisation (*e.g.*, through atmospheric nitrogen deposition; Farquhar *et al.*, 1989; Stewart *et al.*, 1995; McCarroll 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 $\delta^{13}\text{C}$ (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 (McCarroll and Loader, 2004). Thus, records of natural $\delta^{13}\text{C}$ 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_{CO_2} -dependence can be quantified.

“Modern” conditions anchor many quantitative estimates of palaeoclimate, *e.g.*, $\delta^{13}\text{C}$ -based estimates of MAP are normalised to AD 2000 data ($p_{\text{CO}_2} = 370$ ppmv, $\delta^{13}\text{C}_{\text{CO}_2} = -8.0$ ‰). If C3 plant $\delta^{13}\text{C}$ does depend on p_{CO_2} , $\delta^{13}\text{C}$ values from periods of low p_{CO_2} (*e.g.*, late Pleistocene) are anomalously high, and must be downward corrected for any calculations ($\Delta^{13}\text{C}$ increases); conversely $\delta^{13}\text{C}$ values from periods of high p_{CO_2} (*e.g.*, Eocene) must be upward corrected ($\Delta^{13}\text{C}$ decreases; Fig. 1a). In comparison with the modern dependence of C3 plant $\delta^{13}\text{C}$ 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_{CO_2} is known either from measurements in ice cores or from geochemical proxies. Thus, p_{CO_2} -effects on C3 $\delta^{13}\text{C}$ values can now be evaluated from ancient sediments and fossils, albeit with careful consideration of sometimes substantial errors in proxy estimates of p_{CO_2} and MAP (see Supplementary Information).

This study evaluates p_{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;

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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- p_{CO_2} (<250 ppmv) and high- p_{CO_2} (>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 $\delta^{13}C$ (especially MAP, carbon sources) and ascribe any residual effect to p_{CO_2} .

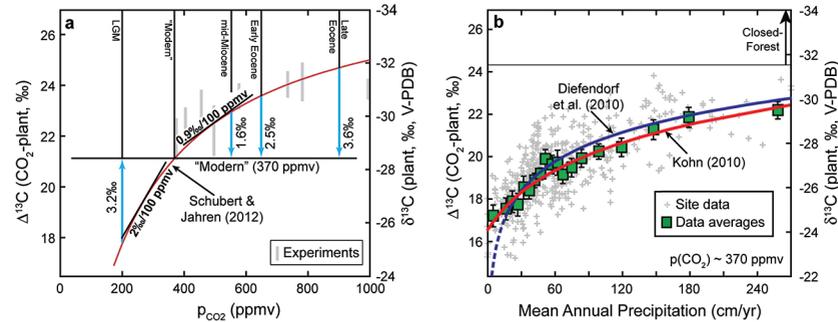


Figure 1 Proposed models for factors that influence $\delta^{13}C$ of C3 plants. (a) p_{CO_2} . Differences are illustrated between geological conditions vs. AD 2000 ($p_{CO_2} = 370$ ppmv, average $\delta^{13}C = -28.5$ for C3 biomass). LGM = Last Glacial Maximum. Note inverse relationship between $\delta^{13}C$ and $\Delta^{13}C$. Experiments are for above-ground biomass (Schubert and Jahren, 2012), shifted to fit preferred curve. (b) Mean annual precipitation (data and data averages from Kohn, 2010).

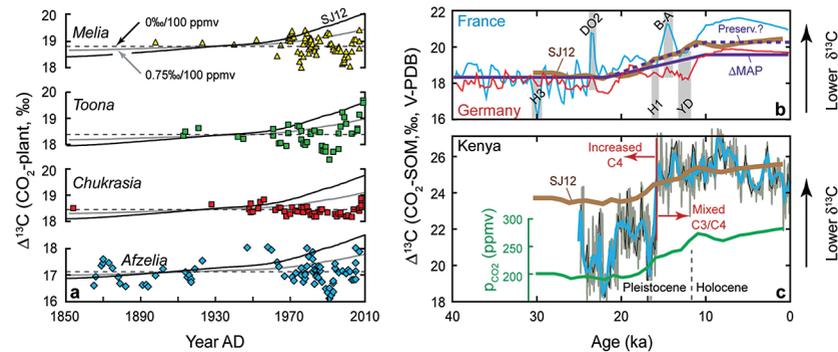


Figure 2 Tree ring and Pleistocene-Holocene records. (a) Tropical data from Thailand show near-zero p_{CO_2} effect. Models are anchored on oldest 5-10 analyses (where any p_{CO_2} effects should be smallest). SJ12 = model of Schubert and Jahren (2012). (b) Correction for changes in mean annual precipitation ("ΔMAP"), and possibly for organic matter preservation ("preserv.") reproduces records independent of a direct p_{CO_2} -dependence. Brief climatic events also correlate with changes in $\Delta^{13}C$ independent of p_{CO_2} . H1, H3 = Heinrich events 1 and 3; DO2 = Dansgaard-Oeschger event 2; B-A = Bølling-Allerød; 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).

Because plants track the $\delta^{13}C$ of atmospheric CO₂, which has changed through time, data are presented in terms of isotope discrimination ($\Delta^{13}C$):

$$\Delta^{13}C(\text{CO}_2 - i) = \frac{\delta^{13}C_{\text{CO}_2} - \delta^{13}C_i}{1 + \delta^{13}C_i/1000} \quad \text{Eq. 1}$$

By correcting for secular changes to atmospheric $\delta^{13}C$ 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

Modern/Historical records. Linear regression of modern leaf $\Delta^{13}C$ (Kohn, 2010), treating p_{CO_2} as an independent variable (Table S-1), results in a p_{CO_2} coefficient for $\Delta^{13}C$ of -1.2 ± 1.0 ‰/100 ppmv (2σ). These data do not generally support a positive p_{CO_2} -dependence for $\Delta^{13}C$ 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 p_{CO_2} (0.62 ± 1.05 ‰/100 ppmv, 2 s.e.; Supplementary Information), but are also strongly influenced by an up-tick in $\Delta^{13}C$ between 2000 and 2010 AD (Fig. 2a; *Toona*, *Chukrasia*), which might reflect other factors. For example, 10-20 yr, 1-2 ‰ oscillations $\delta^{13}C$ at all sites (*e.g.*, *Melia*, *Azelia*, Fig. 2a) probably reflect susceptibility to environmental factors besides precipitation and p_{CO_2} , and such an effect might explain specific slopes. Tree ring isotope data across Europe, corrected for climate variables, suggest a negative p_{CO_2} -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 p_{CO_2} -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 p_{CO_2} -effect: a gradual 2 ‰ increase in $\Delta^{13}C$ between 20 and 10 ka parallels p_{CO_2} (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 p_{CO_2} -effect must be $\leq \sim 1.0$ ‰/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 $\Delta^{13}C$ and the logarithm of soil organic C content, (*e.g.*, Poage and Feng, 2004) with a minimum slope of c. 0.7 ‰ per $\log_{10}[C]$ (Balesdent *et al.*, 1993). If the striking increase in organic C content in the European records represents differential degradation, $\Delta^{13}C$ 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 p_{CO_2} -effects.



Alternatively, an estimate of ecosystem impacts on $\Delta^{13}\text{C}$ can be made for the French record in reference to the Dansgaard-Oeschger 2 (DO2) and the Bølling-Allerød (B-A) warming events, which caused brief 2-2.5 ‰ spikes in $\Delta^{13}\text{C}$ 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 $\Delta^{13}\text{C}$ 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 destabilise 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 $\Delta^{13}\text{C}$, 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 ~ 0.0 ‰/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 $\Delta^{13}\text{C}$ for the Pleistocene and underestimates $\Delta^{13}\text{C}$ for the Tertiary (Fig. 3a,b). Similarly, isotopically-based estimates of MAP without correction of p_{CO_2} reproduce independent estimates within uncertainties (Fig. 3c), whereas estimates from the p_{CO_2} -dependent model strongly overestimate MAP for Pleistocene data, and strongly

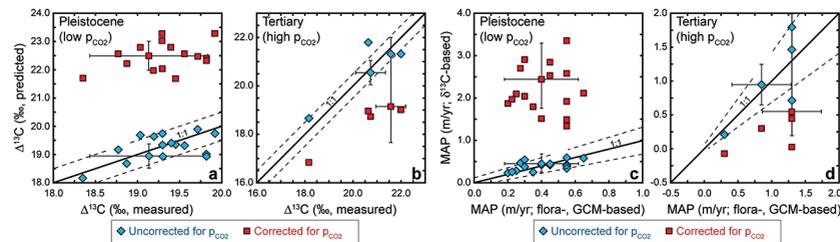


Figure 3 Cenozoic herbivore data. (a-d) Calculated vs. measured $\Delta^{13}\text{C}$, and calculated vs. independently estimated MAP, showing good correspondence with p_{CO_2} -independent model. Representative error bars (2σ) reflect propagated uncertainties in isotope compositions and tissue-diet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

underestimate MAP for Tertiary data (Fig. 3d). Uncertainties in estimates of MAP, p_{CO_2} , or the $\delta^{13}\text{C}$ of atmospheric CO_2 do not likely bias interpretation of Pleistocene data because p_{CO_2} and $\delta^{13}\text{C}$ 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 $\Delta^{13}\text{C}$ 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 $\Delta^{13}\text{C}$ (CO_2 -plant), high $\delta^{13}\text{C}$ (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 and Oligocene (Fig. 4a). A histogram of p_{CO_2} -dependent predictions (Fig. 4c) yields unrealistically abundant hyperarid deserts (MAP < 0) and rainforests (>2.5 m/yr).

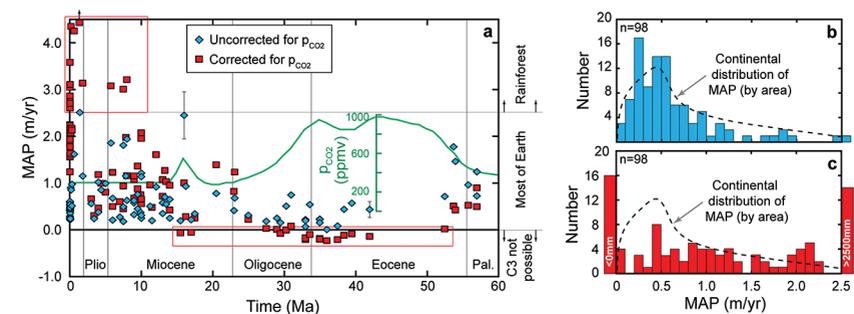


Figure 4 (a) Estimates of MAP for the Cenozoic based on fossil herbivore isotope compositions show a U-shaped distribution. p_{CO_2} -corrections imply widespread rainforests in the Pleistocene, and hyper-deserts in mid-Cenozoic. p_{CO_2} curve simplified from Beerling and Royer (2011). (b-c) Histograms 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.



Perspective and Recommendations

As discussed elsewhere (Schubert and Jahren, 2012), studies investigating p_{CO_2} -effects rarely account for other factors that may influence $\delta^{13}\text{C}$, making cross-study comparisons difficult. One recent study that did attempt to account for such factors (Frank *et al.*, 2015) concluded that p_{CO_2} has no effect on tree $\delta^{13}\text{C}$ (-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 (Loader *et al.*, 2011; MAP c. 3 m/yr) also imply a p_{CO_2} -effect indistinguishable from zero (0.0 ± 0.2 ‰/100 ppmv; Supplementary Information). Early Eocene isotopes of angiosperms further support p_{CO_2} -independence (Diefendorf *et al.*, 2015). At present, the most discrepant study (Schubert and Jahren, 2012) represents short-term experiments on two forbs (*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 p_{CO_2} , but on evolutionary timescales (decades to centuries) may evolve towards an optimal physiology whose isotopic fractionation is p_{CO_2} -independent. Short-term experiments might have relevance for modern rapid changes to p_{CO_2} , but not for ancient isotope records.

Overall, natural data either do not resolve a p_{CO_2} -dependence or indicate an effect far smaller than recent models. On geologic timescales, a best estimate for a p_{CO_2} -dependence between c. 200 and c. 700 ppmv averages -0.04 ± 0.26 ‰/100 ppmv (2 s.e.; Table S-3), *i.e.* p_{CO_2} -dependencies are negligible. Because no correction for p_{CO_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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