Paleoceanography and Paleoclimatology

RESEARCH ARTICLE
10.1029/2021PA004408

Key Points:

- Some CO₂ proxy estimates from the Late Cretaceous-early Paleocene are low (<400 ppm), seemingly at odds with elevated sea surface temperature.
- We apply a leaf gas-exchange model to Platanites leaves of four early Paleocene localities from the San Juan Basin, New Mexico.
- Our CO₂ estimates, between ~660 and 1,140 ppm, are congruent with more recent estimates from several other proxy methods.

Supporting Information:
Supporting Information may be found in the online version of this article.

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Citation:
Milligan, J. N., Flynn, A. G., Kowalczky, J. B., Barclay, R. S., Geng, J., Royer, D. L., & Peppe, D. J. (2022). Moderate to Elevated Atmospheric CO₂ During the Early Paleocene Recorded by Platanites Leaves of the San Juan Basin, New Mexico. Paleocene localities from the San Juan Basin, New Mexico (65.66–64.59 Ma). We first calibrate the model on two modern Platanus species, Platanus occidentalis and P. × acerifolia, where we find the leaf gas-exchange model accurately predicts present-day CO₂, with a mean error rate between 5% and 14%. Applying the model to the early Paleocene, we find CO₂ varies between ~660 and 1,140 ppm. These estimates are consistent with more recent CO₂ estimates from boron, leaf gas-exchange, liverwort, and paleosol proxies that all suggest moderate to elevated levels of CO₂ during the Late Cretaceous and early Paleocene. These levels of atmospheric CO₂ are more in keeping with the elevated temperature during this period.

Plain Language Summary
Throughout Earth history, temperature and atmospheric CO₂ usually track each other. During the Late Cretaceous to early Paleocene (~70–60 Ma), global mean surface temperature was ~8–12.5°C higher than today. However, CO₂ estimates are variable, with some estimates equal to or less than present-day CO₂ (~415 ppm) and at odds with the estimated global temperatures. Here we use a proxy based on leaf gas-exchange principles (i.e., photosynthesis) to estimate early Paleocene CO₂ from fossil Platanites leaves (family Platanaceae) of four early Paleocene localities from the San Juan Basin, New Mexico (65.66–64.59 Ma). We first test and calibrate the proxy on two modern Platanus species, Platanus occidentalis and P. × acerifolia. We find the leaf gas-exchange model accurately predicts present-day CO₂. Applying the leaf gas-exchange model to the early Paleocene, we find CO₂ varies between ~660 and 1,140 ppm. Our results are consistent with other proxies, such as boron, paleosol, leaf gas-exchange, and liverwort proxies, that all suggest moderate to elevated levels of CO₂ during the Late Cretaceous and early Paleocene. These levels of atmospheric CO₂ are more in line with elevated temperature during this period, consistent with most observations of CO₂ and temperature throughout the Phanerozoic.

1. Introduction

Human alteration of land cover and combustion of fossil fuels has elevated atmospheric CO₂ levels to over 415 ppm. If very high greenhouse gas emissions continue, CO₂ will be between 750 and 1,300 ppm by 2100 (IPCC, 2013), levels not seen in almost 35 million years (Ma) (e.g., Beerling & Royer, 2011; Foster et al., 2017). Through Earth history both CO₂ and temperature have varied, and thus, these variations in the past act as archives of Earth system responses to changes in climate. These paleo-records of CO₂ and temperature can therefore help provide context to present day climate change (Royer, 2016; Tierney et al., 2020).

In general, estimated CO₂ levels from CO₂ proxies correlate well with independent records of temperature through much of the geologic record (Lunt et al., 2010; Montañez et al., 2007; Royer, 2006; Tierney et al., 2020). However, there are notable exceptions, such as during the Late Cretaceous and early Paleocene (70–60 Ma) (Tierney et al., 2020). During this interval there are several major perturbations to the global carbon system, including:

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(a) the Deccan volcanism (e.g., Fendley et al., 2020; Schoene et al., 2019; Schoene et al., 2021; Sprain et al., 2019); (b) a bolide impact (e.g., Hull et al., 2020; Schulte et al., 2010), and (c) other minor carbon cycle perturbations as recorded by negative carbon isotopic excursions (e.g., Late Maastrichtian warming event, Dan-C2 event, the Latest Danian event, and Danian/Selandian Transition; Barnet et al., 2019; Coccioni et al., 2010; Schulte et al., 2013). Many studies have focused on the climatic and atmospheric response to these carbon perturbations (e.g., Beerling et al., 2002; Henehan et al., 2019; Hull et al., 2020; MacLeod et al., 2018; Milligan et al., 2019; Nordt et al., 2002; Steinhorsdottir et al., 2016; Taylor et al., 2018; Upchurch et al., 2007; Vellekoop et al., 2014; Wilf et al., 2003; Zhang et al., 2018). However, these perturbations are geologically brief, and when assessing long term trends, there appears to be discordance between CO$_2$ and temperature of the Late Cretaceous to early Paleocene, as global mean surface temperature is ∼8–12.5°C higher than the pre-industrial average (Westerhold et al., 2019) while estimated background CO$_2$ varies between <400 and >1,000 ppm depending on age, proxy, and study (Figure 1; Barclay & Wing, 2016; Beerling et al., 2002; Beerling et al., 2009; Foster et al., 2017; Henehan et al., 2019; Huang et al., 2013; Kowalczyk et al., 2018; Milligan et al., 2019; Nordt et al., 2002; Nordt et al., 2003; Royer, 2003; Royer et al., 2001; Steinhorsdottir et al., 2016; Wang et al., 2020; Zhang et al., 2018).

While many previous estimates of background CO$_2$ during the Late Cretaceous to early Paleocene have been low (<400 ppm; Beerling et al., 2002; Foster et al., 2017; Nordt et al., 2002; Steinhorsdottir et al., 2016; Royer et al., 2001), recent improvement in proxy methodologies (e.g., boron; Henehan et al., 2019, leaf gas-exchange; Kowalczyk et a, 2018; Milligan et al., 2019) have started to converge on moderate to elevated CO$_2$ (600–1,500 ppm; Henehan et al., 2019; Kowalczyk et al., 2018; Milligan et al., 2019; Zhang et al., 2018). Nonetheless, more studies are needed to fill the temporal gaps during this period (Figure 1).

Here we use the leaf gas-exchange model of Franks et al. (2014) to estimate CO$_2$ from fossil Platanites leaves (Platanaceae family) of four geochronologically well-constrained early Paleocene floral localities from the San Juan Basin (SJB), New Mexico (65.66–64.59 Ma). Critically, compared to traditional stomatal index and stomatal ratio proxies, leaf gas-exchange models provide more robust CO$_2$ estimates, especially at elevated CO$_2$ (Konrad et al., 2021; but see; Barclay & Wing, 2016) and can be used on most canopy-forming C$_3$ plant species (Franks et al., 2014). While the leaf gas-exchange model is robust across plant taxa (Royer et al., 2019), estimates can be improved by using information from taxonomically or ecologically similar living species for some of the model inputs (Kowalczyk et al., 2018; Maxbauer et al., 2014; Milligan et al., 2019; Reichgelt & D’Andrea, 2019; Royer et al., 2019). In general, when using leaf gas-exchange models it is better to use a multi-taxon approach, as reconstruction of atmospheric CO$_2$ can be species specific (e.g., Kowalczyk et al., 2018; Londoño et al., 2018; Milligan et al., 2019; Porter et al., 2019; Royer et al., 2019; Reichgelt & D’Andrea, 2019). This is especially true when taxonomic affinities are uncertain. However, estimates based on a single taxon can be improved when modern calibration is applied (e.g., Kowalczyk et al., 2018; Maxbauer et al., 2014; Milligan et al., 2019; Reichgelt & D’Andrea, 2019; Royer et al., 2019). This single taxon approach is advantageous when that taxon is common throughout Earth’s history, such as Platanaceae (plane tree or sycamore family) which is found throughout the Cenozoic of North America (Kváček et al., 2001; Pigg & DeVore, 2010). Therefore, we first test the model on two modern relatives of Platanaceae—Platanus occidentalis and Platanus × acerifolia—and then use that information to apply the method to fossil sycamore taxa from the SJB to reconstruct early Paleocene CO$_2$.

2. Materials and Methods

2.1. Leaf Samples

For modern calibration of the Franks et al. (2014) leaf gas-exchange model we used leaves from a single mature tree at the Blandy Experimental Farm, Virginia (P. occidentalis; 2019) and at Wesleyan University, Connecticut (P. × acerifolia; 2014) (Table 1).

Early Paleocene fossil Platanites leaves were collected from the lower Nacimiento formation in the SJB, New Mexico (Figure 2). The SJB preserves a nearly continuous succession of lower Paleocene terrestrial sediments (e.g., Cather et al., 2019; Flynn et al., 2020; Williamson, 1996; Williamson et al., 2008). A high-resolution age model for the basin exists for the first ~3.5 Ma of the Paleocene (Flynn et al., 2020), which provides precise age constraints on the fossil leaf localities (often ≤0.05 Ma; Table 1). The ages of the leaf localities are calculated using sediment accumulation rates based on the local stratigraphic position of magnetostratigraphic boundaries (Flynn, 2020; Flynn et al., 2020), and range in age from 65.66 Ma to 64.59 (Table 1; Figure 1). The fossil
Platanites leaves in our study come from four localities in the SJB: the De-Na-Zin Wilderness Area (sites AF1405 and DP1304) and Kimbeto Wash (sites AF1528 and DP1311; Figure 2). Fossils from site AF1405 were collected from a finely bedded carbonaceous shale interpreted to have been a swamp or ponded deposit (Table 1). Sites DP1304 and AF1528 were collected from a series of interbedded muds and sands interpreted to have been an overbank or crevasse splay deposit (Table 1). Lastly, site DP1311 fossils were collected from a carbonaceous shale interpreted to have been a ponded crevasse splay or overbank deposit. Fossils were assigned to the genus Platanites based on foliar architecture and leaf venation (e.g., Flynn, 2020; Flynn & Peppe, 2019). In addition, stomata have a raised ledge over the guard cell, which is characteristic of modern Platanaceae (Carpenter et al., 2005).

2.2. Leaf Gas-Exchange Model

We use the leaf gas-exchange model of Franks et al. (2014) to reconstruct atmospheric CO₂ (Equation 1). This mechanistic model is based on well-established relationships between the rate of CO₂ assimilation of plants ($A_p$), total leaf conductance to CO₂ ($g_{c(tot)}$), and gradient between atmospheric ($c_a$) and leaf intercellular CO₂ ($c_c$; Farquhar & Sharkey, 1982; Von Caemmerer, 2000). Definitions for all abbreviations are in Table 2.

$$C_c = \frac{A_p}{g_{c(tot)} \times \left(1 - \frac{c_i}{c_a}\right)}$$  \hspace{1cm} (1)

Overall, the model has 18 required inputs that inform the three main input categories of Equation 1 (Tables 2–3; Franks et al., 2014; Kowalczyk et al., 2018). When applied to the fossil record, stomatal density ($D$), stomatal pore length ($p$), and single guard cell width (GCW; as a proxy for stomatal pore depth) are used to partially determine $g_{c(tot)}$; carbon isotopes of leaf tissue ($\delta^{13}C_L$) and atmospheric air ($\delta^{13}C_a$) determine $c_i/c_a$; and physiology of modern plants help constrain both $A_p$ and $g_{c(tot)}$. For our fossil Platanites, physiology constraints (i.e., $A_p$ photosynthetic rate at a measured CO₂; $c_i/c_a$, present-day $c_i/c_a$; and physiology of modern plants help constrain both $A_p$ and $g_{c(tot)}$) were measured on modern P. occidentalis. We note that the leaf gas-exchange model of Franks et al. (2014) assumes light-saturated photosynthesis. All but one leaf in this study comes from high light environments based on measurements of undulation of leaf epidermal cells (Milligan et al., 2021; Milligan et al., 2022; Supporting Information S1). Therefore, this leaf was excluded.

The use of P. occidentalis and P. × acerifolia as modern analogs was guided by the work of Royer (2003). Royer (2003) reconstructed CO₂ from the Paleocene using the stomatal ratio method by comparing stomatal indices of P. guillelmæ to those of modern P. occidentalis, P. orientalis, and their hybrid P. × acerifolia. The extant species were selected based on similarities in morphology and ecology to both Platanites raynoldsii Newberry and P. guillelmæ (Royer et al., 2003).

To apply the model, we use the R script of Kowalczyk et al. (2018). Ten thousand Monte Carlo simulations are used to propagate errors and CO₂ estimates are reported as the median value. All input parameters can be found in Table 3 and the number of leaves used for each input parameter in Table 1. All raw values are available in Milligan et al. (2022).
2.2.1. Physiology

We measured physiology inputs needed for the leaf gas-exchange model of Franks et al. (2014), including $A_n$, operational stomatal conductance ($g_{c_{op}}$), and $c_i/c_a$ on extant *Platanus* with a LI-COR 6400 portable photosynthesis system (Li-Cor Inc, Lincoln, Nebraska, USA). Gas-exchange measurements were made on 12 leaves of *P. × acerifolia* on 23 June 2014, and 18 leaves of *P. occidentalis* on 21st June 2019–23rd June 2019. Physiology measurements were made on leaves that received full sunlight (i.e., sun leaves; selected from the outer portion of the canopy on the eastern or south-eastern side of the tree). All measurements were made between 9 a.m. and 12 p.m. to avoid midday stomatal closure, with the following settings: leaf fan speed = slow, air flow rate = 400 μmol s⁻¹, stomatal ratio = 0, leaf area = 6 cm², block temperature = 25°C, reference CO₂ = 400 ppm, and PAR = 1,000 μmol m⁻² s⁻¹.

![Geologic map of the San Juan Basin, New Mexico, showing Upper Cretaceous through lower Eocene strata](image)

**Figure 2.** Geologic map of the San Juan Basin, New Mexico, showing Upper Cretaceous through lower Eocene strata (modified from Flynn et al., 2020 and Williamson et al., 2008). Black boxes indicate geographic location of fossil leaf sites.
Leaf vapor pressure deficit averaged 1.4 ± 0.2 and 1.6 ± 0.2 for *P. occidentalis* and *P. × acerifolia*, respectively. During the gas-exchange measurements, a leaf was kept in the chamber for enough time to allow the photosynthetic rate to stabilize (approximately 2–3 min) and IRGAs were “matched” regularly throughout each working period. After the measurement, the leaf was picked, and chamber boundaries were marked on the leaf edges outside of the chamber with permanent marker. For one specimen, *P. × acerifolia* sample 5, the leaf did not fill the entire 6 cm$^2$ (∼5.89 cm$^2$) of the LI-COR; so, gas-exchange parameters were recalculated with the correct area following equations in the LI-COR manual (LI-COR, 2011).

### 2.2.2. Stomatal Measurements

On extant leaves, an approximately 1 cm$^2$ section was removed from the leaf from the area where physiology measurements were taken. Leaves were macerated using 5% NaOH. Maceration took 1–3 days and NaOH was replaced when discolored. Samples were then placed in household bleach for 1–5 min to clear the tissue. All
samples were water mounted for light microscopy and 7 fields of view at 20x and 5 fields of view at 40x objective lens were taken with an Olympus BX51 microscope and Leica DFC450 digital camera for stomatal density and stomatal size measurements, respectively.

Macrofossil leaves were prepared following the overlay technique of Kouwenberg et al. (2007). In brief, an Olympus BX51 microscope with epifluorescence (420–490 nm) was first used to determine which side of the leaf was facing up (adaxial or abaxial). As most leaves were adaxial side up, the polyester overlay was adhered to the cuticle and gently peeled to expose the abaxial surface. The overlay was then placed in a 10% HCl/10% HF solution for 24 hr to remove any carbonates or silicate matrix that would obscure the epidermal cells. The overlay-stomatal cuticle method of Barclay et al. (2002) following the protocols of Poole and Kürschner (1999). Therefore, two additional pieces of cuticle were prepared by using the dispersed cuticle method of Barclay et al. (2010). For this method, ~150 g of dry rock from site AF1405 was placed in concentrated HCl (36.5%–38%) for two weeks, rinsed with DI water, placed in concentrated HF (48%) for two weeks, and rinsed with DI water. The >500 μm fraction was separated out using a 500 μm sieve. For all pieces of cuticle, ~5–7 fields of view at 20x and 5 fields of view at 40x objective were taken using an Olympus BX51 microscope with epifluorescence (420–490 nm) and Leica DFC450 digital camera or Fluorescence Microscope IX-81 (Olympus Corp) with DP81, Peltier cooled 12.5 MP digital camera (450–490 nm) for D and stomatal size measurements.

Stomatal density (D) and stomatal size measurements were measured in Photoshop. For D, all counts were done within a 200 × 200 micron area (0.04 mm²) following the protocols of Poole and Kürschner (1999). A 0.04 mm² box was used to ensure that most veins, which generally do not contain stomata, were excluded and to provide consistency between modern and fossil measurements; fossil peels were often patchy and did not contain large intact areas. Stomata touching the left and bottom line of the box were counted as “in” (Figures 3a and 3c). p and GCW were measured on 10 to 15 stomata per specimen. GCW was taken as the average of the width of the
two guard cells. GCW was measured from the outside edge of the guard cell to the start of the cuticular ledge (Figures 3b and 3d). $g_{c(max)}$ was estimated following Franks and Beerling (2009):

$$g_{c(max)} = \frac{d \times \ln(a_{max})}{\epsilon \left(1 + \frac{1}{2} \times \sqrt{\frac{a_{max}}{\epsilon}}\right)}$$  \hspace{1cm} (2)

where constants $d$ and $\nu$ are the diffusivity of CO$_2$ in air and the molar volume of air, $D$ is stomatal density, $l$ is stomatal pore depth (approximated as GCW), and $a_{max}$ is the maximum stomatal aperture. For this study $a_{max}$ is approximated as a circle with diameter equal to the stomatal pore length ($a_{max} = \pi p^2/4$), following the recommendations of Franks et al. (2014).

2.2.3. Carbon Isotopes

Leaf specimens were analyzed for $\delta^{13}C$ using a Delta-V Advantage mass spectrometer at Baylor University. For $\delta^{13}C_p$ analysis all extant specimens were sampled near the same location where stomatal and physiology measurements were taken using a hole punch. For fossil specimens, cuticle from a subset of fossil leaves was gently scraped from the rock, taking care to remove as little matrix with the cuticle as possible. The scraped material was submerged in HCl (36.5%–38%) to remove carbonate, rinsed in distilled water, treated with HF (48%) to dissolve silicates, rinsed again in distilled water, and then oven dried at 60°C.

For $P. \times$ acerifolia we used a $\delta^{13}C_{atm}$ value of $-8.50\%e$ from Maxbauer et al. (2014) derived for May–June 2012 of Middletown, CT. For $P. occidentalis$, air was sampled on 23 June 2019, using 100 ml two arm glass flasks, and analyzed for $\delta^{13}C$ of atmospheric CO$_2$ using a Thermo Finnigan Delta Plus Advantage (IRMS) connected with a
When applying the leaf gas-exchange model to the fossil record, constraints are needed based on modern plant physiology. The choice of modern analog for physiology measurements is important, as the leaf gas-exchange model is particularly sensitive to changes in both $A_p$ and $\zeta$, especially when $\zeta$ is low (i.e., <0.1; Kowalczyk et al., 2018; Maxbauer et al., 2014; McElwain et al., 2016a; Milligan et al., 2019; Royer et al., 2019). When the taxonomic affinity of fossils is unknown, Franks et al. (2014) offer values of $A_p$ for broad taxonomic groups (12 $\mu$mol m$^{-2}$s$^{-1}$ for angiosperms, 10 for conifers, and 6 for ferns and ginkgo) and recommend a constant value for $\zeta$ (0.20). Reichgelt and D’Andrea (2019) found that CO$_2$ estimates can be improved when $A_p$ is constrained by: (a) family level and (b) habitat. Similarly, several studies have found improved model accuracy when $A_p$ and $\zeta$ are measured on extant species (e.g., Maxbauer et al., 2014; Kowalczyk et al., 2018; Milligan et al., 2019; but see; Royer et al., 2019); especially since $\zeta$ can range from 0.007 to 0.86 depending on species and methodology used to calculate $g_{\text{c(max)}}$ (Dow et al., 2014; Franks et al., 2014; McElwain et al., 2016b; Murray et al., 2020; Xiong & Flexas, 2020).

Our physiology measurements of $P. occidentalis$ ($A_p = 12.2 \mu$mol CO$_2$ m$^{-2}$ s$^{-1}$; $g_{\text{c(op)}} = 0.16$ mol CO$_2$ m$^{-2}$ s$^{-1}$; $\zeta = 0.08$; $c_i/c_a = 0.74$) and $P. \times acerifolia$ ($A_p = 13.2 \mu$mol CO$_2$ m$^{-2}$ s$^{-1}$; $g_{\text{c(op)}} = 0.13$ mol CO$_2$ m$^{-2}$ s$^{-1}$; $\zeta = 0.07$; $c_i/c_a = 0.67$) are consistent with other published values for $A_p$ and $g_{\text{c(op)}}$ for $P. occidentalis$ (Xiong & Flexas, 2020; You et al., 2021), providing confidence in using these values for estimating paleo-CO$_2$. For our fossil reconstructions, we chose to use the physiology input parameters of $P. occidentalis$ due to the better prediction of present-day CO$_2$ compared to $P. \times acerifolia$ (Figure 4; Table 3). The use of physiology measurements of $P. \times acerifolia$ increases estimates of early Paleocene CO$_2$ by ~20% due to an increase in $A_p$ and lower $\zeta$.

Taken together, these results provide support for the application of leaf gas-exchange models to fossil Platanaceae. These results have broad utility because Platanaceae is ubiquitous across Laurasia in the Cenozoic (Kvaček et al., 2001; Figg & DeVore, 2010) and early Cretaceous (Crane et al., 1993; Upchurch, 1984; Wang et al., 2011), and thus the gas-exchange model calibrated for Platanaceae could be widely applied. However, future work that evaluates the leaf gas-exchange model at the family level could help provide confidence in our estimates because Platanaceae is composed of seven extant tree species (Nixon & Poole, 2003) and there may be cross-species variation in physiology.

### 3.2. Moderate to Elevated Early Paleocene CO$_2$

Our estimates of early Paleocene CO$_2$ range from 665 to 1,143 ppm (Figure 1; Table 3). Our estimates are, on average, higher than other similar-aged early Paleocene estimates that use the stomatal index and stomatal ratio.

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**Figure 4.** Atmospheric CO$_2$ estimates from modern $P. occidentalis$ (red) and $P. \times acerifolia$ (blue). The error bars indicate the 95% confidence interval for each CO$_2$ estimate. Lines represent the mean atmospheric CO$_2$ value for the respective year (2019, 2014) based on data from Mauna Loa (https://gml.noaa.gov/webdata/ccgg/trends/co2/co2_annmean_mlo.txt).
methods (Beerling et al., 2009; Kowalczyk et al., 2018; Steinthorsdottir et al., 2016; Wang et al., 2020), which range from ~250 to 570 ppm, and some paleosol proxies (Foster et al., 2017) that can range from implausibly low values (e.g., 0; see Nordt et al., 2003) to ~650 ppm. Instead, our estimates are more in line with recent work based on leaf gas-exchange (Kowalczyk et al., 2018; Milligan et al., 2019), liverworts (Kowalczyk et al., 2018), boron (Henehan et al., 2019) and paleosols (Zhang et al., 2018; Figure 1). Specifically, our estimate of 1,143 at 65.66 Ma is comparable to estimates from Henehan et al. (2019; 1,166–1,704 ppm at 65.61 Ma) and Zhang et al. (2018; 1,048 ppm at 65.69 Ma). In general, these moderate to elevated atmospheric CO₂ estimates are more in line with the elevated temperatures observed for the early Paleocene (Westhorst et al., 2020).

Our earliest CO₂ estimate of 1,143 at 65.66 Ma (site AF1405), is roughly coincident with an early Paleocene pulse in Deccan volcanism (e.g., Fendley et al., 2020; Schoene et al., 2019; Schoene et al., 2021) and at the tail end, or just after, the carbon isotope excursion of the Dan-C2 event (Barnet et al., 2019; Lyson et al., 2019). Thus, it may reflect a brief episode of relatively high CO₂ conditions in the early Paleocene. After 65.66 Ma, our record documents a ~40% swing in CO₂ from a drop of 1,143 ppm at 65.66 a.m. to 665 at 65.29 Ma before returning to ~1,000 ppm by 64.79 Ma. A drop in CO₂ over 300 kys is plausible, because the removal of a rapid release of CO₂ into the atmosphere typically requires up to 100–200 kys (Archer, 2005; Colbourn et al., 2015; Schaller et al., 2011; Zeeb & Zachos, 2013), and could reflect intensified weathering of Deccan Traps that were erupting during the Late Cretaceous and early Paleocene (Fendley et al., 2020; Schoene et al., 2019; Schoene et al., 2021; Sprain et al., 2019). Assuming an early Paleocene Earth system sensitivity of ~3–4.5°C (e.g., Farnsworth et al., 2019; Kowalczyk et al., 2018; Royer, 2016), we would expect to observe a 3–4.5°C cooling in response to this halving in CO₂. In the Denver Basin, fossil leaves record a ~2°C drop in mean annual temperature from 65.66 to 65.29 Ma (Lyson et al., 2019), but there is no evidence for a decrease in temperature based on the deep-sea foraminifera record (e.g., Westhorst et al., 2020), suggesting that there was not a global change in temperature. Therefore, more evidence is needed to confirm if these large but transitory changes in CO₂ are real. Critically, though, the lower end of our CO₂ estimates is still distinctly higher than most estimates for this time from the older literature.

4. Summary

Here we validated a leaf gas-exchange model on two modern species of Platanus, P. occidentalis and P. × acerifolia, by measuring the three main inputs: (a) physiology, (b) stomatal density and size, and (c) carbon isotopes. We find that the model accurately predicts modern day CO₂, with a mean error rate of ~5%–14%. Based on physiology constraints from modern Platanus in this study, we then applied the leaf gas-exchange model to fossil Platanites of four early Paleocene localities from the SJB, New Mexico. Estimated CO₂ ranged from ~660 to 1,140 ppm, which is 2–3x higher than some previous studies. Our new estimates are comparable with more recent studies based on a variety of proxies (i.e., boron; leaf gas-exchange; liverworts; paleosols) and thus more compatible with the elevated temperatures seen in the early Paleocene.

Data Availability Statement

All data used to produce modern and paleo-CO₂ estimates in this study are archived in the Texas Data Repository (Milligan et al., 2022). The R script to run the Franks et al. (2014) leaf gas-exchange model can be found in the Supporting Information of Kowalczyk et al. (2018).

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