Moderate levels of Eocene pCO₂ indicated by Southern Hemisphere fossil plant stomata

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ABSTRACT

Reducing the uncertainty in predictions of future climate change is one of today’s greatest scientific challenges, with many significant problems unsolved, including the relationship between pCO₂ and global temperature. To better constrain these forecasts, it is meaningful to study past time intervals of global warmth, such as the Eocene (56.0–33.9 Ma), serving as climatic analogues for the future. Here we reconstructed pCO₂ using the stomatal densities of a large fossil Lauraceae (laurel) leaf database from ten sites across the Eocene of Australia and New Zealand. We show that mostly moderate pCO₂ levels of ~450–600 ppm prevailed throughout the Eocene, levels that are considerably lower than the pCO₂ forcing currently needed to recreate Eocene temperatures in climate models. Our data record significantly lower pCO₂ than inferred from marine isotopes, but concur with previously published Northern Hemisphere Eocene stomatal proxy pCO₂. We argue that the now globally consistent stomatal proxy pCO₂ record for the Eocene is robust and that climate sensitivity was elevated and/or that additional climate forcings operated more powerfully than previously assumed.

INTRODUCTION

The anthropogenic rise in CO₂ concentrations (pCO₂) is predicted to result in a global average temperature increase of up to 4 °C by the year 2100 (IPCC, 2014), with severe socioeconomic and ecosystem impacts predicted. However, the exact relationship between pCO₂ and temperature—or climate sensitivity (the equilibrium response in mean global surface temperature to a doubling of pCO₂, generally reported as ~3 °C)—is still not well understood, and is probably state-dependent; i.e., dependent on baseline pCO₂ and temperature. Scientists therefore look to past time intervals of global warming, which can serve as “climatic analogues”, for clues about our future. The Eocene epoch was such a time interval, with average global temperatures 4–15 °C higher than at present (Zachos et al., 2001; Huber and Caballero, 2011; Anagnostou et al., 2016; Cramwinckel et al., 2018). In the earliest Eocene (ca. 55.5 Ma), there was a transient episode of extremely elevated temperatures—the Paleocene-Eocene Thermal Maximum, or PETM (McInerney and Wing, 2011). Later, after the peak warmth of the Early Eocene Climatic Optimum (EECO, ca. 52–50 Ma), a gradual cooling began, briefly interrupted by a major warming reversal at ca. 40 Ma, called the Middle Eocene Climatic Optimum (MECO) (Zachos et al., 2001; Cramwinckel et al., 2018). The Eocene climate still constitutes one of the greatest unsolved problems in paleoclimate research. Temperatures were globally much higher than today, with a significantly weaker equator-to-pole temperature gradient and a muted seasonal cycle compared to today, referred to as the “Eocene equable climate problem” (Sloan and Barron, 1990; Greenwood and Wing, 1995; Greenwood et al., 2003a). Climate modeling has been able to reconstruct this pattern with very high pCO₂ levels (up to ~4500 ppm: Huber and Caballero, 2011), but such extremely elevated pCO₂ is not documented by proxy records. It is therefore assumed that Eocene climate sensitivity—often defined as Earth system sensitivity for longer time scales, including both “fast” and “slow” feedbacks (Lunt et al., 2010)—was elevated compared to present, and/or that other mechanisms, in addition to the dominant forcing of pCO₂, were in operation (Caballero and Huber, 2013; Anagnostou et al., 2016; Zeebe et al., 2016; Carlson and Caballero, 2016; Cramwinckel et al., 2018; Keery et al., 2018). A variety of geochemical and biological proxies as well as carbon cycle modeling have been used to estimate Eocene pCO₂, but these estimates still differ hugely (with values ranging from hundreds to thousands of parts per million pCO₂); however, there is some convergence forming (Holdgate et al., 2009; Beerling and Royer, 2011; Foster et al., 2017). To further constrain Eocene pCO₂, additional proxy records of sufficient quality and resolution are urgently required. Here, we contribute to this quest by presenting a new terrestrial record of Eocene pCO₂ using a stomatal proxy method of paleo-pCO₂ reconstruction.

MATERIAL AND METHODS

We photographed and analyzed 92 fossil Lauraceae (angiosperm) specimens from six Australian and four New Zealand localities (Fig. 1), derived from ten relatively well-dated stratigraphic levels spanning the Eocene. The database of specimens consists of permanently mounted cuticle samples on microscope slides, prepared in connection with previous taxonomic work, following standard paleobotanical procedures. The database derives from two separate collections, with 46 specimens hosted at Melbourne Museum, Melbourne, Victoria, Australia, and the remaining 46 at the School of Environment, University of Auckland, New Zealand (see Appendix DR1 in the

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GSA Data Repository1 for details). We reconstructed paleo-pCO2 using the stomatal proxy, founded on the observed inverse relationship between the density of leaf stomata and pCO2 (Woodward, 1987; McElwain and Steinthorsdottir, 2017). Stomatal density of plant leaves was quantified from microscope images as stomatal index (SI [%] = proportion of stomata relative to all epidermal cells). Three methods of stomatal proxy paleo-pCO2 reconstructions are currently in use:

1. The semiquantitative empirical stomatal ratio method, which utilizes the ratio between the SI of fossil plants and the SI of extant nearest living relatives or equivalents (NLRs or NLEs), grown in known pCO2 (living or herbaria specimens), to estimate paleo-pCO2 (McElwain, 1998);

2. The also empirical transfer function method, which uses herbarium and/or experimental data sets of NLR-NLE responses to variations in pCO2 to construct regression curves on which fossil SI can be plotted to infer paleo-pCO2 (e.g., Barclay and Wing, 2016);

3. Mechanistic gas exchange modeling, which is taxon-independent (relying on morphological measurement data), but also requires input of additional parameters, such as leaf δ13C and paleotemperature (Konrad et al., 2008; Franks et al., 2014; Konrad et al., 2017).

Here the Lauraceae database is without leaf δ13C data, so we used the stomatal ratio and transfer function methods to reconstruct Eocene pCO2, employing multiple NLEs to minimize interspecies variation and reach best-consensus pCO2. The NLE species used in the stomatal ratio method were Litsea glutinosa (Indian laurel), L. fascata, L. stockii, Neoilisca dealbata (bolly gum), and Cinnamomum camphora (camphor laurel), and Laurus nobilis (bay laurel) was used in the transfer function (from Kürschner et al. [2008], including the recommended correction factor of +150 ppm), using the equations:

Stomatal ratio:

\[
pCO_{2\text{paleo}} = \frac{SI_{\text{NLE}}}{SI_{\text{fossil}}} \times pCO_{2\text{modern}},
\]

Transfer function:

\[
pCO_{2\text{paleo}} = 10^{\frac{1.73}{10}} \left[ 0.5499 \times \log (SI_{\text{fossil}}) \right] + 150.
\]

(Fors details on the stomatal proxy pCO2 reconstruction, stratigraphic setting, and chronology, see Appendix DR1, including Figs. DR1 and DR2, and data set Appendix DR2 in the Data Repository).

RESULTS AND DISCUSSION

Southern Hemisphere Stomatal Proxy pCO2 Reconstruction

Early Eocene (ca. 54–50 Ma) Lauraceae leaf cuticles from the Otaio River (South Island, New Zealand) and Regatta Point (Tasmania) record SIs of 11.5% and 11.2%, respectively, and those from Dean’s Marsh (southern Australia), 13.4% (Table 1). The early Eocene SIs translate into average pCO2 of ∼520–540 ppm and ∼450 ppm, respectively (Fig. 2, pink dots). These results are highly comparable to previously published stomatal proxy pCO2 estimates (Fig. 2, green diamonds), but much lower than contemporaneous marine boron isotope pCO2, which mostly record 800–1400 ppm (Pearson et al., 2009; Zhang et al., 2013; Anagnostou et al., 2016), whereas existing paleosol records form less internal consensus, recording ∼80–1300 ppm, and mostly derive from the narrow time interval 54–52 Ma (Foster et al., 2017). Error bars on the x-axis show the full likely chronological range of each sample locality (see also Fig. DR1).

Comparison to Existing pCO2 Records and Implications

The Eocene pCO2 results obtained using Southern Hemisphere Lauraceae mostly fall in the relatively moderate interval of ∼450–600 ppm, which is highly comparable to previously published coeval stomatal proxy records (Fig. 2), but lower than marine records, which mostly record pCO2 of ∼800–1400 ppm (Pearson et al., 2009; Zhang et al., 2013; Anagnostou et al., 2016; Frost et al., 2017). Here the lower range of marine isotope–based pCO2 estimates from three separate localities in this study and from well-dated contemporaneous Metasequoia (redwood) needles (Doria et al., 2011), this seems unlikely. Finally, in the late Eocene (ca. 35 Ma), we record a SI from Huntly Mine (North Island, New Zealand) at 7.7%, translating to pCO2 of ∼750 ppm (Table 1; Fig. 2). These results are based however on only two specimens, and should not be considered robust. We note nonetheless that the high estimate agrees with previously published coeval stomatal pCO2 results (Roth-Nebelsick et al., 2012), as well as with the lower range of marine isotope–based pCO2 estimates (Fig. 2).
climatic events of the Eocene recorded by the deep ocean–derived temperature record, such as rising pCO$_2$ at the transition into the EECO or MECO (Fig. 2).

The most striking feature of the Eocene stomatal proxy record is that some of the highest pCO$_2$ is indicated in the early middle Eocene (until ca. 46–44 Ma), well beyond the end of the EECO, in reasonable agreement with the couple of marine isotope data points in this interval, whereas the deep-ocean proxy compilation tracks a gradual temperature decline between the EECO and MECO (Fig. 2). After ca. 46–44 Ma, a decrease in stomatal pCO$_2$ is recorded prior to the MECO, followed by a moderate increase at the transition into the MECO (Fig. 2). These trends do not fully agree with the deep-ocean compilation, but it should be noted that terrestrial mean annual temperature (MAT) records suggest a correlation between stomatal-recorded pCO$_2$ and MAT during this time (e.g., Greenwood et al., 2003a; Pancost et al., 2013). In the latter part of the late Eocene, stomatal and marine isotope records show a fairly high range in coeval pCO$_2$ values, with the stomatal record displaying a closer congruence with the deep-ocean compilation temperature than the marine pCO$_2$ record (Fig. 2).

Stomatal proxy pCO$_2$ reconstructions currently offer the highest-resolution record of Eocene pCO$_2$, with almost 50 data points, compared to ~10 each derived from marine alkane and boron isotopes, and ~20 from paleosols. The numerous studies, using various fossil isomers as well as the fossil gymnosperms Ginkgo and Metasequoia, in the three stomatal proxy methods currently in use mostly agree that the Eocene pCO$_2$ was more moderately elevated compared to what marine proxies and climate modeling suggest (McElwain, 1998; Kürschner et al., 2001; Royer et al., 2001; Greenwood et al., 2003b; Retallack, 2009; Smith et al., 2010; Doria et al., 2011; Grein et al., 2011; Roth-Nebelsick et al., 2012; Franks et al., 2014; Maxbauer et al., 2014; Liu et al., 2016; Steinthorsdottir et al., 2016; Wolfe et al., 2017). The discrepancy between the marine isotope and stomatal proxy pCO$_2$ results is considerable, with the marine isotope values recording pCO$_2$ currently assumed to be more consistent with the elevated Eocene temperatures recorded by numerous proxies and the workings of the Earth’s climate system (Cramwinckel et al., 2018). Our results provide new SI data from the previously sparse Southern Hemisphere record, suggesting that the terrestrial pCO$_2$ proxy data may indeed be robust with an internally consistent global record of moderate Eocene pCO$_2$ levels. Although it is premature to make strong statements, this would imply that Earth system sensitivity was likely in the range of ∼4–8 °C during the Eocene, significantly elevated compared to the “modern” climate sensitivity of ∼3 °C (Lunt et al., 2010; Royer et al., 2012; Maxbauer et al., 2014; Wolfe et al., 2017; Keery et al., 2018; Schneider et al., 2019). However, the various feedback mechanisms affecting Earth system sensitivity in an ice-free world are still poorly understood.

In summary, we find pCO$_2$ of ~450–600 ppm recorded by Southern Hemisphere fossil plants throughout the Eocene—significantly less than the forcing required by modeling, suggesting that climate sensitivity was elevated and/or that other climate forcings were stronger than previously assumed.
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