

# High Arctic forests during the middle Eocene supported by moderate levels of atmospheric CO<sub>2</sub>

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## ABSTRACT

Fossils from Paleogene High Arctic deposits provide some of the clearest evidence for greenhouse climates in the past and offer the potential to improve our understanding of Earth system dynamics in a largely ice-free world. One of the most well-known and stunningly preserved polar forest sites, Napartulik, crops out of middle Eocene (47.9–37.8 Ma) sediments on eastern Axel Heiberg Island, Nunavut, Canada (~78°N paleolatitude). An abundance of data from Napartulik suggests mean annual temperatures at least 30 °C warmer than today and atmospheric water loads 2× current levels. Despite this wealth of paleontological and paleoclimatological data, there are currently no direct constraints on atmospheric CO<sub>2</sub> levels for Napartulik or any other polar forest site. Here we apply a new plant gas-exchange model to *Metasequoia* (dawn redwood) leaves to reconstruct atmospheric CO<sub>2</sub> from six fossil forest horizons at Napartulik. Individual reconstructions vary between 392 ppm and 474 ppm, with a site median of 424 ppm (351–523 ppm at 95% confidence). These estimates represent the first direct constraints on CO<sub>2</sub> for a High Arctic forest and suggest that the temperate conditions present at Napartulik during the middle Eocene were maintained under CO<sub>2</sub> concentrations ~1.5× pre-industrial levels. Our results support the case that long-term climate sensitivity to CO<sub>2</sub> in the past was sometimes high, even during largely ice-free periods, highlighting the need to better understand the climate forcings and feedbacks responsible for this amplification.

## INTRODUCTION

It was clear to paleobotanists as early as 1878 that the discovery of Paleogene fossil plants from well above the Arctic Circle similar to plants “now existing only in the south of the United States and in Mexico...[is evidence that] climatic conditions in the polar regions have undergone a [considerable] change” (Heer, 1878, p. 67, 72). Subsequent discoveries of early Paleogene Arctic fossils with temperate extant relatives and independent paleoclimate data support the notion that warm and wet conditions persisted in the Arctic for much of the Paleocene and Eocene (Eberle and Greenwood, 2012) when global temperatures were also elevated (Fig. 1; Zachos et al., 2008).

The Napartulik (Inuk for “place of trees”) fossil forest site crops out of middle Eocene (47.9–37.8 Ma) sediments on eastern Axel Heiberg Island in the Canadian High Arctic (79.92°N, 89.03°W; Fig. 2) and has historically been the topic of extensive research (for a review, see Jahren, 2007; for an age discussion, site pictures, and stratigraphic context, see Appendix DR1 in the GSA Data Repository<sup>1</sup>). The productivity of the Napartulik forests and

their associated climate are comparable to those of extant temperate and coastal forests of Chile, east Asia, and the Pacific Northwest of North America (Francis, 1991; Schubert et al., 2012; Williams et al., 2003) despite growing under an extreme light environment of ~4 months continuous summer light and ~4 months continuous winter darkness at a paleolatitude of ~78°N (LePage et al., 2012). Proxy data from Napartulik highlight the drastic differences between our current climate and the middle Eocene climate that supported these forests: mean annual temperature (MAT) reconstructions range from 9 to 15 °C for the Napartulik fossil forests compared with -19.7 °C today; atmospheric water loads were as much as 2× current levels, with a mean annual precipitation of ~1330 mm compared to 75 mm today (Eberle and Greenwood, 2012; present-day values are for nearby Eureka, from <http://climate.weather.gc.ca>).

There are comparatively few constraints on atmospheric CO<sub>2</sub> concentration for the middle Eocene (Fig. 1). Furthermore, there are no CO<sub>2</sub> estimates that come directly from the sites of Paleogene polar forests, including Napartulik. Because of the role that CO<sub>2</sub> plays in regulating Phanerozoic climate (Royer, 2014), the potential for CO<sub>2</sub> to vary substantially on geologically short time scales (<10<sup>6</sup> yr), and the poorly constrained age range for the Napartulik site (Appendix DR1), this lack of CO<sub>2</sub> data limits our ability to place existing paleoenvironmental data from Napartulik in its fullest and proper context. Here we present estimates of CO<sub>2</sub> obtained directly

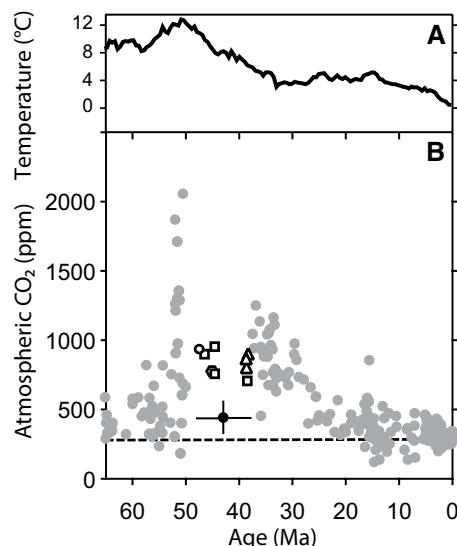


Figure 1. Proxy record of Cenozoic CO<sub>2</sub> and temperature. A: Likely minimum global mean surface temperature, calculated from the benthic foraminifera  $\delta^{18}\text{O}$  compilation of Zachos et al. (2008) following methods of Royer et al. (2012) and Hansen et al. (2008). B: CO<sub>2</sub> proxy record from Royer (2014), with additional data from Badger et al. (2013a, 2013b), Cotton and Sheldon (2012), Erdei et al. (2012), Foster et al. (2012), Grein et al. (2013), Huang et al. (2013), Hyland et al. (2013), Hyland and Sheldon (2013), Roth-Nebelsick et al. (2012), and Zhang et al. (2013). CO<sub>2</sub> site mean reconstruction from Napartulik (Nunavut, Canada) is shown in black; error bars for CO<sub>2</sub> are the 2.5 and 97.5 percentiles. Open triangles come from the marine alkenone method, open squares from traditional stomatal approaches, open pentagon (partially covered) from the paleosol carbonate method, and open circle from the alternative gas-exchange model of Konrad et al. (2008). Dashed black line indicates pre-industrial CO<sub>2</sub> (280 ppm).

from a Paleogene fossil forest using a recently developed gas-exchange model applied to well-preserved *Metasequoia occidentalis* Newberry (Chaney) foliage (LePage et al., 2012).

## USING STOMATA TO RECONSTRUCT CO<sub>2</sub>

One popular CO<sub>2</sub> proxy relies on the species-specific relationship between stomatal frequency and the partial pressure of CO<sub>2</sub> (Royer, 2001). This approach applies the stomatal frequency response of an extant species to the same species in the fossil record; it is thus lim-

<sup>1</sup>GSA Data Repository item 2014357, site overview (Appendix DR1), detailed methods (Appendix DR2), model validation with extant *Metasequoia glyptostroboides* (Appendix DR3), raw data (Appendix DR4), and stomatal index (Appendix DR5), is available online at [www.geosociety.org/pubs/ft2014.htm](http://www.geosociety.org/pubs/ft2014.htm), or on request from [editing@geosociety.org](mailto:editing@geosociety.org) or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.



**Figure 2.** Map showing location of Napartulik (Nunavut, Canada; black dot) during the middle Eocene. Reconstructed paleolatitude is ~78°N (Irving and Wynne, 1991). Map is redrawn and modified from Markwick et al. (2000).

ited to fossil species that persist to the present day. Additionally, the CO<sub>2</sub> transfer functions are based on empirically measured responses, not physiological theory, and above 500–1000 ppm the upper error limits often become unbounded (e.g., Jordan, 2011). Recently, Franks et al. (2014) applied principles of leaf gas-exchange theory to develop a new CO<sub>2</sub> proxy that largely avoids these problems (see Appendix DR2.1 for details).

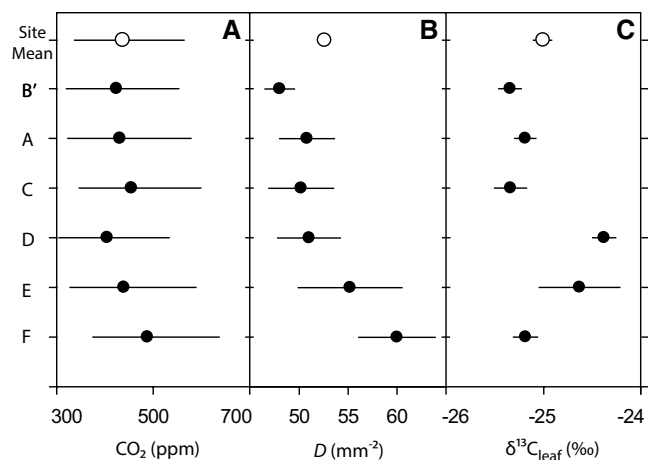
In brief, a well-vetted model for photosynthesis (Farquhar and Sharkey, 1982) can be solved for atmospheric CO<sub>2</sub> concentration (C<sub>a</sub>):

$$C_a = \frac{A}{g_{c_{tot}} \left(1 - C_i / C_a\right)}, \quad (1)$$

where *A* is the photosynthetic rate (μmol m<sup>-2</sup> s<sup>-1</sup>), *g*<sub>c<sub>tot</sub></sub> is the total operational conductance to CO<sub>2</sub> diffusion from the atmosphere to sites of photosynthesis within the leaf (mol m<sup>-2</sup> s<sup>-1</sup>), and *C*<sub>i</sub> is leaf intercellular CO<sub>2</sub> (μmol m<sup>-2</sup> s<sup>-1</sup>). *g*<sub>c<sub>tot</sub></sub> can be derived from measurements of stomatal size and density, *C*<sub>i</sub>/*C*<sub>a</sub> from the carbon isotope fractionation (Δ<sup>13</sup>C) between leaf and air, and *A* from measurements on extant analogs. The model robustly estimates present-day CO<sub>2</sub>, experimentally elevated CO<sub>2</sub>, the recent rise in CO<sub>2</sub> over the past 40 yr, and the rise in CO<sub>2</sub> across the last glacial-interglacial transition (Franks et al., 2014). This approach marks a significant advance over traditional stomatal methods because it retains sensitivity at high CO<sub>2</sub>, is not limited to fossil species that are still alive today, and is driven by gas-exchange theory, not empirical functions (Franks et al., 2014).

We analyzed *M. occidentalis* foliage from the six fossil forest horizons at Napartulik where cuticle preservation was sufficient; these six horizons likely span 10<sup>5</sup> yr (see Appendix DR1). We estimated CO<sub>2</sub> with the Franks et al. (2014) model using measurements of stomatal geom-

**Figure 3.** Key leaf data from Napartulik (Nunavut, Canada) fossil forest horizons. Stratigraphic nomenclature follows Francis (1991) and Jahren et al. (2009) (see Appendix DR1 [see footnote 1]). **A:** Median estimated CO<sub>2</sub> concentrations. Error bars are the 2.5 and 97.5 percentiles. **B:** Whole-leaf stomatal density (*D*) for *Metasequoia occidentalis*. Values are scaled from within-band *D* based on percentage of leaf surface composed of stomatal bands. Errors represent ±1 standard error of the mean (s.e.m.). **C:** δ<sup>13</sup>C<sub>leaf</sub> for fossil *M. occidentalis* relative to Vienna Peedee belemnite. Errors represent ±1 s.e.m.



etry and bulk leaf δ<sup>13</sup>C (see Appendix DR2 for methods). Reported CO<sub>2</sub> is the median of 10,000 resamples using Monte Carlo methods (Franks et al., 2014). The model resamples each input parameter assuming a Gaussian distribution centered about its mean value. Because we are interested in how close the measured (or modeled) means in these input terms are to their true means, and not their variances, standard errors of the mean (s.e.m.) are used to build the distributions. For most input variables the s.e.m. is a measured value. For those inputs not measured for *Metasequoia*, we assume that ±5% of the mean corresponds to ±1 s.e.m.; these modeled errors are typically larger proportionately than the measured errors. For each of the 10,000 resamples, a CO<sub>2</sub> estimate is produced that incorporates error in every input term. The 10,000 CO<sub>2</sub> estimates are then used to create a probability density function (PDF). The reported uncertainties associated with the median values are similar to a 95% confidence interval (2.5 and 97.5 percentiles).

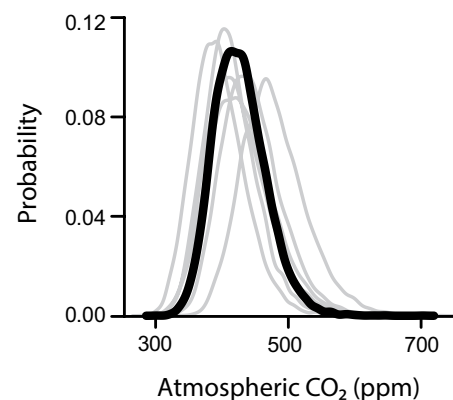
As an important check on the model, we estimated present-day CO<sub>2</sub> using extant *M. glyptostroboides* Hu et Cheng; the 431 ppm estimate is within 9% of the observed value, validating our approach for *Metasequoia* (Appendix DR3; see Appendix DR2.4 for methods). We were unsuccessful in applying another gas exchange-based model (Konrad et al., 2008) to extant *M. glyptostroboides*, and so we did not apply it to the Napartulik fossils.

### CO<sub>2</sub> RECONSTRUCTION FOR NAPARTULIK

Fossil CO<sub>2</sub> reconstructions for Napartulik fluctuate between 392 ppm and 474 ppm, with a site median of 424 ppm (351–523 ppm at 95% confidence) and a net decline of 65 ppm progressing upsection (Fig. 3; see Appendix DR4 for data). All PDFs display similar distributions, supporting a broad equivalence in reconstructed

CO<sub>2</sub> across fossil forest horizons (Fig. 4). Preservation of epidermal cell boundaries was sufficient at layer C to estimate CO<sub>2</sub> using stomatal indices (the percentage of epidermal cells that is stomatal complexes), one of the traditional, calibration-based stomatal approaches. The similarity in estimated CO<sub>2</sub> (441 ppm versus 471 ppm for gas-exchange and stomatal index, respectively; Appendix DR5) boosts confidence that the presented CO<sub>2</sub> reconstruction is reliable. Two key input variables, stomatal density (*D*) and leaf δ<sup>13</sup>C, display somewhat offsetting patterns, which contribute to the stable CO<sub>2</sub> estimates (Fig. 3). There is a positive correlation between *D* and reconstructed CO<sub>2</sub> (Figs. 3A and 3B), opposite of the typical inverse relationship. This highlights the advantage of gas-exchange modeling over traditional approaches.

Our CO<sub>2</sub> estimates are lower than coeval estimates (~715–965 ppm; Fig. 1) that come primarily from traditional stomatal methods and the marine alkenone approach (open squares and triangles in Fig. 1). Imprecise dating of the



**Figure 4.** Probability density functions for all CO<sub>2</sub> reconstructions from Napartulik (Nunavut, Canada). Thin gray lines represent reconstructions from individual layers; thick black line represents the site mean reconstruction.

Napartulik site makes direct comparison of our estimates with other work difficult, however as already described our gas exchange-based estimates are likely more robust than estimates from traditional stomatal methods. Nonetheless, some newer estimates for the early Eocene, an interval warmer than the middle Eocene, are more in line with our estimates (e.g., Hyland and Sheldon, 2013); also, recent climate modeling efforts have simulated early Eocene warmth with a CO<sub>2</sub> level of only 560 ppm (2× pre-industrial levels) (Sagoo et al., 2013).

## IMPLICATIONS FOR CLIMATE SENSITIVITY

The regional paleoclimate data from Napartulik, along with its rich floral record, demonstrate that temperate conditions persisted during the middle Eocene at very high latitudes (Eberle and Greenwood, 2012). The CO<sub>2</sub> constraints we present are the first for a High Arctic forest, and together with the existing body of paleoclimate data suggest that a largely ice-free Arctic was maintained under CO<sub>2</sub> levels only ~1.5× pre-industrial values (0.60 doublings). The juxtaposition of a considerably warmer climate under only moderately elevated CO<sub>2</sub> has potentially important implications for Earth's sensitivity to CO<sub>2</sub>.

Climate sensitivity, defined as the equilibrium response in mean global surface temperature to a doubling of CO<sub>2</sub> above the pre-industrial level (e.g., IPCC, 2013), typically only includes “fast feedbacks” in Earth's climate system (e.g., snow, sea ice, and water vapor content); numerous studies support a climate sensitivity of ~3 °C (e.g., IPCC, 2013; Rohling et al., 2012). Earth system sensitivity (ESS), in contrast, includes both “fast” and “slow” (e.g., continental ice-sheet dynamics) feedbacks (Hansen et al., 2008; Lunt et al., 2010; Pagani et al., 2010). Estimates of ESS for an icehouse Earth are high (6+ °C) owing to the ice-albedo feedback associated with continental ice sheets (Hansen et al., 2008; Lunt et al., 2010; Pagani et al., 2010; Park and Royer, 2011). During times with little to no ice, such as the middle Eocene, it may be expected that ESS was ~3 °C; nonetheless, preliminary constraints on greenhouse ESS during the Cretaceous and early Paleogene suggest values above 3 °C (~3–5 °C; Hansen et al., 2013; Higgins and Schrag, 2006; Pagani et al., 2006; Royer et al., 2012; Zeebe et al., 2009). Data from Napartulik can be used to constrain ESS by assuming a site-mean CO<sub>2</sub> of 424 ppm and likely minimum mean global surface temperatures for the probable age range of the site (47.9–37.8 Ma) of ~6–11 °C warmer than pre-industrial conditions (see Fig. 1; Hansen et al., 2008; Royer et al., 2012). Following the methods of Royer et al. (2012), this implies a mean ESS of 4–8 °C over the last 48–38 m.y. These calculated ESS values are likely minima and have been adjusted

for concurrent changes in the radiative effects of solar evolution and paleogeography (see Royer et al., 2012). The CO<sub>2</sub> constraints presented here support a growing body of work for a greenhouse ESS sometimes exceeding 3 °C.

A number of hypotheses for boosts in polar temperatures, and thus ESS, have been offered in recent years. Increased polar stratospheric clouds (Abbot et al., 2009; Sloan and Pollard, 1998), increased methane and other trace greenhouse gases (Beerling et al., 2011; Jähren et al., 2004; Sloan et al., 1992), and increased latent heat transport (Ufnar et al., 2004) have all been argued as complementary warming mechanisms that may have acted during greenhouse climates. However, at present, a clear answer to this longstanding problem remains elusive, suggesting that our understanding of basic climate forcings and feedbacks during greenhouse periods is incomplete.

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