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# Estimating paleoatmospheric $pCO_2$ during the Early Eocene Climatic Optimum from stomatal frequency of *Ginkgo*, Okanagan Highlands, British Columbia, Canada

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ABSTRACT

Estimates of $pCO_2$ for the early Paleogene vary widely, from near modern-day levels to an order of magnitude greater, based on various proxy measures. Resolving the relationship between climate and $pCO_2$ during this globally warm period is a key task in understanding climate dynamics in a warmer world. Here, we use the stomatal frequency of fossil *Ginkgo adiantoides* from the Okanagan Highlands of British Columbia, Canada to estimate $pCO_2$ during the Early Eocene Climatic Optimum (EECO), the interval of peak warmth in the Cenozoic. We also examine a dataset of modern *Ginkgo biloba* leaves to critically assess the accuracy and precision of stomatal frequency as a proxy indicator of $pCO_2$. Early Eocene fossil *G. adiantoides* has significantly lower stomatal frequency than modern *G. biloba*, suggesting $pCO_2$ levels $>2\times$ modern pre-industrial values. This result is in contrast to earlier studies using stomatal frequency of *Ginkgo* that indicated near modern-day levels of $pCO_2$ in the early Paleogene, though not including samples from the EECO. We also find that levels of $pCO_2$ as indicated by stomatal frequency are correlated with trends in climate (mean annual temperature) over time at the Falkland fossil locality, suggesting that climate and $pCO_2$ were coupled during the EECO hyperthermal.

## 1. Introduction

The Early Eocene Climatic Optimum (EECO), ca. 53–50 Ma, was the warmest interval of the Cenozoic, indicated by multiple proxy mean annual temperature estimates for sea and land surfaces (Zachos et al., 2001, 2008). However, estimates of $pCO_2$ during the early Eocene from geochemistry (Demicco et al., 2003; Yapp, 2004; Lowenstein and Demicco, 2006), modeling (Berner and Kothavala, 2001; Thrasher and Sloan, 2009), and paleobotanical proxies (McElwain, 1998; Kürschner et al., 2001; Retallack, 2001; Royer et al., 2001; Greenwood et al., 2003; Royer, 2003) show a wide range of values, from near modern-day levels to an order of magnitude greater. In part, the variability in estimates may reflect high oscillations in $pCO_2$ during this time period (Pearson and Palmer, 2000; Demicco et al., 2003). However, the differences in estimates may reflect real issues of accuracy and precision with various proxy datasets. Climate models at global and regional scales have been unable to produce simulations that reconcile both $CO_2$ levels and climate estimates from paleontological data for the early Eocene (Thrasher and Sloan, 2009). Resolving the $pCO_2$ record for this time period, and thereby correlating it with trends in temperature, is a key task in understanding the interaction of climate and $pCO_2$ in globally warm periods.

Greenhouse periods in Earth history provide the best available evidence for developing and refining models to predict future impacts of global climate change on terrestrial ecosystems (Royer, 2008; Zachos et al., 2008). Therefore, the development of paleobotanical proxy measures of paleoenvironmental parameters has received growing attention in recent years, as have concerns over both accuracy and precision of these proxies (Royer, 2001, 2006; Greenwood, 2007). One such proxy measure is the stomatal frequency of land plants, which has been shown in some species to vary inversely with atmospheric $pCO_2$ (Woodward, 1987), and has been used to estimate paleo-$pCO_2$ for multiple geological time periods, including the Paleozoic (e.g. McElwain and Chaloner, 1995; Beerling, 2002), the Mesozoic (e.g. McElwain and Chaloner, 1996; McElwain et al., 1999; Haworth et al., 2005; Passalia, 2009; Quan et al., 2009; Barclay et al., 2010), and the Cenozoic (e.g. Beerling et al., 1992; Van Der Burgh et al., 1993; Royer, 2003; Kürschner et al., 2008). Given the potential practical applications in refining and testing climate models, there is a need to expand the available datasets as well as to critically assess the validity of this proxy. This paper applies the stomatal frequency technique to estimating paleo-$pCO_2$ during the EECO using fossil material of *Ginkgo adiantoides* (Unger) Heer from the Falkland macroflora, part of the Okanagan Highlands series of fossil localities in British Columbia, Canada (Fig. 1; Greenwood et al., 2005; Moss et al., 2005; Smith et al., 2009). In addition, we explore the issue of natural variability in modern populations of *Ginkgo biloba* L., expanding on earlier work by Chen et al. (2001) and Sun et al. (2003).

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## 2. Background

Studies based on historical herbarium material and fossil leaves, as well as experimental studies under $CO_2$ enrichment (or depletion), have shown a general, though not universal, inverse relationship between $CO_2$ levels and stomatal frequency (for a review see Royer, 2001). Stomata are the controlled pores through which plants exchange gases with their environments, and play a key role in regulating the balance between photosynthetic productivity (rate of carbon uptake) and water loss through transpiration. Stomatal response to atmospheric $pCO_2$ varies by species, suggesting caution in comparing data across taxonomic boundaries (Salisbury, 1927; Royer, 2001; Beerling and Royer, 2002b; Greenwood et al., 2003; Royer, 2003; Sun et al., 2003). Therefore, studies tracking correlations between stomatal frequency and $CO_2$ levels should, as far as possible, be based on single-species correlations and ideally under similar habitat conditions (Beerling and Chaloner, 1992; Beerling and Royer, 2002; Greenwood et al., 2003; Royer, 2003; Haworth et al., 2010). Difficulty in identifying appropriate modern analogs for fossil taxa at the species level presents a significant obstacle in the extrapolation of paleoclimate signals from stomatal characteristics in fossil material. For this reason, stomatal frequency of the "living fossil" *Ginkgo biloba* in combination with its fossil analogs is often used in applications of this technique, as there is little evidence of morphological change in this lineage since the Cretaceous (Royer et al., 2003).

Stomatal frequency in *Ginkgo biloba* has been shown to vary inversely with atmospheric $pCO_2$ in experimental studies and in studies based on herbarium material representing the past 150 yr, where $pCO_2$ levels are known (Beerling et al., 1998; Royer, 2003; Beerling et al., 2009). Based on this observed inverse relationship, a number of studies have used fossil *Ginkgo* to estimate paleo-$pCO_2$ for various time periods in the Mesozoic and Cenozoic. Beerling et al. (1998) found that *Ginkgo* from the Triassic and Jurassic showed stomatal frequencies similar to *G. biloba* grown under moderately enriched $pCO_2$ (560 ppmV) in experimental trials, and significantly lower stomatal frequency compared to *G. biloba* grown under ambient $pCO_2$. The Mesozoic is generally recognized as a warm period in Earth history, and thus these results suggest a coupling of elevated $pCO_2$ and temperatures during this period. Passalia (2009) found evidence of modest levels of enrichment of $pCO_2$ (466–777 ppmV) in the Lower Cretaceous (middle Aptian, ~117–120 Ma) based on Ginkgoales, but found higher $pCO_2$ levels indicated by stomatal frequencies of other taxa for this time period. Quan et al. (2009) inferred a gradual decline in $pCO_2$ during the Campanian (Late Cretaceous) based on SI of *Ginkgo adiantoides* from China, with background levels of $pCO_2$ higher than modern at ~550–590 ppmV. In addition, they observed short-term fluctuation in $pCO_2$ during the upper Campanian, with a transient increase to ~690 ppmV.

Royer and colleagues (Royer et al., 2001; Royer, 2003) used *Ginkgo* to track $pCO_2$ levels for the early Paleogene (Paleocene to early Eocene, ca. 65–53 Ma), another warm period in Earth history (Zachos et al., 2001, 2008). Their results indicated that $pCO_2$ levels were similar to the present day (between ~300 and 450 ppmV), suggesting that factors other than $pCO_2$ may have been at work in forcing climate. Recently, however, Beerling et al. (2009) revisited this dataset with a revised statistical approach to estimating paleo-$pCO_2$ from fossil leaves and quantifying uncertainty. The application of their method resulted in an upward revision of these estimates by 150 to 250 ppmV, suggesting $pCO_2$ levels of ~450 to 700 ppmV for the early Paleogene from the same fossil dataset. Retallack (2001) found much higher levels of atmospheric $pCO_2$ in the early Paleogene (~1500–4500 ppmV) based on stomatal frequency of *Ginkgo*, but used a different transfer function than Royer and colleagues. However, Retallack's study relied on previously published images of *Ginkgo* cuticle (representing an unknown range of variability within samples) and in some cases utilized fewer than five leaf fragments to obtain average counts, which is the minimum number deemed adequate by most workers in the field (Beerling and Royer, 2002; Royer, 2003; Quan et al., 2009). In addition, the $pCO_2$ estimates in some cases are based on a transfer function that extrapolates beyond

**Fig. 1.** Map showing location of the Falkland fossil site, and select Okanagan Highlands localities (Republic, Princeton, Quilchena, McAbee and Horsefly). A) Outline map of Canada, with GIS data provided by The Atlas of Canada (Department of Natural Resources Canada). B) Detail of portion of British Columbia, Canada and Washington, USA. World shaded relief map data provided by ESRI ArcGIS Online and data partners.