



A reduced order model to analytically infer atmospheric CO₂ concentration from stomatal and climate data



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ABSTRACT

To address questions related to the acceleration or deceleration of the global hydrological cycle or links between the carbon and water cycles over land, reliable data for past climatic conditions based on proxies are required. In particular, the reconstruction of palaeoatmospheric CO₂ content (C_a) is needed to assist the separation of natural from anthropogenic C_a variability and to explore phase relations between C_a and air temperature T_a time series. Both T_a and C_a are needed to fingerprint anthropogenic signatures in vapor pressure deficit, a major driver used to explain acceleration or deceleration phases in the global hydrological cycle. Current approaches to C_a reconstruction rely on a robust inverse correlation between measured stomatal density in leaves (ν) of many plant taxa and C_a . There are two methods that exploit this correlation: The first uses calibration curves obtained from extant species assumed to represent the fossil taxa, thereby restricting the suitable taxa to those existing today. The second is a hybrid eco-hydrological/physiological approach that determines C_a with the aid of systems of equations based on quasi-instantaneous leaf-gas exchange theories and fossil stomatal data collected along with other measured leaf anatomical traits and parameters. In this contribution, a reduced order model (ROM) is proposed that derives C_a from a single equation incorporating the aforementioned stomatal data, basic climate (e.g. temperature), estimated biochemical parameters of assimilation and isotope data. The usage of the ROM is then illustrated by applying it to isotopic and anatomical measurements from three extant species. The ROM derivation is based on a balance between the biochemical demand and atmospheric supply of CO₂ that leads to an explicit expression linking stomatal conductance to internal CO₂ concentration (C_i) and C_a . The resulting expression of stomatal conductance from the carbon economy of the leaf is then equated to another expression derived from water vapor gas diffusion that includes anatomical traits. When combined with isotopic measurements for long-term C_i/C_a , C_a can be analytically determined and is interpreted as the time-averaged C_a that existed over the life-span of the leaf. Key advantages of the proposed ROM are: 1) the usage of isotopic data provides constraints on the reconstructed atmospheric CO₂ concentration from ν , 2) the analytical form of this approach permits direct links between parameter uncertainties and reconstructed C_a , and 3) the time-scale mismatch between the application of instantaneous leaf-gas exchange expressions constrained with longer-term isotopic data is reconciled through averaging rules and sensitivity analysis. The latter point was rarely considered in prior reconstruction studies that combined models of leaf-gas exchange and isotopic data to reconstruct C_a from ν . The proposed ROM is not without its limitations given the need to a priori assume a parameter related to the control on photosynthetic rate. The work here further explores immanent constraints for the aforementioned photosynthetic parameter.

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1. Introduction

It has been known for some time now (Allen and Ingram, 2002; Held and Soden, 2006; Katul et al., 2012) that long-term changes in atmospheric CO₂ concentrations (C_a) and concomitant air temperature (T_a) alter the long-term balance between global precipitation

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P_g and evaporation E_g as:

$$\frac{\Delta P_g}{P_g} = \frac{\Delta E_g}{E_g}, \quad (1)$$

where ΔP_g and ΔE_g signify the climate-induced precipitation and evaporation changes due to changes in C_a and T_a , respectively. When representing $E_g = \gamma VPD$ (γ denotes a bulk transfer coefficient to water vapor and is a function of wind speed, C_a and T_a , VPD is the vapor pressure deficit), the acceleration ($\Delta P_g > 0$) or deceleration ($\Delta P_g < 0$) of the global hydrological cycle can be reasonably constrained by

$$\frac{\Delta P_g}{P_g} = \frac{\Delta \gamma}{\gamma} + \frac{\Delta VPD}{VPD}. \quad (2)$$

The $VPD = e^*(T_a)(1 - RH)$ is governed by the saturation vapor pressure ($e^*(T_a)$), given by the Clausius-Clayperon equation) and air relative humidity (RH) that appears to be robust to large climatic changes. A few approximations described elsewhere (Katul et al., 2012, especially their Figure 2) result in $\Delta VPD/VPD \approx 0.0675 \Delta T_a$. Climate simulation estimates of $\Delta P_g/P_g$ appear to be a factor of 2 smaller than estimates based only on $\Delta VPD/VPD$ (i.e. ignoring $\Delta \gamma/\gamma$) prompting interest in how this quantity is altered by changes in atmospheric CO_2 (past and future) over land and oceans. Over land, inferring $\Delta \gamma/\gamma$ is particularly complicated by the fact that the plant component of γ impacts and is impacted by C_a at a broad range of time scales. This complication may be turned around into an advantage when attempting reconstruction of past C_a , which is fraught with much more uncertainty when compared to its ΔT_a counterpart. In fact, a solid estimation exists and summarized by the IPCC Fourth Assessment Report that covered some 14 reconstruction methods for ΔT_a that are all roughly converging. It is, however, more difficult to obtain sound data for the past C_a (Jordan, 2011) as needed to assess past trends in the hydrological cycle or indirect expressions of it such as the time-evolving phase relation between ΔT_a and C_a . While all aspects of this problem remain well beyond the scope of a single study, reconstruction of global C_a from various proxies that include stomatal data of fossil plants continues to be a subject of inquiry (Beerling and Woodward, 1996; Beerling and Chaloner, 1992; 1993a; Crowley and Berner, 2001; Franks et al., 2014; Grein et al., 2013; Haworth et al., 2005; Kürschner et al., 2008; Maxbauer et al., 2014; Royer, 2001; Royer et al., 2001; Rundgren and Beerling, 1999; Steinthorsdottir et al., 2013; Wagner et al., 1999). Specifically, what is often disputed are the uncertainties in C_a associated with reconstruction efforts using fossil plants (Franks et al., 2014; Poole et al., 1996), which as shown here can benefit from imposition of eco-hydrological and physiological constraints and constitutes the main novelty of this contribution.

The basic premise to all reconstruction schemes utilizing anatomical stomatal measurements is a robust negative correlation between stomatal density ν and C_a that is often observed on extant plants (either experimentally or with herbarium material). While other factors modulate the rate of change of ν with C_a , the robustness of the negative correlation between these two variables appears in numerous species (Royer, 2001). In fact, Woodward (1987) demonstrated that more than 67% reduction in ν occurs due to C_a increases from 280 ppm to 340 ppm in arboreal species collected over a 200 year period. The original reconstruction technique was based on calibration curves obtained from extant taxa showing a change in ν with increasing C_a . These curves are then applied to fossil data sets where measured changes in ν is used to infer C_a . Using such calibration curves is limited to fossil material belonging to still extant taxa and extrapolations beyond the calibration conditions can be questionable (Beerling, 1999). This limitation prompted interest in alternative methods that are mecha-

nistic yet do not *a priori* assume a negative correlation between ν and C_a and frame the scope here.

The basic premise behind the mechanistic eco-hydrological-physiological approaches is that if a negative correlation between ν and C_a exists, it must be attributed to an adaptation of the plant gas exchange system to the availability of atmospheric CO_2 . Some studies refute this claim (Bettarini et al., 1998) but many others support it (see e.g. Beerling et al., 1993; Hetherington and Woodward, 2003; McElwain and Chaloner, 1995; Peñuelas and Matamala, 1990; Wagner et al., 1996). Short-term exposure (several years) of plants to changing C_a have minor to no impact on ν as demonstrated by a number of Free Air CO_2 Enrichment (FACE) experiments, gradient-type chamber experiments, or field studies (Estiarte et al., 1994; Malone et al., 1993; Reid et al., 2003). Hence, reconstruction of C_a from ν cannot be explored from short-term manipulation experiments that do not allow long-term evolutionary adaptation. To link ν and C_a mechanistically, models of plant gas exchange that connect the supply of atmospheric CO_2 to the photosynthetic demand are required. The supply side is commonly represented by Fick's law of gas diffusion through stomates and the biochemical photosynthetic demand side is represented by the widely used photosynthesis model of Farquhar et al. (1980). During the last years, efforts were made to estimate C_a from fossil stomatal data directly by using such balance between supply and demand for atmospheric CO_2 (Franks et al., 2014; Konrad et al., 2008). The rationale for developing these models are (1) to ensure the reconstruction method is independent from the stratigraphic range of extant taxa, (2) to allow such reconstruction to utilize other data sources such as isotopic measurements (e.g. $\delta^{13}C$) for constraining C_a (Van De Water et al., 1994), and (3) to explore the eco-physiological basis for the emergence of stomatal density responses to increased atmospheric CO_2 . While such models do not address all aspects of the sought-after $\Delta \gamma/\gamma$, they do offer a novel eco-hydrological perspective on how to constrain some of its components on time scales commensurate with plant evolution.

It should be mentioned that besides ν , the size of the stomatal pore can change during evolution (de Boer et al., 2016; Franks and Beerling, 2009). Thus, adjustment of pore size is perhaps a further adaptive element to fine-tune the gas exchange apparatus to shifting CO_2 (Assouline and Or, 2013; 2015; Roth-Nebelsick et al., 2012). Stomatal mechanics also varies among plant groups, which may also constrain guard cell size (Franks and Farquhar, 2007). It is therefore necessary to obtain the stomatal pore length above and beyond ν when modeling gas exchange using measured leaf anatomical traits. Models describing the effects of increased C_a on ν and gas exchange can be complex depending on the manifold of parameters and processes considered. Within the confines of the C_a reconstruction problem here, model complexity cannot be divorced from available parameters, fossil data, and the stratigraphic age of the material. In this contribution, a reduced order model (ROM) resulting in a single-equation that can be used to analytically infer C_a from stomatal data of C_3 -plants (including ν), leaf carbon isotope data and basic climatic conditions is proposed and tested. This ROM is based on approximations to a detailed model linking the soil-plant-atmosphere system described elsewhere (Konrad et al., 2008) but where the measurable macroscopic properties of this system (or order parameters) are substantially reduced without significant loss in accuracy with regards to the inference of C_a . The usage of the term ROM here differs from its popular form used in computational physics, where a phase-space of a high-dimensional model can be reconstructed using lower-order modes derived from a projection (e.g. proper-orthogonal decomposition). However, the definition here retains the original intent of ROM, which is a reduction in degrees of freedom leading to an approximation of a high-dimensional model covering many aspects of the soil-plant-atmosphere system.

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