Fossil leaves: Effective bioindicators of ancient CO₂ levels?

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[1] Past variations in the concentration of the greenhouse gas CO₂ are thought to have played a major role in controlling Earth’s climate on pre-Quaternary and Quaternary timescales. To identify the contribution of CO₂ to past climatic change requires accurate quantification of its content in the ancient atmosphere, and a number of proxies have been developed for this purpose (for a review see Royer et al. [2001a]). For the Late Quaternary, there is the unique opportunity to measure directly the composition of fossil air samples trapped in bubbles preserved in the polar ice sheets. Results from Antarctic ice cores reveal that the glacial-interglacial changes characterizing Quaternary climate were accompanied by variations in the atmospheric concentration of CO₂ [Petit et al., 1999; Shackleton, 2000; Mudelsee, 2001].

[2] Detailed ice core data from the last glacial period indicate temperature-CO₂ covariation on shorter, millennial, timescales [Stauffer et al., 1998]. However, such detailed studies are rarely feasible because the CO₂ concentrations retrieved from the ice cores are inherently smoothed by diffusion during air enclosure, an effect controlled by ice accumulation rate. It is therefore not a surprise that ice cores drilled at low accumulation sites show little evidence of abrupt CO₂ change during the last deglaciation [Minnin et al., 2001] and the Holocene [Indermühle et al., 1999]. A temporally detailed understanding of global carbon cycle dynamics over shorter, century to millennial timescales, might be achieved with sufficiently sensitive and reliable CO₂ proxies.

[3] Of the various CO₂ proxies available, the carbon isotope composition of phytoplankton and the boron isotope composition of calcium carbonate shells of foraminifera have temporal resolutions
suitable for detecting CO₂ changes on $10^3$–$10^4$ years [Royer et al., 2001a], but only the stomatal method has the capability to record century scale CO₂ dynamics. Moreover, it is also arguably the most direct, with cellular differentiation taking place as the leaves sense CO₂ in the environment. The CO₂ signal was encoded in fossil leaf cuticles because as atmospheric CO₂ concentrations increase, leaves of terrestrial vascular plants develop fewer stomatal pores for regulating gaseous exchange with the atmosphere [Woodward, 1987]. However, the recovery of quantitative information from this unique paleobotanical CO₂ archive is still in its infancy and has yet to gain widespread critical acceptance. To achieve this goal, its performance deserves to be critically evaluated against empirical data drawn from field studies, laboratory experiments, ice cores and the plant fossil record.

An important criterion for any CO₂ proxy is that the fidelity of the CO₂ signal remains undiminished by changes in other features of the environment. Paleo-CO₂ estimates from leaf fossils which utilize measurements of stomatal index (SI, defined as the percentage of leaf epidermal cells that are stomata) are likely to be secure. This is because observations on leaves of tree and shrub populations growing across natural climatic gradients, and controlled environment experiments, show SI is relatively insensitive to soil water supply, irradiance, atmospheric moisture and temperature [Beerling, 1999; Royer, 2001]. The stability of SI arises because it is a proportional quantity independent of leaf expansion; CO₂ actually changes the number of epidermal cells that develop into stomatal pores [Woodward, 1987]. In fact, altering the growth atmospheric CO₂ concentration is one of the few means of inducing a marked change in the SI of leaves within a given species. Stomatal density, in contrast, simply expresses the number of stomata per unit area of leaf, and is influenced by the climate-controlled degree of leaf expansion (see Figure 1).

If measurements of fossil leaf SI securely reflect past CO₂ changes, how do the stomatal-based paleo-CO₂ reconstructions compare with benchmark CO₂ records reported from ice core studies? A key demonstration of the capacity of the technique to capture and retrieve the past CO₂ history of the atmosphere derives from temporally detailed measurements on radiocarbon-dated Holocene fossils, made exclusively with leaves of the dwarf willow (Salix herbacea) [Rundgren and Beerling, 1999]. The resulting reconstruction shows a pattern of CO₂ accumulation in the atmospheric reservoir over 7000 yrs that closely tracks the Taylor Dome Antarctic ice core CO₂ record, although the stomatal record shows a greater amplitude [Indermühle et al., 1999] (see Figure 1). Both records also reveal minor fluctuations during the so-called Medieval Warm Period and the Little Ice Age climatic oscillations, as well as the more recent exponential rise in CO₂ due to fossil fuel burning and deforestation (see Figure 1).

For the Holocene, the CO₂ patterns compare favourably, but terrestrial high-resolution CO₂ reconstructions [Beerling et al., 1995; McElwain et al., 2002; Wagner et al., 2002; Rundgren and Björck, 2003] through millennial-scale climate variations of the last deglaciation have revealed interesting new information that is absent from ice cores. They show that the steady rise in CO₂ during deglaciation was apparently interrupted by an abrupt fall in CO₂ coinciding with the beginning of the Younger Dryas stadial (see Figure 1). In addition, a temporary CO₂ decline is registered at the time of the Preboreal oscillation, an early Holocene cooling event. Measurements on the Dome C Antarctic ice core indicate a more gradual glacial CO₂ increase [Monnin et al., 2001] without the relatively high-amplitude changes suggested by stomatal data. The trends in the two sets of data are, however, almost identical (see Figure 1). This discrepancy can partly be accounted for by the smoothing of ice core CO₂ records caused by diffusion. The age distribution of enclosed air at the Dome C site, for example, lies between 200 and 550 yrs [Monnin et al., 2001], which is an order of magnitude larger than in a single sample of fossil leaves (30–40 yrs). If the fossil leaves are accurately portraying Lateglacial global carbon cycle dynamics, they suggest a higher sensitivity to climate than previously realized (see Figure 1) and demand a coherent explanation from the modelling community.
Figure 1. Stomata and CO$_2$. (a) Effects of climate on leaf stomatal density (SD) and stomatal index (SI). Under droughted conditions, leaf epidermal cells are small and the stomata tightly packed. Under non-droughted conditions epidermal cells are fully expanded forcing the spacing of the stomatal pores further apart, thereby decreasing SD. Because the proportion of epidermal cells that are stomata has not changed between either condition, SI remains constant. (b) Comparison of a Holocene terrestrial reconstruction of atmospheric CO$_2$ partial pressure, based on changes in the SI of fossil S. herbacea leaves [Rundgren and Beerling, 1999], with atmospheric CO$_2$ records from Antarctic ice cores [Etheridge et al., 1996; Indermühle et al., 1999]. The SI record is in CO$_2$ partial pressure because stomata respond to partial pressure rather than mole fraction [Woodward, 1987], and the leaf materials were cored from a site 999 m above sea level. The approximate timing of the Medieval Warm Period (MWP) and Little Ice Age (LIA) are indicated. (c) Comparison of Lateglacial CO$_2$ changes reconstructed from fossil leaves of three species of dwarf shrubs, each independently calibrated, for the Lateglacial [Rundgren and Björck, 2003], and the Dome C ice core record [Monnin et al., 2001]. Fossil leaves were obtained from a Swedish site close to sea level enabling direct reconstruction of past CO$_2$ concentrations in parts per million (ppmv). Timescales in Figures 1b and 1c are in years before present (BP) = years before AD 1950. Green lines in Figures 1b and 1c are the locally weighted regression and 5 point running means, respectively. Black line in Figure 1c is the high resolution oxygen isotope curve from the Greenland Ice Core Project [Johnsen et al., 2001].
[7] Other early Holocene and Lateglacial records [Wagner et al., 1999; McElwain et al., 2002] have reproduced similar CO₂ patterns, indicating self consistency in the approach both between species and sites. Some stomatal-based records however have reconstructed atmospheric CO₂ values higher (maximum 40 ppmv) than those obtained in ice core studies [Wagner et al., 1999, McElwain et al., 2002; Wagner et al., 2002]. The overestimations in these studies may relate to the use of fossil leaf assemblages containing a mixture of closely related species. Leaf SI responds to CO₂ in a strongly species-specific manner [Royer et al., 2001a]; even closely related species capable of hybridising with each other differ in their CO₂ responsiveness [Rundgren and Björck, 2003]. Additionally, studies involving fossil Betula leaves may be compromised by developing calibration functions with trees of very restricted genotypic diversity [Birks et al., 1999].

[8] However, how important are such mismatches relative to the performance of the other three leading paleo-CO₂ proxies? And should they be allowed undermine stomatal-derived paleo-CO₂ estimates? The paleosol CO₂ barometer has typical errors of ±300–500 ppmv and is unsuitable for tracking ice core CO₂ variations because of the time required for the formation of soil carbonates (10³–10⁴ yrs) [Cerling, 1992]. Atmospheric CO₂ records derived from the carbon isotope composition of alkenones track the CO₂ variations of the last glacial-interglacial seen in ice cores, but significant (c. 20 ppmv or more) mismatches are evident [Jasper et al., 1994]. As recently shown by Pagani et al. [2002], accurate CO₂ reconstruction by this approach requires parallel estimates of marine phosphate concentration. CO₂ records based on the boron isotopic method are likely to be influenced by changes in upwelling [Palmer and Pearson, 2003], and its accuracy is called into question because it suggests that whole-ocean pH was stable over the last glacial-interglacial cycle [Anderson and Archer, 2002].

[9] An implicit assumption for paleo-CO₂ proxies involving the biota is that the growth of an organism in responses to its environment is the same on ecological and evolutionary timescales. For vascular land plants such as S. herbacea it is probably a quite reasonable assumption because atmospheric CO₂ values reconstructed with fossil leaves dating back to the last interglacial (the Eemian, 130–115 kyrs BP) [Rundgren and Bennike, 2002] are directly comparable with CO₂ data reported from the Vostok Antarctic ice core [Petit et al., 1999]. On a multimillion year timescale, the relationship between SI and CO₂ exhibited by modern Ginkgo trees has been validated by analyses of changes in the SI of early Paleogene fossil Ginkgo leaves and independent CO₂ estimates from paleosols spanning some 3 Myr [Beerling and Royer, 2002]. Strong arguments exist therefore to expect a similarity between the phenotypic and genotypic responses of plants to past histories of CO₂; arguments which are critical to establishing the credibility of stomatal-based paleo-CO₂ estimates.

[10] The elegance of the stomatal paleo-CO₂ proxy is that it rests on a simple inverse correlation between CO₂ and stomatal formation which is underpinned by a gene involved in the signal transduction pathway controlling stomatal numbers at elevated CO₂ [Gray et al., 2000]. Encoded into the leaf fossil record therefore is a rich archive detailing how the CO₂ content of the ancient atmosphere has varied. Over the last decade, surprisingly rapid progress has been made in recognizing and recovering this valuable source of CO₂ information. It has, for example, provided clues to the causes of mass extinction events [McElwain et al., 1999] and new constraints on radiative forcing by CO₂ in the Tertiary [Royer et al., 2001b]. With the capacity to record millennial and century-scale CO₂ changes, the stomatal approach to paleo-CO₂ estimation offers the potential to identify new undetected rapid reorganizations of the global carbon cycle, as already suggested for the last deglaciation (see Figure 1).

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