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Biophysical analysis of plant gas exchange and reconstruction of palaeoclimate

Wilfried Konrad (1), Anita Roth-Nebelsick (2), and Michaela Grein (2)

(1) University of Tuebingen, Institute for Geosciences, Sigwartstrasse 10, D-72076 Tuebingen, Germany, wilfried.konrad@uni-tuebingen.de, (2) State Museum of Natural History Stuttgart, Rosenstein 1, D-70191 Stuttgart, Germany

We present a systematic derivation of the relation between stomatal density and CO2concentration based upon (i) a quantitative model of C3-photosynthesis, (ii) the physics of diffusion, and (iii) an optimisation principle which asserts that plants adjust stomatal conductance such that assimilation is maximised and transpiration is minimised. Since maximum stomatal conductance per leaf area is related to stomatal density the model leads to an equation connecting parameters which describe (a) the environment (stomatal density, atmospheric CO2-concentration, leaf temperature, atmospheric humidity, soil water content, insolation, wind velocity) (b) leaf and stoma anatomy, (c) C3photosynthesis.

Due to the formulation of the model in terms of analytic functions, sensitivity studies can easily be performed. According to the results, stomatal density depends strongly on atmospheric CO2concentration, leaf temperature, atmospheric humidity, soil water content, stomatal area, stomatal depth and one of the photosynthetic parameters. Compared to these, the influence of the other parameters (for example, wind speed) is negligible. It is usually assumed that the stomatal index is largely independent from climate and represents therefore a more robust quantity for reconstructing CO2. However, the stomatal index does 1) not consider the changes in stomatal anatomy that can often observed in a lineage (for example, pore length) and 2) the stomatal index itself may also be influenced by climate. Additionally, it is often not possible to determine the density of epidermal cells which is a prerequisite for calculating the stomatal index.

We suggest to focus on stomatal density for CO2 reconstruction. Stomata of fossil leaves are often well preserved and photosynthetic biochemical parameters are comparatively conservative. Hence, the model ties essentially the four environmental quantities atmospheric CO2-concentration, temperature, atmospheric humidity and soil water content to the fossil stomatal density and stomatal anatomy. In other words, if three of these environmental quantities are already known, the fourth is provided by the mathematics of the model. Attempts to obtain the atmospheric CO2concentration from stomatal density (or stomatal index) should therefore accompanied by additional palaeoclimate studies of the considered sites.