

Calibrating the silica-phytolith paleothermometer

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Paleoclimate potential of phytolith $\delta^{18}\text{O}$ values

Plants absorb aqueous silicic acid from soils and precipitate silica phytoliths in cells along the transpiration stream. Phytoliths are composed of opal-A and can accumulate in soils when plants decay. Ancient phytoliths can provide paleoclimate information because their $\delta^{18}\text{O}$ values vary with temperature and the $\delta^{18}\text{O}$ values of plant water. However, a detailed understanding is required of how the $\delta^{18}\text{O}$ values of phytoliths vary in response to fluctuations in temperature and plant water $\delta^{18}\text{O}$ values over the growing season.

Horsetail (*Equisetum hyemale*) plants were grown under constant temperatures for 6 months. The $\delta^{18}\text{O}$ values of watering-water, plant-water and atmospheric-water vapour were monitored monthly and the $\delta^{18}\text{O}$ values of phytoliths were determined after the plants reached maturity. Fluctuations in plant-water $\delta^{18}\text{O}$ values resulted from changes in the $\delta^{18}\text{O}$ values of atmospheric vapour, the maturity of the plant and related changes in transpiration. Higher plant-water $\delta^{18}\text{O}$ values occurred in the warmer growth chambers but also toward the apex each plant and these values increased over time. Phytolith $\delta^{18}\text{O}$ values increased from 35.9, 37.1, 37.5 to 43.4 ‰ in the 15, 20, 25 and 30 °C growth chambers, respectively.

Comparison to opal-A paleothermometers

Plant-water and phytolith $\delta^{18}\text{O}$ values were used to evaluate the fit of the observed phytolith oxygen-isotope fractionation to existing opal-A paleothermometer equations developed for diatoms and phytoliths grown under field conditions where temperatures were variable [1,2]. A linear relationship between $1000\ln\alpha$ and $10^6/T^2$ was not observed for the phytoliths when the plant-water $\delta^{18}\text{O}$ values were averaged over the growing season. Instead, the phytolith paleothermometer equation most closely resembles recent diatom paleothermometers [1] when plant-water $\delta^{18}\text{O}$ values from the latter half of the growing season are used for plants grown at 20-30°C and when plant-water from the mid-growing season is used to calculate $1000\ln\alpha$ for the plants grown at 15°C. These results support earlier finding [2] that the $\delta^{18}\text{O}$ values of phytoliths are dominated by phytoliths produced later in the growing season. Horsetails grown at 15°C were unhealthy at the end of the experiment and phytolith deposition was likely restricted after the fifth month.

This study demonstrates that the oxygen-isotope fractionation between phytoliths and water is similar to that observed for diatom opal-A. However, interpretation of a phytolith oxygen-isotope paleothermometer must consider the timing of silica deposition. Non-ideal growth conditions can limit phytolith formation, creating disequilibrium between silica and average seasonal plant water.

[1] Dodd & Sharp (2010) *Geochim. Cosmochim. Acta* **74**, 1381-1390. [2] Shahack-Gross et al. (1996) *Geochim. Cosmochim. Acta* **60**, 3949-3953.

Plankton diversity and ocean circulation regulate the ocean nitrogen reservoir

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Regulation of the ocean N reservoir

The average elemental composition of marine plankton is closely matched to the availability of the major nitrogen (N) and phosphorus (P) nutrients. This is understood to arise from biological control over the ocean's N budget, in which removal of N by denitrification selects for diazotrophic phytoplankton that add new N to the ocean when it limits the growth of other species. Current understanding of this feedback mechanism derives from box models of the ocean, which lack a realistic representation of physical mixing and the spatial heterogeneity of biological processes.

Role of plankton diversity and ocean circulation

We show that in the context of a realistic ocean circulation and a uniform 'Redfieldian' N:P ratio of plankton biomass, this feedback mechanism consistently yields too little N relative to observations. The solution lies in the large-scale variability of phytoplankton N:P ratios, which range from ~10:1 in diatom-dominated regions to >20:1 in low-diatom regions [1]. Because diazotrophs compete with high N:P subtropical plankton, the N reservoir is restored towards a higher value than in the Redfieldian case. However, low N:P communities outside the subtropics do exert some leverage over the ocean's nutrient balance, because their stoichiometric signature is transported to diazotrophic habitats through shallow pathways of ocean circulation.

Conclusions

Our study demonstrates that a combination of local ecosystem dynamics, plankton biogeography, and large-scale circulation patterns control the availability of fixed N in the ocean, and thus ocean fertility and carbon storage over millennial timescales.

[1] Weber & Deutsch (2010) *Nature* **467**, 550-554.