Differences in carbon isotope fractionation between angiosperm and gymnosperm woody plants, and their significance for paleoatmosphere and hydroclimate reconstruction.

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In terrestrial contexts, the stable carbon isotopic composition of fossil C_3 plant matter is widely used as a proxy of past hydroclimate and atmospheric CO_2 concentration. Presently, differences in carbon isotope discrimination ($\Delta^{13}C$) between the two major vascular plant groups, angiosperms and gymnosperms, are relatively small (2–3‰). Yet, an increasing body of evidence suggests that larger differences occurred across geological times (up to 6–7 ‰). Unfortunately, an accurate first principles understanding of how different C_3 plant groups respond to variable environments and atmospheres (e.g. CO_2 and O_2 concentrations) is currently uncertain, with important consequences for the interpretation of the fossil record, and the accuracy of paleo-proxies.

Here we develop a comprehensive *ab initio* model of discrimination, to show how differences in $\Delta^{13}C$ between angiosperms and gymnosperms arise from three key physiological differences: (1) the ratio of cost factors for transpiration to carboxylation (higher in angiosperms); (2) the ratio of mesophyll to stomatal conductance of CO_2 (lower in gymnosperms); and (3) differences in photorespiration. As a result of these factors, angiosperm $\Delta^{13}C$ is more sensitive to CO_2, and gymnosperm $\Delta^{13}C$ is more sensitive to VPD. Isotopic data from 20th century leaves, tree rings (n >7000) and previously-published plant chamber experiments, along with geological data from the Cenozoic, agree with our model over a range of O_2:CO_2 ratios from 100 to 650 mol mol^{-1} (equivalent to a CO_2 range of around 323 - 2000 ppm at 21% O_2), and VPD levels between 0.45 and 1.1 kPa.

Our new framework offers a refined explanation for secular trends in $\Delta^{13}C$ in the geological record, and reconciles previously unexplained observations, such as covariation of modern tree ring $\Delta^*_{a\text{-}g}$ with latitude (and VPD), variable O_2, and differences during glacial maxima. We show how incorporating differences in plant responses can improve estimates of past hydroclimate and atmospheres, by applying the new framework to the Mid-Miocene Climatic Optimum (MMCO, 17 to 15 Ma ago). We find a likely range of CO_2 between 550 and 700 ppm, at VPD levels between 0.8 and 1.4 kPa, in broad agreement with other paleo-CO_2 proxies from phytane, and $\delta^{11}B$.