Beyond the cellulose: Measuring shifts in water regime using oxygen isotopes of plant lipids

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There is sustained interest in isotopic proxies for assessing and scaling plant to ecosystem water balance, but the use of oxygen isotope composition ($\delta^{18}O$) has been mostly limited to plant cellulose, which does not persist after deposition. Here we compare $\delta^{18}O$ signals in bulk plant lipid extracts with cellulose $\delta^{18}O$, using field experiments with several C_3 and C_4 species, to validate the use of recalcitrant lipids as an explicit hydrological proxy. We show that manipulations of evapotranspiration (ET) replenishment yield unequivocal signals in both cellulose and lipid $\delta^{18}O$, regardless of species-specific variations in molecular composition (determined by Fourier Transform Infrared Spectroscopy - FTIR). Larger effects of shifts in water balance were observed in C_3 compared to C_4 plants, with the latter generally showing heavier (1-4‰) $\delta^{18}O$ values. Despite this intrinsic difference in absolute $\delta^{18}O$, our data provide concrete evidence of a predictable relative enrichment (>1‰ with a 30% reduction in water supply relative to ET loss), with no post-synthetic exchange and the effect of growing conditions preserved in C_3 and C_4 species ($\delta^{18}O_{LIP} = 0.3045\ \delta^{18}O_{CELL} + 6.0216$). In C_4 species, lipid $\delta^{18}O$ better reflects variation in water regime than cellulose, allowing comparisons that cannot be made using carbon isotope composition ($\delta^{13}C$), a common proxy for water use efficiency that is only applicable in C_3 plants. Moreover, in contrast to cellulose, lipid $\delta^{18}O$ signals are expected to persist following deposition (e.g., in soils and sediments) and can be used to address long-standing questions regarding past and ongoing changes in the terrestrial water cycle. The consistency of our results also indicate that bulk lipid $\delta^{18}O$ better integrates plant-mediated hydrological changes than more difficult (compound specific) hydrogen isotope (δD) analysis, as numerous hydrogen transfer reactions during lipid biosynthesis result in large variation and unpredictability of δD signals among species and commonly employed biomarkers. The next phase of understanding will come from the use of multiple proxies, advancing lipid $\delta^{18}O$ alongside its physiological controls, to improve our ability to reconstruct and predict shifts in water regime across spatiotemporal scales.