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Intramolecular stable isotope variation: Consequences for conventional isotope measurements and elucidation of new ecophysiological signals

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Isotope ratios (13C/12C and 2H/1H) have long been used in plant ecophysiology and for reconstruction of environmental variables. For decades it has also been known that heavy isotopes are distributed unevenly IN biological metabolites. In other words, the isotopomers of metabolites have unequal abundances. Consequently, conventional δ values are whole-molecule averages over varying intramolecular values. However, this biochemical knowledge has not been applied in plant ecophysiology or biogeochemistry, because the first measurements of intramolecular isotope distributions were extremely cumbersome, requiring breakdown of metabolites into small molecules and IRMS measurements on those. Since then, NMR methodology has advanced so that intramolecular isotope distributions can routinely be measured (Chaintreau et al., Anal. Chim. Acta 2013), although large samples are needed. Here we demonstrate the importance of intramolecular isotope distributions with several examples.
1. We show that 13C is distributed unevenly in tree-ring cellulose. While this is not surprising given previous observations, it has important consequences: When wood enters soil organic matter and is broken down, the δ13C of respired CO_2 will only follow δ13C of cellulose if the glucose units are fully respired. If part of the glucose molecules enters other pathways, such as the oxidative pentose phosphate pathway, δ13C of liberated CO_2 can deviate markedly from the whole-molecule value. This may have consequences for using δ13C of CO_2 to unravel ecosystem C exchange fluxes.
2. Intramolecular isotope distributions are created by enzyme isotope effects, hence they constitute fingerprints of biosynthetic pathways and can report on regulation of metabolism on time scales up to millennia. As particular advantage, this information can be encoded in ratios of isotopomer abundances (Augusti et al., Chem. Geol. 2008), and can be extracted independent of the isotope ratio of the whole molecule, and of the isotope source (Ehlers et al., PNAS 2015).
3. We demonstrate that intramolecular 13C distributions of the glucose units of tree-ring cellulose vary over time. This implies that 13C fractionations mechanisms beyond the well-known stomata-Rubisco mechanism exist. The time-dependent intramolecular variation constitutes new ecophysiological information.
4. When δ13C or δD are used as proxies for ecophysiological parameters, correlation coefficients between both quantities are restricted to low values, limiting the power of isotope-based reconstructions. We show that this limitation is at least partly caused by intramolecular isotope variation. Conversely, higher correlation coefficients can be observed between intramolecular isotope parameters – position-specific carbon isotope ratios or deuterium isotopomer ratios – and ecophysiological parameters. Thus, intramolecular isotope data allow for more powerful reconstructions of physiological and environmental parameters.