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Carbon isotope composition of plant photosynthetic tissues reflects a Crassulacean Acid Metabolism (CAM) continuum in the majority of CAM lineages

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The stable carbon isotope composition of plant tissues, commonly expressed as delta C-13, holds a wealth of information about photosynthetic pathway, water relations and stress physiology. Crassulacean acid metabolism (CAM) is a derived form of photosynthesis that allows plants to fix carbon at a higher water-use efficiency compared to the ancestral C-3 photosynthesis. While the central carbon-fixing enzyme of C-3 plants, Rubisco, strongly discriminates against the heavy C-13 isotope, CAM is characterized by a dual use of Rubisco and the much less discriminating PEP carboxylase as carbon-fixing enzymes, causing the delta C-13 values of CAM plant tissues to be generally less negative than those found in C-3 plants. Past studies of delta C-13 variation in CAM plant lineages have repeatedly found a bimodal distribution with very few samples representative of the range around -20 parts per thousand that is intermediate between C-3- and CAM-like values. Although delta C-13 values of facultative CAM plants have long been known to extend well into the range below -20 parts per thousand, this value is often tentatively used as threshold for character coding to distinguish C-3 from CAM species in studies of CAM evolution. Compiling 6623 delta C-13 values reported in the literature for CAM/C-3 vascular plant lineages and presenting new data for 581 accessions mainly of the succulent Mesembryanthemoideae (Aizoaceae) and Aeonieae (Crassulaceae), we here investigate the diverse patterns of delta C-13 distribution in different plant families and sub-familial taxa and demonstrate that a bimodal distribution is not universally present in all lineages. Moreover, we show by means of mixture modelling that the bimodal distribution of delta C-13 values in the full dataset as well as in the very well-sampled Bromeliaceae is best described by a combination of three rather than two Gaussian distributions with one intermediary cluster between the more evident clusters of C-3- and CAM-like values. In view of these results and the furthermore emerging unimodal distribution of delta C-13 values in Mesembryanthemoideae with mean close to -20 parts per thousand, we conclude that the evident continuum between CAM and C-3 photosynthesis cautions against the usage of a delta C-13 threshold in macroevolutionary studies. Finally, the observed diversity of delta C-13 distribution patterns between monophyletic lineages urges for lineage-specific reconstructions rather than a unifying model of CAM evolution.
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