CRASSULACEAN ACID METABOLISM

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CRASSULACEAN ACID METABOLISM IN SUBMERGED AQUATIC PLANTS

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The submerged aquatic *Isoetes howellii* possesses CAM comparable to that found in terrestrial CAM plants. Substantial net CO_2 uptake occurs in the dark and is stored as malic acid. Overnight acidification is followed by daytime deacidification of the same magnitude observed in terrestrial CAM plants. Maximum malic acid production rates (20 μM mg^{-1} Chl h^{-1}) can be accounted for by net dark CO_2-uptake rates (35 μM mg^{-1} Chl h^{-1}) which, in turn, can be accommodated by PEP carboxylase activities (37 μM CO_2 mg^{-1} Chl h^{-1}). This pathway is shut off in the light and C_3 type CO_2 assimilation is possible. Day and night CO_2 uptake is known from terrestrial plants exhibiting CAM. Submerged *Isoetes* species differ from the prototype CAM plant ("Super-CAM" of Kluge and Ting) in that they lack stomata (or functional stomata); thus, they also lack a diurnal pattern of changes in stomatal conductance which (in terrestrial CAM plants) results in the bulk of the carbon gain occurring at night. However, such a pattern of CO_2 uptake may occur in *I. howellii*, being controlled by diurnal changes in CO_2 availability rather than by changes in stomatal conductance.

Diurnal acid metabolism of the order of magnitude found in terrestrial CAM plants is widespread in submerged aquatic *Isoetes* species and apparently absent in terrestrial *Isoetes* species. With few exceptions, aquatic *Isoetes* are found in one of two habitats: temporary seasonal pools or oligotrophic lakes. A survey of non-*Isoetes* aquatics shows acid metabolism in at least two other species--*Crassula aquatica* (Crassulaceae) from a vernal pool and *Littorella uniflora* (Plantaginaceae) from an oligotrophic lake. Overnight acid or malate accumulation has been reported (in the literature) for species found in habitats unlike these, though levels for such species are an order of magnitude less than that observed in *Isoetes howellii*.

My working hypothesis on the functional significance of CAM in aquatic plants is that it was selected as a means of enhancing carbon gain in carbon-limiting environments. Evidence to date is not definitive, but is consistent with this hypothesis. The two aquatic habitats *Isoetes* predominates--seasonal pools and oligotrophic lakes--are both potentially carbon-limited environments. In seasonal pools, free CO_2 may be depleted during the day and pH conditions of the pool may limit photosynthesis part of the day. The extremely low inorganic carbon levels (for aquatic environments with a high diffusive resistance to CO_2) characteristic of oligotrophic lakes may likewise limit photosynthesis. Both conditions could place a selective advantage on nighttime CO_2 uptake.