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BRIEF COMMUNICATION

Lack of Diurnal Acid Metabolism in Two Terrestrial *Isoetes* Species*

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Abstract

Even though the Crassulacean Acid Metabolism (CAM) has recently been demonstrated in fifteen submerged aquatic *Isoetes* species distributed worldwide, the present report shows that CAM is absent in the two terrestrial species *I. nuttallii* and *I. butleri* grown under both "natural" drained or "unnatural" submerged conditions. The terrestrial *I. nuttallii* survives up to five months of submergence and does not show any evidence of diurnal acid metabolism.

The submerged aquatic *I. howellii* Engelmann (*Isoetaceae*) has recently been shown to possess Crassulacean Acid Metabolism (CAM) comparable in magnitude to that observed in terrestrial CAM plants (Keeley 1981). CO_2 assimilated in the dark is fixed into malic acid which accumulates overnight. During the day acid levels drop resulting in a diurnal change of 100—300 μeq malic acid g^{-1}(f.m.). Accompanying daytime deacidification is a movement of dark-fixed carbon from organic acids to 3-phosphoglycerate and phosphorylated sugars.

The genus *Isoetes* includes over 60 species distributed worldwide, largely in "temperate" climates and freshwater aquatic or seasonally wet habitats (Pfeiffer 1922). Fifteen aquatic species of *Isoetes* from North America, Central America, Europe and Australia have been sampled and all show a distinct diurnal change in titratable acidity and malic acid while under submerged conditions (Keeley 1982 and unpublished data).

Worldwide, only a few *Isoetes* species are strictly terrestrial (Pfeiffer 1922). In North America there are two: the western *I. nuttallii* A. Br. ex. Engelmann, and the eastern *I. butleri* Engelmann. I report here the lack of diurnal acid metabolism in these two species (Table 1).

The absence of any flux in acidity is true whether it is measured at an endpoint of pH 6.4 or pH 8.3 (data not shown). The relatively constant malic acid (malate) levels are approximately the same as those levels observed in aquatic *Isoetes* at the end of the day, though the titratable acidity levels are several times lower than observed in aquatic *Isoetes* at the end of the day (Keeley 1982).

I. nuttallii lacks CAM whether it is maintained under "natural" drained conditions or "unnatural" submerged conditions. This terrestrial species survives five months of submergence and remains healthy without the diurnal acid metabolism characteristic of aquatic *Isoetes*.

The absence of CAM in *I. nuttallii* and *I. butleri* likely are related to their terrestrial condition. CAM is found in all aquatic species so far surveyed even though they represent tremendous variation in habit; diurnally submerged in tidal creeks, seasonally submerged in pools and permanently submerged in lakes (Keeley 1982).

The apparent lack of CAM in these terrestrial *Isoetes* is consistent with the observation that aquatic *Isoetes* shut off the CAM pathway upon emergence. Both of these findings are consistent

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Table 1

Afternoon and morning levels of titratable acidity (to pH 6.4) and malic acid in leaves of the terrestrial *Isoetes nuttallii* and *I. butleri* ($\bar{X} \pm$ S.D.). *I. nuttallii* was collected from Butte Co., CA, U.S.A., and *I. butleri* from Newton Co., AR, U.S.A. Growing conditions and assay methods were as described in Keeley (1982).

	N	Titratable acidity [μeq g^{-1}(f. m.)]		Malic acid [μmol g^{-1}(f. m.)]	
		1700	0700	1700	0700
I. nuttallii					
drained soil	4	6 ± 1	5 ± 1	28 ± 3	22 ± 2
submerged 1 week	2	5 ± 3	6 ± 0	20 ± 2	14 ± 1
submerged 2 weeks	2	5 ± 1	3 ± 1	18 ± 1	23 ± 4
submerged 5 weeks	2	2 ± 1	6 ± 2	20 ± 1	9 ± 5
submerged 6 weeks	2	12 ± 2	7 ± 0	17 ± 4	11 ± 1
submerged 5 months	2	1 ± 1	5 ± 1	22 ± 4	28 ± 5
I. butleri					
submerged 4 weeks	2	8 ± 2	9 ± 1	14 ± 3	5 ± 4

with the hypothesis that CAM has been selected in aquatic *Isoetes* as a means of enhancing carbon gain in certain carbon-limited aquatic environments.

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