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Photosynthetic Inorganic Carbon Use by Aquatic Carnivorous Plants

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Photosynthetic uptake of inorganic carbon by submerged aquatic plants is limited mostly by the concentration of inorganic carbon and light availability. It is generally accepted that aquatic plants compete for inorganic carbon and that use of HCO_3^- as a carbon source is ecologically advantageous in standing waters (Allen and Spence, 1981; Maberly and Spence, 1983). CO_2 concentration in water depends strongly on pH, according to the following equation (Helder, 1988):

$$\text{pH} = 6.37 + \log ([\text{HCO}_3^-] / [\text{CO}_2]).$$

Thus, the lower the pH is at a given total alkalinity (TA),

$$\text{TA} = [\text{HCO}_3^-] + 2 \cdot [\text{CO}_3^{2-}] + [\text{OH}^-] + [\text{H}^+],$$

the higher is the CO_2 concentration in water.

The majority of aquatic carnivorous species usually grow in soft or medium-hard, acid or neutral, dystrophic waters; but some species of *Utricularia* may grow in hard and slightly alkaline waters (Komiya, 1966; Moeller, 1978; Kadono, 1982; Fraser et al., 1986; Arts and Leuven, 1988; Hough and Fornwall, 1988). These species can grow in waters that differ widely in TA and pH conditions (Kadono, 1982; Fraser et al., 1986; Arts and Leuven, 1988) and at very different CO_2 and HCO_3^- concentrations. Aquatic plants are plastic concerning their photosynthetic affinity for CO_2 and HCO_3^- and are able to change the affinities according to the ratio of $\text{CO}_2/\text{HCO}_3^-$ concentrations in water (Sand-Jensen and Gordon, 1986). In studies performed so far, *Utricularia purpurea* (Moeller, 1978) and *U. vulgaris* (Hough and Fornwall, 1988) were found to use only CO_2 . Aquatic carnivorous plants either have strict or facultative requirements for organic substances in water (Ashida, 1937). These substances enhance plant growth substantially while some of the organic compounds used by the plants are taken up from water, and the plants probably also use organic compounds derived from prey bodies (for a review see Lüttge, 1983, p. 492-493; Juniper et al., 1989: p. 131). In this paper, three European aquatic *Utricularia* species and *Aldrovanda vesiculosa* were tested for HCO_3^- use and CO_2 affinity, *Utricularia australis* R.Br. and *U. minor* L. were collected from sites in the Ceska Lipa

District, N. Bohemia, Czech Republic. pH values in these stands were measured using a combined pH electrode and a battery-powered pH meter (+0.1 pH). *Utricularia vulgaris* L. and *Aldrovanda vesiculosa* L. plants used for the experiments were grown in an outdoor culture at the Institute of Botany in Trebon, Czech Republic. Eurasian water milfoil, *Myriophyllum spicatum* L., known as an efficient HCO_3^- user (Maberly and Spence, 1983), was used as a control for HCO_3^- use. TA in natural and cultivation waters was determined by titration with 0.01 M HCl to the end-point pH of 4.4. CO_2 affinity was determined using a simple "final-pH" test (Allen and Spence, 1981; Maberly and Spence, 1983). Plants were closed in a "light bottle" in a solution of a known TA. The final pH reached was a measure of HCO_3^- use and, in HCO_3^- non-users, indicated the CO_2 compensation point of photosynthesis calculated according to the above equations.

Healthy apical parts of the shoots, 4-5 cm long, were placed in 10 ml tubes in the filtrated fishpond water of known TA or in a 1 mM NaHCO_3 solution. The tubes were closed with plastic plugs, with an air bubble left inside. The whole internal volume was evenly filled with the plants. The tubes were exposed to natural light in water at temperatures of 21-24 °C. Photosynthetically active radiation (400-700 nm) stayed within the range of 80-120 W.m^{-2} , allowing the saturation of photosynthesis. Final pH values were measured after the plants were exposed for 4 h. All experiments were repeated twice and mean values were always stated. The replicates never differed by more than 0.2 pH.

As shown in Table I, the species were not able to alkalize media above a pH of 9.2, which indicates CO_2 use only. The corresponding CO_2 compensation points of *U. australis* and *U. minor* (2.3-4.5 μM) collected from natural sites were lower than those in *U. vulgaris* and *Aldrovanda* (5.9-7.2 μM) cultivated in containers. However, it is not possible to determine whether the latter two species naturally have lower CO_2 affinities or if the results were due to their cultivation conditions. A similar range of values (1.5-6.7 μM CO_2) was also found in *U. purpurea* (Moeller, 1978). These compensation points are consistent with values of 1.5-10 μM generally found in aquatic non-carnivorous plants (Maberly and Spence, 1983). Although the aquatic carnivorous plants usually grow in shallow dystrophic waters with a more or less elevated CO_2 concentration (Komiya, 1966; Adamec, 1993, unpublished), they may also grow in mildly alkaline waters where CO_2 concentration is rather low (Hough and Fornwall, 1988; see also Table I for *U. minor*). Under such conditions, carnivory may be an important means for obtaining additional organic carbon. The extent of this contribution, however, is not known.

The paper is dedicated to Dr. Slavomil Hejny from Prague, Czech Republic, on the occasion of his 70th birthday.

Table I. Alkalization of media as a measure of photosynthetic affinity to CO_2 . A, plants collected from natural sites and fishpond water used as the experimental medium; B, the plants cultivated outdoors and 1 mM NaHCO_3 solution used. *Myriophyllum spicatum*, an efficient HCO_3^- user, was used as a control. Final $[\text{CO}_2]$ corresponds to CO_2 compensation point of photosynthesis. TA in meq.l^{-1} ; $[\text{CO}_2^*]$ in μM .

Species and habitat	Growth conditions		Expt. TA	Final	
	pH	TA		pH	[CO ₂]
A.					
<i>U. australis</i> , shallow fen pool	7.2	0.81	1.35	9.2	1.8
<i>U. australis</i> , drainage canal	7.6	0.0	1.35	8.95	3.3
<i>U. australis</i> , dystrophic fishpond	8.3	1.86	1.35	9.15	2.0
<i>U. minor</i> , reed belt of a fishpond	7.2	1.80	1.35	9.1	2.3
<i>U. minor</i> , alkaline fen pool	8.9	3.45	1.24	8.9	3.4
<i>U. minor</i> , alkaline fen pool	8.9	3.45	3.45	9.2	4.5
<i>H. spicatum</i> (control), fishpond	8.3	1.86	1.35	10.9	0.0

B					
<i>U. vulgaris</i> , outdoor cultivation	8.0 ca	1.2	1.00	8.5	7.2
<i>A. vesiculosa</i> , Italian plants. outdoor cult.	7.4 ca	0.5	1.00	8.6	5.9
<i>A. vesiculosa</i> , Polish plants, outdoor cult.	6.9 ca	0.8	1.00	8.5	7.2

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Literature Review

Cheek Martin. 1994. *Pinguicula greenwoodii* (Lentibulariaceae), a new butterwort from Mexico. Kew Bull. 49:813-815.

Yet another new Mexican pinguicula comes to light, this one being most closely related to *P. jackii*, the latter occurring in Cuba and heretofore the only member of Section *Homophyllum*. It is found in a shaded dripping limestone cliff in Oaxaca. The plant's leaves are monomorphic; that is the leaves do not become the typically small, succulent type of other Mexican pinguiculas in winter. The flower is relatively small, pale and bilabiate, the corolla lacks a palate and the leaves are thin and membranous. This brings to a total of 17 new Mexican species since Casper's monograph, most of these in the orchid flowered section where distinctions are often difficult.

Heard, Stephen B. 1994. Pitcher-plant midges and mosquitoes: A processing chain commensalism. Ecology 75:1 647-660.

Working in the field in Newfoundland, the author studied the coexistence of a midge larva (*Metriocnemus knabi*) and a mosquito larva (*Wyeomyia smithii*) in the pitchers of *Sarracenia purpurea*. Trying to determine whether there was competition or not, the author made some interesting studies. The midges sought food by chewing on prey carcasses (mostly ants in this location) deep in the narrow part of the pitcher. The mosquito larvae floated near the fluid surface and are filter feeders, feeding on particles and bacteria excreted by the midge larvae. Thus the mosquito larvae benefitted from the presence of the midges who essentially processed food for them, while the midges gained nothing from the mosquito larvae but did not suffer either. Thus this is an example of what the author calls processing chain commensalism. The author performed several manipulations on over 100 pitchers to discover the relative value of numbers of either larvae, with and without ant food, in pitchers.

Labat, Jean-Jacques, and Paul Starosta (Photography). 1993. L'Univers des plantes carnivores. DuMay, Paris. 140 pp.

IN FRENCH

This is the latest hard cover book addition to the CP literature. The book is nicely jacketed and bound and measures 25 x 31 cm. The first 113 pages are full color photos of at least one per genus of CP, often more, and many of the photos being full page size. Closeups are effective in certain cases such as *Nepenthes* spp. and *Cephalotus* in 25 x