



Photosynthetic inorganic carbon acquisition in 30 freshwater macrophytes[☆]

Liyan Yin^{a,b}, Wei Li^{b,*}, Tom V. Madsen^c, Stephen C. Maberly^d, George Bowes^e

^a Hainan Key Laboratory for Sustainable Utilization of Tropical Bioresources, Hainan University, Haikou 570228, China

^b Key Laboratory of Aquatic Botany and Watershed Ecology, Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan 430074, China

^c Department of Biological Science, Aarhus University, Plant Biology, Ole Worms Allé 1135, 8000 Aarhus C, Denmark

^d Lake Ecosystems Group, Centre for Ecology & Hydrology, Lancaster Environment Centre, Library Avenue, Lancaster LA1 4AP, UK

^e Department of Biology, 220 Bartram Hall, University of Florida, Gainesville, FL 32611, USA

ARTICLE INFO

Article history:

Received 9 March 2015

Received in revised form 30 April 2016

Accepted 3 May 2016

Available online 4 May 2016

Keywords:

Bicarbonate use

CAM

C₄ metabolism

Photosynthesis

Freshwater macrophytes

ABSTRACT

Photosynthetic inorganic carbon (C_i) acquisition mechanisms were surveyed in 30 freshwater macrophytes grown under uniform, nutrient-sufficient, low C_i conditions where C_i is a potentially limiting factor on plant photosynthesis. In pH-drift experiments there was evidence for HCO₃⁻ use in 21 of the 30 species that were able to raise the solution pH above 10.0. Titratable acidity had distinct diel fluctuations in the leaves of *Nechamandra alternifolia*, *Egeria densa*, *Vallisneria spinulosa*, *Deinostema violaceum*, and *Isoetes sinensis* (aerial and submersed), which suggests some degree of Crassulacean Acid Metabolism (CAM) in these species. Incubation of *D. violaceum* under low C_i conditions substantially increased the amount of acidity and the difference between night and day. The phosphoenolpyruvate carboxylase (PEPC) activity in *Hydrilla verticillata*, *V. spinulosa*, *E. densa*, *D. violaceum*, *Ottelia acuminata*, and *O. alismoides* ranged from 32.4 ± 6.6 to 156.8 ± 5.3 μmol mg⁻¹ protein h⁻¹ and the ratio of PEPC to ribulose biphosphate carboxylase-oxygenase (Rubisco) activity ranged from 1.0 to 2.9. When *O. alismoides* and *D. violaceum* were incubated under conditions that greatly reduced daytime C_i, the PEPC activity was around 1.5 times higher than in untreated leaves. A high PEPC to Rubisco activity ratio, and the increased ratio under low C_i conditions, is consistent with a facultative C₄ or CAM system. These results indicated that most of the freshwater macrophytes tested can use HCO₃⁻ as a carbon source, while *O. alismoides*, and *D. violaceum* may possess C₄ or CAM characteristics like *H. verticillata* and *I. howellii*, and thus are worthy of further study.

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1. Introduction

Most lakes are oversaturated with CO₂ as a result of direct input of CO₂ from the catchment (Maberly et al., 2013) or via oxidation of terrestrially produced dissolved organic carbon (Duarte and Prairie, 2005). However, in productive aquatic systems with high biomass, carbon fixation can greatly exceed rates of carbon supply, leading to depletion of CO₂ virtually to zero (Maberly, 1996). A number of factors impinge on the ability of submersed macrophytes to acquire inorganic carbon (C_i): the rate of CO₂ diffusion

is about 10⁴-fold lower in water than in air (Raven, 1970); and a substantial unstirred layer at the leaf/water interface further limits the diffusion of CO₂ into the leaf (Smith and Walker, 1980). Thus the low availability of C_i can be a significant barrier to the success of submersed macrophytes in aquatic habitats (Vadstrup and Madsen, 1995).

Freshwater macrophytes compensate for this situation with various anatomical, morphological, physiological, and biochemical features to maximize C_i uptake in the aquatic environment. Morphological and anatomical strategies to minimize C_i limitation may include possession of aerial or floating leaves to access atmospheric CO₂, and lacunal connections via the roots to utilize the high concentrations of CO₂ in the sediments (Nielsen and Borum, 2008; Raven et al., 1988; Wium-Andersen, 1971). Physiological and biochemical strategies include various mechanisms of HCO₃⁻ use and adaptations in the photosynthetic process, such as Crassulacean Acid Metabolism (CAM) and C₄-like metabolism (Maberly

[☆] This article is part of a special feature entitled: "Macrophytes in freshwater habitats—Perspectives from Asia. Proceeding of the second International Symposium of Aquatic Plant Biology (MACROPHYTE 2014, Wuhan, China)" published at the journal Aquatic Botany 140C.

* Corresponding author.

E-mail addresses: liweil@wbgcas.cn, lapp@public.wh.hb.cn (W. Li).

and Madsen, 2002). Use of HCO_3^- is the most widespread carbon acquisition strategy, and was till the present work estimated to occur in some 50% of submersed angiosperms (Maberly and Madsen, 2002). It is more common in lakes of high alkalinity and in the elodeid growth form (Maberly and Spence, 1983; Vestergaard and Sand-Jensen, 2000), while most species in sites with very high concentrations of CO_2 , such as rivers fed from groundwaters, lack the ability to use HCO_3^- even though alkalinity can be very high (Maberly et al., 2015). Bicarbonate is the most abundant form of C_i in freshwaters where the pH ranges from 6.3 to 10.1. When the pH changes from 7 to 8.5, the $\text{HCO}_3^- : \text{CO}_2$ ratio can rise from 4 to 140. Three mechanisms for HCO_3^- use have been described: (a) H^+ and HCO_3^- symport system (such as in some Characeae); (b) the external acidification of the water in the leaf boundary layer caused by H^+ extrusion that facilitates the conversion of HCO_3^- into CO_2 (such as in some *Potamogeton* species); and (c) an increased rate of inter-conversion of HCO_3^- and CO_2 by the action of the enzyme carbonic anhydrase (such as in *Chlamydomonas*) (Prins and Elzenga, 1989; Moroney et al., 2011).

The Crassulacean acid metabolism (CAM) photosynthetic pathway occurs largely in xeric-adapted terrestrial succulents where it plays a major role in the water-use efficiency of the plant (Silvera et al., 2010). The discovery of CAM in the submersed aquatic fern ally *Isoetes howellii* Engelmann (Isoetaceae) (Keeley, 1981; Keeley and Bowes, 1982) and the subsequent confirmation of its occurrence in other species of the genus *Isoetes* provided an additional perspective on the evolutionary, ecological, and functional significance of this photosynthetic pathway (Keeley, 1982). Several other freshwater macrophytes have been shown to possess CAM, including the angiosperms *Littorella uniflora* (Madsen, 1987a,b), *Crassula helmsii* (Newman and Raven, 1995; Klavsen and Maberly, 2009) and *Vallisneria spiralis* (Keeley, 1998). Underwater, CAM acts as a carbon-conserving mechanism that reduces the loss of respiratory carbon at night and exploits nocturnal $[\text{CO}_2]$ that are often higher than during the day (Klavsen et al., 2011). CAM has also been shown to enhance underwater photosynthesis and reduce photorespiration in *Isoetes australis* (Pedersen et al., 2011).

Most terrestrial plants with the C_4 photosynthetic system have specialized 'Kranz anatomy', with fixation by PEPC of HCO_3^- into C_4 acids in the mesophyll cell layer that surrounds the bundle-sheath cells. Transport of C_4 acid to the bundle-sheath cells then leads to its decarboxylation and donation of the CO_2 for subsequent refixation by Rubisco (Raghavendra and Sage, 2011). This system concentrates CO_2 around Rubisco in the bundle-sheath chloroplasts and overcomes the inhibitory effects of O_2 on photosynthesis, thus enhancing the fixation rate.

The CO_2 diffusion limitations in water tend to constrain the thickness of most submersed leaves to only two to four cell layers, so C_4 -like 'Kranz anatomy' is absent. Thus it was surprising when a variant of the C_4 system was discovered in the submersed monocot, *Hydrilla verticillata*, Hydrocharitaceae, which lacks the traditional C_4 anatomy (Holaday and Bowes, 1980; Bowes, 2011). Instead the division of labour is between the cytosol and chloroplast, with PEPC located in the former and decarboxylation, CO_2 concentrating, and refixation by Rubisco in the latter. Thus the C_4 cycle operates in a "single-cell". Subsequently, single-cell C_4 systems have been found in some terrestrial plants (Voznesenskaya et al., 2001). The system in *H. verticillata* is facultative in that it is induced by conditions that produce a low $[\text{C}_i]$ in the water. A similar C_4 mechanism appears to operate in another submersed monocot, *Egeria densa* (Hydrocharitaceae), but is less well documented than in *H. verticillata* (Casati et al., 2000). Recently, evidence for C_4 metabolism has been found in two other macrophytes from the Hydrocharitaceae, *Ottelia alismoides* and *O. acuminata* (Zhang et al., 2014).

Most of the studies on freshwater macrophyte C-acquisition strategies have been undertaken on species from Europe and USA

on material collected from a range of different environmental conditions. In this study we surveyed Chinese populations of 30 macrophytes grown under uniform, nutrient-sufficient, low C_i conditions to compare, using several techniques, how these species potentially acquire C_i for photosynthesis. The selected 30 species are widely distributed in China and were available in the ponds and tanks at Wuhan Botanical Garden.

2. Materials & methods

2.1. Plant material

Thirty freshwater macrophytes were used in this experiment: *Blyxa echinosperma* (Clarke) Hook. f., *Blyxa japonica* (Miq.) Maxim., *Cabomba caroliniana* Gray, *Ceratophyllum demersum* L., *Deinostema violaceum* (Maxim.) Yamazaki, *Egeria densa* Planch., *Elodea nuttallii* (Planch.) St. John, *Hydrilla verticillata* (L. f.) Royle, *Isoetes sinensis* Palmer, *Limnophila sessiliflora* (Vahl) Blume, *Myriophyllum aquaticum* (Vell.) Verdc (Synonym *M. brasiliense* Camb), *Myriophyllum spicatum* L., *Najas marina* L., *Najas oguraensis* Miki, *Nechamandra alternifolia* (Roxb.) Thw., *Nuphar pumila* subsp. *pumila* (Timm) de Candolle (Synonym: *Nuphar lutea* ssp. *pumila* (Timm) E.O. Beal), *Ottelia acuminata* (Gagnep.) Dandy, *Ottelia alismoides* (L.) Pers., *Potamogeton* × *anguillanus* Koidz, (Synonym: *Potamogeton intortifolius* J.B. He et al.) *Potamogeton crispus* L., *Potamogeton lucens* L., *Potamogeton maackianus* A. Benn., *Potamogeton oxyphyllus* Miq., *Stuckenia pectinata* (L.) Borner (Synonym: *Potamogeton pectinatus* L.), *Potamogeton perfoliatus* L., *Potamogeton pusillus* L., *Potamogeton wrightii* Morong Bull. (Synonym: *Potamogeton malaianus* (Miq.), *Potamogeton natans* L., *Vallisneria natans* (Lour.) Hara, *Vallisneria spinulosa* Yan. Of the 30 species, *Cabomba caroliniana*, *Egeria densa*, *Elodea nuttallii* and *Myriophyllum aquaticum* are aliens, but rather common now especially in southern China. All the plant material was grown in tanks or ponds in Wuhan Botanical Garden of the Chinese Academy of Sciences, containing water pumped from nearby Donghu Lake (30°55'N 114°42'E). Donghu is a hypereutrophic lake (total nitrogen around 0.12 mM; total phosphorus around 1.2 μM) (Li et al., 2008) with a high alkalinity (about 2 mequiv L^{-1}). Plants were grown outside in full sun or in minimal shade conditions. The water temperature ranged between 26 and 33 °C and the pH was around 7.3 early in the morning and around 9.9 late in the afternoon.

2.2. pH-drift

Plants were sampled in September and tested immediately on collection, or after being kept for up to 24 h at 25 °C under low irradiance. The material was washed in tap water and rinsed twice in the test solution which comprised equimolar concentrations of NaHCO_3 and KHCO_3 at an overall concentration of 1 mM. About 0.2–0.3 g fresh weight of leaves or shoots were incubated in 50 mL glass bottles with glass stoppers. A small (1–2 mL) volume of air was left in each bottle to minimise the build-up of oxygen in solution. The bottles were incubated in a chamber (Zhujiang LRH-150-G) at 25 °C and 35–60 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ PAR (400–700 nm). After 24 h continuous irradiance, the final pH (after this time, there was no further pH increase) was measured with a Metrohm combination pH electrode connected to a Metrohm 718 stat Titrino. The electrode was calibrated with buffers at pH 7 and 10. Water from three triplicate bottles was combined and the alkalinity measured on an aliquot by Gran titration with 0.1 mM HCl dispensed by a digital burette (Brand Gmbh, Wertheim, Germany). Carbon-speciation was calculated using the equations described by Maberly (1996).

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