The role of roots in carbon uptake by the submersed macrophytes *Myriophyllum spicatum, Vallisneria americana,* and *Heteranthera dubia*

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Abstract

The carbon uptake by the roots of three common submersed macrophytes, *Myriophyllum spicatum, Heteranthera dubia* and *Vallisneria americana,* was measured *in situ* under a range of pH and dissolved inorganic carbon (DIC) concentrations. After 4–8 weeks of growth in ^{14}C labelled sediments, less than 1.5% of the total C found in the shoots originated from root uptake. Between species, significant differences in C uptake by the root were found and root development alone could explain most of the observed variance (84%). C uptake by the roots of aquatic macrophytes thus appears to be restricted to small, rosette-shaped plants growing in poorly mineralized waters.

Introduction

Dissolved inorganic carbon (DIC) has been observed to affect the development and productivity of aquatic macrophytes (Bristow 1969; Adams *et al.* 1978). Bristow (1969) and Raven (1970) suggested that the assimilation by the root and upward translocation of sediment DIC could explain the successful growth of submersed macrophytes characterizing the vegetation of poorly mineralized lakes where DIC concentrations are usually very low.

Subsequently, this mechanism was experimentally demonstrated by Wium-Andersen (1971), Sand-Jensen & Sondergaard (1978), Sondergaard & Sand-Jensen (1979) for *Lobelia dortmanna* and *Littorella uniflora.* In particular, Sand-Jensen and Sondergaard found that up to 95% of the carbon photosynthetically fixed by *L. dortmanna* originated from the sediment. DIC uptake by the root has also been found in the seagrasses *Zostera marina, Thalassia testudinum* and *Halodule wrightii* (McRoy & Goering 1974; Wetzel & Penhale 1979; Penhale & Thayer 1980), but was more reduced (0.3–4.1% of the total fixed carbon). Adams *et al.* (1978) have shown that short-term ^{14}C uptake by *Myriophyllum spicatum* was DIC limited in a range of natural habitats and suggested that primary production was limited by DIC availability. If DIC limitation is indeed common in submersed macrophytes, DIC uptake by the root constitutes a potentially important additional source of inorganic carbon to the plant and should be quantified for various species and environments.

The present study was thus undertaken to measure the contribution of the root in C uptake by three ecologically important species characteristic of the medium to hard waters of northern U.S. and southern Canada.

Methods

Approach

So far, all available data on DIC uptake by the roots of submersed macrophytes has been obtained from short-term incubations under laboratory conditions. Short-term laboratory incubations of roots

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or shoots in ^{14}C labelled media have the disadvantage of exposing the plants to highly unnatural conditions. Moreover, although this method may give an accurate measure of the rate of C uptake by the shoot or by the root, it only provides a minimum estimate of the rate of C translocation from root to shoot since the extent of isotope dilution occurring within the plant is unknown.

We have, therefore, chosen an approach similar to the one described in Carignan & Kalff (1980) and measured root contribution in C uptake on plants grown *in situ* from sprouts to mature plants on ^{14}C labelled sediments of known DIC specific activity, with the shoots in free contact with the unlabelled overlying water. When grown under these conditions, the contribution of the root in C uptake can be easily measured as the ratio of macrophyte C to sediment DIC specific activities. Specific activity refers here to the $^{14}C/^{12}C$ ratio expressed as counts per minute per micromole of carbon (CPM · μM^{-1}). As the relative importance of root and shoot in phosphorus and nitrogen uptake has been found to depend on the relative availability of these nutrients in the sediments and overlying waters (Nichols & Keeney 1976; Carignan & Kalff 1980), we measured DIC uptake by the root under a range of DIC concentration and pH values in sediments and overlying waters.

Experimental

During the 1979 growth season, three species of submerged macrophytes were studied in two different locations: *Myriophyllum spicatum* in Quinn Bay, Lake Memphremagog (Québec–Vermont, 45°06′N, 72°15′E) and *M. spicatum, Heteranthera dubia* and *Vallisneria americana* in Rivière du Sud (Québec, 45°07′N, 73°15′E). Sediments were collected with a Peterson dredge from the littoral zone of both sites. They were labelled by adding 5–8 μCi of $NaH^{14}CO_3$ to 100–400 kg batches that were thoroughly homogenized with a 1 m^3 commercial mortar mixer and left to equilibrate for 6–8 weeks prior to use. A single sediment batch was collected from Rivière du Sud whereas four identical batches amended with various levels of $NaHCO_3$ or $CaCO_3$ (Table 1) were used in Lake Memphremagog.

In early summer, sprouting plants (5–10 cm) were collected, weighed and potted in 10 liter polyethylene pails filled with labelled sediments and closed with an opaque cover. Three plants were potted in each container and the stems allowed to exit the cover through split soft neoprene stoppers. The plants were then grown *in situ* for 30–60 days. Openings through the cover normally closed with rubber stoppers allowed the regular sampling of the labelled sediment pore water for measurement of DIC concentration and specific activity. The pore water was obtained by dialysis from samplers made of 7 ml polyethylene LSC vials in which two 1 × 2 cm windows were cut and covered with a biologically inert P.V.C. membrane (Gelman, DM 450). The samplers were left in the sediments for 7–12 days, preliminary tests having shown a half equilibration time of 15 h in these sediments.

Table 1. Location and respective treatment of experimental sediments.

Treatment	Sediments	Additions
T1	Quinn Bay, Lake Memphremagog	Unamended
T2	Quinn Bay, Lake Memphremagog	44.1 g. $NaHCO_3$ to 110 liters
T3	Quinn Bay, Lake Memphremagog	117.6 g. $NaHCO_3$ to 110 liters
T4	Quinn Bay, Lake Memphremagog	75.0 g. $CaCO_3$ to 110 liters
T5	Newport, Lake Memphremagog	Unamended
T6	Riviere du Sud	Unamended

DIC was measured on a Beckman IR-215 infrared gas analyzer following a gas stripping procedure (Stainton *et al.* 1977). The ^{14}C activity of the same samples was then measured by trapping the evolved CO_2 in Oxyfluor (NEN) and counting in a Beckman liquid scintillation system.

Upon harvesting, the shoots were separated from the roots, cut into three equal sections and each part was vigorously shaken with filtered lake water to remove as much periphyton and sediment as possible. The plant material was then dried at 70 °C for 48 h and finely ground. Before weighing or analysis, the plant material was exposed to HCl fumes for 10 min to remove any $CaCO_3$ and dried again. The total plant-C was measured on a Carlo Erba CHN analyzer. The ^{14}C activity of the plant material was measured following combustion in a carbon oxydizer (Oxymat, Intertechnique). The CO_2 was trapped in Oxyfluor and all counts were corrected

for counting efficiency using an external standard method (Wang *et al.* 1975).

The contribution of the root in C uptake was calculated from the measured plant C and mean pore water DIC specific activities. The mean pore water DIC specific activity was obtained by integrating over the growth period the best fitting relation describing the evolution of the pore water DIC specific activity with time. This method assumes a constant shoot/root ratio with time.

Natural pore water DIC profiles were obtained by inserting in the sediments a compartmented dialysis sampler (Hesslein 1976) fitted with a DM 450 membrane. The sampler was allowed 15 days to equilibrate. pH was measured by direct insertion of a combination electrode in cores obtained with a Brown piston corer.

Results and discussion

Sediment characteristics and plant growth

The observed concentrations of DIC and pH for the overlying water and the undisturbed and experimental sediments of both sites are presented in Fig. 1 and Table 2. Although the experimental manipulation of the sediments did not change by much their natural pH or DIC speciation (as H_2CO_3, HCO_3^- and CO_3^{2-}), the DIC levels of the unamended control sediments increased 2–4 times when compared to undisturbed sediments (Fig. 2a). This increase was probably due to the confinement of the sediments in closed containers where diffusive loss of metabolically produced CO_2 could not occur. Higher DIC levels in the container are also attributable to the homogenization within the bulk sediment of an organically rich and metabolically active surface layer (Carignan, unpubl.).

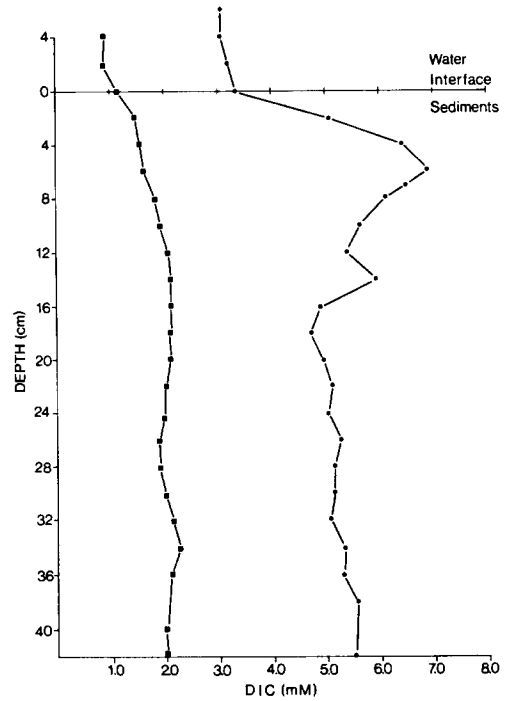

Fig. 1. Midsummer interstitial dissolved inorganic carbon profiles for Quinn Bay, Lake Memphremagog (-■-), and for Riviere du Sud (-●-).

Table 2. Water and sediment dissolved inorganic carbon (DIC) and pH at two study sites. DIC speciation was calculated from DIC, pH and temperature values with $pK_1 = 6.38$ and $pK_2 = 10.37$ at 20 °C (Stumm & Morgan 1970). Concentrations are in millimolar.

Study sites and treatments	pH	DIC	H_2CO_3	HCO_3^-	$CO_3^{2=}$
Quinn Bay, Lake Memphremagog					
Water	8.50	0.88	0.01	0.86	$11.0\ 10^{-3}$
Undisturbed sediments	6.65	2.00	0.70	1.30	$0.2\ 10^{-3}$
Treatment T1	6.50	7.03	3.04	3.99	$0.5\ 10^{-3}$
Treatment T2	6.70	9.49	3.08	6.41	$1.3\ 10^{-3}$
Treatment T3	6.80	14.22	3.91	10.30	$2.7\ 10^{-3}$
Treatment T4	6.65	8.76	3.07	5.69	$1.1\ 10^{-3}$
Treatment T5	6.70	9.91	3.22	6.69	$1.4\ 10^{-3}$
Riviere du Sud					
Water	7.60	3.10	0.18	2.92	$0.5\ 10^{-3}$
Undisturbed sediments	6.60	5.50	2.07	3.43	$0.6\ 10^{-3}$
Treatment T6	6.60	10.64	4.00	6.64	$1.1\ 10^{-3}$

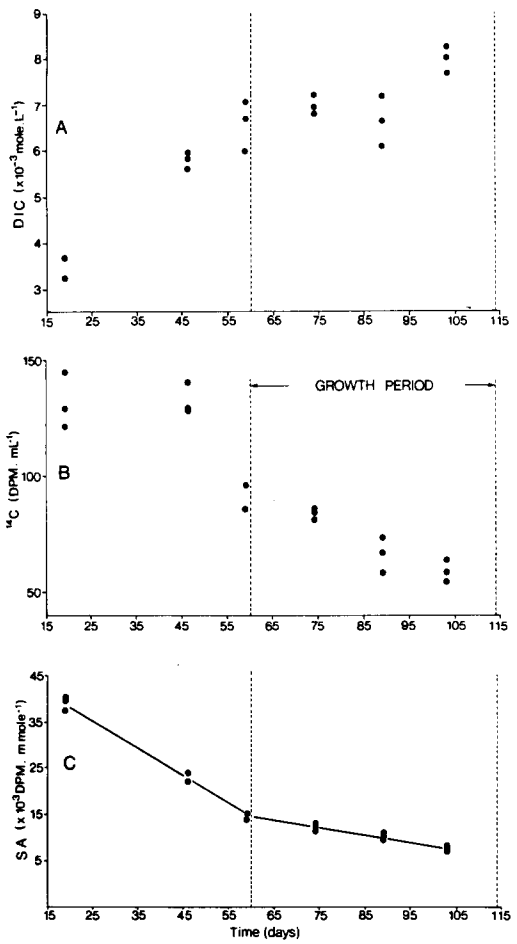

Fig. 2. Interstitial dissolved inorganic carbon concentration (a), ^{14}C activity (b), and specific activity (c) versus time for sediments T1.

The addition of inorganic carbon as $NaHCO_3$ or $CaCO_3$ to treatments C_2, C_3 and C_4 resulted in DIC increases (25–102%) mainly in the HCO_3^- form, and somewhat inferior to that expected (50–125%). This can be caused by CO_2 reduction, known to occur in these sediments (LaZerte 1981), partial dissolution or precipitation of $CaCO_3$, or DIC adsorption.

In all treatments, the interstitial ^{14}C activity decreased continuously (Fig. 2b). This suggests again a constant loss or transformation of interstitial DIC by CO_2 reduction into CH_4, precipitation as a carbonate mineral, or DIC adsorption. The interstitial DIC specific activity also decreased markedly with time (Fig. 2c) as the result of the simultaneous increase in total DIC and loss of $DI^{14}C$. The slope change around day 60, upon initiation of the growth experiments, is presumably the result of a temperature decrease which occurred when the containers were moved from a stagnant shallow area (0.3 m) to the deeper and cooler experimental sites (2.0 m).

Because of the dynamic nature of the DIC pool in the sediments used, its specific activity does not seem to be stabilize after labelling. Consequently, the eight weeks equibration period allowed in this study to obtain a stable specific activity was probably unnecessary.

With the exception of the plants rooted in Newport sediments, the growth of the plants rooted in the labelled sediments appeared normal compared to nearby plants rooted in undisturbed sediments. Table 3 shows that the yield of the plants rooted in Newport sediments was three times higher than those in Quinn Bay sediments. Nutrient limitation in the Quinn Bay sediments might explain this difference as they showed much lower interstitial reactive phosphorus and ammonia concentrations (185 and 3 000 $\mu g \cdot l^{-1}$) than the Newport sediments (2 000 and 6 000 $\mu g \cdot l^{-1}$).

Carbon uptake by the root

The results of the ^{14}C uptake experiments for the three species and six treatments are presented in Table 4. In all treatments, the root accounted for not more than 1.5% of the total C uptake by the plants. Although small, the contribution of the root to C uptake was significantly different ($P > 0.05$) for the three species grown in R. du Sud sediments. Small but significant differences were also observed for *M. spicatum* growing in the five Quinn Bay treatments but could not be related to the DIC

Table 3. Mean biomass for *Myriophyllum spicatum* grown under different treatments in Quinn Bay, Lake Memphremagog. The number of replicates is given in parentheses.

Treatment	Biomass (g dry weight)		
	Mean	SE	n
T1	0.524	0.240	(6)
T2	0.793	0.427	(6)
T3	0.633	0.415	(6)
T4	0.689	0.344	(6)
T5	1.808	0.422	(6)

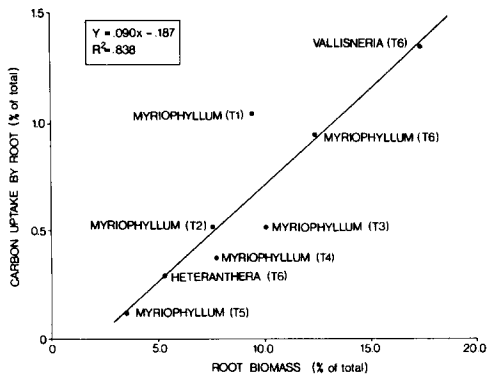

Fig. 3. Relationship between carbon uptake by the root and root development for three species grown under various dissolved inorganic carbon concentrations (treatments T1 to T6).

speciation or concentration in these sediments. There was, however, a significant positive correlation ($r = 0.92$, Fig. 3.) between the amount of sediment-derived C found in the shoot, and root development expressed as root/total plant dry weight ratio. Between species and treatments, root development explained 84% of the observed variance in root uptake.

Values for carbon uptake by the root measured in this study probably represent maximum estimates since the interstitial DIC concentrations to which the plants were submitted were two to four times higher than in the undisturbed sediments of the same sites. The amount of C originating from the sediments is thus negligible for these species when growing under a relatively high but nevertheless limiting (Adams *et al.* 1978) DIC availability in the water. Our results thus corroborate, for these plants, the validity of primary production measurements by the ^{14}C method were only the surrounding water DIC pool is labelled.

So far, quantitatively important DIC uptake by the root seems to be restricted to small rosette-shaped plants such as *Lobelia, Litorella* and *Isoetes* occurring in acidic, DIC impoverished environments.

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