CARBON UPTAKE IN AQUATIC PLANTS DEDUCED FROM THEIR NATURAL ^{13}C AND ^{14}C CONTENT

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ABSTRACT. δ^{13}C and ^{14}C activity measurements were made on terrestrial, marsh and aquatic plants growing in their natural habitat of the Plitvice Lakes in northwest Yugoslavia. δ^{13}C values were ca $-47‰$ for aquatic mosses, which indicate that the carbon source was dissolved inorganic carbon (DIC) from alkaline karst waters, following a C_3 pathway, and ca $-25‰$ for marsh plants, indicating the carbon source was atmospheric CO_2. ^{14}C activity of true aquatic plants and submerged parts of helophytes was close to ^{14}C activity of DIC, whereas that of emergent parts of helophytes and terrestrial plants was similar to atmospheric CO_2 activity. Aquatic plants which use DIC in freshwater for their photosynthesis are not suitable for ^{14}C dating, unless the initial activity of incorporated carbon is known. δ^{13}C values of plant material also depend on the carbon source and cannot be used for ^{14}C age correction.

INTRODUCTION

Varying δ^{13}C values in terrestrial plants reflect three major photosynthetic carbon pathways: C_3, C_4 and CAM (Bender, 1971; Smith & Epstein, 1971). Most authors agree that the enrichment of ^{12}C with respect to atmospheric CO_2 in the metabolic intermediates of plants occurs at the primary enzymatic ribulose 1,5-biphosphate-carboxylase (RuBP) step for C_3 plants or at the phospho-phenolpyruvate-carboxylase (PEP) step for C_4 plants (Benedict, 1978; Wong, Benedict & Kohel, 1979; O'Leary, 1981; Osmond, Winter & Ziegler, 1982). Carbon atoms of glucose and malate in C_4 plants are 2 to 3‰ enriched in ^{12}C, and intermediates in C_3 plants are enriched 15–18‰ with ^{12}C in respect to atmospheric CO_2 (Whelan, Sackett & Benedict, 1973). In crassulacean acid metabolism plants (CAM) CO_2 fixation occurs in the dark by PEP- and in the light by RuBP-carboxylase (Osmond, Winter & Ziegler, 1982). Other factors may also contribute to fractionation of carbon isotopes (O'Leary, 1981).

δ^{13}C values ranging from -22 to $-40‰$ can be found for terrestrial C_3 plants, whereas, for C_4 plants, values from -6 to $-20‰$ are typical and, for CAM plants, intermediate values from -9 to $-25‰$ are quoted (Smith & Epstein, 1971; O'Leary, 1981; Osmond, Winter & Ziegler, 1982; Press *et al*, 1987). The only relevant source of carbon in terrestrial plants is atmospheric CO_2 with an isotopic content equal to $-7.8‰$ with respect to the PDB standard.

In contrast to atmospheric carbon which has a relatively uniform isotopic composition because of intensive circulation of air masses, isotopic

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composition of inorganic carbon in freshwater is subject to considerable variations. The large scatter in $\delta^{13}C$ values of aquatic plants has been partly attributed to variations in the $\delta^{13}C$ content of the carbon source itself: dissolved inorganic carbon (DIC) in water. $\delta^{13}C$ values in several aquatic plants reflect, besides the photosynthetic pathway, the difference in water chemistry, water depth, water flow, seasonal and other ecological factors (Osmond *et al,* 1981), which makes the interpretation of isotopic data even more difficult. Thus, in aquatic plants, of which most fall within the C_3 category, at least biochemically, the situation is complicated by the influence of various ecological factors as well as lack of knowledge of the exact photosynthetic steps following carbon uptake.

Dark CO_2 fixation of CAM-type plants has also been reported in some aquatic Isoetids (Richardson *et al,* 1984). However, no plant of this group was found in the investigated area (Figure 1).
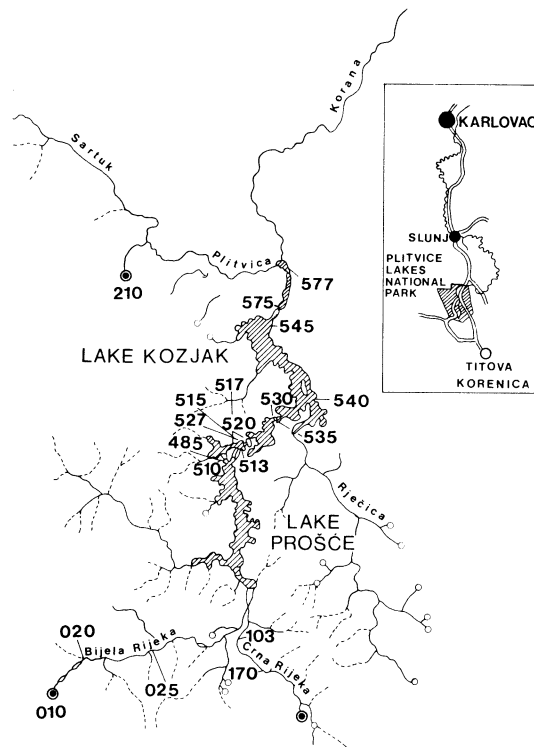

Fig 1. Location of study site

Some algae and aquatic vascular plants may also use HCO_3^- when the CO_2 supply is limited. In this case, an active transport and carbon concentrating mechanism seems to be involved, which further complicates the interpretation of data (Benedict, 1978, Raven, 1985). Some authors consider that aquatic plants do not belong to any of the known photosynthetic pathways

(eg, Salvucci & Bowes, 1983). Most freshwater algae are considered C_3 plants (Lloyd, Canvin & Culver, 1977).

The $\delta^{13}C$ values of submerged aquatic plants which take carbon from water, quoted in the older literature, are best understood when knowledge of the composition of the carbon source is available. Thus, $\Delta^{13}C = (\delta^{13}C$ plant $- \delta^{13}C$ source carbon) was introduced (Osmond *et al,* 1981; Richardson *et al,* 1984).

Another factor relevant to the interpretation of these processes is the determination of the source of carbon used by aquatic plants during photosynthesis, from air or from water. For this measurement, ^{14}C seems to be more reliable due to significant difference in ^{14}C content between DIC and atmospheric CO_2 in most areas. Namely, DIC in freshwater always contains a fraction derived from dissolved mineral carbonates (limestone, dolomites, etc), which does not contain ^{14}C, resulting in total DIC ^{14}C activity significantly below that of atmospheric CO_2. For example, the DIC activity in spring water in the investigated area ranges between 60% of modern activity (Crna Rijeka spring) up to 84% (Bijela Rijeka and Plitvica springs) as opposed to atmospheric CO_2 activity which changed during the investigation period from 130% (1984) to 120% (1988). Since our ^{14}C measuring system can resolve a 1% difference in ^{14}C activity of samples, there was no ambiguity in determining the source of carbon in measured aquatic plants. Thus, we decided to compare the aquatic and terrestrial mosses, submerged and emerged leaves of aquatic macrophytes, as well as freshwater amphibious plants in areas subject to periodic flooding. The location of the study site is shown in Figure 1.

MATERIALS AND METHODS

All plants, except the terrestrial moss, *Neckera crispa,* grew in an aquatic environment: alkaline karst waters in the Plitvice Lakes area. The chemical and isotopic properties of the aquatic system consisting of karst springs, streams, waterfalls and lakes are reported elsewhere (Srdoč *et al,* 1985, 1986a).

Samples weighing several grams when dried were analyzed for ^{14}C content by using a conventional ^{14}C dating method consisting of a proportional gas counter in a heavy lead shield at Ruđer Bošković Institute, Zagreb. Samples weighing 0.2–1.0 g (mostly cyanobacteriae and algae) were measured by liquid scintillation counting at the Research School of Earth Sciences, Australian National University, Canberra. The $\delta^{13}C$ isotope determinations were carried out using a mass spectrometer at Jožef Stefan Institute, Ljubljana and ANU, Canberra. Samples heavily encrusted with calcium carbonate were treated with dilute HCl prior to combustion.

The isotopic content of plant material is expressed as deviations from standards chosen by convention. The $\delta^{13}C$ results are expressed as a deviation from the PDB standard (*Belemnitella americana*), in per mil. The concentration of the radioactive isotope of carbon is expressed as percent of ^{14}C concentration in an undisturbed atmosphere. For this purpose, a NBS oxalic acid is used as a standard.

TABLE 1

Comparison of ^{14}C activity and $\delta^{13}C$ values of terrestrial
and aquatic plants and DIC in water

Plant	Site (Fig 1) Code	Name	$\delta^{13}C$ ‰ vs PDB Plant	DIC	^{14}C % modern
Prokaryota					
Cyanobacteriophyta					
Nostoc verrucosum	170	Crna Rijeka	–40.4	–12.5	
Rivularia haematites	575	M Trnina Falls	–28.5	–10.0	
Phormidium uncinatum	010	Bijela Rijeka, spring	–46.2	–12.5	
Eukaryota					
Phycophyta (Algae)					
Xanthopyceae					
Vaucheria geminata	010	Bijela Rijeka, spring	–41.9	–12.5	
Chlorophyceae					
Charales					
Nitella opaca	025	Bijela Rijeka	–40.7	–12.5	
Chara sp	520	Lake Galovac, 1987			85.0
Chara sp	025	Bijela Rijeka, (shallow pond)	–36.0		92.3
Bryophyta (Mosses)					
Hepaticae					
Fegatella conica	513	Okrugljak–Malo Jezero (grown on calcareous rock, spray zone)	–27.9		
Musci					
Neckera crispa* (terrestrial moss)	210	Plitvica spring area, (grown on *Fagus silvatica*, epiphytic)	–27.5		124.0
Cratoneurum commutatum (moss growing in spray zone near waterfalls)	510	Špiljski Vrt	–40.6	(–10.7)**	101.0
Cratoneurum commutatum	530	Lake Gradinsko	–37.0	(–10.0)	82.0
Cratoneurum commutatum	577	Lake Kaluđerovac	–34.6	(– 9.8)	108.2
Cratoneurum commutatum	010	Bijela Rijeka	–35.2	–12.5	82.6
Cratoneurum commutatum	210	Plitvica spring area			82.5
Cratoneurum commutatum	485	Waterfalls above Lake Okrugljak			
a) underwater					81.7
b) above water in dry period					81.8
Fontinalis antipyretica	025	Bijela Rijeka	–47.5	–12.5	78.7
Cinclidotus aquaticus	103	Crna Rijeka	–47.9	–12.0	
Mniobrium albicans	517	Lake Vir	–32.8	–10.2	83.0
Pteridophyta					
Equisetatae					
Equisetum palustre	010	Bijela Rijeka, spring	–26.5	(–12.5)	
Spermatophyta					
Magnoliophytina (Angiosperms)					
Magnoliatae (Dicotyledons)					
Ranunculaceae					
Caltha palustris	010	Bijela Rijeka, spring (leaf)	–26.0	(–12.5)	

TABLE 1 (continued)

Plant	Site (Fig 1) Code	Name	δ^{13}C ‰ vs PDB Plant	DIC	^{14}C % modern
Caltha palustris	010	Bijela Rijeka, spring (whole plant)	−28.0	(−12.5)	
Ranunculus trichophyllus	020	Bijela Rijeka, (fast waterflow)	−28.7	−12.5	
Ranunculus trichophyllus	545	Lake Kozjak, (very slow waterflow)	−26.1	−10.0	
Halorragidaceae *Myriophyllum verticillatum*	527	Mali Prštavci Falls	−29.7	−10.1	
Callitrichaceae *Callitriche truncata*	010	Bijela Rijeka, spring	−35.7	−12.5	
Brassicaceae *Nasturtium officinale*	010	Bijela Rijeka, spring	−38.2	(−12.5)	
Boraginaceae *Myosotis scorpioides*	010	Bijela Rijeka	−27.5	(−12.5)	
Scrophulariaceae *Veronica anagallis aquatica* submerged, coll 1988-4-3	010	Bijela Rijeka, spring	−34.9	(−12.5)	
Veronica anagallis aquatica submerged part of plant emergent part of plant	515	Between Malo and Veliko Jezero	−34.8 −31.0	(−10.5)	81.3 119.0
Veronica anagallis aquatica submerged part of plant emergent part of plant, coll 1988-5-18	010	Bijela Rijeka, spring	−38.9 −30.0	−12.5	76.0 114.0
Veronica beccabunga	020	Bijela Rijeka	−27.2	(−12.5)	
Veronica scutellata	480	Lake Prošće – Labudovac	−28.5	(−11.5)	
Lamiaceae *Mentha* sp	010	Bijela Rijeka, spring	−29.4	(−12.5)	
Mentha pulegium	010	Bijela Rijeka, spring	−29.9	(−12.5)	
Asteraceae *Petasites albus* (leaf)	535	Burgetić, 1988	−27.7	(−10.0)	114.4
Petasites albus (root)	535	Burgetić, 1988	−28.6	(−10.0)	117.6
Liliatae (Monocotyledons) Alismataceae *Alisma plantago*	540	Lake Kozjak	−28.4	(−10.0)	
Hydrocharitaceae *Vallisneria spiralis*	540	Lake Kozjak	−32.0	(−10.0)	
Potamogetonaceae *Potamogeton fluitans*	020	Bijela Rijeka	−29.7	(−12.5)	
Potamogeton perfoliatus	545	Lake Kozjak	−28.0	−10.0	
Potamogeton pusillus	510	Lake Okrugljak	−27.9	−10.5	83.4
Cyperaceae *Carex goodenowii (nigra)*	480	Lake Prošće – Labudovac	−25.6	(−11.5)	
Poaceae *Glyceria maxima*	020	Bijela Rijeka	−34.2	(−12.5)	103.3
Glyceria maxima	577	Lake Kaluđerovac	−31.5	(− 9.8)	
Phragmites communis	577	Lake Kaluđerovac	−28.1	(− 9.8)	

* Collected sample obviously contained plant material from previous years, when the activity of atmospheric CO_2 was higher.

** Values in parentheses are for partly emergent plants.

RESULTS AND DISCUSSION

$\delta^{13}C$ Values of Aquatic Plants

The $\delta^{13}C$ values of several terrestrial and aquatic plants that belong to different systematic divisions of the plant kingdom: cyanobacteriae, algae, mosses, and vascular plants, were measured. The results are shown in Table 1. The $\delta^{13}C$ values of total DIC in water at the collecting site are given in Table 1. Values in parentheses are for cases when at least part of the plant was found growing emergent in atmospheric environment, eg, for *Ranunculus aquatilis,* only flowers were growing above the water surface.

The isotopic composition of DIC in spring water, streams and lakes was extensively studied in the area where plants were sampled (Srdoč *et al,* 1986a). We concluded that the isotopic composition of DIC in karst areas covered by limestone and dolomites is a result of dissolution of bedrock by H_2CO_3 derived from microbial degradation of plant detritus in topsoil and the subsequent exchange process between the liquid and gaseous phases. The fact that the measured isotopic composition of DIC did not correspond to stoichometrically calculated $\delta^{13}C$ and ^{14}C values, indicated at the exchange process between dissolved CO_2 in soil water during seepage and gaseous CO_2. Two distinct sources of CO_2 are available for exchange: plant-derived CO_2 from topsoil ($\delta^{13}C = -25$ to $-30‰$, ^{14}C activity $= 115–120$ pMC) and atmospheric CO_2 ($\delta^{13}C = -7.8‰$, ^{14}C activity $= 115–120$ pMC). The next component is bedrock isotopic composition ($\delta^{13}C = 0.0$ to $+1.5‰$, ^{14}C activity below detectable limit, ~ 0.1 pMC). With these data in hand, we then calculate the contributions of each component to the DIC for karst groundwater with a very short mean residence time (1–3 years). Thus, the stoichometric values $\delta^{13}C = 1/2 [\delta^{13}C \text{ (plant)} + \delta^{13}C \text{ (bedrock)}] \approx -15‰$ and the corresponding ^{14}C activity pMC (DIC) $= 1/2$ [pMC (plant) + pMC (bedrock)] $\approx 60\%$ have been modified by exchange with atmospheric CO_2 to $\delta^{13}C$ (DIC) $\approx -12.5‰$ and ^{14}C activity up to 80 pMC at karst springs. It should be emphasized that the surface flow of water brings about further changes of isotopic composition of DIC due to the exchange of carbon isotopes between the liquid (surface water) and gaseous (atmosphere) phase, especially at points where turbulent flow mode enhances the exchange process (rapids, cascades, waterfalls). The $\delta^{13}C$ values of the DIC in water ranged from $-12.0 \pm 0.2‰$ in the spring area up to $-9 \pm 0.2‰$ in the downstream direction. The ^{14}C activity of DIC steadily increases going downstream due to the same process. CO_2 concentration in water varied from 0.6 mM/L in the spring area to 0.03 mM/L in the lower reaches (Srdoč *et al,* 1986a).

The $\delta^{13}C$ values of plants ranged from $-25.6‰$ in the marsh plant *Carex goodenowii* to $-47.9‰$ in the aquatic moss *Cinclidotus aquaticus*. $\delta^{13}C$ values differed partly because of the different carbon source. In this connection we can distinguish 1) true aquatic plants like freshwater algae (*Nitella, Chara*) aquatic mosses *Fontinalis* and *Cinclidotus;* submerged aquatic phanerogams (hydrophytes) like *Ranunculus aquatilis, Myriophyllum verticillatum, Vallisneria spiralis, Callitriche truncata, Potamogeton perfoliatus, Potamogeton pusillus;* 2) partly submerged and partly emerged plants (helophytes like *Veronica anagallis aquatica, Veronica beccabunga, Veronica*

scutellata, Mentha sp, *Alisma plantago, Potamogeton fluitans* (with partly submerged and partly floating leaves on the surface of water) and *Phragmites communis;* 3) plants growing in the spray zone around the waterfalls, cascades and streams like the cyanobacterium *Rivularia hematites,* the siphonal alga *Vaucheria geminata,* the mosses *Cratoneurum commutatum* and *Mniobrium albicans,* the grass *Glyceria;* 4) true terrestrial plants like the moss *Neckera crispa.* The $\delta^{13}C$ value of total carbon in *Phragmites communis* (-28.1‰) differs slightly from values recorded in the literature (-26.6‰, Bender, 1971; -24.6‰, Smith & Brown, 1973).

Generally, $\delta^{13}C$ values of roots and stems are a little less negative than that of leaves, which agrees with the data recorded by O'Leary (1981). A small difference in $\delta^{13}C$ values with respect to other parts of the plant was also observed in flowers, but the data are still too scarce (Table 2).

TABLE 2

Comparison of $\delta^{13}C$ values of plant carbon in different organs of plants living in aquatic environment

Plant	$\delta^{13}C$ value			
	Root	Stem	Leaves	Flower
Caltha palustris (helophyte)		–25.4	–26.0	–25.7
Nasturtium officinale (helophyte)	–31.2	–31.1	–31.6	
Petasites albus (hygrophyte)	–28.6		–27.7	–30.6
Glyceria fluitans (helophyte)	–28.4	–29.3	–30.0	
Veronica beccabunga (helophyte)	–26.7	–25.9	–27.0	

Petasites albus and *Equisetum palustris* were growing at the edge of a stream exposed to moist air (hygrophytes). *Nasturtium officinale* and the cyanobacterium *Nostoc verrucosum* were submerged at the time of collection.

The emergent parts of *Veronica anagallis aquatica* contained $\delta^{13}C$ (-31.0‰) and ^{14}C (119% pMC) values comparable to those of terrestrial plants in the area, whereas the submerged parts of the same plant showed isotopic characteristics of true aquatic plants ($\delta^{13}C = -34.8$‰, $^{14}C = 81\%$ pMC).

The $\delta^{13}C$ value of the emergent leaves in *Veronica anagallis aquatica* was less negative than that of submerged leaves in two different habitats in contrast to the $\delta^{13}C$ values in the same species found by Osmond *et al* (1981) but agreed with most aquatic plants found by the same authors. The difference may be due to habitat – still pond water in Britain and fast flowing water in the Plitvice Lakes. It is obvious that the carbon used is derived from different sources in submerged and emergent parts of the plant, which is even more substantiated by ^{14}C measurements, and that the transport of incorporated carbon between the two sections of the plant is slow or negligible.

Our investigations indicate the influence of the aquatic environment on $\delta^{13}C$ values of aquatic plants growing in different natural habitats. Contrary to the popular view that $\delta^{13}C$ values of aquatic plants are often significantly more positive than those of terrestrial plants (see review in O'Leary, 1981)

our investigations showed extremely negative values for aquatic mosses. Our data are comparable to those of Osmond *et al* (1981) for aquatic plants in Britain.

The calculation of $\delta^{13}C$ values in plants from carbon source values (DIC or atmospheric CO_2) via various photosynthetic pathways (C_3, C_4, CAM) is still not feasible. An interplay of several factors such as the use of aquatic and atmospheric carbon in the case of *Cratoneurum commutatum* and *Glyceria maxima* in a spray zone or a similar phenomenon of using both sources of carbon simultaneously by *Veronica anagallis aquatica* (see Table 1, ^{14}C data), makes any calculation unrealistic. Also, preferential use of dissolved CO_2 *vs* bicarbonate ions results in ca 10.2‰ more negative $\delta^{13}C$ values of incorporated carbon. Transport resistance, i e slow diffusion of CO_2 in the water as compared to air at the boundary layer (Richardson *et al,* 1984), is another characteristic of submerged aquatic plants. Another possibility for less negative values is the dark fixation of CO_2 via the CAM pathway, or use of the HCO_3^- ion. Measured aquatic mosses show distinctly negative $\delta^{13}C$ values which indicates the use of free CO_2 via Rubisco. The supply of CO_2 in the spring area is most probably not the limiting factor due to extensive circulation of water and high CO_2 concentration. In *Ranunculus* and *Myriophyllum,* a significant dark fixation of CO_2 is excluded (Salvucci & Bowes, 1983). As they grow mostly in ponds and lakes with low water circulation, isotope fractionation may not be so expressed. $\delta^{13}C$ values of *Ranunculus trichophyllus* indicate the influence of the carbon source but not the water flow rate (Table 1).

^{14}C Content of Aquatic Plants

Our results were complemented with ^{14}C data which clearly indicated the actual carbon source, a prerequisite for further interpretation of the possible contribution of physiological processes to isotope fractionation of aquatic plants. The $\delta^{13}C$ values of total carbon in plants alone are not sufficient to evaluate the carbon uptake in the investigated aquatic plants. Beside the photosynthetic pathway itself, we must determine whether the source of carbon is atmospheric CO_2 or DIC in water. The ^{14}C content of the plant is the most reliable indicator for the carbon source (Table 1).

The sources of carbon are 1) air, for terrestrial moss *Neckera crispa,* emergent parts of *Veronica anagallis aquatica,* and *Petasites albus* growing in a moist environment; 2) air and water, for the moss *Cratoneurum commutatum* and 3) water, for the algae *Chara* sp and aquatic moss *Fontinalis antipyretica,* moss *Mniobryum albicans* growing mostly in water, submerged parts of *Veronica anagallis aquatica,* and aquatic plants *Vallisneria spiralis* and *Potamogeton pusillus.* The $\delta^{13}C$ value of *Caltha Palustris,* which grows underwater in early spring, indicates that the carbon used for growth comes from storage tissue formed during exposure of the plant to atmospheric CO_2 during the previous season. *Cratoneurum commutatum,* which grows in the spray zone around waterfalls and karst springs, seems to use CO_2 from both reservoirs depending on environment and season.

CONCLUSION

The interpretation of the $\delta^{13}C$ values of aquatic plants growing in a natural habitat requires an individual approach for almost every species. Thus, the use of aquatic and atmospheric carbon in spray or boundary zones, or exposure of floating leaves to atmospheric CO_2, prevented calculation of $\delta^{13}C$ values in investigated plants via various photosynthetic pathways (C_3, C_4, CAM). On the other hand, the very negative $\delta^{13}C$ values of lower plants (aquatic cyanobacteriae and mosses) agree with expected values for a true C_3 plant which uses only free CO_2. The results agree with the findings of Osmond *et al* (1981) in *Fontinalis* found in a similar environment in Britain (fast flowing water where CO_2 supply is not limited).

The $\delta^{13}C$ and ^{14}C data presented in Tables 1 and 2 for aquatic plants which use DIC from freshwater for photosynthesis clearly indicates that these plants and their fossil remains do not fit into the basic scheme for ^{14}C dating of organic plant-derived material (initial activity = 100 pMC, $\delta^{13}C = -25‰$). The true age of aquatic plants in the Crna Rijeka region can be as much as 4200 yr younger than their ^{14}C age, and any age correction based on $\delta^{13}C$ values is very questionable. The use of both sources of carbon simultaneously by *Veronica anagallis aquatica* (DIC by submerged parts and atmospheric CO_2 by emerged parts of the plant) is an interesting phenomenon from the point of view of plant physiology, however, its fossil remains buried in, e g, lake sediment, will show a grossly erroneous ^{14}C age.

In principle, it is possible to correct the ^{14}C age of DIC-derived calcareous deposits or plant remains (Srdoč *et al*, 1986b) provided that the initial ^{14}C activity of the carbon source is known. For example, dating terrestrial plants (driftwood, leaves, etc) embedded in sediment helps determine the initial activity of matrix material. A less successful attempt to use aquatic moss *Drepanocladus crassicostatus* for ^{14}C dating of the "ice-free corridor" of western Canada has been reported by MacDonald *et al* (1987). An apparently inconsistent value of the initial activity of the aquatic moss prevented the calculation of the true age of the "ice-free corridor".

REFERENCES

Bender, M M, 1971, Variations in the $^{13}C/^{12}C$ ratio of plants in relation to the pathway of photosynthetic carbon dioxide fixation: Phytochemistry, v 10, p 1239–1244.

Benedict, C R, 1978, Nature of obligate photoautotrophy: Ann Rev Plant Physiol, v 29, p 67–93.

Gupta, S K and Polach, H, 1985, Radiocarbon dating practices at ANU: Lab. monograph, 171 p.

Håkansson, S, 1979, Radiocarbon activity in submerged plants from various south Swedish lakes, *in* Berger, R and Suess, H E, eds, Radiocarbon dating, Internatl ^{14}C conf, 9th, Proc: Berkeley, Univ California Press, p 433–443.

Lloyd, N D H, Canvin, D T and Culver, D A, 1977, Photosynthesis and photorespiration in algae: Plant Physiol, v 59, p 936–940.

MacDonald, G M, Beukens, R P, Kieser, W E and Vitt, D H, 1987, Comparative radiocarbon dating of terrestrial plant macrofossils and aquatic moss from the "ice-free corridor" of western Canada: Geology, v 15, p 837–840.

O'Leary, M, 1981, Carbon isotope fractionation in plants: Biochemistry, v 20, p 553–567.

Osmond, C B, Valaane, N, Haslam, S M, Uotila, P and Roksandić, Z, 1981, Comparisons of $\delta^{13}C$ values in leaves of aquatic macrophytes from different habitats in Britain and Finland: some implications for photosynthetic processes in aquatic plants: Oecologia, v 50, p 117–124.

Osmond, C B, Winter, K and Ziegler, H, 1982, Functional significance of different pathways of CO_2 fixation in photosynthesis, *in* Lange, O L, Nobel, P S, Osmond, C B and Ziegler, H, eds, Physiological plant ecology II. Water relations and carbon assimilation: Berlin – Heidelberg, Springer, p 480–535.

Polach, H, Kaihola, L, Robertson, S and Haas, H, 1988, Small sample ^{14}C dating by liquid scintillation spectrometry: Radiocarbon, v 30, no. 2, p 153–155.

Press, M C, Shah, N, Tuohy, J M and Stewart, G R, 1987, Carbon isotope ratios demonstrate carbon flux from C_3 host to C_4 parent parasite: Plant Physiol, v 85, p 1143–1145.

Raven, J A, 1985, The CO_2 concentrating mechanism, *in* Lucas, W J and Berry, J A, eds, Inorganic carbon uptake by aquatic photosynthetic organisms: Am Soc Plant Physiologists, Rockville, Maryland, p 67–82.

Richardson, K, Griffiths, H, Reed, M L, Raven, J A and Griffiths, N M, 1984, Inorganic carbon assimilation in the Isoetids, Isoetes lacustris and Lobelia dortmanna: Oecologia, v 61, p 115–121.

Salvucci, M E and Bowes, G, 1983, Two photosynthetic mechanisms mediating the low photorespiratory state in submerged aquatic angiosperms: Plant Physiol, v 73, p 488–496.

Smith, B N and Brown, W V, 1973, The Kranz syndrome in the Gramineae as indicated by carbon isotope ratio: Am Jour Bot, v 60, p 505–513.

Smith, B N and Epstein, S, 1971, Two categories of $^{13}C/^{12}C$ ratio for higher plants: Plant physiol, v 47, p 380–384.

Srdoč, D, Horvatinčić, N, Obelić, B, Krajcar, I and Sliepčević, A, 1985, Calcite deposition processes in karst waters with special emphasis on the Plitvice Lakes, Yugoslavia: Carsus Yugoslaviae, 11/4–6, p 101–203 (In Serbo-Croatian, with extended abs, fig captions and table headings in English).

Srdoč, D, Krajcar-Bronić, I, Horvatinčić, N and Obelić, B, 1986a, The increase of ^{14}C activity of dissolved inorganic carbon along the river course, *in* Stuiver, M and Kra, R S, eds, Internatl ^{14}C conf, 12th, Proc: Radiocarbon, v 28, no. 2A, p 436–440.

Srdoč, D, Obelić, B, Horvatinčić, N, Krajcar-Bronić, I, Marčenko, E, Merkt, J, Wong, H K and Sliepčević, A, 1986b, Radiocarbon dating of lake sediments from two karstic lakes in Yugoslavia, *in* Stuiver, M and Kra, R S, eds, Internatl ^{14}C conf, 12th, Proc: Radiocarbon, v 28, no. 2A, p 495–502.

Whelan, T, Sackett, W M and Benedict, C R, 1973, Enzyme fractionation of carbon isotopes by phosphoenolpyruvate carboxylase from C_4 plants: Plant Physiol, v 51, p 1051–1054.

Wong, W W, Benedict, C R and Kohel, R J, 1979, Enzymic fractionation of the stable carbon isotopes of carbon dioxide by ribulose-1.5-biphosphate carboxylase: Plant Physiol, v 63, p 852–856.