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Sources of organic carbon in the littoral of Lake Gooimeer as indicated by stable carbon isotope and carbohydrate compositions

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Abstract. The relative importance of potential carbon sources in the littoral of Lake Gooimeer, a lake in the centre of the Netherlands, was studied using a combination of $^{13}C/^{12}C$-ratio analysis and carbohydrate composition analysis. The littoral is covered on the land side by a 80 m wide *Phragmites australis* bed. Potential carbon sources were macrophyte litter, seston and benthic algae. Samples of potential carbon sources, sediments and benthic macrofauna from inside and outside the bed were analyzed for their $^{13}C/^{12}C$-ratio and some for their carbohydrate composition. Results indicate that inside the bed, macrophyte litter was the main source of carbon for both the sediment organic matter and the benthic macrofauna, and that algal material was of minor importance. Outside the bed, production by benthic algae was the main carbon source, with seston as a second source. No macrophyte derived material could be detected outside the reed bed.

Abbreviations: DOC (Dissolved Organic Carbon), SOM (Sediment Organic Matter)

Introduction

In littoral systems of lakes, a number of primary producers might be important as organic carbon sources for the food web and the sediment organic matter. A high production of both submerged and emergent macrophytes is characteristic for most littorals, and in addition to phytoplankton, other algal sources like epiphytes and benthic algae are present. Also, terrestrial material can be transported to the littoral by run-off or winds (Wetzel 1992). Information on the relative importance of these carbon sources is important to our understanding of the structure and functioning of wetlands and of littoral regions in particular.

A number of techniques have been applied to trace the flow of carbon in ecosystems. The $^{13}C/^{12}C$-ratio in organic matter has been used extensively to trace carbon sources in sediments and in food webs (Fry & Sherr 1984;

Peterson & Fry 1987; Gearing 1991). The method is based on differences in $^{13}C/^{12}C$-ratios among primary producers caused by differences in CO_2 fixation metabolism and CO_2 source. Emergent C3 plants have a ratio of around −27‰ ($\delta^{13}C$ notation; see method section for definition) whereas C4 plants are relatively enriched (−13‰). Phytoplankton of lakes is variable and ranged in a number of lakes from −17‰ to −45‰ (Siller 1979; Rau 1980; LaZerte 1983; Estep & Vigg 1985; Takahashi et al. 1990). The isotopic fractionation is in general small during the assimilation of food by heterotrophic organisms and the same applies for diagenetic processes acting on the bulk organic matter in sediments. This means that both heterotrophic organisms and sediment organic matter have a ratio close to their carbon source. By comparing $^{13}C/^{12}C$-ratios of potential carbon sources with ratios in sediments and/or heterotrophic organisms, conclusions can be drawn about the relative importance of these sources in an ecosystem. A prerequisite is that the potential carbon sources have a different $^{13}C/^{12}C$-ratio.

Problems arise when more than two major carbon sources are present in the system. In that case, intermediate $^{13}C/^{12}C$-ratios of sediments or organisms can originate from a number of different mixtures of the carbon sources. Conclusions can only be drawn unequivocally if sediments or animals have $^{13}C/^{12}C$-ratios comparable to one of the extremes in the range spanned by the carbon sources. In most ecosystems, littoral zones included, there are more than two carbon sources present. Therefore, combinations of the $^{13}C/^{12}C$-ratio method with other stable isotope or chemical composition-derived parameters have been used to increase the resolution of the analysis (Hedges & Parker 1976; Fry & Sherr 1984; Peterson et al. 1985).

This study is part of a project on the decomposition of organic matter in a reed bed covering a section of the littoral of Lake Gooimeer. The purpose of the study was to determine the most important sources of organic matter for the sediment from inside and outside the bed. To answer this question, stable carbon isotope measurements were combined with determinations of the neutral carbohydrate composition. The latter measurement can be used to discriminate between algal and macrophyte sources in sediments (Cowie & Hedges 1984a). Results indicate that inside the reed bed, primarily macrophyte derived material was present in the sediment and algal material was of minor importance. Outside the bed, no macrophyte material could be detected and benthic algal production was the most important source, followed by sestonic material.

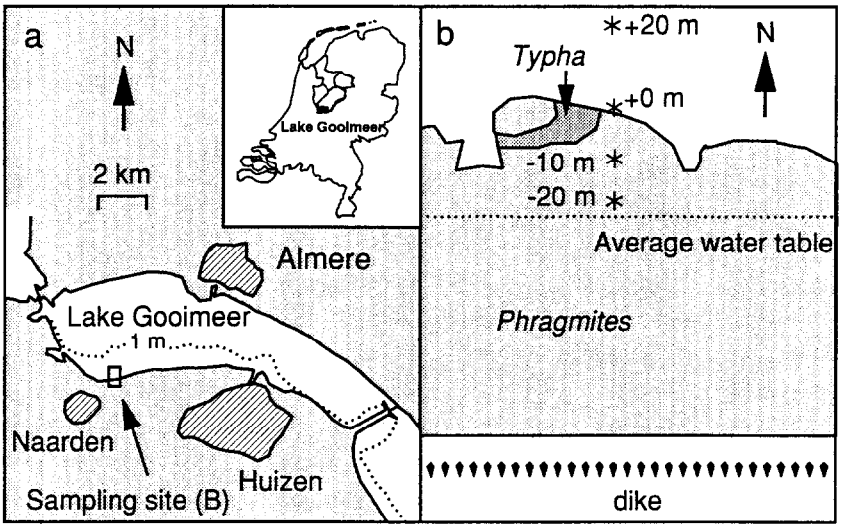

Fig. 1. Map of Lake Gooimeer (a) showing the sampling site (b); small map (a) shows location of Lake Gooimeer in the Netherlands. Sampling points (b) for stable carbon isotope and carbohydrate measurements are indicated by stars and by their distance from the edge of the reed bed. Average water depth at the lake side of the reed bed was about 20 cm and at point 20 m about 30 cm. Nearby cities are indicated by striped areas.

Description of sampling site and methods

Sampling site

The 'Gooimeer' is a very shallow lake (mean depth of 3.6 m, surface area 24 km^2) with a sandy sediment in the centre of the Netherlands (Fig. 1, De Haan et al. 1993). On the southern shore, there is a reed bed of approximately 80 m wide and 4 km long, with *Phragmites australis* (Cav.) Trin. Ex Steudel (common reed) as the dominant macrophyte species and some patches of *Typha augustifolia* L. (cat-tail) on the lake side of the bed. Outside the bed some *Potamogeton pectinatus* L. plants were present from May to July and the sediment was covered with benthic algae during the whole sampling period. The bed is bordered on the landside by a dike. Sedimentary organic matter is accumulating inside the bed and increases in concentration from <0.5% at the lake side to 1% at 10 m and to 30% at 20 m inside the bed.

The lake is eutrophic, with summer chlorophyll-a concentrations of about 60 $\mu g\ l^{-1}$. The phytoplankton was dominated by the cyanobacterium *Oscillatoria agardhii* Gom. during most of the year. Green algae were present in varying numbers throughout the year, and diatoms bloomed in early spring

(H.L. Hoogveld, NIE-CL, pers. comm.). The pH varied between 7.5 in winter and 8.8 in summer.

Horizontal gradients in the water column

During 1990–1991, overlaying water was collected in a gradient from inside to outside the reed bed at fixed sampling points marked with a stick. Care was taken to sample the water phase without resuspending the sediment. Water samples were first sieved over 150 μm to remove larger floating particles and zooplankton; the latter was present in high numbers inside the reed bed especially during summer and obscured possible gradients in seston originating from the open water. The material that passed the sieve contained mainly phytoplankton and some detritus. The organic matter concentration in the seston (>150 μm) was measured by filtering 200 to 500 ml through a Whatman GF/F glass-fibre filter. The filter was dried overnight at 105 °C and organic matter on the filter was determined as the subsequent loss of weight after 4 hours at 550 °C. DOC in the filtrate was determined using photochemical (UV) oxidation with persulfate (Schreurs 1979).

Sampling and sample treatment

Samples for stable carbon isotope ratio and carbohydrate composition measurements were mainly collected during two periods: (i) from October 1990 to August 1991, when samples were taken of potential carbon sources, sediments and macrofauna from 20 m inside (−20 m) the bed, and (ii) from October 1992 to March 1993, when samples were taken from inside (−20 m) and outside (20 m) the bed. Sediments from −10 m and +0 m were sampled for carbohydrate analysis on several occasions. Furthermore, monocultures of a green algae (*Scenedesmus obligus*) and a cyanobacterium (*Limnotrix limnetica),* both grown under light limitation in continues cultures, were analyzed for carbohydrates.

Emergent macrophytes were sampled at the end of the growing season when plants started to become yellow. *Potamogeton pectinatus* was not sampled because densities were low and it was only present during a short period of the year. Macrophyte litter was taken by hand from the top layer of the sediment and gently washed to remove sediment particles. SOM was sampled from the top 1 cm of three sediment cores (id 7 cm). For SOM samples from outside the bed, sand was removed by repeatedly shaking the sediment sample with water and decanting the SOM suspension; SOM was concentrated by centrifugation. Seston was collected by centrifugation of a 25 l water sample taken 20 m outside the reed bed. Centrifugation was performed with a Sorvall SR-5C centrifuge equipped with a continues flow angle rotor (Sorvall SS-

34/KSB system) at 10,000 rpm and a flow of 5 l/min (Sorvall Instruments, Du Pont, Wilmington, Del.). More than 90% of the particles were removed with this method, as determined by seston analysis (see above) before and after centrifugation. Seston samples for stable isotope and carbohydrate measurements were not sieved over 150 μm as for the horizontal gradient study, since samples were taken outside the bed and contained neither zooplankton nor course macrophyte litter. Seston and SOM samples were pretreated overnight with 0.25 N HCl to remove any carbonate minerals present. Macrofauna was sorted by hand from sediment material collected on a 0.7 mm sieve. Only dominant macrofauna species were collected and were grouped as chironomids, oligochetes, *Asellus* sp, leeches (Hirudinea) or Heteroptera. All samples were lyophilized and ground to a fine powder before further analysis.

Stable carbon isotope measurements

After combustion of the organic carbon to CO_2, stable carbon ratios were determined on a VG SIRA2 mass spectrometer (VG MassLab, UK) for the first sampling period and on an Europa 20-20 mass spectrometer (Europa Scientific, UK) for the second period. All carbon isotope data are given in the $\delta^{13}C$ notation:

$$\delta^{13}C\ (‰) = (R_{sample}/R_{standard} - 1) \times 1000,$$

where R is the $^{13}C/^{12}C$-ratio and the standard is PeeDee Belemite. The mean $\pm$ SD for the difference between duplicate subsamples was 0.19‰ $\pm$ 0.11 (n = 60).

Carbohydrate composition

The neutral carbohydrate composition of potential carbon sources and sediment samples was determined in duplicate after acid hydrolysis (H_2SO_4) according to Cowie & Hedges (1984b). Carbohydrates in the hydrolysates were determined with a Dionex 2000i/SP ion chromatograph. A Dionex PA1 column, with Milli-Q water as eluent (flow rate: 1 ml/min), was used to separate carbohydrates. Prior to use, the column was preconditioned with 100 mM NaOH plus 25 mM NaAcetate (flow rate: 1 ml/min) for one hour to reduce retention times. To optimize the detection, a post column addition of 1.6 M NaOH (flow rate: 0.3 ml/min) was performed using an AMMS II anion-micromembrane reactor (Haginaka et al. 1989). Carbohydrates were detected with a Dionex PED detector in the pulsed amperometric mode. A gold electrode with an $AgCl_2/Cl$ reference electrode was used, and pulsed

amperometric waveforms were optimized according to LaCourse & Johnson (1991). Hydrolysates were analyzed for fucose, arabinose, rhamnose, galactose, glucose, xylose, mannose and ribose (listed in order of increasing retention time) using external standards. No other compounds were identified. The detection limit was between 5 and 15 nM, depending on the compound analyzed. The hydrolysis efficiency was checked with cellulose (MN300, Hachery Nagel & Co). The carbohydrate yield from cellulose was 83.0% ± 0.7 ($n = 2$). No corrections for hydrolysis efficiency were made.

Results

Gradient measurements in the overlaying water (Fig. 2) showed that seston concentrations were lower inside the reed bed than outside on all sampling dates except on 17-March-92. DOC gradients were less evident; only on 8-July-91 and on 9-September-91 DOC concentrations were clearly higher inside the reed bed. On the other dates DOC concentration tended to be higher (<2 mg C/l) inside the bed, but differences were small compared to variability in the DOC determination (±1 mg C/l).

Seston, sampled 20 m outside the reed bed for stable carbon isotope and carbohydrate analysis, was examined by microscope and contained mainly phytoplankton with little detritus and no zooplankton. Stable carbon isotope measurements of seston (Fig. 3) showed a pattern with more negative values in the winter period and values comparable or somewhat enriched to the macrophytes during summer. In March, a dip in the $^{13}C/^{12}C$-ratios of seston was found, which coincided with a bloom of diatoms (see Method section). Seston $^{13}C/^{12}C$-ratios for both sampling periods (1990–1991 and 1992–1993) were in agreement with each other during the winter period; they were clearly depleted in ^{13}C compared to the macrophytes and showed the lowest value in March. *Phragmites australis* and *Typha augustifolia* had similar ratios of −27.0‰ ± 0.15 (mean for all samples) indicating a C4 type of CO_2 fixation metabolism for both species.

Sediment organic matter and macrofauna were sampled on six dates (Fig. 3): four during the winter period when seston and macrophytes had clearly different $\delta^{13}C$ values, and two during summer when seston and reed had similar values. Although, there was an overlap between the range in $\delta^{13}C$ for litter and SOM from inside the bed and the range for macrophytes, the data for litter and SOM were somewhat shifted to more negative ratios (on average −0.7‰, Fig. 4). SOM from outside the reed bed (+20 m) had variable but clearly higher $\delta^{13}C$ values than could be explained by either a seston or a macrophyte source. Coarse recognizable litter was never found on the sediment outside the reed bed.

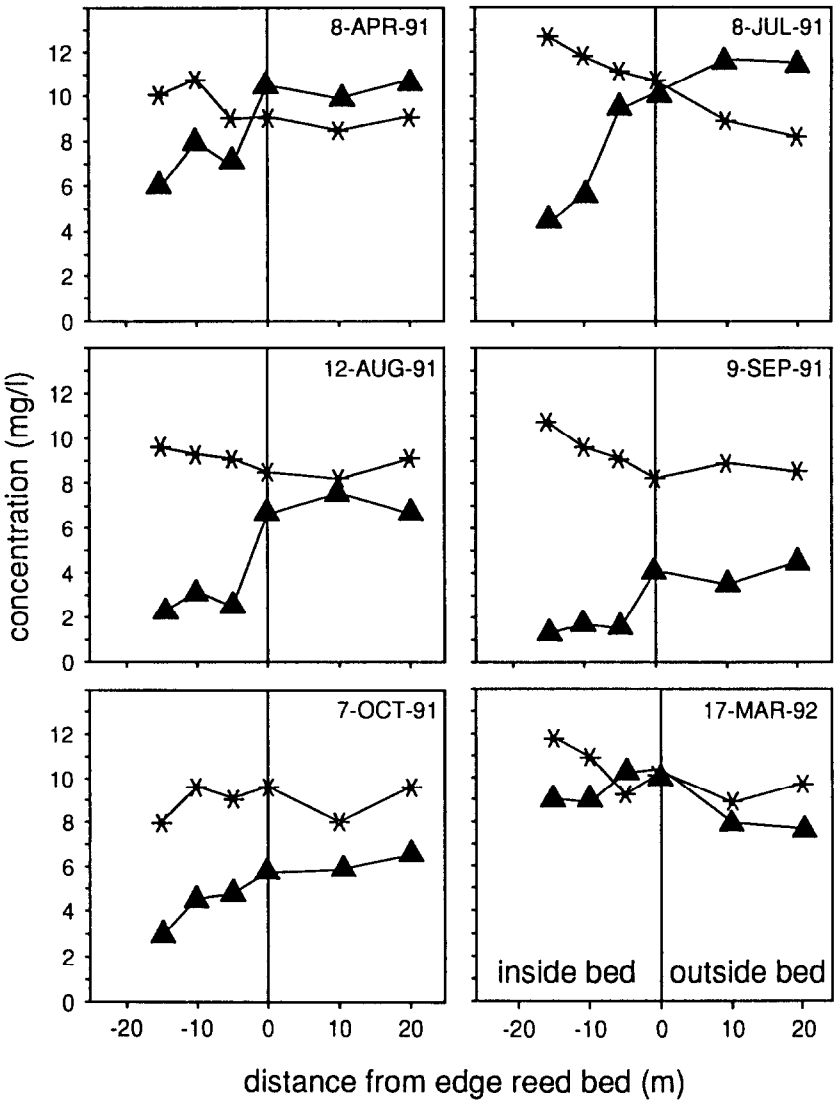

Fig. 2. Horizontal gradient measurements of seston (mg OM/l <150 μm, black triangles) and DOC (mg C/l, stars) in the water phase of the littoral on several dates.

Stable carbon isotope values for macrofauna from inside the bed (Fig. 4) did not vary much between sampling dates (mean values ± SD, −25.5‰ ± 0.9). Values for macrofauna inside the bed were comparable to seston in summer, macrophytes and litter. There was no correlation ($r^2 = 0.09$) between $\delta^{13}C$ values of seston and $\delta^{13}C$ values of macrofauna from inside the bed (Fig. 5a). Macrofauna from outside was clearly enriched in ^{13}C and fell between

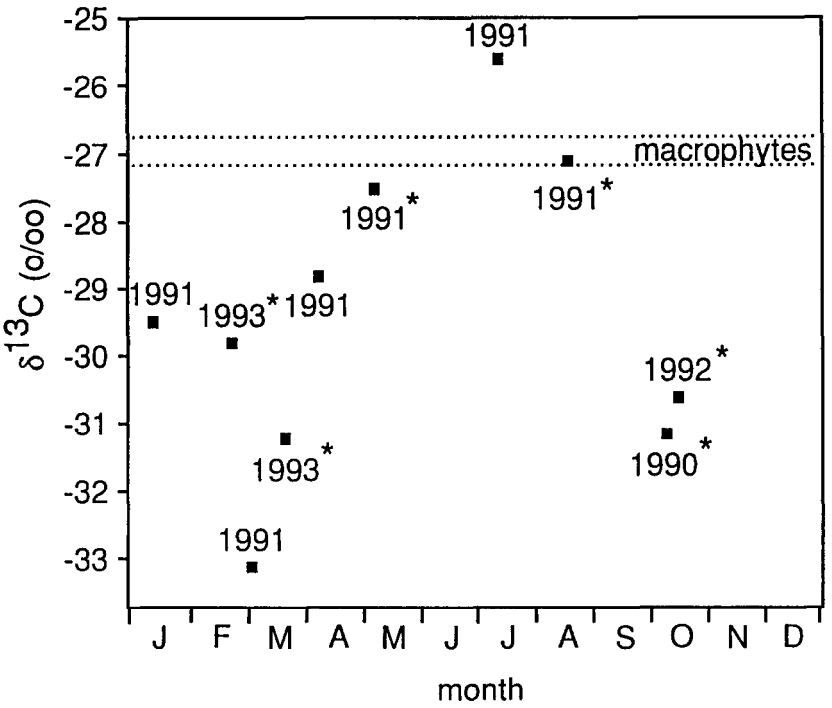

Fig. 3. Seston $\delta^{13}C$ values through the year. Black squares represent results from one seston sample analyzed in duplicate. For comparison, values for the two sampling periods are plotted on a one year scale. Years next to the $\delta^{13}C$ values indicate when samples were taken. Years labelled with stars show when sediment and macrofauna were sampled for $\delta^{13}C$ analysis. The range of $\delta^{13}C$ values for macrophytes is indicated by dotted lines.

seston in summer and SOM from +20 m. Although data from outside the bed were too sparse for a reliable correlation analysis, $\delta^{13}C$ values of chironomids seemed to correlate with values of seston (Fig. 5b). Outside the bed (Fig. 5b) the two sampled macrofauna groups appeared to behave differently; inside (Fig. 5a) no such differences were found between the five dominant groups and all macrofauna data were pooled for correlation analysis.

Results of carbohydrate analysis are shown in Table 1. Xylose and deoxy-sugars (fucose+rhamnose) showed the highest variability between different types of samples. A plot of xylose against deoxy-sugars, as percentages on a glucose free basis (total carbohydrates minus glucose), gave good graphical separation between macrophyte and algal based materials (Fig. 6). Glucose was excluded in the calculations for Fig. 6 because its dominance in all samples tends to obscure differences among the less abundant carbohydrates (Cowie & Hedges 1984a). Macrophytes, litter and SOM from −20 m had high % xylose and low % deoxy-sugars (Fig. 6). Monocultures of algae, SOM from

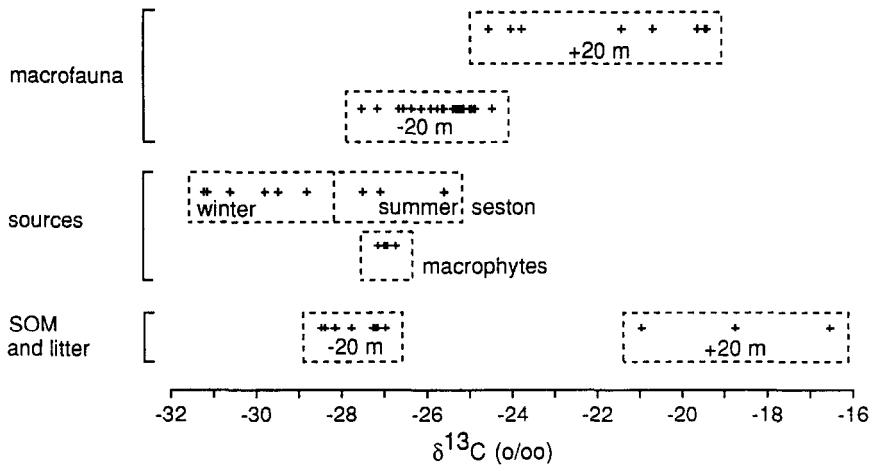

Fig. 4. Summary of all $\delta^{13}C$ data of potential carbon sources, sediments and macrofauna at 20 m inside (−20 m) and 20 m outside the reed bed (+20 m). Symbols represent results from one sample analyzed in duplicate.

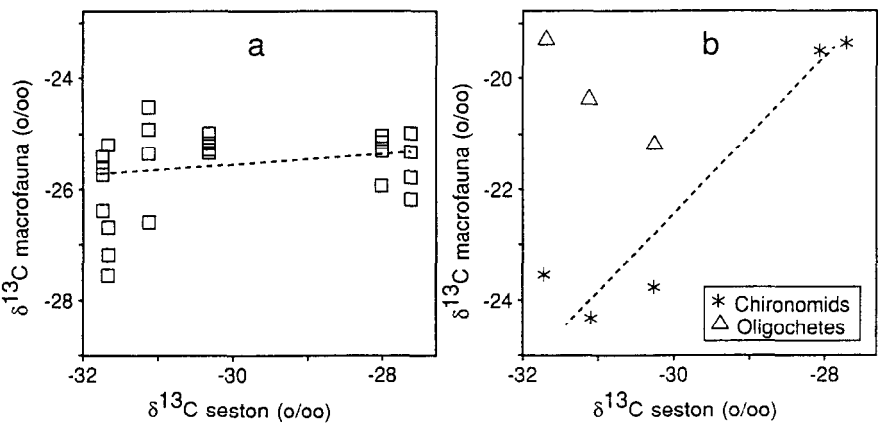

Fig. 5. Plot of $\delta^{13}C$ values of macrofauna from 20 m inside the reed bed (a) and 20 m outside the reed bed (b) against seston from the same sampling date. Lines show results of linear regression analysis (a: animals = $-21.7 + 0.1 \times$ seston, $r^2 = 0.09$; b: animals = $15.3 + 1.3 \times$ seston, $r^2 = 0.90$); for b) only chironomid data were included in the regression although data are very sparse.

outside the bed and seston had low % xylose compared to macrophytes. The % deoxy-sugars was higher in seston than in algae and SOM from outside. This might have been due to differences in algal populations, since % deoxy-sugars can vary between 0 and 63% depending on the species analyzed (Haug

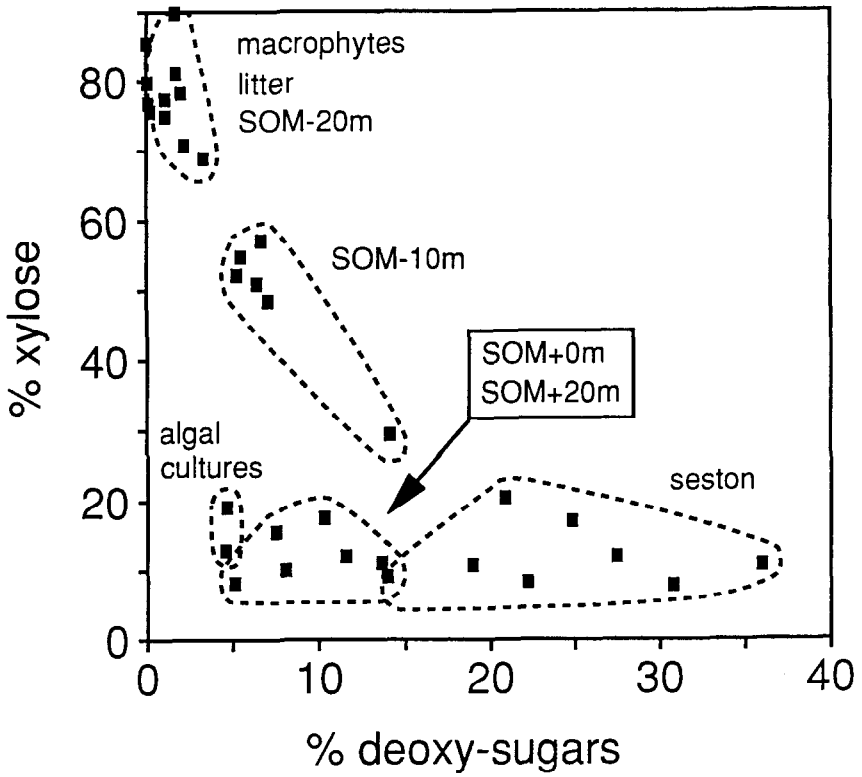

Fig. 6. Plot of weight % xylose against weight % deoxy-sugars (fucose + rhamnose) calculated on a glucose free basis in hydrolysates of sources, litter and SOM. Also shown are results from two monocultures of algae.

& Myklestad 1976; Vaidya & Mehta 1989; Brown 1991). SOM from −10 m had intermediate % xylose, which suggested the presence of a mixture of algal and macrophyte derived material.

Discussion

In this study, three main potential sources of carbon for the sediment were considered: litter of emergent macrophytes, seston and benthic algae. All three sources were visually abundant in the littoral. The gradient study showed consistently lower seston concentrations inside the reed bed, which suggested that the bed acted as a sink for sestonic material. The importance of seston as a carbon source for the reed bed sediment could not be estimated from these gradients. The gradient study also suggested a small flux of DOC to the

Table 1. Carbohydrate composition of selected samples from the littoral of Lake Gooimeer. Showing percentage of organic matter explained by carbohydrates and concentrations of individual compounds.

Sample	Date	%	% of total carbohydrates							
		of OM	Fucose	Arabinose	Rhamnose	Galactose	Glucose	Xylose	Mannose	Ribose
Macrophytes										
Phragmites[1]	01-Oct-90	54.1	(2)	6.4		2.5	54.0	36.7	0.4	
Phragmites[1]	01-Oct-90	54.8		5.3	0.9	3.0	48.5	42.3	0.1	
Typha	01-Oct-90	58.3		5.5	0.9	3.1	55.0	35.4		
Macrophyte litter										
−20 m	06-Oct-92	60.8		6.8		2.7	54.9	34.2	1.3	0.1
−20 m	22-Mar-93	51.0	0.1	6.9		3.7	54.9	34.3	0.2	
−10 m	06-Oct-92	46.6		6.2		2.7	55.6	34.3	1.3	
−10 m	22-Mar-93	50.2		4.2		2.4	54.5	38.9		
Algal cultures										
Limnotrix		5.6	0.2	0.8	3.2	32.0	28.7	13.8	21.3	
Chlamydomonas		11.3	1.0	0.6	1.9	37.8	37.5	8.2	12.9	
Seston										
	14-Jan-91	16.5		2.0	7.0	6.6	66.7	6.8	7.7	3.2
	08-Apr-91	12.9	1.3	1.6	5.1	10.3	68.6	3.6	7.5	2.1
	06-May-91	19.9	1.5	0.2	6.1	9.1	68.7	2.8	8.4	3.2
	08-Jul-91	23.8	1.5	0.2	5.0	10.0	58.3	4.2	17.9	3.0
	17-Mar-92	15.1	5.7	2.9	7.2	14.9	55.4	5.0	8.9	
	06-Oct-92	7.1	4.3	1.6	20.4	22.9	36.6	7.3	6.9	
	23-Feb-93	14.2	1.5	1.8	7.0	9.8	68.8	5.8	5.3	
	22-Mar-93	19.0	1.4		10.2	10.7	64.7	3.0	6.1	4.0

Table 1. Continued.

Sample	Date	% of OM	% of total carbohydrates							
			Fucose	Arabinose	Rhamnose	Galactose	Glucose	Xylose	Mannose	Ribose
Sediments (0–1 cm)										
−20 m	01-Oct-90	38.4		7.6	0.6	4.7	42.6	43.6	0.9	0.1
−20 m	08-Jul-91	22.6		5.5	0.5	2.8	53.8	35.6	1.8	
−20 m	23-Feb-93	45.1		7.7	1.4	4.3	54.0	28.6	4.0	
−20 m	19-Apr-93	22.6		5.2	0.5	3.0	57.7	31.6	2.1	
−10 m	01-Oct-90	14.2		4.4	3.2	6.5	51.9	27.5	6.5	
−10 m	14-Jan-91	8.1		7.7	3.9	7.7	45.0	31.1	4.5	
−10 m	06-May-91	17.2	2.0	5.6	4.0	8.8	61.1	12.5	6.0	
−10 m	08-Jul-91	22.1	0.6	8.3	2.1	7.2	50.6	26.5	4.8	
−10 m	06-Oct-92	18.9	1.1	7.1	2.5	8.1	50.2	25.0	5.9	
−10 m	23-Feb 93	19.8	0.6	7.8	2.2	6.7	50.6	27.9	4.3	
+0 m	06-Oct-92	24.4	0.7	2.6	2.3	7.8	64.3	3.7	14.9	3.7
+0 m	23-Feb-93	13.6	0.9	2.7	3.8	10.7	58.8	6.7	16.2	0.2
+0 m	22-Mar-93	18.5	0.6	1.3	3.4	9.3	68.0	4.2	11.3	2.0
+20 m	06-Oct-92	15.6	0.1	2.6	2.0	8.4	60.4	3.4	23.0	
+20 m	23-Feb-93	13.2	0.6	2.4	3.0	10.9	54.1	7.4	19.5	2.1
+20 m	22-Mar-93	16.2	0.7	0.8	4.2	10.3	66.5	4.0	9.5	4.1

[1] The *Phragmites* sample was analyzed on two occasions

[2] Blanc enteries were not detected

open water. Input of terrestrial material was probably not important, since the land side of the system was bordered by a dike that prevented direct transport of terrestrial material to the littoral. Submerged macrophytes with epiphytic algae attached to them show a high productivity in some littoral systems (Wetzel 1992), but were almost absent and restricted to a short period in summer in the littoral of Lake Gooimeer. Therefore, submerged macrophyte derived material was not considered to be an important source of organic carbon.

We used two parameters to trace carbon inside the littoral of Lake Gooimeer: $^{13}C/^{12}C$-ratios and neutral carbohydrate compositions. It is important to notice that these methods are not equivalent. With the $^{13}C/^{12}C$-ratio method all carbon is taken into account, whereas the carbohydrate composition method considers only the carbohydrate fraction in the sample. The carbohydrate fraction of macrophytes and litter (total carbohydrate yield of 45 to 60%, this study) is higher than that of algal sources (5 to 25%, this study). The percentage total carbohydrates will also change during decomposition, since polysaccharides in macrophyte litters are selectively faster degraded then lignin (Wilson et al. 1986; Benner et al. 1987).

The carbohydrate measurements showed that emergent macrophytes, litter and SOM from −20 m had a comparable composition with high percentages of xylose and low percentages of deoxy-sugars, which are characteristic for macrophyte-derived material (Cowie & Hedges 1984a; Moers et al. 1990), and had a composition clearly different from algae, seston and sediments from outside the bed (Fig. 6). The $\delta^{13}C$ values of sediment and litter from inside the bed were on average slightly lighter (−0.7‰) but in the same range as the macrophytes (Fig. 4). Small differences between sediment $^{13}C/^{12}C$-ratios and their likely carbon sources have been noted before (Fry & Sherr 1984) and in our case this might have been caused by the selective decomposition of the isotopically heavier polysaccharides in macrophyte litters resulting in an enrichment of the lighter lignin (Benner et al. 1987). In summary, the carbohydrate analysis indicated that SOM at 20 m inside the reed bed was dominated by macrophyte-derived material with little or no algal derived material present. The $\delta^{13}C$ determinations were in agreement with this indication.

Inside the bed, stable carbon ratios for macrofauna ranged from similar to clearly enriched compared to macrophytes. On average, macrofauna from inside the bed was 1.5‰ heavier than the macrophytes, which is in the range of fractionations between animals and their carbon source of ± 2‰ found in literature (Fry & Sherr 1984). Seston in summer had $\delta^{13}C$ values comparable or somewhat enriched to macrophytes, but in winter seston ratios were clearly depleted in ^{13}C compared to the macrophytes. This variation in sestonic $\delta^{13}C$

did not correlate with the ratios of the macrofauna from inside the bed, which suggested that seston was of little importance as a carbon source. An alternative explanation for the macrofauna ratios inside the bed might be that a mixture of seston and benthic algae was used as food source in addition to the abundant litter. However, production by benthic algae inside the bed was not likely to be high, because they would be heavily shaded by the macrophytes. In August, less than 10% of the incident light intensity reached the sediment; the remainder was absorbed by the vegetation (data not shown, similar to Rodewald-Rudescu 1974; Roos & Meulemans 1987).

Outside the reed bed, $\delta^{13}C$ values of SOM were higher than could be explained by either macrophytes or seston, which meant that another source or sources of carbon were present. We believe that this other source was most likely material produced by benthic micro-algae, which were visually present on the sediment of this shallow water during the whole sampling period. The low % xylose of the SOM outside the bed also indicates that algal material dominated and that little macrophyte derived material was present (Haug & Myklestad 1976; Cowie & Hedges 1984a; Vaidya & Mehta 1989; Brown 1991). Recent measurements with oxygen micro-electrodes have shown a high primary production in the toplayer of the sediment from outside the bed (K. Buis, NIE-CL, pers. comm.). The presence of isotopically heavy material derived from C4 macrophytes was not likely, since the dominant species in the littoral system were of the C3 type and carbohydrate compositions showed that little macrophyte derived was present outside the reed bed.

Outside the bed, macrofauna had $\delta^{13}C$ values similar to or lower than SOM. Since carbohydrate analysis suggested that macrophyte material was neither present in the SOM outside the bed nor in the seston, the macrofauna outside the bed probably used a mixture of SOM and seston as food. Based on our $\delta^{13}C$ data, a simple two source mixing model (formula on page 216 of Gearing 1991) with SOM and seston as sources, suggested that chironomids used 35% to 50% seston in their food and oligochetes 5% to 20% during the second sampling period.

Carbohydrate composition measurements showed a gradient in the SOM, with macrophyte derived material dominating at 20 m inside the bed and algal material dominating outside the bed. Algal material also appeared to be important at 10 m inside the bed, although the standing stock of macrophytes was similar at this point as at 20 m inside the bed (data not shown). It seemed that most of this standing stock, which will eventually die and enter the sediment, did not remain at – 10 m but was transported elsewhere. Macrophyte material could not be detected outside the reed bed, which meant that there was little transport of macrophyte litter towards the open water or that the material was diluted beyond the detection limit of the methods used.

LaZerte (1983) showed that in Lake Memphremagog approximately 40 to 50% of the organic carbon in the pelagic sediment was terrestrial in origin, whereas up to 100% was terrestrial in littoral sediments. Similarly, results of Rau (1980) indicated that terrestrial material was important as food sources for certain aquatic insects species in the subalpine Findley Lake. Both lakes are situated in a relatively large forested watershed compared to the area of the lake. In the littoral of Lake Gooimeer, terrestrial or emergent macrophyte influence on the sediment organic carbon was only present inside the reed bed and no macrophyte material could be detected outside the bed. The surface ratio between the macrophyte covered area and the lake is an additional important factor in determining the importance of macrophyte derived material in lakes. For Lake Gooimeer, this ratio is rather small, about 0.025.

Our results suggested that production by benthic algae was the primary carbon source outside the reed bed. A recent study showed that benthic microalgal production is also an important component in the food web of a salt marsh (Sullivan & Moncreiff 1990). Based on feeding habits and $\delta^{13}C$ values, Rau (1980) suggested that periphyton (algae that grow attached to a substrate) might be a food source for a mayfly larvae in Findley Lake. These data show that benthic microalgal production should also be considered in studies on carbon flow in other littoral systems.

In conclusion, combined results of stable carbon isotope and carbohydrate composition measurements suggest that mainly macrophyte-derived material was present in the sediment at 20 m inside the reed bed of Lake Gooimeer, and that macrophyte-derived material was probably also the most important food source for benthic macrofauna. Outside the reed bed, in the open part of the littoral, benthic algal production was of primary importance as source of carbon, with a variable contribution of seston depending on the macrofauna group.

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