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Sources of organic carbon in mangrove sediments: variability and possible ecological implications

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Abstract

Mangrove sediments from three different mangrove ecosystems (Coringa Wildlife Sanctuary in the Godavari Delta, Andhra Pradesh, India, and Galle and Pambala, south-west Sri Lanka) were analysed for their organic carbon content, elemental ratios (C:N) and carbon stable isotope composition. Organic carbon content (0.6 – 31.7% dry weight), C/N ratios (7.0 – 27.3) and δ^{13}C (between −29.4 and −20.6‰) showed a wide range of values. Lower stocks of organic carbon coincided with low C/N (atom) ratios and less negative δ^{13}C values, indicating import of marine or estuarine particulate suspended matter. High organic carbon stocks coincided with high C/N ratios and δ^{13}C values close, but not equal, to those of the mangrove vegetation. The variations observed in this study and published literature data could be adequately described by a simple two-end mixing model, whereby marine/estuarine suspended matter and mangrove litter were taken as end members. Thus, while in some mangrove ecosystems or vegetation zones, organic carbon stocks can be very high and are almost entirely of mangrove origin, there also appear to be cases in which deposited estuarine or marine suspended matter is the dominant source of organic carbon and nitrogen in mangrove sediments. This situation is remarkably similar to that observed in temperate salt marsh ecosystems where the importance of local vascular plant production to the sediment organic carbon pool is equally variable. The observed high variability in organic matter origin is thought to have a major impact on the overall carbon dynamics in intertidal mangrove ecosystems.

Introduction

Intertidal mangrove ecosystems are an important interface for the carbon cycle in some tropical coastal environments. The most extensive areas of mangrove forests occur on sedimentary shorelines, where large rivers discharge in low gradient coastlines. They can obtain high net primary production rates, and under certain conditions may export organic carbon to the adjacent aquatic environment either as leaf litter, particulate or dissolved organic matter (reviewed by Lee, 1995). On the other hand, mangroves enhance sedimentation of suspended matter during flooding and thus may act as a sink for allochtonous material (e.g. Furukawa et al., 1997). Sedimentation rates in mangrove forests are difficult to measure, and although in some cases rates of up to 10 mm/yr have been reported, they are estimated to be usually less than 5 mm/yr (Twilley et al., 1992; Ellison, 1998). Although a number of studies have recently investigated the -possible- outwelling of organic matter (e.g. Dittmar et al., 2001) and its potential fate in the aquatic environment (e.g. Bouillon et al., 2000, 2002a) very little attention has been given to possible ‘inwelling’ of organic matter, even though some authors have suggested that this might be one of the sources of the nitrogen enrichment observed in many mangrove sediments (Morell & Corredor, 1993; Kazungu, 1996; Middelburg et al., 1996).

Mangrove ecosystems are able to store large amounts of organic carbon (e.g. Matsui, 1998; Fujimoto et al., 1999) and in some mangrove ecosystems organic-rich sediments of several meters depth have been found (e.g. Twilley et al., 1992; Lallier-Verges et al. 1998). The sources of organic carbon stocks in mangrove sediments have rarely been studied in detail, although this should be an important factor when constructing any carbon budget of mangrove ecosystems.

A recent study in an east Indian mangrove forest indicated that mangrove leaf litter was not the dominant carbon source for most benthic invertebrate species in the intertidal zone (Bouillon et al., 2002b). It was suggested that this may not be a general feature of mangrove ecosystems yet might be related to e.g. the sources of organic matter in the sediment available for higher consumers. Recently, Lee (1999) argued that more research attention should focus on the interplay between physical and biotic influences in the ecology of mangrove ecosystems. A prime example of this interaction is provided by sediment organic carbon dynamics, as the amount and origin of organic carbon in mangrove sediments should be influenced by both physical (e.g. tidal amplitude) and biological (e.g. consumption, removal, degradation) factors, and may in turn influence the quality and availability of food sources for benthic faunal communities. In this paper, we discuss the variabiltity of sedimentary organic carbon sources in different mangrove ecosystems for which we expected to find large differences in the stocks and sources of organic carbon, and argue that this may be a key factor in some aspects of mangrove ecosystem functioning which deserves further research.

Materials and methods

Study areas

Surface sediment samples were collected in three different vegetation zones in the Coringa Wildlife Sanctuary located in the Godavari Estuary along the Bay of Bengal coast (between 82° 15′ and 82° 22′ E, 16° 43′ and 16° 52′ N), i.e. an *Avicennia officinalis* L. fieldplot, an *Excoecaria agallocha* L. fieldplot (both sampled at approximately monthly intervals during 1996 and early 1997), and a mixed *Avicennia-Excoecaria* zone (sampled in November 1999). More details on these sites and a general description of the area can be found in Dehairs et al. (2000) and Bouillon et al. (2002b). Briefly, the mangroves in this area are located in the estuary of the Gautami Godavari, the northern branch of one of India's largest rivers which opens into the Bay of Bengal on the east coast of India in the state of Andhra Pradesh. Tidal amplitude in the coastal zone varies between 0.5 and 2 m.

Two sites along the south-west coast of Sri Lanka were also selected for sampling of sediments in November 1999: the basin/riverine forest in Unawatuna-Galle (06° 01′ N – 80° 14′ E), covering an area of about 1.5 km^2, and the fringing mangroves ($\sim$3.5 km^2) at Pambala-Chilaw lagoon (07° 35′ N – 79° 47′ E). In Galle, sediments were taken from a *Rhizophora apiculata* Bl. zone and from an *E. agallocha* zone, whereas in Pambala, a mixed *R. apiculata* - *R. mucronata* Lamk. and an *A. officinalis* zone were sampled. Tidal amplitude at both sites is very low ($<$1 m) and rarely exceeds 15 cm in a 7-day period (Dahdouh-Guebas et al., 2002). More detailed descriptions of these sites can be found in Dahdouh-Guebas et al. (2000) and Dahdouh-Guebas (2002).

Sampling and analytical techniques

All surface sediment samples (up to 5 cm depth) were collected by hand and were cleared from large debris and shell remains. Sediments were dried at 60 °C for 24–48 h and ground to a fine powder using a mortar and pestle. All samples were acidified with dilute (5%) HCl before analysis to remove carbonates, as described by Nieuwenhuize et al. (1994). Mangrove leaves were collected by hand, washed, and dried at 60 °C for 48–72 h. Leaf samples contain 1 leaf/sample, but as the inter-leaf variability showed to be relatively small, pooled samples of 10 leaves were chosen in some cases.

Concentrations of organic carbon, total nitrogen, and elemental ratios (C/N) were determined by combusting preweighed samples in a Carlo Erba NA-1500 Elemental Analyser, and acetanilide (Merck) was used for calibration. All samples for carbon stable isotope analysis were combusted in a Carlo Erba NA-1500 Elemental Analyser, and the resulting CO$_2$ was cryogenically separated using a manual extraction line. Stable isotope ratios were determined on a Finnigan

Table 1. Carbon isotopic composition of mangrove leaves from the different study sites (average ± 1 s.d.). *n* = number of samples

Site/species	δ^{13}C (in ‰)
Coringa Wildlife Sanctuary	
Various species (n = 16)	−28.7 ± 1.1‰*
Galle	
Rhizophora apiculata (n = 9)	−31.5 ± 1.4‰
Excoecaria agallocha (n = 4)	−28.1 ± 2.0‰
Pambala	
Avicennia officinalis, pooled leaves (n = 10)	−30.5‰
Rhizophora apiculata, pooled leaves (n = 10)	−29.3‰
Rhizophora apiculata (n = 4)	−29.1 ± 1.2‰
Rhizophora mucronata, pooled leaves (n = 10)	−31.0‰
Rhizophora mucronata (n = 4)	−31.3 ± 0.9‰

* data from Bouillon et al. (2002b).

Mat Delta E Isotope Ratio Mass Spectrometer, and are expressed relative to the conventional standard (PDB limestone) as δ values, defined as:

$$\delta^{13}\mathrm{C} = \frac{\mathrm{X}_{\mathrm{sample}} - \mathrm{X}_{\mathrm{standard}}}{\mathrm{X}_{\mathrm{standard}}} * 10^3 [‰]$$

where X = ^{13}C/^{12}C. Internal reference materials included IAEA-C6 (sucrose) and IAEA-CH-7 (polyethylene). The standard deviation of δ^{13}C for ten aliquots of the same sample was lower than 0.2 ‰.

Results

Data on organic carbon content (% OC), elemental ratios (C/N, atom), and carbon stable isotopic composition (δ^{13}C) of sediments from the three study sites are shown in Figure 1A and 1B. Overall, the organic carbon content of mangrove sediments was found to vary over almost two orders of magnitude (0.6 – 31.7%), and C/N ratios varied between 7.0 and 27.3. Carbon stable isotope ratios showed a ^{13}C-enrichment relative to the average mangrove leaf material of the specific sites (Fig. 1A, Table 1), and varied between −29.4 and −20.6‰. Sediments under *Rhizophora* spp. showed a much higher OC content than that under *Excoecaria agallocha* (in Galle) or *Avicennia* spp. (in Pambala). Organic carbon content in sediments from the Coringa area was much lower than that found in the two Sri Lankan mangrove forests. Lower concentrations of organic carbon and low C/N ratios coincided with less negative δ^{13}C values, whereas sediments rich in organic carbon and with higher C/N ratios had δ^{13}C values which are much closer to those of the mangrove vegetation (Fig. 1A, 1B).

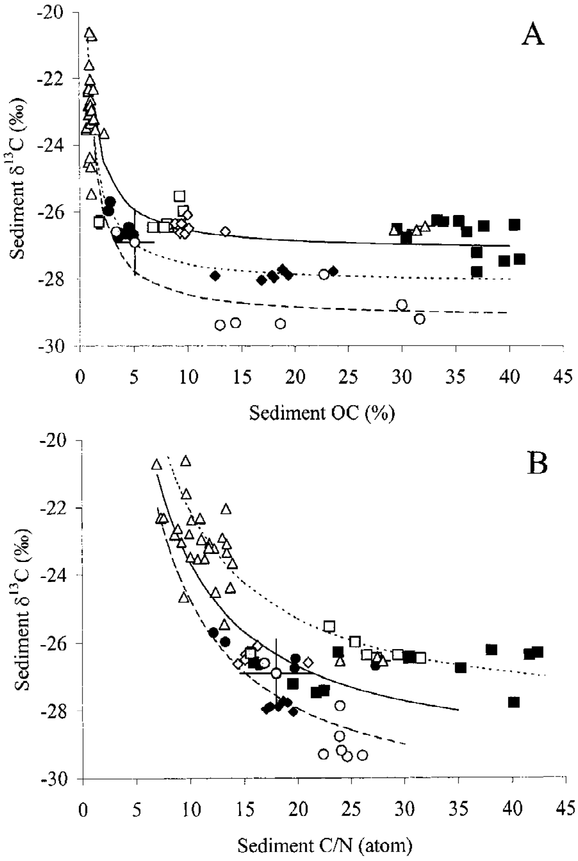

Figure 1. (A) δ^{13}C (in ‰) of organic carbon *versus* organic carbon content (% dry weight) of surface sediments from various mangrove ecosystems, and (B) δ^{13}C (in ‰) of sediment organic carbon *versus* C/N (atom) ratios of sediments from various mangrove ecosystems. Open triangles represent data from the Coringa Wildlife Sanctuary, full circles: *Excoecaria agallocha* zone (Galle), open circles: *Rhizophora* spp. zone (Galle), open diamonds: *Avicennia* spp. zone (Pambala), full diamonds: *Rhizophora* spp. zone (Pambala), open squares: data from Kazungu (1996), grey square: data from Dittmar & Lara (2001), grey circles: data from Jennerjahn & Ittekkot (2002), grey triangles: data from McKee et al. (2002), and black squares: data from Lallier-Verges et al. (1998). Error bars: 1 s.d. Different curves correspond to different assumptions for δ^{13}C and organic carbon content or C/N ratios for the two end-members (see text for details).

Differences in leaf δ^{13}C between sites and species were also found, with *Rhizophora* spp. from Galle being most ^{13}C-depleted with an average value of −31.5 ± 1.4‰ (Table 1).

Discussion

$\delta^{13}C$ values of organic carbon in 'peaty' mangrove sediments (such as those in the *Rhizophora* zones at the two Sri Lankan sites) were relatively similar to that of the mangrove vegetation and showed high C/N ratios between 17 and 25, whereas organic matter in 'mineral' sediments such as those from the Coringa area is enriched in ^{13}C by up to 8.5‰ and showed C/N ratios of on average about 10 but sometimes as low as 7.0 (Fig. 1B). Other organic carbon-rich sediments such as those described by Lallier-Verges et al. (1998) have also been shown to display high C/N ratios (up to 43) and $\delta^{13}C$ values close to that of the mangrove vegetation. The organic matter stocks in these systems can be extremely high: when assuming a carbon content of 40% (dry weight) for mangrove organic matter (e.g. Lallier-Verges et al., 1998), some of the *Rhizophora* sediments from Galle (Fig. 1) can be estimated to consist of up to 75% organic matter. On the other extreme, Machiwa (2000) found a distinct gradient in $\delta^{13}C$ in a mangrove ecosystem in Zanzibar, where sediments on the marine fringe showed $\delta^{13}C$ values of -17.6 ± 0.8‰, but lower values of -24.3 ± 1.1‰ in the landward zones. The more enriched values were attributed to inwelling of marine organic matter, including relatively ^{13}C-enriched seagrass material. An enrichment in ^{13}C of the sediment organic matter has also been recorded in other mangrove sediments (e.g. Hemminga et al., 1994; Kazungu, 1996).

When combining the data from the three study sites, it appears that there is an inverse relationship between the organic carbon content and the corresponding $\delta^{13}C$ values (Fig. 1A) and between the sediment C/N ratios and the corresponding $\delta^{13}C$ values (Fig. 1B). Middelburg et al. (1997) found a similar OC% – $\delta^{13}C$ relationship in sediments from temperate salt marsh ecosystems, with sediments low in organic carbon reflecting allochtonous sources and organic-rich sediments having $\delta^{13}C$ values close to the dominant vegetation (note that in the case of salt-marshes the vegetation – mainly grasses – is usually enriched in ^{13}C relative to allochtonous sources). Following the arguments of Middelburg et al. (1997), two-end mixing curves were constructed to describe the relationship between sediment $\delta^{13}C$ values and the corresponding OC% and C/N values, and these are represented in Figure 1A and 1B by the full and dotted curves (the different curves represent different values for the input parameters).

By defining an autochtonous component, i.e. mangrove leaf litter, and an allochtonous component (suspended particulate matter), we can calculate the $\delta^{13}C$ values of sediments for a given OC% or C/N ratio as follows. First, we calculate the fraction of the *bulk sediment* which is from mangrove origin, $X_{mangrove}$, as:

$$X_{mangrove} = \frac{C_{sediment} - C_{allocht}}{C_{mangrove} - C_{allocht}}$$
$$0 < X_{mangrove} < 1 \qquad (1)$$

Where $C_{sediment}$, $C_{allocht}$, and $C_{mangrove}$ are the organic carbon content of the sediment, the allochtonous component, and mangrove litter, respectively (in g/g dry weight).

This allows us to calculate the fraction of the *organic carbon* in the sediment which is of mangrove origin, $X_{mangroveC}$ (expressed in g/g dry weight) as:

$$X_{mangroveC} = $$
$$= \frac{X_{mangrove} * C_{mangrove}}{X_{mangrove} * C_{mangrove} + (1 - X_{mangrove}) * C_{allocht}}$$
$$0 < X_{mangroveC} < 1 \qquad (2)$$

Thirdly, we calculate the expected $\delta^{13}C$ of the sediment organic matter, $\delta^{13}C_{sediment}$ (expressed in ‰), as:

$$\delta^{13}C_{sediment} = X_{mangroveC} * \delta^{13}C_{mangrove} +$$
$$(1 - X_{mangroveC}) * \delta^{13}C_{allocht} \qquad (3)$$

where $\delta^{13}C_{mangrove}$ and $\delta^{13}C_{allocht}$ are the carbon isotopic composition of mangrove litter and the allochtonous component, respectively. Similarly equations were derived for the relationship between sediment C/N (atom) ratios and sediment $\delta^{13}C$ values.

Some of the parameters used in constructing these two-source mixing curves are, of course, subject to significant variability. C/N ratios of mangrove leaf litter are variable, and will depend on factors such as the nutrient status, the degradation stage and the species considered (e.g. Twilley et al., 1986; Dehairs et al., 2000). The suspended organic matter in mangrove creeks and nearshore waters may have a wide range of $\delta^{13}C$ signatures and C/N ratios (Cifuentes et al., 1996; Bouillon et al., 2000), but is on average more ^{13}C-enriched than the mangrove-derived carbon. In our mixing curves (Fig. 1A), we have used a value between -23.0 and -20.5‰ in order to account for the observed variability, and although δ^{13}C are expected to be lower in some cases (e.g. Bouillon et al., 2000, 2002a), this would not change the general trend of the mixing curves and its consistence with the data – except for the samples with the most enriched δ^{13}C values. C/N ratios of suspended particulate organic matter are usually much lower than those of mangrove litter, e.g. in the Coringa area it was shown to have C/N ratios of on average 8–10 (Dehairs et al., 2000). The suspended matter usually consists of a large, but variable, fraction of inorganic material (e.g. Twilley et al., 1992; Wolanski et al., 1998; Tanaka et al., 1998). Using the data of Dehairs et al. (2000) and Murthy (1997), the POC contribution to suspended matter in our study area in the Coringa Wildlife Sanctuary is estimated to be – on average – between 1.8 and 3.7%. As sedimentation results in the preferential deposition of inorganic material, we have used slightly lower values in constructing the mixing curves. Finally, the δ^{13}C signature of mangroves used in our mixing model are slightly more enriched than those measured in leaf tissues. The rationale behind this approach is that (i) inputs from other parts of mangrove tissues such as roots or wood may be significant (Middleton & McKee, 2001) and the latter are usually slightly enriched in ^{13}C, and (ii) a slight degree of enrichment is often observed between the dominant inputs and the resulting soil or sediment organic matter. The latter is currently thought to be mainly the result of an increase in bacterial and fungal residues in this organic matter pool (see Ehleringer et al., 2000 for a recent review on this issue).

Notwithstanding these sources of variability in our end-members, the general trend of the curve remains similar when the values of the end-member parameters are slightly modified, as represented by the different curves in Figures 1A and B ($\delta^{13}C_{\mathrm{allocht}}$ between -23.0 and -20.5‰, $\delta^{13}C_{\mathrm{mangrove}}$ between -29.0 and -27.0‰, sediment OC between 0.8 and 1.5%, C/N_{mangrove} between 30 and 43). Thus, the two-source mixing model appropriately describes our dataset, and the available literature data (Kazungu, 1996; Lallier-Verges et al., 1998; Dittmar & Lara, 2001; Jennerjahn & Ittekkot, 2002; McKee et al., 2002) also fit in this pattern, confirming the validity of the model. Although organic carbon in sediments from some intertidal mangrove ecosystems, such as in the *Rhizophora* zones of the two Sri Lankan sites studied and the one described by Lallier-Verges et al. (1998), originates entirely or almost entirely of decomposing mangrove-derived organic matter, this appears not to be a general feature. In fact, the data from the Coringa area indicate that organic matter in the sediments originates mainly from the water column suspended matter, and phytoplankton-derived matter is presumably a major fraction of this material (Bouillon & Dehairs, 2000). Thus, there appear to be large differences in carbon dynamic between ‘flow-through’ systems where exchange of organic carbon (both import and export) between the intertidal regions and the adjacent aquatic environment is possible, and more closed ‘accumulation’ systems where local mangrove production accumulates in the underlying sediments. When considering the relatively high tidal amplitude in the Coringa area, and the very low tidal amplitude in the two Sri Lankan sites and the Guadeloupan site studied by Lallier-Verges et al. (1998), it becomes clear that this may be an important factor determining the stocks and sources of organic carbon in intertidal mangrove sediments. To which extent the bacterial biomass or local primary producers such as benthic microalgae and cyanobacteria may contribute to the sediment organic matter pool remains unresolved in our approach, and other techniques would be required to assess the possible contribution of these sources.

Such large variations in availability and sources of organic matter can be expected to have major consequences for the overall carbon pathways in intertidal mangrove forests. For instance, Boschker et al. (1999) showed that the contribution of local plant material to bacterial production in sediments was of little importance in ‘mineral’ salt marshes (i.e. those with low organic carbon content), but dominant in ‘organic’ salt marshes (i.e. systems where local plant production accumulated to form organic-rich sediments). It thus appears that carbon sources used by bacteria in intertidal ecosystems do not necessarily originate from the dominant local vegetation (Boschker et al., 2000), but that algal sources are preferred when available. Although there is as yet no direct evidence, it is possible that a similar situation occurs in mangrove sediments. Many invertebrates in mangrove environments feed – selectively or not – on the sediment organic matter, and the often assumed close link between mangrove primary production and the invertebrate community may not be valid in flow-through ecosystems where mangrove litter is not a major component of sediment organic matter. A recent study on resource utilisation by benthic invertebrates in the Coringa area using on carbon and nitrogen stable isotope ratios as natual tracers (Bouillon et al., 2002b) showed that incorporation of mangrove-derived carbon was detectable in only a limited number of species, whereas the majority of invertebrates did not show significant assimilation of mangrove-derived carbon. In this context, it is worth noting that several authors have mentioned that organic matter should have a C/N ratio lower than 17 in order to be of nutritional use to invertebrates (Russel-Hunter, 1970). As can be seen in Figure 1B, this would imply that bulk sediment organic matter can only be of importance where allochtonous sources contribute to the sediment pool. Several authors have drawn attention to the fact that mangrove leaf litter is of little nutritional value due to its high C/N ratios – even after considerable degradation – (e.g. Micheli, 1993; Lee, 1997) and the relatively N-rich material deposited during high tides may offer some invertebrates an easily accessible N-source. The large variations observed in the origin of organic matter in mangrove sediments provide an excellent opportunity to study the effects of the availability of different sources on the carbon and nitrogen dynamics of these systems.

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