

Plant-mediated methane emission from an Indian mangrove

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Abstract

Mangroves have been considered for a long time to be a minor methane source, but recent reports have shown that polluted mangroves may emit substantial amounts of methane. In an unpolluted Indian mangrove, we measured annual methane emission rates of $10 \text{ g CH}_4 \text{ yr}^{-1}$ from the stands of *Avicennia marina*. This rate is of the same order of magnitude as rates from Northern wetlands. Methane emission from a freshwater-influenced area was higher, but was lower from a stunted mangrove growing on a hypersaline soil. Methane emission was mediated by the pneumatophores of *Avicennia*. This was consistent with the methane concentration in the aerenchyma, which decreased on average from 350 ppm_v in the cable roots to 10 ppm_v in the emergent part of the pneumatophores. However, the number of pneumatophores varied seasonally. The minimum number occurred during the monsoon season, which reduced methane emissions largely. Ebullition from unvegetated areas may also be important, at least during monsoon season when measured bubble fluxes were occasionally about five times as high as pneumatophore-mediated emissions.

Keywords: mangrove, marine, methane emission, plant-mediated transport, pneumatophore

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Introduction

Methane is the most important greenhouse gas after carbon dioxide. More than half of the net source comes from systems under human control, while natural wetlands contribute between 26% and 40% to the total emission (Hein *et al.*, 1997; Houweling *et al.*, 1999). The atmospheric methane concentration has been increasing over the last 300 years and has currently reached a mixing ratio of approximately 1.8 ppm_v . The increasing trend has slowed down to nearly zero in 1992 but was again considerably high at the end of the 1990s (Dlugokencky *et al.*, 2001, 2003; Intergovernmental Panel on Climate Change, 2001). Superimposed on this trend is a considerable inter-annual variation (Dlugokencky *et al.*, 1998). While the increase has been attributed mainly to human activities, the variations may also be influenced by natural wetlands (Hogan & Harriss, 1994; Dlugokencky *et al.*, 2001; Walter *et al.*,

2001). Until now, field experiments were focused mainly on northern and temperate wetlands. Tropical wetlands were recognized as important, but empirical studies are rare.

Mangroves are trees that are well adapted to the transition zone between land and sea, where they form intertidal forests. These forests are also named mangroves or sometimes mangal (Tomlinson, 1994). Mangroves grow preferentially in the tropics and reach their highest species diversity and area extent in South-east Asia.

Most water-saturated soils and littoral sediments are anoxically very close to the sediment–water interface (Brune *et al.*, 2000). While the rhizosphere of emerging plants may be supplied with oxygen through the plant's aerenchyma, the bulk soil or sediment stays anoxic (Conrad & Frenzel, 2002). Methanogenesis is the prevalent terminal process in anoxic freshwater sediments and sulphate reduction in anoxic marine sediments. Nevertheless, methanogenesis may occur in marine sediments, if the so-called noncompetitive substrates are available (Oremland & Polcin, 1982; King, 1988), or if the organic input is large enough to support both sulphate reducers and methanogens.

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However, methanogenesis in and methane emission from unpolluted mangroves have been regarded as minor, both in a particular ecosystem and on a regional scale (Sotomayor *et al.*, 1994; Giani *et al.*, 1996; Alongi *et al.*, 2000, 2001). More recently, however, we observed high methane emissions from both polluted and unpolluted coastal wetlands in South India (Purvaja & Ramesh, 2000a, 2001). These observations indicated for the first time that coastal ecosystems of the tropics might emit considerable amounts of methane. Therefore, we decided to study the seasonal pattern of methane emissions from mangroves together with the pathways and controls of emission.

Material and methods

Site and vegetation

The Pichavaram mangrove is located at the northern end of the Cauvery delta at 11°27'N and 79°47'E. The mangrove is an estuarine type, connected to the Vellar estuary in the North and the Coleroon estuary in the South, with a well-developed backwater system. It is separated from the Bay of Bengal by a narrow sand bar during summer and is periodically flushed with neritic waters by the incoming tidal waters. Spring and neap tides have an amplitude of about 1 and 0.3 m, respectively. Freshwater enters the mangrove through the Coleroon and Vellar rivers, the former being more important. The average monthly discharge from the Coleroon river for the years 1985–1990 was used as the best estimate of the seasonally changing inflow of freshwater (MSSRF, 1996). Agriculture is the primary human activity and is based mainly on wetland rice cultivation. Hence, the mangrove receives agricultural run-off from the adjacent paddy fields. However, nutrient levels were at least two orders of magnitude lower than in polluted mangroves that are known as significant methane sources (Purvaja & Ramesh, 2000b). Local fishing is for subsistence and done by women wading with fishing baskets and nets in the shallow flats, or from rafts and dugout canoes. The average grain size distribution in the sediments of the Pichavaram mangrove is (ranges, if available, are given in brackets) clay: 25% (20–30%), silt 15% (10–20%), fine sand 45%, and coarse sand 15% (Untawale, 1987).

The total area of the wetland of the Vellar–Pichavaram–Coleroon estuarine complex is about 2336 ha, of which 241 ha are occupied by dense mangrove vegetation (Krishnamoorthy, 1996). The vegetation is composed of 14 exclusive mangrove species, including as dominants *Avicennia marina*, *A. officinalis*, *Excoecaria agallocha*, *Rhizophora apiculata* and *R. mucronata*. In

addition, at least 18 associated species occur, among which *Suaeda maritima* is the most abundant. Further biological information has been summarized recently (Kathiresan, 2000).

Rhizophora forms a band of about 4–10 m wide along the tidal creeks and channels. Summing up the values of relative frequency, relative dominance density to an importance value index the genus *Avicennia* is most important, covering ca. 80% of the mangrove area. *A. marina*, a high-salinity tolerant mangrove, is the most frequent species (MSSRF, 1996).

Avicennia has a highly differentiated root system with cable roots growing horizontally in the sediment, and pneumatophores projecting from the cable roots upwards and connecting it to the atmosphere (Tomlinson, 1994). Below the sediment surface, the pneumatophores and to a lesser extent the cable roots have laterals, the so-called fine or feeding roots. In order to measure the rooting depth, a transparent acrylic cylinder (inner diameter 6.5 cm) was put over individual pneumatophores and pressed down into the sediment until it cut through the cable root. The depth and architecture of the root system was determined by dissecting the core.

The relative volume of the aerenchyma was measured by pycnometry (Archimedes' principle: Curran *et al.*, 1996) in roots sampled from INTSAL on January 2003. The roots were separated into cable roots, pneumatophores below the soil surface, basal and distal half of the emerging part of the pneumatophores, and fine roots. Roots were cut to pieces ca. 1 cm long. About 6 g (fine roots) to 11 g (other parts) fresh weight were filled into bottles of known volume and weighed. The bottles were closed with a rubber septum, weighed again, filled bubble-free with water by syringe and needle, and reweighed. The volume of the roots was calculated from the difference between the volume of the bottle and the weight of the water times the temperature-corrected density.

The water was then drained off again and a coarse mesh made from stainless steel was inserted in order to keep the roots at the bottom of the bottle during the following treatment. The bottles were closed with rubber septa and evacuated via a needle for 10 min. While connected to the vacuum, water was injected until the roots became submerged. The atmospheric pressure was re-established by disconnecting the bottles from the pump with the needle open to the atmosphere. After repeating this procedure three times, virtually no bubbles escaped under vacuum, indicating that the aerenchyma was completely filled with water. The steel mesh was removed, and the bottles were filled again bubble free with water and reweighed. The volume of the aerenchyma was calculated from the difference between water displacement before and after

exchanging the gas in the aerenchyma by water. The experiment was done in triplicate.

Sampling plots

The sampling plots were situated around the centre of the mangrove area and 1–2 km away from the closest settlement. Three different zones based on water salinity were chosen; average values and ranges are given in brackets: HISAL – high-salinity zone (34.2; 30–38‰), INTSAL – intermediate salinity (20.7; 15–28‰), and LOWSAL – low salinity (17.8; 11–27‰). The minimum corresponds to the monsoon season while the maximum was measured during the dry period. HISAL receives tidal waters from the Bay of Bengal, while LOWSAL is affected by effluents from rice fields located upstream along the River Colleroon. The *Avicennia* trees were well developed in LOWSAL and HISAL, but were stunted and not much higher than 1.5 m in HISAL.

In each salinity zone a plot of 50 × 50 m² was selected within the area dominated by *A. marina*. A summary of the sampling schedule is given in Table 1. Seasonal sampling was undertaken during premonsoon (September 1998), monsoon (December 1998), postmonsoon (March 1999) and summer (June 1999) seasons. In addition, a year-round monthly sampling was carried out from September 1998 until August 1999 at INTSAL.

Flux measurements

Methane fluxes were measured in a Perspex-chamber (53 × 37 × 71 cm³, length × width × height), (Custom-made Perspex[®] Chamber) which was placed on the grooves of an aluminium base (57 × 37 × 10 cm³, length × width × height). The base was inserted between three and 5 h prior to sampling with the lower edge pressed firmly into the sediment. The aluminium base enclosed the pneumatophores of *A. marina*; the actual number of pneumatophores was counted. A battery-operated air circulation pump with a flow rate

of 1.5 L min⁻¹ (M/S Aerovironment Inc., Monrovia, CA, USA) was connected to mix the air inside the chamber and was also used to transfer air samples from the chamber into the glass sampling bottles. The samples were collected at regular intervals of 15 min for 1 h. The sampling bottles were fitted with two stopcocks and initially filled with water. To prevent gaseous contaminations the water had been flushed prior to use with nitrogen. The gas samples were collected into the sampling bottles by connecting the pump outlet to one stopcock and displacing the water with sample air. The bottles were closed after all the water had been replaced. Water inside the chamber was on average 35 cm deep. Water level fluctuations because of tides and air temperature were measured in parallel. Methane emissions were calculated from the linear increase of methane mixing ratio with time, taking into account the volume of the chamber.

Gas bubbles and aerenchyma

Gas bubbles entrapped in the sediment were stirred up from unvegetated plots that had an overlying water column of 0.5 m. These plots were 2–3 m distant from the sites where the flux chamber was installed. Bubbles were collected below the water surface in an inverted funnel (20 cm diameter) fitted with a silicone rubber septum in its stem. The gas was withdrawn using a disposable syringe and was transferred into 10-mL Venoject[®] (Terumo Europe N.V., Leuven, Belgium) tubes. The tubes had been prefilled with a saturated NaCl solution. Excess salt solution was expelled during injection through an additional needle (Krüger *et al.*, 2001). Gas bubbles released naturally (without stirring) were collected once in June 1999. The funnel was left undisturbed for 3 h (from 09:00 hours in the morning until 12:00 hours) at each location on consecutive days at HISAL, INTSAL and LOWSAL, respectively. The gas volume was estimated from the reading of the syringe used for withdrawing the sample from the funnel.

Table 1 Sampling schedule

Experiment	HISAL	INTSAL	LOWSAL
Methane emission	Seasonal* (2, 4)	Monthly [†] (2, 12)	Seasonal (2, 4)
Methane concentration in gas bubbles	Seasonal (2, 4)	Monthly (2, 12)	Seasonal (2, 4)
Methane concentration in pneumatophores	Seasonal (2, 4)	Monthly (2, 12)	Seasonal (2, 4)
Methane concentration in cable roots	Two seasons (2, 2)	Monthly (2, 6)	Two seasons (2, 2)
Rooting depth	January 2000	January 2000	January 2000
Environmental variables	Seasonal (2, 4)	Monthly (2, 12)	Seasonal (2, 4)

*Seasonal: September 1998 (premonsoon), December 1998 (monsoon), March 1999 (postmonsoon) and June 1999 (summer).

[†]Monthly: September 1998–August 1999.

Numbers in parentheses indicate the number of samples in a site followed by the number of measurements per sampling schedule.

Otherwise, the samples were processed as described above.

Gas samples were also collected from the aerenchyma of the cable roots, and from the pneumatophores below and above the water level. One millilitre samples were taken by syringe and needle from at least five pneumatophores originating from the same cable root and pooled into 5 mL Venoject-tubes (Terumo). For sampling the cable roots, a hole was dug following a pneumatophore until the root could be felt and the needle inserted into it. Because the hole filled rapidly with water, the syringe was below the surface during sampling. This avoided any contamination from the atmosphere. Samples were stored as described above.

Environmental parameters

Electrical conductivity and pH were measured in the field with a battery-operated multimeter. Temperature of surface water and sediment at 10 cm depth was measured using an alcohol thermometer. Salinity of the floodwater was calculated from chlorinity that was measured by Mohr's titration. Dissolved oxygen in the floodwater was measured by a standard Winkler titration. Total organic matter in sediment was quantified as loss-on-ignition. Predried soil (5 g) was dried in a quartz crucible for 2 h at 105 °C, weighed and heated in a muffle furnace at 550 °C overnight.

Gas analysis

Gas samples were analysed on a Hewlett Packard GC 6890 (Hewlett Packard, Albertville, Minnesota, USA) fitted with a flame ionization detector and a HayeSep-B column (HayeSep, Alltech, Unterhaching, Germany). Column, injector and detector temperatures were 60 °C, 100 °C and 250 °C, respectively. The carrier was nitrogen at a flow rate of 30 mL min⁻¹. For flux measurements, the GC was calibrated before and after each set of measurements using 1.77 ppm_v methane in nitrogen (Matheson Inc., Parsippany, NJ, USA). Pure methane (99.99%) and 1195 ppm_v methane in nitrogen were used as standards for the analysis of methane in gas bubbles and in the aerenchyma of roots and pneumatophores, respectively (Bhoruka Gases, Bangalore, India). Gas samples were taken with pressure-lock syringes (Dy-natech, Baton Rouge, LA, USA) from the sampling bottles or tubes and injected. The GC was regularly checked for linearity by injecting various volumes (0.1–1.0 mL) of the standards.

Statistics

All calculations and tests were done with SYSTAT Ver. 10 (SPSS Inc., Chicago, IL, USA).

Results

Some of the environmental variables were highly correlated, e.g. salinity with conductivity and water temperature with soil temperature. Hence, we selected the variables discharge, salinity, dissolved oxygen, soil organic matter and soil temperature to perform a factor analysis (Fig. 1). After varimax rotation, factors one and two explained 49% and 35% of the overall variance, respectively. We interpret factor one as a seasonal factor with high scores for the seasonally changing discharge from the River Coleroon and the seasonal variation of the environmental variables. In contrast, factor two covers the spatial gradient of salinity, dissolved oxygen and soil organic matter (Table 2).

The correlations of average methane emissions with factor one ($r^2 = 0.55$) and factor two ($r^2 = 0.32$) indicated that site-specific influences were less important than seasonal factors. Indeed, emissions from LOWSAL and INTSAL were nearly identical, while those from HISAL were slightly lower (Fig. 2).

Chamber measurements are prone to artefacts that may be caused by the unavoidable temperature increase during the incubation. During the closure times with 40 chamber measurements, a maximum decrease of 4 °C and a maximum increase of 7 °C were observed. The effect of temperature change on methane

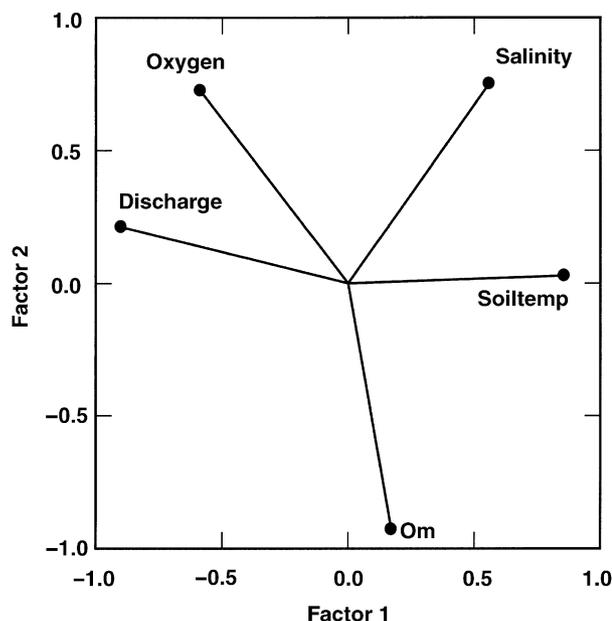


Fig. 1 Factor loadings of environmental variables. Clockwise from left: Discharge, average monthly discharge from the River Coleroon; Oxygen, dissolved oxygen in water; Salinity, salinity in water; Soiltemp, soil temperature, ca. 10 cm deep; OM, soil organic matter. See also Table 2.

Table 2 Environmental parameters in the Pichavaram mangrove

Site	Water					Soil			Factor Scores	
	Conductivity (mS)	Salinity (‰)	Phosphate (µM)	Total inorganic		Temperature (°C)	OM (%)	Temperature (°C)	Factor 1	Factor 2
				Nitrogen (µM)	Oxygen (mLL ⁻¹)					
LOWSAL	34.5 ± 4.8	17.8 ± 2.0	2.7 ± 0.2	67.1 ± 12.9	4.6 ± 0.8	27.6 ± 1.8	11.8 ± 1.2	26.0 ± 1.2	-0.83 ± 0.02	0.02 ± 0.56
INTSAL	40.3 ± 2.9*	20.7 ± 3.7	2.6 ± 0.2	49.2 ± 7.2	8.1 ± 2.1	25.8 ± 0.6	10.1 ± 1.5	26.8 ± 1.9	-0.20 ± 0.28	-0.28 ± 0.61
HISAL	70.4 ± 6.5	34.2 ± 1.6	2.1 ± 0.2	68.0 ± 29.0	9.1 ± 1.3	28.7 ± 1.3	3.1 ± 0.4	27.5 ± 1.3	1.3 ± 1.35	0.37 ± 0.4

LOWSAL, low-salinity zone; INTSAL, intermediate salinity zone; HISAL, high-salinity zone.

Data from seasonal sampling; average ± standard error, n = 4.

*n = 3.

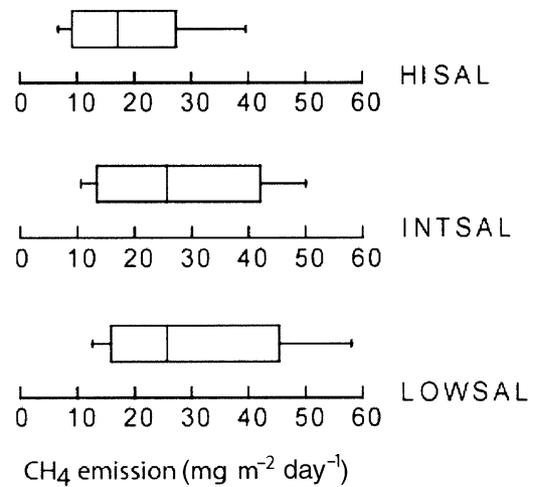


Fig. 2 Box plot of methane emissions ($\text{mg CH}_4 \text{m}^{-2} \text{day}^{-1}$) from the different sites. Combined data from March, June, September and December. The vertical bar marks the median, the box the inner quartiles, and the horizontal lines the range. Number of samples $n = 12$.

emission was detectable but insignificant ($r = 0.28$, $n = 40$, $\alpha > 0.10$).

The seasonal curve of methane emission runs antiparallel to the long-term average of the discharge from the main tributary (Fig. 3). Emissions were highest during the dry season except from HISAL, where emissions and number of pneumatophores had already decreased before the beginning of the monsoon. In general, methane emissions were highly correlated with the number of pneumatophores (Fig. 4a; $r = 0.78$, $n = 40$, $\alpha < 0.01$) while the number of pneumatophores was inversely correlated with discharge ($r = -0.49$, $n = 40$, $\alpha \leq 0.001$). The correlation held also if the sites were analysed separately. In particular, the methane emission per pneumatophore was higher in the dry than in the wet season (low and high discharge: Fig. 4b). This finding is consistent with occasional observations that the pneumatophores showed signs of senescence and decay during the monsoon season. Bubble fluxes were measured only once at the end of the monsoon season in June 1999. The emissions were 66, 188 and $522 \text{ mg CH}_4 \text{m}^{-2} \text{day}^{-1}$ in HISAL, INTSAL and LOWSAL, respectively.

The structure of the root system and its position relative to the soil surface differed between the sampling sites (Table 3). The aerenchyma made up 50% of the total volume and even more in most parts of the root system, with the exception of the distal half of the pneumatophores (Table 4). We found in all sites a strong methane gradient from the soil through the root system to the atmosphere (Fig. 5). Overall, the median

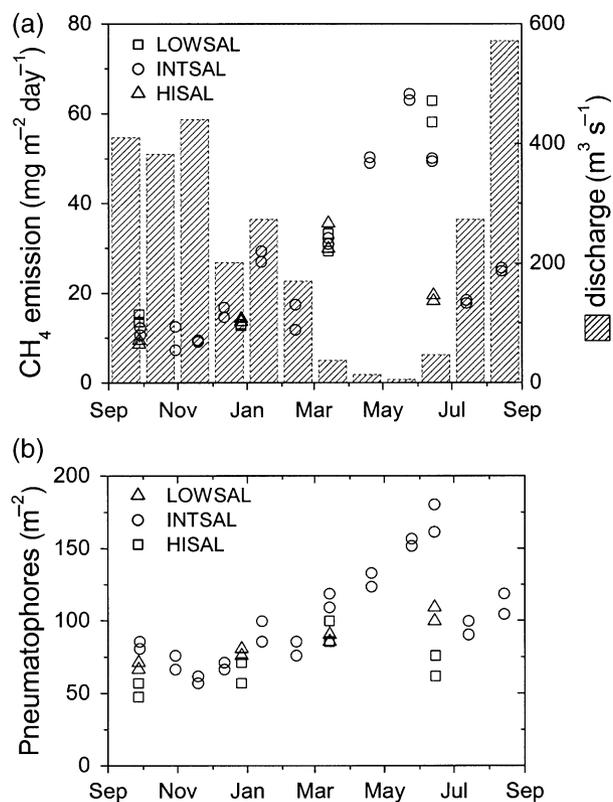


Fig. 3 (a) Seasonal change of methane emission from the Pichavaram mangrove and the average discharge from the River Coleroon (columns). (b) Seasonal change of the number of pneumatophores.

mixing ratio decreased from ca. 30% in gas bubbles through ca. 300 ppm_v in cable roots and 150 ppm_v in the submersed parts of the pneumatophores to ca. 5 ppm_v in the pneumatophores above the water table.

Discussion

The peak and average values for methane emission from an *Avicennia* mangrove are comparable with emissions measured from freshwater wetlands (Table 5). Our estimate of 10 g CH₄ yr⁻¹ is the sum of the monthly average values from INTSAL and valid only for the *Avicennia* stand itself. For this, it is probably a minimum estimate, because methane may also be emitted via the leaves of the mangroves. However, it was not technically feasible to build enclosures that covered entire trees. Unfortunately, we have no seasonal data about the natural ebullition from unvegetated plots that may be important from time to time. Methane concentrations in bubbles were high (Table 3), reaching values comparable with those reported from freshwater wetlands and rice fields

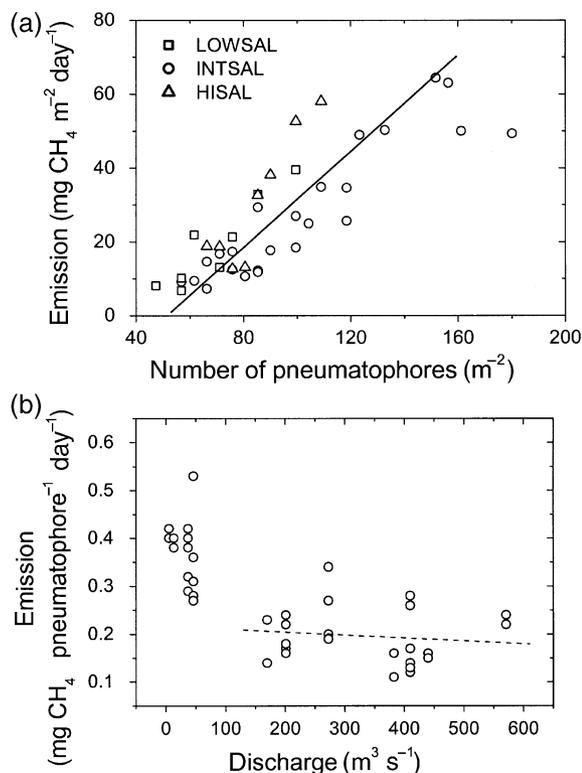


Fig. 4 Methane emission and pneumatophores. (a) Methane emission as a function of the number of pneumatophores. The line shows the common regression for the data from all sites. (b) Methane emission per single pneumatophore as a function of average discharge from the Coleroon River. The stippled line shows the regression for a discharge ≥ 100 m³ s⁻¹. The correlation for this subset is not significant ($r = -0.13$, $n = 23$; $P = 0.56$).

(King *et al.*, 1981; Shannon *et al.*, 1996; Frenzel & Karofeld, 2000; Krüger *et al.*, 2002). However, the few bubble fluxes measured in June 1999 were about five times as high as the pneumatophore-mediated emissions at the same time. It is known that polluted mangroves emit considerable quantities of methane (Sotomayor *et al.*, 1994; Purvaja & Ramesh, 2001), but unpolluted sites were assumed to be less important. Recent micrometeorological measurements in another Indian mangrove, the Sundarbans, confirm that high emissions are possible (Mukhopadhyay *et al.*, 2001, 2002). Our observations are further supported by occasional flux measurements from a mangrove in East Africa that showed a potential for high emission rates (Lyimo *et al.*, 2002).

Current global estimates of methane emissions from wetlands vary between 25% and 45% of the global methane source. However, methane budgets for tropical areas are notoriously uncertain. Recent attempts to overcome this uncertainty include the application of a

Table 3 Depth distribution (cm) of the rooting system of *Avicennia marina* in the Pichavaram mangrove

	HISAL	INTSAL	LOWSAL
Depth of cable roots	9	25	47
Depth of fine (= feeding) roots	4–8	5–10	24–40
Total length of pneumatophores from cable root to tip	28	47	50

LOWSAL, low-salinity zone; INTSAL, intermediate salinity zone; HISAL, high-salinity zone.

Table 4 Proportion of the aerenchyma in different parts of the root system of *Avicennia marina* (average \pm standard error, $n = 3$)

	Aerenchyma (%)
Cable roots	57.7 \pm 3.4
Pneumatophores below ground	67.2 \pm 1.4
Emerging part of the pneumatophores, basal half	50.8 \pm 9.9
Emerging half of the pneumatophores, distal half	30.6 \pm 0.8
Fine roots	48.4 \pm 5.3

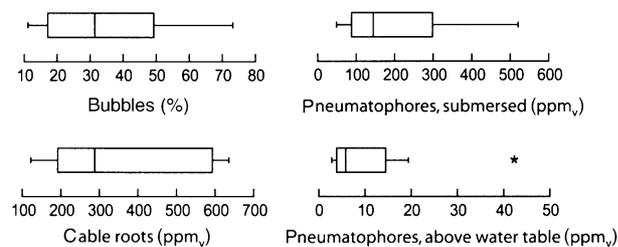


Fig. 5 Box plot of the methane mixing ratio in gas bubbles stirred up from the sediment and in different compartments of the root system of *Avicennia marina*; combined data from all sites. The vertical bar marks the median, the box, the inner quartiles and the horizontal lines the range; the asterisk marks an outlier. Number of samples $n = 12$ except for the cable roots with $n = 6$.

process-based wetland model. This model behaved well in high latitudes of the northern hemisphere, but showed discrepancies in the tropics (Walter *et al.*, 2001). Our results may help to close one of the many gaps in our current knowledge.

To our knowledge, no data are available about the global area covered by *Avicennia* species. In total, mangroves cover approximately 180 000 km² (Spalding *et al.*, 1997; Burke *et al.*, 2002). However, it is not certain that all these mangroves are methane sources. Assuming similar annual emission rates for mangroves and

boreal wetlands (Table 5), the boreal wetlands play the prominent role simply by their vast area of 600 000 km² (Lelieveld *et al.*, 1998). In a world influenced largely by human activities, the methane emitting rice fields that cover 1 300 000 km² (Denier van der Gon, 2000) dominate the overall emission from wetlands. Nevertheless, mangroves can no longer be ignored and are, among natural wetlands, a potentially significant source for atmospheric methane.

Our findings are also important for the reconstruction of past emissions from the era before men started to modify methane sources. Recent marine and terrestrial paleoresearch suggests that variations in Holocene monsoon circulation affected the lower latitudes worldwide (Kröpelin & Petit-Maire, 2000). Given the large seasonal variation in the methane emission from the Pichavaram mangrove (Fig. 3), the source strength of tropical coastal ecosystems may have fluctuated largely in the past, depending on extent and water regimen.

One expects a stimulation of methanogenesis and hence of methane emission during monsoon, because the impact of freshwater should shift the electron flow from sulphate-reducing bacteria to methanogens. However, we observed that emission peaked in the dry season and dropped during monsoon (Fig. 3). Instead, methane emission was correlated with the seasonally fluctuating number of pneumatophores (Fig. 4a). To the best of our knowledge, nothing is known about seasonal dynamics of the roots and pneumatophores of *Avicennia*, and cyclic changes in the number of pneumatophores. We positioned the flux chamber at various sites within a defined sampling area, but always on top of pneumatophores. Considering this sampling strategy, a plausible explanation for our results is that high water levels during monsoons reduced the number of pneumatophores protruding into the air. However, the relatively higher methane emission per pneumatophore during the dry period at low discharge rates (Fig. 4b; $r = -0.7$, $n = 40$, $\alpha < 0.001$) suggests an additional seasonal effect on source strength and/or on transport capacity. The latter is in accordance with occasional observations that the pneumatophores showed signs of senescence and decay during the monsoon.

The pneumatophores' primary function is that of a conduit allowing oxygen to be transported from the atmosphere down to the roots growing below the surface. In addition, they are pathways through which methane may be transported from the sediment to the atmosphere. The voluminous aerenchyma facilitates this gas exchange. The measured relative volume of the aerenchyma (Table 4) agrees well with values given for entire roots systems of 1-year-old *A. marina australasica*

Table 5 Methane emissions from mangroves, northern wetlands and rice fields

Site and reference	Method	Remark	Latitude	Flux (mg CH ₄ m ⁻² day ⁻¹)	Flux (g CH ₄ m ⁻² yr ⁻¹)
Mangrove (<i>Avicennia</i>), South India, this work	Chamber	Flux through pneumatophores	11°N	7.4–63.7	10*
Mangrove (<i>Bruguiera</i>), Hainan (Lu <i>et al.</i> , 1999)	Chamber	Flux from water surface and soil	18°N		0.12–0.39
Mangrove, Sundarban (Mukhopadhyay <i>et al.</i> , 2002)	Gradient	Micrometeorological measurement	22°N	–16–32	43†
Mangrove (<i>Avicennia</i>), Puerto Rico (Sotomayor <i>et al.</i> , 1994)	Chamber	Gradient from pristine (low emission) to polluted (high)	18°N	4–42	n.a.
Rice agriculture (Denier van der Gon, 2000)	Geostatistical analysis	Global average‡	n.a.	n.a.	22
Lowlands West of River Yennisei, Siberia (Bosse and Frenzel 2001)	Chamber	Weighted average, 32% mires by area	61°N	25§	3.0¶
Hudsonbay Lowlands, coastal marshes (Roulet <i>et al.</i> , 1994)	Chamber	Weighted average	50–58°N	84.3	8.0
Hudsonbay Lowlands, open fens (Roulet <i>et al.</i> , 1994)	Chamber	Weighted average	50–58°N	78.6	6.7

n.a. = not available or not applicable.

*INTSAL, from monthly averages.

†Calculated from the annual net flux of the Sundarban mangrove divided by the area; numbers taken from Mukhopadhyay *et al.*, 2002.

‡Calculated from a global estimate of 28 TG a⁻¹ and a rice growing area of 1 300 000 km².

§Summer flux.

¶Assuming a vegetation period of 120 days.

(Curran *et al.*, 1996). Different mechanisms of gas exchange have been discussed, including mass-flow driven by the tide (Westermaier, 1900). Indeed, the water-level changes measured in the flux chamber (difference between start and end, minimum = –10 cm, maximum = +10 cm) were correlated to the methane emission per pneumatophore ($r = 0.35$, $n = 40$, $\alpha = 0.027$). However, the average water level inside the chambers showed a closer, but negative correlation to the emission per pneumatophore ($r = -0.54$, $n = 40$, $\alpha < 0.001$). This suggests diffusion as the transport mechanism, because gas exchange takes place at the lenticles (Scholander *et al.*, 1955; Ish Shalom-Gordon & Dubinsky, 1992). One may hypothesize that when pneumatophores become flooded, the gas transfer between the aerenchyma and the atmosphere becomes impeded, and vice versa. Furthermore, in a stepwise regression analysis with four independent variables, the discharge from the River Coleroon ($r = -0.70$) was the most powerful predictor of the emission per pneumatophore, followed by the average water level inside the chamber ($r_{\text{partial}} = -0.55$), the water level change (the tide; $r_{\text{partial}} = 0.25$), and the temperature change (chamber effect; $r_{\text{partial}} = 0.16$).

To summarize, we found a control of methane emission by the water level, which operated via the pneumatophores. In a tidal area this will produce variations in methane emissions on the diurnal time scale. In addition, we found a strong seasonal variation that can largely be attributed to the seasonally changing number of pneumatophores. Site-specific factors also have an influence on methane emissions, but are less important than seasonal factors with the monsoon as the main force.

The observed seasonality raises the issue of what happens to the methane during monsoon. If the production is constant with season, one has to look for alternative pathways like ebullition, emission from leaves, or export by the flood water. However, with respect to the enormous number of pneumatophores – more than 10 000 have been counted for a single *Avicennia* tree standing only 2–3 m tall (Scholander *et al.*, 1955) – the transport through pneumatophores seems to be most important. Nevertheless, other scenarios are possible. Methane may become entrapped in gas bubbles and contribute later to the elevated emission during the dry season (Fig. 4a), uncoupling production and emission. Last but not least, the processes of methane production, aerobic methane oxidation and anaerobic methane oxidation may vary as well. Hence, the microbial processes form the next level that has to be analysed for an understanding of the controls of methane emission from mangroves.

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