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Methane flux and production from sediments of a mangrove wetland on Hainan Island, China

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Abstract

Methane fluxes from sediments in different zones of a *Bruguiera sexangula* mangrove wetland were determined by closed static chamber techniques during one whole year period, at Changning River estuary, northeast of Hainan Island, China. Methane productions were also measured by anaerobically incubating sediment samples. Impacts of salinity, sulphate and temperature on methane production rates were studied *in vitro*. Great differences of annual methane fluxes were observed in three zones, with the values of 0.39, 0.20 and 0.12 g m^{-2} in the outer zone, middle zone and inner zone, respectively, in part due to the differences of sediment water contents and crab bioturbation . The highest fluxes in each zone occurred in autumn and the lowest in winter. Large diurnal fluctuations in fluxes were caused by the changes of tidal conditions rather than the changes of air or sediment temperatures. The temporal and spatial patterns of methane production differed somewhat from those of methane flux. There was great seasonality for methane production and the highest productions were found in autumn and the lowest in spring. Different horizontal and vertical patterns occurred in different seasons and different zones, suggesting the complexity of factors controlling methane production. The *in vitro* control experiments indicated that salinity and sulphate had negative effects whereas temperature (20–50°C) had positive effects on methane production rates. However, there were different sensitivities for the different levels of the three factors.

Introduction

Methane is an important greenhouse gas with a warming potential per molecule about 21 times that of carbon dioxide. Although it may have an important role in the radiative and chemical balance of the earth, its global budget is not well known (Khalil and Rasmussen, 1989, 1990; Steele et al., 1992). Recent investigations have shown that the atmospheric methane has increased 1% per year during the last century, although the rate at present may be slowing (Steele et al., 1992). The rate of increase in atmospheric methane has been much faster than that of atmospheric carbon dioxide and methane may become an even more important greenhouse gas in near future (Wang, 1993).

Sources of methane are widespread such as wetlands, animals, landfills, natural gas production and consumption, coal burning, biomass burning, termites, etc. Global budget estimates for methane have shown that wetlands are the largest biogenic source of atmospheric methane, accounting for 40–50% of global source strength (Cicerone and Oremland, 1988; Whiting and Chanton, 1993). Thus, a major effort has been made to map wetlands (Matthews and Fung 1987; Aselmann and Crutzen, 1989), and to determine average fluxes from the biomes. However, current global estimates of methane emissions from wetlands are uncertain. This is due to the paucity of measurements of methane flux, an incomplete understanding of the environmental factors that control methane flux, the great differences in geological distributions, soil types, nutrition inputs and vegetation between different wetland types or even between different wetlands classified

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as the same type. Therefore, it is necessary and urgent to obtain knowledge on methane fluxes from wetlands.

Although most studies of methane's source strengths from wetlands have been focused on inland freshwater wetlands where the largest fluxes have been found to occur (Schütz et al., 1991), methane fluxes from coastal saline marshes have also been well documented (King and Wiebe, 1978; Bartlett et al., 1987), with values ranging from -2.4 to $145\,\mathrm{mg\,m^{-2}\,d^{-1}}$. Coastal saline marshes in temperate areas give way to mangrove swamps in the tropical and subtropical latitudes. Methane fluxes from mangrove swamps have been reported only in red mangrove (*Rhizophora mangle*), black mangrove (*Avicennia germinans*) and white mangrove (*Laguncularia racemosa*) in Florida (Harriss et al., 1988; Barber et al., 1988), with low values of about $0.3\,\mathrm{mg\,m^{-2}\,d^{-1}}$, and in Puerto Rico (Sotomayor et al., 1994), with values of $0.3\,\mathrm{mg\,m^{-2}\,d^{-1}}$ (unimpacted mangroves) and 4–$82\,\mathrm{mg\,m^{-2}\,d^{-1}}$ (impacted mangroves). The reasons why original mangrove swamps have much lower methane fluxes than saline marshes are not fully understood.

The methanogenic food chain is a microbial system that mediates the biodegradation of organic matters in many anaerobic environments. Since methanogenesis is the terminal step in this chain, any perturbation of the chain should be reflected by altered methane production, resulting in the altered methane flux. Therefore, methanogenesis is a key process to study the source of methane's strength from wetlands.

This report is the result of a study on direct measurements of methane fluxes to the atmosphere from another species of mangrove (*Bruguiera sexangula*) swamp to improve the global estimates of methane fluxes from a wetland type that has received scant attention. Supporting data of methane productions are presented. We demonstrate that complex interactions of hydrologic, meteorological, chemical, and biological factors regulate methane emission and production from this wetland. In addition, we have studied the effects of salinity, sulphate, and temperature on methane production rate by *in vitro* controlled experiments.

Material and methods

Study area

The island of Hainan in the south of China is an ideal habitat for mangroves. About 25 mangrove species belonging to 15 genera in 12 families are found around the coast of this island (Lin, 1997). Furthermore, Hainan Island has the largest mangrove resources in China. *B. sexangula* is the most dominant mangrove species in Hainan.

The *B. sexangula* mangrove swamp chosen for this study is at the Changning River estuary, at Dongzai Harbor Mangrove Reserve on the Hainan Island northeast coast adjoining Qiongshan County ($19^\circ 51'$ N, $110^\circ 24'$ E). According to climatic records in 1973–1987 by the nearby Shanjiang Weather Station, this area has typical southern subtropical marine climate with annual mean air temperature of $23.7\,^\circ$C. The lowest monthly mean temperature is $17.3\,^\circ$C (in January) and the highest is $28.7\,^\circ$C (in July). Rainfall is seasonal (annual mean of 1,942 mm).

The *B. sexangula* community is about 60 years old, with smooth canopy and green physiognomy. The community has the canopy height of 6–10 m, the tree density of 32 individuals per $100\,\mathrm{m^2}$, the average tree chest diameter of 9.5 cm ranging from 4.1 cm to 16.2 cm, and the average stem height under the lowest branch of 3 m. *B. sexangula* accounts for 85% of the trees in the forest. *Bruguiera gymnorhiza* and *Rhizophora stylosa* plants are scattered within the forest, and account for 13% and 2% of the trees, respectively.

The swamp is within the mid-intertidal zone, with the average salinity of 14.8 ppt in the surface sediment. The width of the swamp is about 120 m from the land-ward fringe to the river-ward fringe and is here artificially divided into three zones of equal width: outer zone (the river-ward zone), middle zone and inner zone (the land-ward zone). Because the whole swamp is frequently flushed by tidal water, there is little litter fall remaining on the swamp surface. The sediment surface of the outer zone is smooth because of long tidally flushing time . The middle and inner zones are irregular due to the digging activities of crabs. Water contents in surface sediments of the outer, middle and inner zones are 57%, 52% and 48%, respectively.

Methane flux

Three sampling stations were established at random in each zone to measure methane fluxes from sediments by a closed chamber technique. The methane fluxes were determined by covering part of the sediment of the stations with a collector chamber and measuring the temporal increase (or decrease) of the methane concentration of the enclosed air during an observation period. The collector chamber of plexiglass had width and length of 20 cm and height of 15 cm. The top of the chamber had a rubber septum port, with a syringe needle (0.3 mm i.d.) serving as an orifice to maintain equal air pressures between the outside and inside of the chamber. The chamber was set on four bamboo stakes during flooding observation periods, when methane fluxes across water–air interface represented those across swamp–air interface. The height of the stakes was adjusted in such a way that the chamber dipped only slightly (2–3 cm deep) into the water, allowing exchange of the water between the inside and outside of the chamber. During non-flooding observation periods, the chamber was gently pushed 2–3 cm deep into the sediment to ensure a seal against the ambient atmosphere. After each observation period, the chamber was removed and the sediment surface exposed to natural conditions until next observation. The stakes remained at the sampling station for the whole study period to ensure constant experimental conditions. During incubation, the chamber was closed for an observation period of 30 min. Air samples were taken routinely during this 'incubation time' using a 10 ml gas-tight glass syringe through the septum at the chamber top. Four samplings were done in a time series at the onset of incubation and at 10 min intervals thereafter. Leakage from the syringe was inhibited by capping the needle with silicon rubber. Methane fluxes were calculated using a linear least square fit to the time series of concentration for each observation period. Concentrations usually increased (or decreased) linearly with time. Occasional outliers in the time series were omitted. If a few observations at the first time point (0 min) differed markedly from ambient levels, indicating disturbance of the station during emplacement, the entire time series was rejected. About 10% of the data were rejected due to the above criteria. The average methane flux (F) was calculated by Equation (1).

$$F = H\rho\frac{\mathrm{d}m}{\mathrm{d}t} \tag{1}$$

where H is the chamber height above the water–air or air–sediment interface, $\mathrm{d}m/\mathrm{d}t$ is the rate of change of methane concentration inside the chamber during the observation period, and ρ is the density of methane at ambient pressure and temperature.

Diurnal variation of methane fluxes from sediments was studied every 4 h during a 24 h period on 22–23 May 1996 (representing spring). On 25 August 1996 (representing summer), 20 November 1996 (representing autumn) and 20 February 1997 (representing winter), daily observations were made at each station in the mornings when the swamp was not flooded by tidal water.

Methane production

One sediment core was taken with thin-walled PVC tube (5 cm i.d.) from the upper 40 cm of sediment in each zone on each sampling date. The core was sectioned in 10 cm depth intervals.

Methane production was measured by anaerobic incubations of sediment samples. A fresh sediment sample of about 10 g was obtained by inserting a hollow glass tube (1.2 cm i.d. and 10 cm long) into a core section. Each tube containing sediment sample for each core section had a headspace of about 6 ml and was immediately sealed with rubber stoppers at both ends after being flushed with pure nitrogen for 1 min to form a completely anaerobic condition. An air sample of 1 ml was withdrawn from the headspace through the rubber stopper using a 1 ml gas-tight glass syringe 24 h after sealing the tube. Methane production was calculated according to methane accumulation in the headspace, the headspace volume, the dry weight of the sediment sample and the sediment density. All of the incubations were done at the laboratory temperatures (similar to field temperatures). Considering the change of atmospheric pressure in the headspace, we sampled only once and not according to time series. However, our preliminary study demonstrated that during three days' period, different tubes containing sediment samples from the same core section had the same methane production rate even though their sampling times were different (data not shown). Therefore, sampling only at 24 h was presumed valid.

Factors affecting methane production rates

All sediment samples for these experiments were obtained in the 20–30 cm deep sediment layer on 22 May 1996. Sediment samples of about 10 g (fresh weight) were extruded into 40 ml glass tubes. The tubes were sealed after having been flushed with pure nitrogen for 1 min to form a completely anaerobic condition and 5 ml incubation liquid was injected into each of them. Three duplicates were set up for each treatment.

In the salinity experiment, four salinities (0, 15, 25 and 35 ppt) of incubation liquids were applied by dissolving NaCl in distilled and deoxygenated water. In the sulphate experiment, four sulphate concentrations (0, 4, 8 and 12 mM) of incubation liquids were applied by dissolving K_2SO_4 in distilled deoxygenated water. In the temperature experiment, four temperatures (20, 30, 40 and 50 °C) were applied and the added liquid was deoxygenated surface water from the swamp (salinity of about 20 ppt).

Air samples of 1 ml were withdrawn through the stopper with a glass syringe from the headspace of each tube at 24 h after the incubation liquid was added. All incubations were completed at the laboratory temperature (about 25 °C), except for the temperature experiment. Methane production rates were determined from the methane accumulation rate in the tube and corrected for the dry weight of the sediment.

Methane analysis

The methane concentrations in the air samples were analyzed by injection of 1 ml of the sample onto a Varian 3400 gas chromatograph equipped with a flame ionization detector and a GDX-502 column (60/80 mesh, 2 m by 4 mm, stainless steel) maintained at 50 °C. Carrier gas was nitrogen and the flow rate was 30 ml min^{-1}. Injector and detector temperatures were set at 150 °C. All air samples were analyzed within 24 h after being sampled.

Results

Methane fluxes

Large diurnal variations of methane fluxes from sediments were observed in the three flat zones on the spring sampling date (Figure 1). Minimum fluxes were generally negative (representing direction from air to swamp surface water) and occurred at 16:00 and 0:00 when the swamp was inundated by tidal water. Otherwise, fluxes were relatively stable and were positive (representing direction from sediment to air). By including all six time points, the total daily methane flux followed a sequence of outer zone > middle zone > inner zone. The correlation between methane flux and air or sediment temperature was not significant by linear regression.

Throughout all four seasons there was the same order in the magnitude of the methane fluxes: outer zone > middle zone > inner zone (Figure 2). The annual fluxes integrated over the four seasons were 0.39, 0.20 and 0.12 g m^{-2} in outer zone, middle zone and inner zone, respectively. In each zone, the highest flux of the four seasons occurred in autumn. The average fluxes for the three sites were 0.81, 0.50, 1.05 and 0.23 mg m^{-2} d^{-1} in spring, summer, autumn and winter, respectively.

Methane production

Methane production from sediments of the *B. sexangula* mangrove swamp is shown in Table 1. Great differences of methane productions occurred in the four seasons, with much higher values in autumn and winter than those in spring and summer. Zone variations of methane productions were irregular although the sequence of the integrated productions averaged by the values of four seasons from 0–40 cm deep sediment was middle zone > outer zone > inner zone. Different vertical patterns of methane production occurred in the various zones. For the outer zone, higher methane productions generally occurred in the deeper sediment layers, while for the middle and inner zones, the highest methane productions generally occurred in the upper sediment layers.

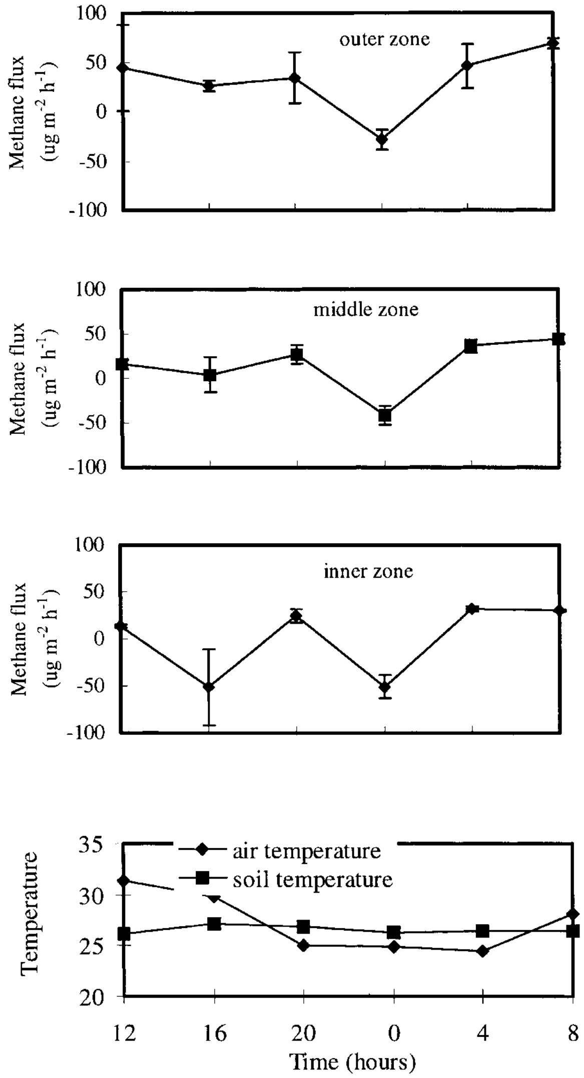

Figure 1. Diurnal variation of methane fluxes from sediments of the *Bruguiera sexangula* swamp (error bar represents standard deviation of methane fluxes by three chambers in each zone) and air and sediment (5 cm deep) temperatures (in °C) during 12:00 May 22 to 8:00 May 23, 1996.

Controlling factors for methane production

Methane production rates decreased with increasing salinity of the incubation liquids (Figure 3). The de-

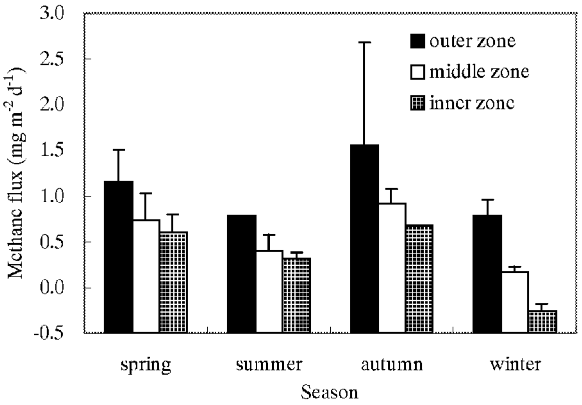

Figure 2. Seasonal and flat variations of methane fluxes from sediments of the *Bruguiera sexangula* mangrove swamp (error bar represents standard deviation for three stations in each zone).

crease of production rates from 0–15 ppt was much less than those from 15–25 ppt (4.34 ng g^{-1} DW d^{-1}) and from 25–35 ppt (2.64 ng g^{-1} DW d^{-1}), respectively, indicating that the sensitivity of methane production to salinity of incubation liquid was less within the lower salinity range than those in the higher salinity ranges.

Methane production rates decreased with the increasing sulphate concentrations of the incubation liquids (Figure 4). The decrease of production rates was most conspicuous from 0 to 8 mM , indicating that the sensitivity of methane production rates to sulphate of incubation liquid was least in the higher sulphate concentration range (8–12 mM).

Within the range of 20–50 °C, methane production rates increased with temperature (Figure 5). The increase of methane production rates was highest from 40–50 °C, 115 and 179 times those from 20–30 °C and from 30–40 °C, respectively.

Discussion

Methane flux

Many reports from wetlands have revealed that air or sediment temperature control the diurnal pattern of methane fluxes (e.g. Shangguan et al., 1993b; Yagi and Minami, 1990). However, our study indicates that tidal conditions, rather than temperature, control the diurnal pattern in the *B. sexangula* mangrove swamp. An important characteristic of mangrove swamps is that they are located in the intertidal zone with frequent inundations. Kelley et al. (1995) reported that methane fluxes from the tidally flooded bank margin vegetated by *Acer* and *Pontederia* varied with the tidal cycle and had greatest fluxes at low tide. The likely causes for low methane fluxes from tidal wetlands during flood periods include (1) increased hydrostatic pressure inhibits gaseous methane emission, (2) part of the methane emitted from the sediment is dissolved in the undersaturated tidal water and (3) part of the methane being released to the oxygenated flood water will be oxidized by methane-oxidizing bacteria in the water column before being released to the atmosphere (de Angelis and Scranton, 1993). That methane fluxes during flood periods were usually negative may be due to the undersaturation of methane in tidal water. Therefore, during flood periods tidal water on the swamp surface may become a methane sink of both sediment and air.

By t-test, at the level of $P < 0.1$, methane fluxes from sediments in outer zone are higher than and significantly different from those in middle zone ($t = 3.897$, $\mathrm{d}f = 3$) and those in inner zone ($t = 1.991$, $\mathrm{d}f = 3$), and methane fluxes in middle zone are higher than but not significantly different from those in inner zone ($t = 0.816$, $\mathrm{d}f = 3$). The spatial pattern of methane fluxes from sediments coincides with that of water contents, indicating that sediment water content is an important factor for methane fluxes, as concluded from other wetlands (Harriss et al., 1988). Through adjusting anaerobic condition in the sediments, sediment water contents control methane fluxes by affecting methanogenesis . Meanwhile, the lower methane fluxes in the middle and inner zones may be caused by crab bioturbation, because crabs will bury into the sediment and thus allow oxygen and other oxygenised compounds to be introduced deep into the sediment.

Most reports about seasonality of methane flux from freshwater wetlands have indicated that higher fluxes occur in warmer seasons (Bubier and Moore, 1993; Shannon and White, 1996). However, the highest methane fluxes was here recorded in autumn for all zones. Bartlett et al. (1987) found that seasonal patterns of flux from saline marshes appear to change along the salinity gradient, with the highest flux in summer for the freshest marsh and the highest flux in autumn for the most saline marsh. A pattern of relatively high emissions continuing well into autumn has been reported for other temperate saline marshes by DeLaune et al. (1983) and Bartlett et al. (1985).

Methane production

There is no definitive method for determining *in situ* methane production (Yavitt et al., 1993). In this study the rates were potential net methane production, because measurements were made under anoxic conditions in the laboratory. The actual production in the

Table 1. Variations of methane productions in different flats and seasons from sediments of the *Bruguiera sexangula* mangrove swamp

Zone	Depth interval (cm)	Methane production (mg m^{-2} d^{-1})				
		Spring	Summer	Autumn	Winter	Annual mean
Outer	0–10	0.084	0.068	0.122	0.282	0.139
	10–20	0.141	0.089	1.140	1.285	0.664
	20–30	0.094	0.102	0.207	2.064	0.617
	30–40	0.094	0.119	3.269	0.706	1.047
	0–40*	0.413	0.378	4.738	4.337	2.467
Middle	0–10	0.093	0.119	0.394	1.144	0.438
	10–20	0.076	0.087	1.346	2.089	0.900
	20–30	0.114	0.093	2.712	0.126	0.761
	30–40	0.080	0.109	2.149	0.149	0.622
	0–40*	0.363	0.408	6.601	3.508	2.721
Inner	0–10	0.102	0.118	1.515	0.143	0.470
	10–20	0.099	0.128	0.156	0.131	0.129
	20–30	0.071	0.099	0.785	0.121	0.269
	30–40	0.084	0.130	0.767	0.110	0.273
	0–40*	0.356	0.475	3.223	0.505	1.141
Mean of all zones	0–40*	0.377	0.420	4.854	2.783	2.110

*Sum of the individual sediment samples for each zone.

field was presumably less, since the surface sediments of the *B. sexangula* mangrove swamp are directly exposed to atmospheric oxygen during low tide periods and are always exposed to an oxygenated water column during high tide periods. These exposures, inhibiting methanogenesis, may result in lower production rates. The potential productions are still good indicators of the potential abilities of methanogens in sediments.

Kelley et al. (1995) compared the methane productions from tidal bank and submerged stations at the White Oak River estuary. They concluded that methane production from sediments of the tidal bank stations was higher than that of the submerged stations because unlike the bank stations, the submerged stations had no rooted macrophytes to directly inject labile organic matter deep into the sediments. Spatial changes of methane production were irregular in the *B. sexangula* mangrove swamp, indicating that the factors affecting methane production are complex. However seasonally average methane production integrated over the upper 40 cm sediments from the middle zone in the *B. sexangula* mangrove swamp was higher than those from the outer and inner zones probably due to the more roots in the middle zone, which is similar to the conclusion by Kelley et al. (1995). However, the inner zone which has more roots than the outer zone had lower methane productions than the outer zone, probably because the inner zone is less influenced by tide and has lower water content in sediment than the middle zone. This is similar to the conclusion by Shangguan et al. (1993) that rice paddy sediments with higher sediment moistures had higher methane productions. From these, the spatial pattern of factors affecting *in situ* methane production should mainly include vegetation and tidal zone.

In the outer zone, the upper sediments have been formed more recently and comprise fewer root materials than the deeper sediments, which resulted in lower methane production in the upper sediments. However, in the middle and inner zones, root materials distributed mainly in the upper sediments, resulting in methane production vertical pattern opposite to that in the outer zone. Some other factors such as profiles of salinity and sulphate maybe also influence the vertical pattern of methane product as reported in other salt marshes (Bartlett et al., 1987).

Different seasonal patterns have been reported in different wetlands. Kelly et al. (1995) reported that there was higher methane production in sediment of tidal bank in warmer seasons than in colder seasons and explained that more root exudates may appear in warmer seasons and thus provide more substrates to methanogenic bacteria. However, Saarnio et al. (1997) reported that methane production in an oligotrophic

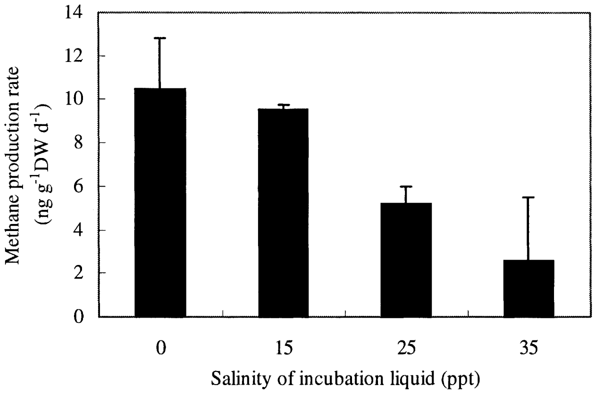

Figure 3. Effects of salinities of incubation liquids on methane production rates from sediments (20–30 cm deep) in the middle zone of the *Bruguiera sexangula* mangrove swamp (error bar represents standard deviation for triplicate treatments; DW represents dry weight of incubated sediment sample).

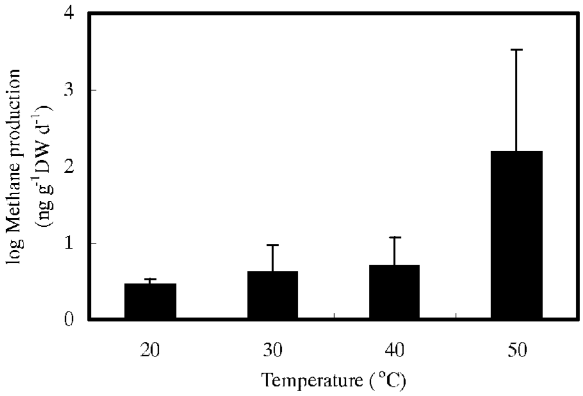

Figure 5. Effects of temperature on methane production rates from sediment (20–30 cm deep) in the middle zone of the *Bruguiera sexangula* mangrove swamp (error bar represents standard deviation for triplicate treatments; DW represents dry weight of incubated sediment sample).

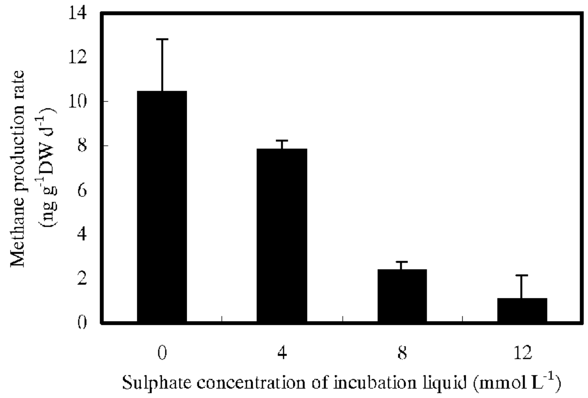

Figure 4. Effects of sulphate concentrations of incubation liquids on methane production rates from sediments (20–30 cm deep) in the middle zone of the *Bruguiera sexangula* mangrove swamp (error bar represents standard deviation for triplicate treatments; DW represents dry weight of incubated sediment sample).

pine fen increased in autumn because the decrease in temperature in autumn certainly reduced *in situ* decomposition processes and possibly left unused substrates in the peat. Our seasonal pattern of methane production in sediment of the *B. sexangula* mangrove swamp is similar to that by Saarnio et al., but we consider that their explanation is not the only factor for our result because root physiology may also be important. Although less root exudates will be provided in colder seasons and result in less substrates for methanogenic bacteria as described by Kelley et al., from another point of view the amount of dead root may increase in colder seasons and their decomposition will provide more substrates for methanogenic bacteria.

In any system, the input of a constituent minus the output (or losses) must equal the change in storage of that constituent. If the storage term is zero (input equals output), then the system is said to be at steady state. In the *B. sexangula* mangrove swamp, methane production did not equal methane flux (output) and their temporal patterns were somewhat different, showing that some other inputs or outputs existed. We considered that methane oxidation (output) was the major cause for these differences as reported by other researchers (Denier and Neue, 1996; Shangguan et al., 1993a).

Methane fluxes from mangrove wetlands have been reported to be 2–3 orders of magnitude less than those from coastal salt marshes, rice paddies, and other freshwater wetlands (Harriss et al., 1988; Schütz et al., 1991). The same differences in methane production as in methane fluxes occur between mangrove swamp and some other wetlands: methane production in the *B. sexangula* mangrove is 2–3 orders of magnitude less than those in coastal marshes and 3 orders of magnitude less than those in rice paddies and peatland (Table 2). We consider that methane production is the decisive microbial process reflecting differences in methane fluxes between different wetlands, though some other microbial processes such as methane oxidation also act on it. Therefore, studies on factors controlling methane production are important to reduce methane emissions from wetlands.

Factors controlling methane production in vitro

A number of reports have considered that methane productions from estuarine sediment decrease with

Table 2. Comparison of methane productions from sediments of some wetlands

Wetland type	Location	Vegetation	Depth (cm)	Methane production ($mg\,m^{-2}\,d^{-1}$)	Data source
Salt marsh	North Carolina	*Acer and Pontederia*	0–30	160	Kelley et al., 1995
Salt marsh	Georgia	*Spartina*	0–11	2304	King et al., 1978
Rice paddy	Italy	*Oryza*		2561	Schütz et al., 1989
Rice paddy	Hunan, China	*Oryza*	0–30	1019	Shangguan et al., 1993a
Peatland	Minnesota	*Sphagnum*	0–40	1500	Williams and Crawford, 1984
Mangrove swamp	Hainan, China	*Bruguiera*	0–40	2	This work

increasing sediment salinities (Bartlett et al., 1985; DeLaune et al., 1983), which is similar to our results of salinity control experiments (Figure 3). However, Sotomayor et al. (1994) concluded that the correlation of methane production and salinity was not statistically significant in red mangrove zones. It was probable that other factors concealed the impacts of salinity on methane production. Comparing methane production at different stations with different salinities may not reveal the true relationship between methane production and salinity.

It has generally been considered that sulphate may inhibit methanogenesis from wetland soils (Jakobsen et al., 1981; Winfrey and Zeikus, 1977). This proved true by our sulphate control experiments. The most likely mechanisms are (1) Methane is consumed by sulphate-reducing bacteria and (2) sulphate reduction and methanogenesis compete for available electron donors (Martens and Berner, 1974). Both mechanisms consider CO_2/H_2 or acetate to be the main substrates for methanogenic bacteria. Oremland and Polcin (1982) reported that methanogenesis and sulphate reduction could operate concurrently in anoxic saline marsh sediment because substrates like methanol and trimethylamine can be used by methanogenic bacteria and not by sulphate-reducing bacteria. Methane production rates from sediments of the *B. sexangula* mangrove swamp decreased with the increasing sulphate concentrations in the incubation liquids, substantiating that the main substrates in these sediments may be CO_2/H_2 or acetate rather than noncompetitive substrates such as methanol or trimethylamine.

It has been well documented that methane production rates (Pr) increases with temperature (T) when the supply of organic matter is sufficient (Chapman et al., 1996). This stimulation can best be quantified by the Arrhenius equation:

$$\ln \mathrm{Pr} = \frac{E_a}{R}\left(\frac{1}{T}\right) + \mathrm{Const.} \qquad (2)$$

where E_a ($kJ\,Mol^{-1}$) is the apparent activation energy and R (8.3110^{-3} $kJ\,Mol^{-1}\,K^{-1}$) is the gas constant (Conrad, 1989). The E_a for this swamp is $100\,kJ\,Mol^{-1}$, which is in the upper range of results from rice paddy soils (Conrad et al., 1987). From our temperature experiments, methanogenic bacteria in the *B. sexangula* mangrove swamp appear to be thermophilic strains with optimum temperature above 50 °C. However, as *in situ* temperature in this swamp is less than 35 °C, methane production will never reach the maximum. Although temperature experiments indicated that methane production rate increases with temperature, the sediments had higher methane productions in colder seasons (autumn and winter) than in warmer seasons (summer and spring), presumably as a result to the phyto-physiological differences in different seasons and other reasons as discussed above.

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