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# Methane Emissions from Subtropical and Tropical Mangrove Ecosystems in Taiwan

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**Abstract:** Mangroves are one of the blue carbon ecosystems. However, greenhouse gas emissions from mangrove soils may reduce the capacity of carbon storage in these systems. In this study, methane (CH<sub>4</sub>) fluxes and soil properties of the top 10 cm layer were determined in subtropical (*Kandelia obovata*) and tropical (*Avicennia marina*) mangrove ecosystems of Taiwan for a complete seasonal cycle. Our results demonstrate that CH<sub>4</sub> emissions in mangroves cannot be neglected when constructing the carbon budgets and estimating the carbon storage capacity. CH<sub>4</sub> fluxes were significantly higher in summer than in winter in the *Avicennia* mangroves. However, no seasonal variation in CH<sub>4</sub> flux was observed in the *Kandelia* mangroves. CH<sub>4</sub> fluxes were significantly higher in the mangrove soils of *Avicennia* than in the adjoining mudflats; this trend, however, was not necessarily recapitulated at *Kandelia*. The results of multiple regression analyses show that soil water and organic matter content were the main factors regulating the CH<sub>4</sub> fluxes in the *Kandelia* mangroves. However, none of the soil parameters assessed show a significant influence on the CH<sub>4</sub> fluxes in the *Avicennia* mangroves. Since pneumatophores can transport CH<sub>4</sub> from anaerobic deep soils, this study suggests that the pneumatophores of *Avicennia marina* played a more important role than soil properties in affecting soil CH<sub>4</sub> fluxes. Our results show that different mangrove tree species and related root structures may affect greenhouse gas emissions from the soils.

**Keywords:** *Avicennia marina*; *Kandelia obovata*; greenhouse gas; methane; pneumatophore; soil

## 1. Introduction

Mangroves are distributed in tropical and subtropical coastal zones that provide many essential ecosystem services. Mangroves not only reduce anthropogenic nutrient loading from upstream inputs [1] but also protect the coastline, mitigate erosion from typhoons [2,3], and alleviate the economic losses of coastal residents [4]. Furthermore, mangroves provide coastal fishery resources for humans [5,6] and nursery places for marine organisms [7].

Carbon sequestration is one of the essential ecosystem services of mangroves [8]. Mcleod et al. [9] indicated that mangroves, seagrass beds, and salt marshes are the three main “blue carbon” ecosystems, and the estimated global carbon storage rate was  $226 \pm 39 \text{ g C m}^{-2} \text{ yr}^{-1}$ . In addition, the carbon sequestration rate was approximately  $1.26 \text{ Mg ha}^{-1} \text{ yr}^{-1}$  in mangroves, which was much greater than that of seagrass beds ( $0.36 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ ) and salt marshes ( $0.39 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ ) in Australia [10]. Thus, mangroves can play an important role in regulating climate and mitigating global warming.

Anaerobic conditions often develop in the frequently flooded soils of coastal wetlands such as mangroves due to the curtailed supply of atmospheric oxygen into the soils. As a result, oxygen is rapidly depleted, soil oxidation reduction potential (Eh) is reduced, and other oxidants are used as electron acceptors for further respiration [11–13]. Anaerobic processes that follow aerobic

respiration ( $O_2 \rightarrow CO_2$ ) include (1) denitrification ( $NO_3^- \rightarrow NO_2^- \rightarrow NO \rightarrow N_2O \rightarrow N_2$ ), (2) manganese reduction ( $Mn^{4+} \rightarrow Mn^{2+}$ ), (3) iron reduction ( $Fe^{3+} \rightarrow Fe^{2+}$ ), (4) sulfate reduction ( $SO_4^{2-} \rightarrow H_2S$ ), and (5) methanogenesis ( $CO_2 \rightarrow CH_4$ ). The greenhouse gases such as  $CO_2$ ,  $N_2O$ , and  $CH_4$  are produced in a chain of reduction reactions by microbial metabolism. Furthermore, since sulfate can be directly acquired from seawater, the reduction reaction of sulfate is generally stronger than methanogenesis at sites immersed in high-salinity seawater, such as mangroves [13]. Consequently,  $CH_4$  emissions from mangroves have been reported to be affected by temperature and soil parameters, e.g., salinity, redox potential (ORP), pH, water content, and sulfate content [14,15]. However, other factors regulating greenhouse gas emissions from mangroves have seldom been discussed.

Previous studies established the carbon budgets in mangrove ecosystems [16,17]. Nonetheless, neglecting the emissions of greenhouse gas in the carbon budgets could possibly overestimate the carbon storage capacity. Based on an Intergovernmental Panel on Climate Change (IPCC) report [18], the global warming potential of  $CH_4$  is 28 times higher than that of carbon dioxide ( $CO_2$ ) over 100 years. Thus, to precisely estimate the carbon storage capacity,  $CH_4$  emissions should be quantified in mangrove ecosystems [19,20].

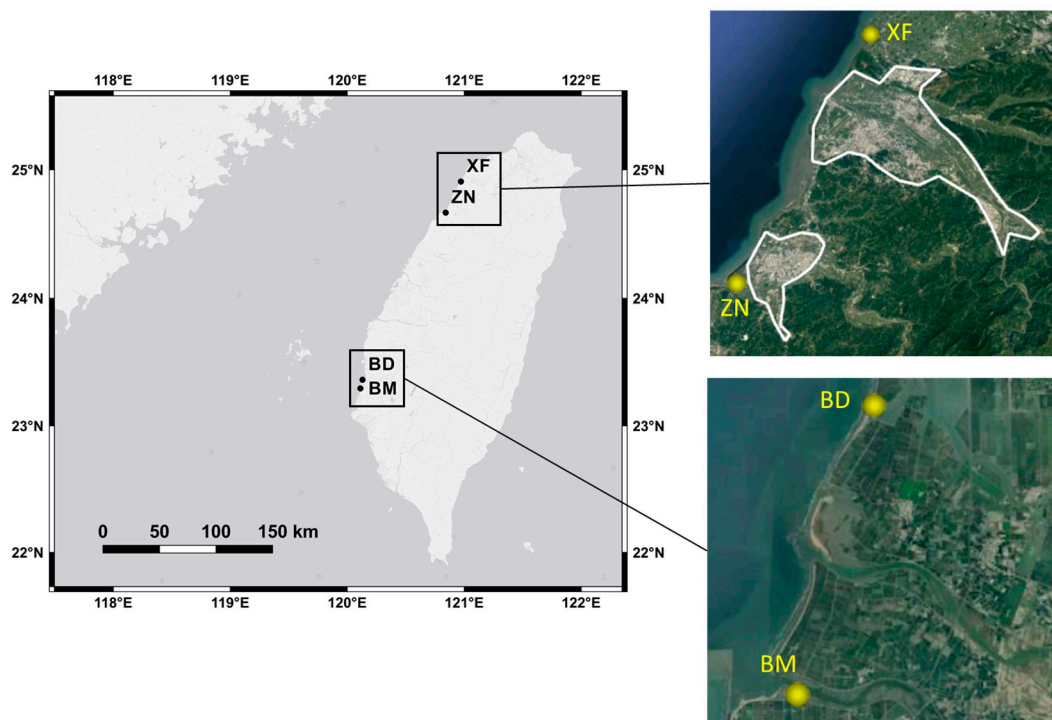
There are large areas of mangroves distributed along the western coast of Taiwan. Four mangrove species (*Avicennia marina*, *Kandelia obovata*, *Lumnizera racemosa*, and *Rhizophora stylosa*) are present in Taiwan. The dominant species are *Kandelia obovata* and *Avicennia marina* on the northwest (subtropical) and southwest (tropical) coasts, respectively. The root structures of the two mangrove species differ. *Kandelia obovata* possesses prop roots, whereas vertical roots or pneumatophores are observed in *Avicennia marina*. In this study, we hypothesized that  $CH_4$  fluxes from the soils of mangrove ecosystems were different among seasons, between habitat types (mangroves and adjoining mudflats), and between mangrove species (*Kandelia obovata* and *Avicennia marina*). The main objectives in this study were to (1) determine seasonal variations in soil  $CH_4$  flux, (2) compare  $CH_4$  fluxes and soil parameters between the mangroves and adjoining mudflats, and (3) compare  $CH_4$  fluxes and soil parameters between the mangroves of *Kandelia obovata* and *Avicennia marina*.

## 2. Materials and Methods

### 2.1. Study Sites

The four study sites (Figure 1), from north to south, were (1) Xinfeng (XF) ( $24^\circ 54' N$ ,  $120^\circ 58' E$ ), (2) Zhunan (ZN) ( $24^\circ 40' N$ ,  $120^\circ 50' E$ ), (3) Budai (BD) ( $23^\circ 21' N$ ,  $120^\circ 7' E$ ), and (4) Beimen (BM) ( $23^\circ 17' N$ ,  $120^\circ 6' E$ ), where the climate is rainy and hot in summer and dry and mild in winter (Table 1). The dominant mangrove species were *Kandelia obovata* at XF and ZN (subtropical) and *Avicennia marina* at BD and BM (tropical). Both tree height and density were higher in the *Kandelia* mangroves than in the *Avicennia* mangroves (Table 1).

Tides were predominantly semidiurnal off the western coast of Taiwan, and the tidal range increased from the southwest (tropical) to the northwest (subtropical; Table 1). The immersion time during flood tides at the four sites averaged 11.5–13.5 h/day. The extended mudflats were wider in the *Avicennia* mangroves than in the *Kandelia* mangroves. As a result, the area ratios of mangroves to mudflats were higher in the *Kandelia* mangroves than in the *Avicennia* mangroves. The mangroves at XF were highly affected by excessive nutrient loading ( $PO_4^{3-}$ : 1.30–72.30  $\mu M$  and  $NO_3^-$ : 41.48–753.84  $\mu M$ ) as a consequence of urban sewage (Figure 1 and Table 1). The mangroves at BD were categorized into an important wetland reserve, which became a habitat for migratory birds and waterfowl. There were several shellfish farms distributed near the mangroves at BM.



**Figure 1.** Map of studied mangrove sites at Xinfeng (XF), Zhunan (ZN), Budai (BD), and Beimen (BM) in Taiwan. The urban areas near XF (15,991 ha) and ZN (3807 ha) are shown by the white polygons. Non-urban area was observed near BD or BM. (Map sources: Left: QGIS 2.18.14; Right: Google Earth).

**Table 1.** Meteorological conditions, mangrove features, soil texture, and water nutrient concentrations at the four mangrove sites: Xinfeng (XF), Zhunan (ZN), Budai (BD), and Beimen (BM).

Site	XF	ZN	BD	BM	
Monthly rainfall (mm)	February (Winter)	41	30.5	9.5	9.5
	April (Spring)	185	169.5	78	72
	July (Summer)	47	67.5	334	545
	October (Fall)	9	17	0	0
Mean temperature (°C)	February (Winter)	16.3	17.1	20.2	20.3
	April (Spring)	22.1	23.1	24.6	24.5
	July (Summer)	28.6	29.4	28.8	28.6
	October (Fall)	23.7	24.8	25.6	25.6
Mean tidal range (cm)	366	388	181	136	
Mean immersion time during flood tides (hours/day)	11.5	12.0	11.3	13.5	
Major mangrove species	<i>Kandelia obovata</i>	<i>Kandelia obovata</i>	<i>Avicennia marina</i>	<i>Avicennia marina</i>	
Presence of pneumatophores	No	No	Yes	Yes	
Mangrove classification (Faunce and Layman [21])	High tide fringe mangroves	Low tide riverine mangroves	Riverine mangroves	High tide fringe mangroves	
Total area of mangrove forests and mudflats (ha)	9.37	19.59	30.2	5.48	
Area ratio of mangroves to mudflats	7.37	2.85	1.27	0.37	
Width of extended mudflats (m)	13–20	7–10	25–70	60–90	
Mean tree height (m)	5.1	5.0	4.0	3.2	
Mean tree density (trees m <sup>-1</sup> )	2.4	1.9	0.9	0.6	
Mean diameter at breast height (DBH) (cm)	5.6	5.9	5.4	6.2	
Soil texture	Fine sand	Very fine sand	Fine sand	Very fine sand	

Table 1. Cont.

Site	XF	ZN	BD	BM	
PO <sub>4</sub> <sup>3-</sup> (μM)	Range	1.30–72.30	2.89–18.30	0.91–5.23	1.46–6.93
	Mean ± standard error	29.94 ± 5.28	8.33 ± 1.16	3.07 ± 0.30	3.40 ± 0.39
NO <sub>3</sub> <sup>-</sup> (μM)	Range	41.48–753.84	2.64–17.09	0.07–8.97	3.24–22.85
	Mean ± standard error	300.24 ± 43.51	8.20 ± 1.04	4.18 ± 0.57	11.39 ± 1.07
NO <sub>2</sub> <sup>-</sup> (μM)	Range	5.57–97.82	0.66–35.22	0.12–2.09	1.99–6.79
	Mean ± standard error	30.06 ± 6.10	13.92 ± 2.28	0.74 ± 0.14	3.74 ± 0.27
NH <sub>4</sub> <sup>+</sup> (μM)	Range	26.10–100.84	93.21–203.75	2.42–17.66	10.62–38.99
	Mean ± standard error	56.08 ± 4.81	129.94 ± 6.12	8.59 ± 0.87	24.16 ± 1.76

## 2.2. Methane Flux Measurement

We determined CH<sub>4</sub> fluxes and soil parameters for a complete seasonal cycle in February (winter), April (spring), July (summer), and October (fall) in 2019. An in situ closed-path chamber connected with an ultraportable greenhouse gas analyzer (LGR915-0001, Los Gatos Research, San Jose, CA, USA) was used to quantify the CH<sub>4</sub> fluxes from the soils in mangrove ecosystems (mangroves and adjoining mudflats) at the four sites during emersion. Measurements of CH<sub>4</sub> flux were carried out in 3–5 replicate (5 in most cases) mangrove and adjoining mudflat soil samples (5 in most cases) at each site in each season. The replicated sites for measurements were chosen randomly within the mangroves and mudflats to represent each habitat type. To avoid any potential disturbance, the distance between two replicated sites was at least 5 m. In the field, a semicircular transparent acrylic chamber with a stainless-steel ring (30 cm in diameter and 16 cm in height) connected with the gas analyzer through a polyvinyl chloride (PVC) tube was pushed into the soil to a depth of 10 cm. The chamber enclosed 10.6 L of air over a 0.071 m<sup>2</sup> surface area. CH<sub>4</sub> concentration exchanges between the soil and the atmosphere were monitored by the gas analyzer and recorded by a data logger with a 20 s logging frequency for 10 min. The CH<sub>4</sub> fluxes were calculated by Equation (1).

$$F = \frac{S * V * 180 * 24}{(RT * A)} \quad (1)$$

where, F: CH<sub>4</sub> fluxes (μmol CH<sub>4</sub> m<sup>-2</sup> day<sup>-1</sup>), S: slope of the linear regression line between CH<sub>4</sub> concentrations (ppm) and recorded frequency (20 s), V: chamber volume (L), R: ideal gas constant = 0.082 (L atm K<sup>-1</sup> mol<sup>-1</sup>), T: absolute temperature (K), A: the area of the bottom part of the chamber (m<sup>2</sup>), 180: time transformation constant = (1 h × (60 min/hour) × ((60 s/min)/20 s), and 24: 1 day = 24 h.

## 2.3. Soil and Water Sampling

After CH<sub>4</sub> measurements at each site in each season, soil parameters in the top 10 cm layer were determined in 5 replicates in the mangroves and 2 replicates in the adjoining mudflats during emersion. Soil temperature and redox potential (ORP) were measured by a redox potential meter (ORP30, CLEAN L'eau, Taoyuan City, Taiwan), and soil pH was determined by a portable pH meter (WD-35634-40, OAKTON Instruments, Vernon Hills, IL, USA) in situ at the four sites during each field visit.

For soil bulk density and water and organic matter content, we collected soil samples by using stainless cores with a 7 cm diameter and 80 cm length. The top 10 cm of the soil core samples were then retrieved as subsamples by applying syringes 2.9 cm in diameter and 5 cm in length (syringe volume = 33.0 cm<sup>3</sup>). The subsamples were stored in 50 mL centrifuge tubes and placed with ice in a portable cooler for laboratory analysis. Each soil subsample was placed on a tin plate ( $W_0$ ) and weighed as  $W_1$ . The sample with the tin plate was placed in an oven at 60 °C until a constant dry weight was attained ( $W_2$ ). The water content and bulk density were calculated by Equations (2) and (3), respectively [17].

$$\text{Water content (\%)} = \frac{(W_1 - W_2)}{(W_1 - W_0)} * 100\% \quad (2)$$

$$\text{Bulk density (g cm}^{-3}\text{)} = \frac{(W_2 - W_0)}{33 \text{ cm}^3} \quad (3)$$

Then, the subsample was placed in an oven at 450 °C for 4 h and weighed as  $W_3$  as the ash-dried weight. The organic matter content was obtained by Equation (4) [17].

$$\text{Organic matter (\%)} = \frac{(W_2 - W_3)}{(W_2 - W_0)} * 100\% \quad (4)$$

Since the soil was too dry to measure the salinity in situ, another subsample was collected from the original core sample and placed in a sealed plastic bag for laboratory analysis. A syringe was used to extract the pore water from the subsample, and the salinity of the pore water was measured by a portable refractometer (Refractometer FG-201, Hangzhou Chincan Trading Co., Ltd., Hangzhou city, Zhejiang province, China).

At the high tide before  $\text{CH}_4$  measurements at each site in each season, water samples collected for nutrient analysis were filtered in the field through 0.45  $\mu\text{m}$  cellulose nitrate membrane filters (GN-6 Metrical, PALL Corporation, Port Washington, NY, USA) and transported back to the laboratory on ice. At the laboratory, these samples were analyzed by a spectrophotometer (U-2001, Hitachi, Japan) for the concentrations of  $\text{NO}_2^-$  [22],  $\text{NO}_3^-$  [23],  $\text{NH}_4^+$  [24], and  $\text{PO}_4^{3-}$  [25].

#### 2.4. Statistical Analyses

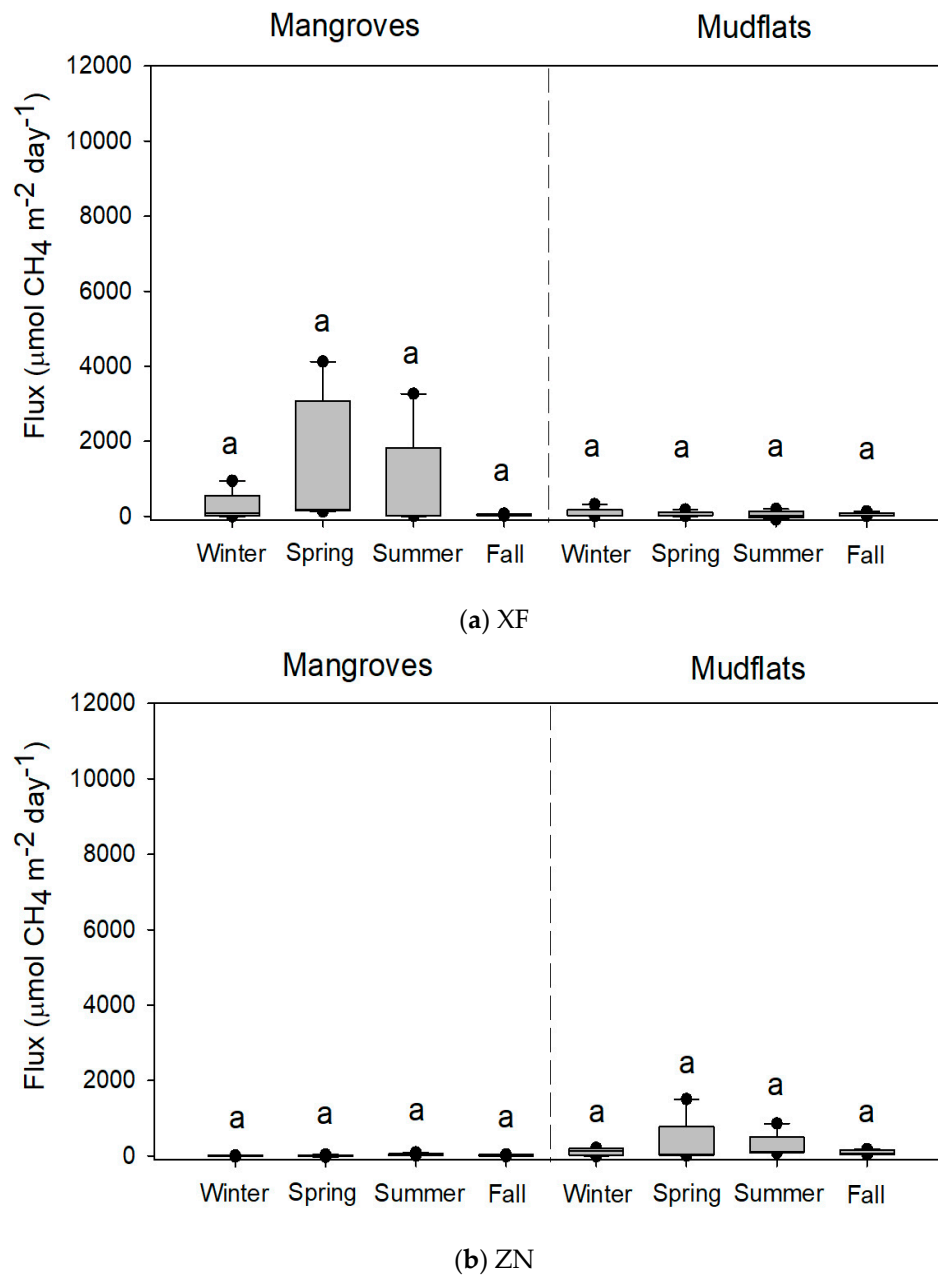
Based on the results of the Shapiro–Wilk test, the data of  $\text{CH}_4$  flux and soil parameters were not normally distributed ( $p$ -value < 0.05). Thus, the Kruskal–Wallis test was applied to evaluate seasonal variations in  $\text{CH}_4$  flux and soil parameters at each site. If the results indicated significance at the 0.05 probability level, the Tukey’s honestly significant difference (HSD) test and the Bonferroni correction for the significance level were used to determine which levels differed. The Wilcoxon rank-sum test was used to compare the differences in  $\text{CH}_4$  flux and soil parameters between (1) mangroves and adjoining mudflats, and (2) the mangroves of *Kandelia obovata* and *Avicennia marina*. Multiple regression analysis was implemented to identify the soil parameters that most affected  $\text{CH}_4$  flux in the mangroves. The statistically significant level was  $p < 0.05$ . The statistical tests in this study were carried out using R software (Version 3.6.1, <https://www.r-project.org/>) [26].

### 3. Results

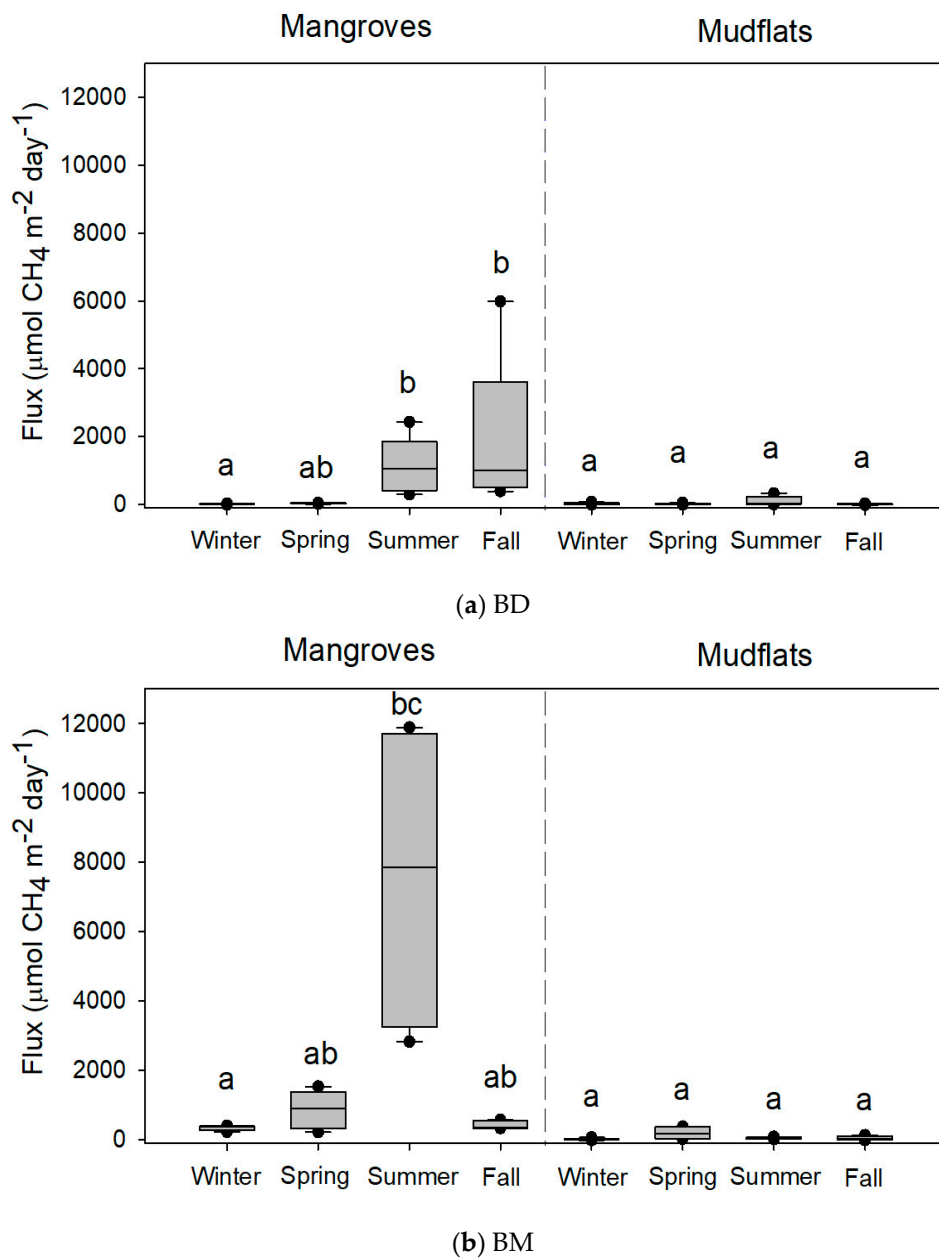
#### 3.1. $\text{CH}_4$ Flux and Soil Parameters

The variations in  $\text{CH}_4$  flux from the mangrove soils were high: 42.4–1326.6, 1.3–39.3, 10.1–1847.8, and 337.6–7606.6  $\mu\text{mol-CH}_4 \text{ m}^{-2} \text{ day}^{-1}$  at XF, ZN, BD, and BM, respectively (Table 2). There were no significant seasonal variations in  $\text{CH}_4$  flux from the soils of XF and ZN mangroves (Figure 2). However,  $\text{CH}_4$  fluxes from the soils of mangroves were significantly higher in summer than in winter at BD and BM (Figure 3). At XF, ZN, and BM, almost all soil parameters were significantly different among seasons (Table 2). At BD, however, there were no significant seasonal variations in many soil parameters.

$\text{CH}_4$  fluxes from the soils of mudflats were 45.2–79.1, 93.9–334.5, 6.6–102.8, and 14.3–192.7  $\mu\text{mol-CH}_4 \text{ m}^{-2} \text{ day}^{-1}$  at XF, ZN, BD, and BM, respectively (Table 3). Seasonal variations in the  $\text{CH}_4$  flux and soil parameters in the mudflats were smaller than the variations in the mangroves at the four sites.



**Figure 2.** Methane fluxes ( $n = 5$ ) from the soils of mangroves of *Kandelia obovata* and adjoining mudflats at (a) Xinfeng (XF) and (b) Zhunan (ZN). Same letters indicate no significant seasonal differences with the Kruskal–Wallis test and Tukey’s honestly significant difference (HSD) test and the Bonferroni correction for the significance level in mangroves and mudflats, respectively.



**Figure 3.** Methane fluxes ( $n = 5$  except at BM, where  $n = 4$  in the summer of mangroves and  $n = 3$  in the spring of mudflats) from the soils of mangroves of *Avicennia marina* and adjoining mudflats at (a) Budai (BD) and (b) Beimen (BM). Different letters indicate significant seasonal differences with the Kruskal-Wallis test and Tukey's honestly significant difference (HSD) test and the Bonferroni correction for the significance level in mangroves and mudflats, respectively.

**Table 2.** Seasonal variations in methane fluxes and soil physiochemical parameters (Mean  $\pm$  standard error) of the four mangrove sites. Different letters indicate significant seasonal differences with the Kruskal–Wallis test and Tukey’s honestly significant difference (HSD) test and the Bonferroni correction for the significance level for each mangrove site. ORP: redox potential.

Site	Season	Methane Fluxes ( $\mu\text{mol-CH}_4 \text{ m}^{-2} \text{ day}^{-1}$ )	Temperature ( $^{\circ}\text{C}$ )	ORP (mV)	pH	Salinity	Bulk Density ( $\text{g cm}^{-3}$ )	Water Content (%)	Organic Matter (%)
XF	Winter	241.6 $\pm$ 178.1 a	17.5 $\pm$ 0.3 a	218.2 $\pm$ 16.2 a	6.4 $\pm$ 0.1 a	0.4 $\pm$ 0.1 a	1.5 $\pm$ 0.0 b	25.9 $\pm$ 1.5 ab	3.9 $\pm$ 0.5 a
	Spring	1326.6 $\pm$ 786.9 a	20.5 $\pm$ 0.1 ab	171.6 $\pm$ 9.5 a	6.2 $\pm$ 0.0 a	0.9 $\pm$ 0.1 ab	1.0 $\pm$ 0.0 a	32.9 $\pm$ 1.5 b	5.2 $\pm$ 0.4 a
	Summer	742.5 $\pm$ 635.3 a	28.6 $\pm$ 0.2 c	160.6 $\pm$ 22.9 a	6.4 $\pm$ 0.1 a	0.9 $\pm$ 0.1 ab	1.0 $\pm$ 0.1 a	34.4 $\pm$ 1.4 b	5.5 $\pm$ 0.4 a
	Fall	42.4 $\pm$ 9.1 a	25.1 $\pm$ 0.5 bc	183.6 $\pm$ 9.9 a	6.2 $\pm$ 0.1 a	1.2 $\pm$ 0.1 b	1.2 $\pm$ 0.0 ab	22.7 $\pm$ 1.2 a	5.5 $\pm$ 1.0 a
ZN	Winter	1.3 $\pm$ 3.4 a	17.4 $\pm$ 0.1 a	139.2 $\pm$ 29.8 ab	6.6 $\pm$ 0.1 ab	2.4 $\pm$ 0.3 a	1.6 $\pm$ 0.0 b	23.7 $\pm$ 1.0 ab	4.1 $\pm$ 0.4 a
	Spring	10.0 $\pm$ 9.5 a	22.8 $\pm$ 0.4 ab	152.2 $\pm$ 2.7 b	6.6 $\pm$ 0.1 ab	2.2 $\pm$ 0.2 a	1.2 $\pm$ 0.0 a	31.1 $\pm$ 0.8 b	4.0 $\pm$ 0.2 a
	Summer	39.3 $\pm$ 13.3 a	27.5 $\pm$ 0.1 c	−3.6 $\pm$ 20.5 a	6.4 $\pm$ 0.1 a	3.1 $\pm$ 0.3 a	1.3 $\pm$ 0.0 a	29.2 $\pm$ 0.9 b	3.8 $\pm$ 0.2 a
	Fall	14.5 $\pm$ 9.3 a	25.7 $\pm$ 0.5 bc	133.6 $\pm$ 10.6 ab	7.0 $\pm$ 0.1 b	3.1 $\pm$ 0.2 a	1.4 $\pm$ 0.0 ab	19.7 $\pm$ 0.6 a	4.3 $\pm$ 0.4 a
BD	Winter	10.1 $\pm$ 5.5 a	23.0 $\pm$ 0.0 a	−274.4 $\pm$ 28.0 a	7.1 $\pm$ 0.1 b	2.9 $\pm$ 0.1 ab	1.1 $\pm$ 0.2 b	43.5 $\pm$ 7.5 a	5.3 $\pm$ 1.1 a
	Spring	32.0 $\pm$ 5.9 ab	27.9 $\pm$ 0.2 bc	−285.0 $\pm$ 9.2 a	6.7 $\pm$ 0.0 ab	4.5 $\pm$ 0.3 c	1.1 $\pm$ 0.1 b	58.0 $\pm$ 2.1 a	7.2 $\pm$ 0.4 a
	Summer	1116.6 $\pm$ 372.3 b	30.5 $\pm$ 0.4 c	−340.8 $\pm$ 13.9 a	6.6 $\pm$ 0.1 ab	2.5 $\pm$ 0.3 a	0.5 $\pm$ 0.1 a	57.6 $\pm$ 2.3 a	8.4 $\pm$ 0.9 a
	Fall	1847.8 $\pm$ 1045.4 b	24.5 $\pm$ 0.1 ab	−290.2 $\pm$ 24.0 a	6.6 $\pm$ 0.2 a	3.8 $\pm$ 0.2 abc	0.8 $\pm$ 0.1 ab	37.8 $\pm$ 5.5 a	6.5 $\pm$ 0.5 a
BM	Winter	337.6 $\pm$ 31.7 a	20.1 $\pm$ 0.3 a	33.0 $\pm$ 37.4 a	6.7 $\pm$ 0.0 a	3.6 $\pm$ 0.4 ab	1.3 $\pm$ 0.0 ab	25.5 $\pm$ 3.6 a	4.3 $\pm$ 0.4 b
	Spring	865.0 $\pm$ 244.5 ab	27.6 $\pm$ 0.2 bc	−8.4 $\pm$ 10.8 a	6.7 $\pm$ 0.1 a	5.6 $\pm$ 0.8 b	2.2 $\pm$ 0.0 b	30.8 $\pm$ 1.2 a	2.6 $\pm$ 0.2 a
	Summer	7606.6 $\pm$ 2304.8 bc	30.1 $\pm$ 0.4 c	−151.4 $\pm$ 54.1 a	7.0 $\pm$ 0.1 a	3.1 $\pm$ 0.1 a	1.0 $\pm$ 0.0 a	38.2 $\pm$ 2.7 a	3.5 $\pm$ 0.2 ab
	Fall	424.7 $\pm$ 54.5 ab	23.7 $\pm$ 0.2 ab	−148.0 $\pm$ 50.3 a	6.6 $\pm$ 0.1 a	4.2 $\pm$ 0.4 ab	1.2 $\pm$ 0.1 ab	29.5 $\pm$ 3.8 a	3.3 $\pm$ 0.2 ab

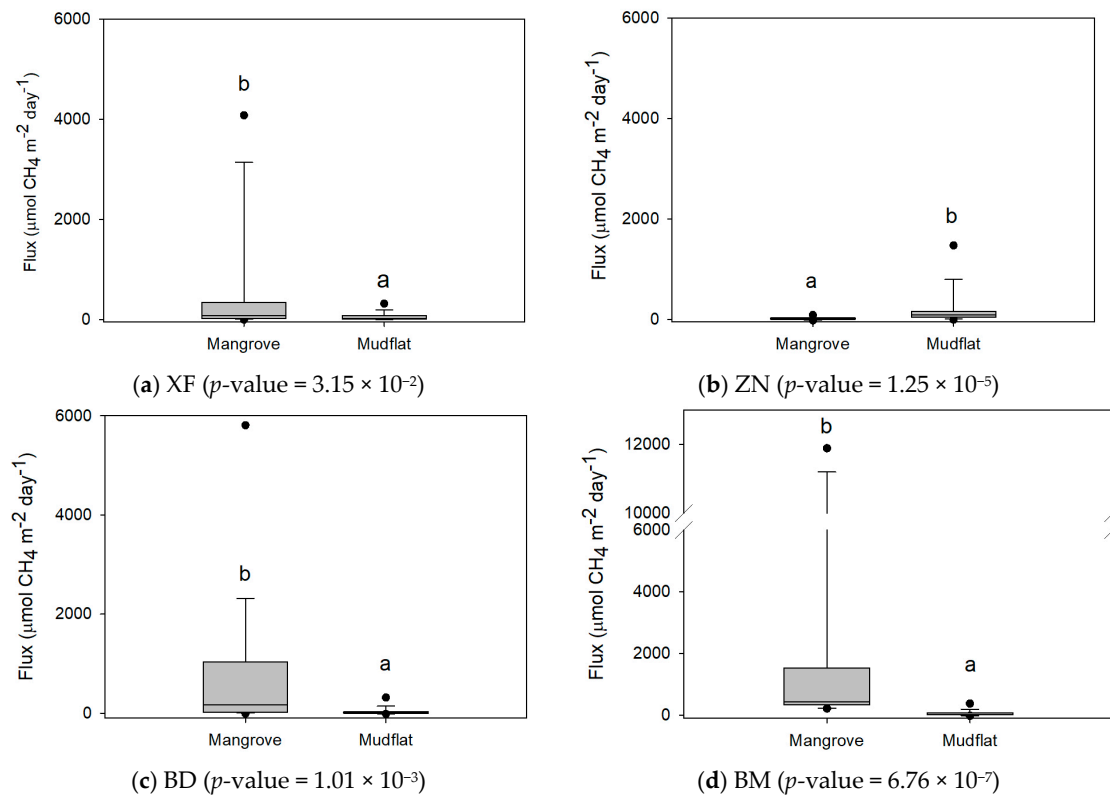


**Table 3.** Seasonal variations in methane fluxes and soil physiochemical parameters (Mean  $\pm$  standard error) of the four adjoining mudflats. No significant seasonal difference was detected for all variables at each mudflat site with the Kruskal–Wallis test and Tukey’s honestly significant difference (HSD) test and the Bonferroni correction for the significance level. ORP: redox potential.

Site	Season	Methane Fluxes	Temperature	ORP	pH	Salinity	Bulk Density	Water Content	Organic Matter
		( $\mu\text{mol-CH}_4 \text{ m}^{-2} \text{ day}^{-1}$ )	( $^{\circ}\text{C}$ )	(mV)			( $\text{g cm}^{-3}$ )	(%)	(%)
XF	Winter	79.1 $\pm$ 61.6	17.5 $\pm$ 0.4	−15.5 $\pm$ 30.5	7.1 $\pm$ 0.2	1.7 $\pm$ 0.0	1.1 $\pm$ 0.0	39.9 $\pm$ 0.4	3.2 $\pm$ 0.0
	Spring	56.3 $\pm$ 32.1	24.7 $\pm$ 0.9	−62.0 $\pm$ 36.0	6.6 $\pm$ 0.0	2.9 $\pm$ 0.2	1.0 $\pm$ 0.0	36.5 $\pm$ 2.1	3.9 $\pm$ 0.1
	Summer	45.2 $\pm$ 46.7	28.6 $\pm$ 0.1	62.5 $\pm$ 86.5	6.9 $\pm$ 0.1	1.8 $\pm$ 0.0	1.1 $\pm$ 0.0	37.8 $\pm$ 0.9	3.8 $\pm$ 0.1
	Fall	48.9 $\pm$ 22.4	24.5 $\pm$ 0.1	47.5 $\pm$ 15.5	7.4 $\pm$ 0.2	3.4 $\pm$ 0.3	1.1 $\pm$ 0.1	31.9 $\pm$ 1.0	3.7 $\pm$ 0.4
ZN	Winter	113.5 $\pm$ 40.8	20.2 $\pm$ 0.0	−19.0 $\pm$ 64.0	7.0 $\pm$ 0.1	1.7 $\pm$ 0.0	1.3 $\pm$ 0.1	33.2 $\pm$ 1.8	3.6 $\pm$ 0.3
	Spring	334.5 $\pm$ 293.2	21.6 $\pm$ 0.4	−31.5 $\pm$ 45.5	6.8 $\pm$ 0.1	3.7 $\pm$ 0.9	1.1 $\pm$ 0.0	34.5 $\pm$ 0.1	3.6 $\pm$ 0.0
	Summer	257.9 $\pm$ 150.8	27.9 $\pm$ 0.0	−196.0 $\pm$ 4.0	7.2 $\pm$ 0.0	1.7 $\pm$ 0.0	1.1 $\pm$ 0.0	36.2 $\pm$ 1.9	3.4 $\pm$ 0.1
	Fall	93.9 $\pm$ 29.1	26.3 $\pm$ 0.1	−54.5 $\pm$ 1.5	7.3 $\pm$ 0.1	3.3 $\pm$ 0.1	1.1 $\pm$ 0.0	30.8 $\pm$ 0.6	4.4 $\pm$ 0.2
BD	Winter	17.0 $\pm$ 14.0	24.7 $\pm$ 0.1	−54.5 $\pm$ 15.5	7.5 $\pm$ 0.1	1.9 $\pm$ 0.0	1.8 $\pm$ 0.0	18.8 $\pm$ 0.3	0.7 $\pm$ 0.1
	Spring	11.3 $\pm$ 10.5	29.5 $\pm$ 0.1	98.5 $\pm$ 5.5	6.9 $\pm$ 0.3	4.8 $\pm$ 0.0	2.8 $\pm$ 0.0	21.2 $\pm$ 0.2	0.8 $\pm$ 0.1
	Summer	102.8 $\pm$ 61.6	34.4 $\pm$ 1.7	−20.0 $\pm$ 30.0	7.3 $\pm$ 0.1	1.7 $\pm$ 0.0	1.4 $\pm$ 0.0	23.8 $\pm$ 2.1	1.5 $\pm$ 0.1
	Fall	6.6 $\pm$ 7.4	22.6 $\pm$ 0.1	−51.0 $\pm$ 27.0	7.3 $\pm$ 0.3	2.3 $\pm$ 0.0	1.5 $\pm$ 0.1	15.9 $\pm$ 0.2	0.8 $\pm$ 0.1
BM	Winter	14.3 $\pm$ 13.5	21.8 $\pm$ 0.2	−40.0 $\pm$ 7.0	7.0 $\pm$ 0.1	4.3 $\pm$ 0.2	1.0 $\pm$ 0.1	41.1 $\pm$ 2.5	4.8 $\pm$ 0.2
	Spring	192.7 $\pm$ 102.2	28.0 $\pm$ 0.1	−281.0 $\pm$ 3.0	6.8 $\pm$ 0.0	7.5 $\pm$ 0.5	2.1 $\pm$ 0.1	32.4 $\pm$ 0.1	1.7 $\pm$ 0.0
	Summer	37.4 $\pm$ 12.1	30.3 $\pm$ 0.6	−73.5 $\pm$ 222.5	7.3 $\pm$ 0.1	1.7 $\pm$ 0.1	1.3 $\pm$ 0.0	25.3 $\pm$ 1.6	1.6 $\pm$ 0.0
	Fall	49.0 $\pm$ 25.7	24.9 $\pm$ 0.2	22.0 $\pm$ 13.0	7.1 $\pm$ 0.1	3.0 $\pm$ 0.5	1.4 $\pm$ 0.1	27.4 $\pm$ 0.3	2.1 $\pm$ 0.2

### 3.2. Comparisons of Methane Flux and Soil Parameters under Various Conditions

Soil CH<sub>4</sub> fluxes were significantly higher in the mangroves than in the adjoining mudflats at XF, BD, and BM, but not at ZN (Figure 4). Many soil parameters differed between the mangroves and the mudflats at XF and BD (Table 4). Only soil ORP was significantly lower in the mudflats than in the mangroves at ZN. There were no significant differences in the soil parameters between the two habitats at BM.



**Figure 4.** Comparisons of methane fluxes between mangroves and adjoining mudflats at (a) Xinfeng (XF), (b) Zhunan (ZN), (c) Budai (BD), and (d) Beimen (BM). Different letters indicate a significant difference ( $p < 0.05$ ) with the Wilcoxon rank-sum test.

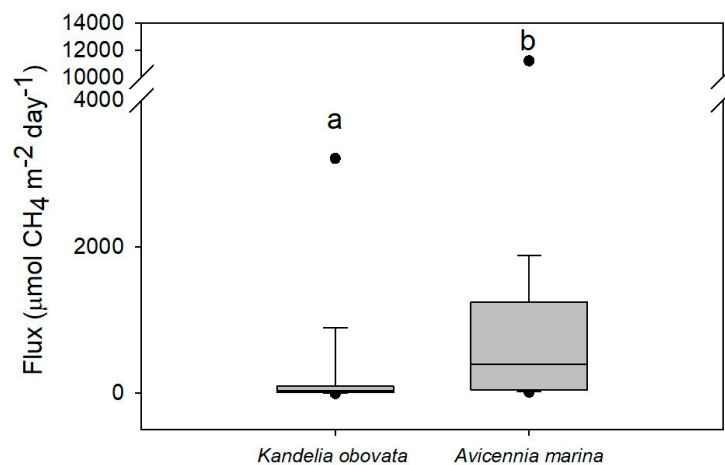
**Table 4.** Comparisons of methane fluxes and soil parameters between mangroves and adjoining mudflats at the four sites with the Wilcoxon rank-sum test (a significant difference at  $p < 0.05$ ; n.s. = no significance). ORP: redox potential.

Parameters	XF		ZN	
	<i>p</i> -Value	Note	<i>p</i> -Value	Note
CH <sub>4</sub> flux	$3.15 \times 10^{-2}$	Mangrove > Mudflat	$1.25 \times 10^{-5}$	Mangrove < Mudflat
Temperature	1.00	n.s.	0.89	n.s.
ORP	$3.04 \times 10^{-2}$	Mangrove > Mudflat	$3.04 \times 10^{-2}$	Mangrove > Mudflat
pH	$2.84 \times 10^{-2}$	Mangrove < Mudflat	0.08	n.s.
Salinity	$2.94 \times 10^{-2}$	Mangrove < Mudflat	1.00	n.s.
Bulk density	0.88	n.s.	0.07	n.s.
Water content	0.11	n.s.	0.06	n.s.
Organic matter content	$4.08 \times 10^{-2}$	Mangrove > Mudflat	0.31	n.s.

Table 4. Cont.

Parameters	BD		BM	
	p-Value	Note	p-Value	Note
CH <sub>4</sub> flux	$1.01 \times 10^{-3}$	Mangrove > Mudflat	$6.76 \times 10^{-7}$	Mangrove > Mudflat
Temperature	0.89	n.s.	0.67	n.s.
ORP	$3.04 \times 10^{-2}$	Mangrove < Mudflat	0.89	n.s.
pH	0.06	n.s.	0.08	n.s.
Salinity	0.31	n.s.	0.89	n.s.
Bulk density	$2.94 \times 10^{-2}$	Mangrove < Mudflat	0.88	n.s.
Water content	$3.04 \times 10^{-2}$	Mangrove > Mudflat	1	n.s.
Organic matter content	$2.94 \times 10^{-2}$	Mangrove > Mudflat	0.31	n.s.

CH<sub>4</sub> fluxes were significantly higher in the soils of *Avicennia* mangroves than in the soils of *Kandelia* mangroves (Figure 5). ORP and bulk density were lower in the soils of *Avicennia* mangroves than in the soils of *Kandelia* mangroves (Table 5). However, pH, salinity, and water content were higher in the soils of *Avicennia* mangroves than in the soils of *Kandelia* mangroves. There was no significant difference in organic matter content between the soils of two mangrove species.



**Figure 5.** Comparison of methane fluxes between the mangroves of *Kandelia obovata* and *Avicennia marina*. Different letters indicate a significant difference ( $p = 1.25 \times 10^{-5}$ ) with the Wilcoxon rank-sum test.

**Table 5.** Comparisons of methane fluxes between the mangroves of *Kandelia obovata* and *Avicennia marina* with the Wilcoxon rank-sum test (a significant difference at  $p < 0.05$ ; n.s. = no significance). ORP: redox potential.

Parameters	p-Value	Note
CH <sub>4</sub> flux	$1.56 \times 10^{-5}$	K < A
Temperature	$4.94 \times 10^{-3}$	K < A
ORP	$4.14 \times 10^{-13}$	K > A
pH	$9.33 \times 10^{-6}$	K < A
Salinity	$1.61 \times 10^{-9}$	K < A
Bulk density	$1.17 \times 10^{-2}$	K > A
Water content	$1.81 \times 10^{-5}$	K < A
Organic matter content	0.84	n.s.

The results of multiple regressions indicate that water content ( $p$ -value = 0.030) and organic matter content ( $p$ -value = 0.038) significantly affected the CH<sub>4</sub> fluxes in the soils of *Kandelia* mangroves. However, none of the soil parameters were detected to significantly influence the CH<sub>4</sub> fluxes in the soils of *Avicennia* mangroves.

#### 4. Discussion

A significant amount of CH<sub>4</sub> was emitted from the studied mangrove soils, which indicates that mangrove soils might act as CH<sub>4</sub> sources. Seasonal variations in CH<sub>4</sub> flux and soil parameters were detected in the mangrove soils at BD and BM. Previous studies also reported a seasonal pattern in other mangrove soils [15,27,28]. The highest and lowest CH<sub>4</sub> fluxes were observed in warm seasons (spring and summer) and in winter respectively, in this study and in other studies [13,14,29]. Previous findings stated that temperature was the main physical factor that affected the amount of CH<sub>4</sub> emission [15,27,30,31]. However, the present study demonstrates that CH<sub>4</sub> fluxes did not vary distinctly among seasons in the mangrove soils at XF and ZN or in the mudflats at the four studied sites. Since seasonal variations in the soil parameters were not detected in the mudflats, it can be expected that the variations in CH<sub>4</sub> fluxes (6.6–334.5 μmol-CH<sub>4</sub> m<sup>-2</sup> day<sup>-1</sup>) from the mudflats were small when compared with those from the mangrove soils (Tables 2 and 3).

In the present study, when comparing the CH<sub>4</sub> fluxes from the mangrove soils with the adjoining mudflats, there were no clear patterns in the studied mangroves. Each mangrove might have its own characteristics. Since greenhouse gases from soils are produced during microbial processes and respiration, the soil parameters (temperature, redox potential, pH, salinity, density, water content, and organic matter content) related to microbial activities are essential [15,31–34]. At XF, although a lower ORP was found in the mudflats (mudflat: −62.0–62.5 mV, forest: 160.6–218.2 mV), organic matter content (mudflats: 3.2%–3.9%, mangroves: 3.9%–5.5%) was greater in the mangrove soils, which indicates that more organic compounds were decomposed and more CH<sub>4</sub> was produced from the mangrove soils. Allen et al. [27] also found that the degradation of more organic matter contents induced a higher production of CH<sub>4</sub>. Furthermore, CH<sub>4</sub> emissions might be inhibited by the higher salinity in the mudflats (mudflats: 1.7–3.4, mangroves: 0.4–1.2). Several studies demonstrated that higher salinity had an inhibitory effect on methanogenic bacterial activities [14,15,27,28,35,36].

At ZN, the higher ORP in the soils of mangroves under aerobic conditions (mudflat: −196.0–−19.0 mV, mangrove: −3.6–152.2 mV) might play a major role in affecting the CH<sub>4</sub> fluxes in the mangroves. Previous studies have identified that redox potential has inverse effects on CH<sub>4</sub> emissions [35,37]. At BD, the lower ORP (mudflats: −54.5 to 98.5 mV, mangroves: −340.8 to −274.4 mV) and bulk densities (mudflats: 1.4 to 2.8 g cm<sup>-3</sup>, mangroves: 0.5 to 1.1 g cm<sup>-3</sup>) and the higher water content (mudflats: 15.9% to 23.8%, mangroves: 37.8% to 58.0%) and organic matter (mudflats: 0.7% to 1.5%, mangroves: 5.3% to 8.4%) led to anaerobic conditions in the mangrove soils, and this then resulted in more CH<sub>4</sub> emissions from the mangrove soils than from the mudflats. Nevertheless, in the present study, the key environmental factors influencing the differences in CH<sub>4</sub> fluxes between the mangrove soils and the mudflats were not found at BM. It appeared that different mangrove tree species might affect CH<sub>4</sub> emissions. Our results show that CH<sub>4</sub> emissions were significantly higher in the mangrove soils of *Avicennia* than in the adjoining mudflats; this trend, however, was not necessarily recapitulated at *Kandelia*.

The results in the present study demonstrate that CH<sub>4</sub> fluxes might be different for the same mangrove species. Since there were more anthropogenic activities at XF than at ZN, higher nutrients and more organic compounds were input from the upstream river to the *Kandelia* mangroves. As a result, a large amount of CH<sub>4</sub> was emitted from the mangrove soils at XF. Previous findings also verified that anthropogenic activities caused a greater amount of nutrient input (total organic carbon, total nitrogen, and total phosphorus) that accumulated in mangrove soils; thus, there might be more organic matter that was taken up by microbial metabolism and produced more CH<sub>4</sub> [13,31,38]. A previous study demonstrated that different mangrove species and related root structures affected greenhouse gases emission [14,27]. The pneumatophores of *Avicennia marina* might become a pathway that transported CH<sub>4</sub> from deeper soils to the atmosphere [14,27,35,39]. In addition, Allen et al. [27] observed that the redox potential of *Avicennia marina* soils was negative, which led to the development of an anaerobic environment in the soils. The results of previous studies support our findings that the soils of *Avicennia* mangroves produced more CH<sub>4</sub> than the soils of *Kandelia* mangroves. The results of multiple regression

analyses show that water and organic matter content in the soils were the main factors regulating CH<sub>4</sub> emissions from the *Kandelia* mangroves. In addition, since bulk density was related to water content in the soils, which might affect the redox potential, this suggests that soil conditions with lower bulk density presented higher water content. As a result, the water and organic matter content contributed significantly to the CH<sub>4</sub> emissions in the *Kandelia* mangroves. However, the results of multiple regression analyses indicate that the assessed soil parameters did not influence the CH<sub>4</sub> emissions significantly in the *Avicennia* mangroves. Since the pneumatophores can transport CH<sub>4</sub> from anaerobic deep soils, it is likely that the pneumatophores of *Avicennia marina* played a more important role than soil parameters in affecting soil CH<sub>4</sub> fluxes. Nevertheless, these results are inconsistent with other research which demonstrated that pneumatophores reduced CH<sub>4</sub> emissions [40,41]. The role of pneumatophores and the mechanisms of transporting CH<sub>4</sub> warrant further investigation.

When comparing this study with other mangrove studies, soil CH<sub>4</sub> fluxes (*Kandelia obovata*: 0.9–884.4, *Avicennia marina*: 6.7–5071.1 µg m<sup>-2</sup> h<sup>-1</sup>) in this study and other mangroves were comparable (Table 6). Thus, the CH<sub>4</sub> fluxes in mangrove ecosystems cannot be neglected when constructing the carbon budgets and estimating the carbon storage capacity.

**Table 6.** Comparisons of soil CH<sub>4</sub> flux in the mangroves of this study and other studies.

Site	Climate	Dominant Mangrove Species	CH <sub>4</sub> Fluxes (µg m <sup>-2</sup> h <sup>-1</sup> )	References
XF and ZN	Subtropical	<i>Kandelia obovata</i>	0.9–884.4	This study
BD and BM	Tropical	<i>Avicennia marina</i>	6.7–5071.1	
North Sulawesi, Indonesia	Equatorial	<i>Rhizophora apiculate</i> and <i>Bruguiera gymnorhiza</i>	0–210.24	[42]
Dar es Salaam, Tanzania	Humid tropical	<i>Sonneratia alba</i> , <i>Avicenniamarina</i> , <i>Ceriops tagal</i> , <i>Rhizophora mucronata</i>	7–233	[40]
Ceará state, NE-Brazil	Tropical	<i>Rhizophora</i> spp.	0.7–8.8	[13]
Odisha state, India	Tropical	<i>Avicennia</i> spp.	80–2300	[28]
Queensland, Australia	Tropical	NA	26.7–698	[36]
Shenzhen, China	Subtropical monsoonal	<i>Kandelia obovata</i>	190.6–4390.9	[31]
Moreton Bay, Australia	Subtropical	<i>Avicennia marina</i>	20–350	[32]
Chelmer, Australia	Subtropical	<i>Avicennia marina</i>	3.0–17,370.0	[27]
Southeast Queensland, Australia	Subtropical	<i>Avicennia</i> spp.	47–1570	[14]

Note: Table was adapted from Nóbrega et al. [13].

## 5. Conclusions

In this study, CH<sub>4</sub> fluxes and soil properties of the top 10 cm layer were determined in subtropical (*Kandelia obovata*) and tropical (*Avicennia marina*) mangrove ecosystems of Taiwan for a complete seasonal cycle. CH<sub>4</sub> emissions were observed in the studied mangrove soils, which indicates that mangrove soils might act as CH<sub>4</sub> sources. This suggests that CH<sub>4</sub> fluxes in mangrove ecosystems cannot be neglected when constructing the carbon budgets and estimating the carbon storage capacity. Our results also indicated that CH<sub>4</sub> fluxes were significantly greater in summer than in winter from the *Avicennia* soils, but no seasonal variation was detected from the *Kandelia* soils. CH<sub>4</sub> fluxes were significantly higher in the mangrove soils of *Avicennia* than in the adjoining mudflats; this trend,

however, was not necessarily recapitulated at *Kandelia*. Multiple regression analyses demonstrated that water and organic matter content were the key factors regulating the CH<sub>4</sub> fluxes from the *Kandelia* soils. However, the assessed soil parameters did not significantly influence the CH<sub>4</sub> fluxes from the *Avicennia* soils. Since pneumatophores can transport CH<sub>4</sub> from anaerobic deep soils, this study suggests that the pneumatophores of *Avicennia marina* played a more important role than soil properties in soil CH<sub>4</sub> fluxes. Our results indicated that different mangrove tree species and related root structures may affect soil greenhouse gas emissions.

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