



Article Effects of Pneumatophore Density on Methane Emissions in Mangroves

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Abstract: Mangroves play an important role in carbon sequestration. However, mangroves can be sources of greenhouse gas (GHG) emissions. In this study, methane (CH₄) emissions and related soil properties were determined in multiple mangroves in Taiwan, including *Kandelia obovata* and *Avicennia marina* mangroves. *K. obovata* possess prop roots, whereas pneumatophores are found in *A. marina*. Our results showed that mangrove soils were significant sources of CH₄ emissions, which should be accounted for in mangrove carbon budgets. In particular, CH₄ emissions in the *A. marina* mangroves were approximately 50- to 100-fold those of the *K. obovata* mangroves and the adjoining mudflats. Multiple regression analyses indicated that the soil salinity and pH in *K. obovata* mangroves and the soil redox potential and organic content in the mudflats were the key factors affecting CH₄ emissions in the *A. marina* mangroves. Thus, compared with the assessed soil properties, the contribution of pneumatophores to the transportation of CH₄ from soil was more significant. In addition to soil properties, our results demonstrated that the root structure may also affect GHG emissions from mangroves.

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

1. Introduction

Anthropogenic activities, such as deforestation and fossil fuel combustion, have generated a great amount of carbon dioxide (CO₂) emissions, with accompanying greenhouse effects and global warming [1,2]. To alleviate climate change, it is essential to develop mitigation strategies to increase the carbon storage capacity and capture ability in natural ecosystems [3,4]. Vegetated coastal ecosystems (VCEs), including mangroves, seagrass meadows, and tidal marshes, are known as the major "blue carbon" sinks, and hold the potential for higher organic carbon (OC) sequestration than terrestrial forests [4,5].

Mangroves provide multiple ecosystem functions and services, such as coastal protection, water quality improvement, nutrient cycling, carbon sequestration, and fisheries [6–8]. Expressed as economic value, the mangrove payment of ecosystem services (PES, ~91,000 \$US dollars ha⁻¹) is much greater than that of seagrass meadows (~13,000 \$US dollars ha⁻¹) and salt marshes (~1500 \$US dollars ha⁻¹) [9]. Serrano et al. [10] reported that the soil carbon stock in 1-m-thick mangroves in Australia was approximately 251 Mg C ha⁻¹, which was 1.5~2.5 times greater than the levels in seagrass meadows (112 Mg C ha⁻¹) and salt marshes (168 Mg C ha⁻¹). In addition, Donato et al. [11] demonstrated carbon storage in mangrove soils to be approximately three to five times higher than that in upland forests in tropical zones. Thus, mangroves play an essential role in sequestering carbon and alleviating climate change.

Recently, mangroves were found to be not only carbon sinks, but also greenhouse gas (GHG) sources [4,12,13]. Frequent tidal inundation has been found to restrict the



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Copyright: © 2021 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). transportation of oxygen across the soil–air surface, creating anaerobic environments in mangrove soils [14]. Subsequently, the redox potential (ORP) of soils was reduced, and other oxidants were substituted as electron acceptors for microbial metabolism. Thus, anaerobic respiration generally occurs after aerobic respiration as follows: (1) denitrification; (2) manganese, iron, and sulfate reduction reactions; and (3) methanogenesis [15,16]. GHGs, including CO₂, N₂O, and CH₄, may be produced and emitted from soils through a series of microbial respiration processes.

To precisely quantify the carbon budgets and storage in mangrove ecosystems, GHG emissions should not be neglected [3,17–19]. Rosentreter et al. [12] demonstrated that carbon storage in carbon dioxide equivalents was reduced by 20% by CH_4 emissions, as the global warming potential of CH_4 is 28 times as great as that of CO_2 over a 100-year time scale. In addition, based on the global methane budget in 2017 [2], wetlands were the major sources of CH_4 in natural ecosystems, especially in subtropical and tropical zones. Thus, to establish carbon budgets accurately, CH_4 emissions from mangrove ecosystems should be considered for evaluation.

Both biotic (e.g., mangrove tree species) and abiotic (e.g., soil properties) factors play important roles in affecting GHG emissions. Soil properties such as water content, organic matter content, pH, salinity, ORP, and temperature can influence CH_4 emissions, as each parameter may regulate microbial processes [18,20–23]. He et al. [24] reported that the root structure of mangrove trees contributed in various ways to CH_4 emissions from soils. The effect of pneumatophores on CH_4 emissions remains uncertain. How biotic and abiotic factors influence CH_4 emissions must be determined and evaluated.

Mangroves are widely distributed along the western coast of Taiwan. Two dominant mangrove species, Kandelia obovata and Avicennia marina, are distributed on the north and south coasts, respectively. Each of these mangrove species has a unique root structureprop roots are observed in the *K. obovata* mangroves and pneumatophores occur in the A. marina mangroves. The pneumatophores of A. marina are known to contribute to CH_4 emissions [25,26]. However, compared with soil properties, the relationship between pneumatophores and CH₄ emissions remains unclear. Our previous study [13] showed that there was a seasonal variation of CH₄ emissions in mangroves, where CH₄ emissions were higher in warm seasons (spring and summer). The study by [13] also found that soil properties affected CH₄ emissions greatly in *K. obovata* mangroves, but none of soil properties significantly influenced CH₄ emissions in *A. marina* mangroves. In this study, we hypothesize that CH₄ emissions would increase with increasing the pneumatophore density. The objectives of this study were (1) to quantify CH_4 emissions from the soils of K. obovata mangroves (prop roots), A. marina mangroves (pneumatophores), and adjoining mudflats; (2) to characterize the effects of soil properties on CH₄ emissions in these three types of habitats; and (3) to determine the effects of pneumatophore density on CH_4 emissions in A. marina mangroves.

2. Materials and Methods

2.1. Site Description

Nine research sites (Figure 1) were established along the western coast of Taiwan, from north to south: A—Wazihwei (WZ); B—Zhuwei (ZW); C—Xinfeng (XF); D—Zhunan (ZN); E1—Fangyuan *Kandelia obovata* (FY-K); E2—Fangyuan *Avicennia marina* (FY-A); F—Budai (BD); G—Beimen (BM); H—Chiku (CK). The climate is dry and mild in winter and humid and hot in summer (Table 1). *K. obovata* mangroves dominated at Site A, B, C, and D. *A. marina* mangroves dominated at Site F, G, and H. At Site E, both species were codominant in the mangroves (E1 and E2). Compared with the *A. marina* mangroves, a higher density and tree height were observed in the *K. obovata* mangroves (Table 1). The tides at all of the mangroves were semidiurnal tides, and the tidal range was highest at Site E and decreased gradually to the north and south. The mean immersion times at the sites during flood periods ranged from 1.2–18.2 h/day. The soil texture for all of the mangroves was silt. The median grain size was the greatest at Site C (0.058 ± 0.017 mm) and the smallest at Site E1 (0.015 ± 0.001 mm).

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Site ID		Α	В	С	D	E1	E2	F	G	Н
Site Name		WZ	ZW	XF	ZN	FY-K	FY-A	BD	BM	СК
Latitude and longitude		25°10′ N, 121°25′ E	25°08′ N, 121°27′ E	24°54′ N, 120°58′ E	24°40′ N, 120°50′ E	23°55′ N, 120°18′ E		23°21′ N, 120°7′ E	23°17′ N, 120°6′ E	23°07′ N, 120°05′ E
Sampling time		2019: all (November)2020: winter (February), spring (May), and summer (July)		2019: spring (April), summer (July), and fall (October)2020: winter (February)		2019: fall (November)2020: winter (February), spring (May), and summer (July)		2019: spring (April), summer (July), and fall (October) 2020: winter (February)		2020: winter (February), spring (May), summer (August), and fall (November)
- Mean seasonal rainfall (mm) ^a -	December– February (winter)	105.7		52	29.7	47.2		4.2	3.5	37.7
	March–May (spring)	234		352	260.3	102		92.2	83.8	147.3
	June–August (summer)	158.3		232.5	267.5	112.5		369.7	419.7	260.3
	September– November (fall)	245.3		44.7	23	3		7.5	34.2	30
- Mean seasonal temperature (°C) ^a -	December– February (winter)	17.4		16.9	17.6	18.2		19.4	19.5	18.7
	March–May (spring)	24.0		21.1	21.9	23.3		23.7	23.7	23.9
	June–August (summer)	29.5		27.8	28.7	30.4		28.6	28.4	29.1
	September– November (fall)	24.0		23.3	24.2	25		25.2	25.1	25.1
Mean tidal range (cm) ^a		220		366	388	410		181	136	139
Mean immersion time at sampling sites during flood tides (hours/day)		8.5	6.9	4.8	1.2	7	7.2	18.2	14.4	7.4

Table 1. Climatic conditions, mangrove characteristics and soil texture at the mangrove sites: A—Wazihwei (WZ); B—Zhuwei (ZW); C—Xinfeng (XF); D—Zhunan (ZN); E1—Fangyuan *Kandelia obovata* (FY-K); E2—Fangyuan *Avicennia marina* (FY-A); F—Budai (BD); G—Beimen (BM); H—Chiku (CK).

Site ID	Α	В	С	D	E1	E2	F	G	Н
Major mangrove species	Kandelia obovata		Kandelia obovata	Kandelia obovata	Kandelia obovata	Avicennia marina	Avicennia marina	Avicennia marina	Avicennia marina
Presence of pneumatophores	No		No	No	No	Yes	Yes	Yes	Yes
Mangrove forest area (ha)	15.8	47.1	9.37	19.59	4.9	68.7	30.2	5.48	5.2
Mean tree height (m)	4.0	3.4	5.1	5.0	4.3	1.8	4.0	3.2	4.0
Mean tree density (trees m^{-2})	1.3	2.3	2.4	1.9	2.2	1.0	0.9	0.6	0.3
Mean diameter at breast height (DBH) (cm)	7.0	4.7	5.6	5.9	8.1	10.5	5.4	6.2	20.1
Soil texture	Silt	Silt	Silt	Silt	Silt	Silt	Silt	Silt	Silt
Median grain size (mm)	0.054 ± 0.003	0.028 ± 0.003	0.058 ± 0.017	0.023 ± 0.004	0.015 ± 0.001	0.035 ± 0.005	0.033 ± 0.004	0.037 ± 0.008	0.025 ± 0.003

Table 1. Cont.

Note: Table 1 was modified from Lin et al. [13]. ^a Data sources: Central Weather Bureau of Taiwan [27].



Figure 1. Location of the research sites: A—Wazihwei (WZ); B—Zhuwei (ZW); C—Xinfeng (XF); D—Zhunan (ZN); E1—Fangyuan *Kandelia obovata* (FY-K); E2—Fangyuan *Avicennia marina* (FY-A); F—Budai (BD); G—Beimen (BM); H—Chiku (CK) in Taiwan (map sources: QGIS 2.18.14).

2.2. Methane Emissions Measurements

The CH₄ emissions and soil properties were determined for a complete seasonal cycle during 2019–2020 (Table 1) within the two species of mangroves and adjoining mudflats (located in the open space outside of mangroves). Mudflats were available for the CH₄ measurements at Site C, D, E2, F, and G. The CH₄ emission measurements were adapted from Lin et al. [13]. Briefly, we used an ultraportable greenhouse gas analyzer (LGR915-0001, Los Gatos Research, San Jose, CA, USA) connected to an in situ closed-path chamber through a polyvinyl chloride (PVC) tube to determine the CH₄ emissions from the soils of the mangroves and mudflats. A semicircular transparent acrylic chamber attached to a stainless-steel ring (with a diameter of 30 cm and height of 15 cm) was placed to avoid crab holes and was inserted into a 10-cm depth of soil to create the air volume (10.6 L) over a 0.071 m² surface area. The CH₄ fluxes within the chamber were monitored by the gas analyzer and were documented by a data logger using a 20-s recording interval in 10-min sessions. The CH₄ emissions were determined by Equation (1).

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

where *F* is the CH₄ emission in terms of μ mol CH₄ m⁻² h⁻¹, *S* is the slope of linear regression line between CH₄ concentration (ppm) and logging time point (20 s), *V* is chamber volume (L), *R* is ideal gas constant = 0.082 (L atm K⁻¹ mol⁻¹), *T* is the absolute temperature (K), *A* is the bottom area of chamber (i.e., 0.071 m²), and 180 is time conversion constant = (1 h × (60 min/hour) × ((60 s/min)/20 s)). The CH₄ detection limit was 0.01 to 100 ppm.

The CH₄ emissions were measured from the soils of the mangroves and mudflats with three to five replications (five in most cases) during emersion periods (2 h before and after

the low tide) at each site in each season. The distance between each randomly selected soil sample was at least 5 m in order to eliminate any potential interactions between the soil samples resulting from the site disturbance.

Based on our previous research [13], significant CH₄ emissions were observed in spring and summer. To determine the effects of pneumatophore density on CH₄ emissions, we quantified CH₄ emissions under different densities of pneumatophores in A. marina mangroves at Sites E2 and G in spring or summer. The density of pneumatophores was classified into the following four levels: (1) 0-20, (2) 20-50, (3) 50-80, and (4) at least 80 pneumatophores within the chamber (0.071 m²; Figure 2). The measurements of the CH_4 emissions at each level were carried out in three replicates. To represent the density of pneumatophores, the number of pneumatophores was divided by the surface area (0.071 m^2) of the chamber.



(a) 0-20

(b) 20-50

(c) 50-80



Figure 2. Photographs of the pneumatophores of *A. marina* within the chambers (diameter = 30 cm): (a) 0–20, (b) 20–50, (c) 50–80, and (d) >80 pneumatophores (unit: number of pneumatophores in 0.071 m^2).

2.3. Soil Sample Analyses

The soil properties in the top 10-cm layer were evaluated after CH4 measurements with five and two replications in the mangroves and mudflats, respectively, at each site in each season. In the field, a portable pH meter (WD-35634-40, OAKTON Instruments, Vernon Hills, IL, USA) was applied to measure the soil pH, and a redox potential meter (ORP30, CLEAN L'eau, Taoyuan City, Taiwan) was used to determine the soil ORP and temperature. As the mangrove soils were wet and free of particles, the instrument manual [28] suggested that the soil pH could be measured in situ. The soil pH and ORP were measured by inserting the meters into the soil at a depth of 5 cm. The soil samples were then collected using stainless-steel cores (with a diameter of 7 cm and length of 80 cm), and syringes (with a diameter of 2.9 cm and length of 5 cm) were used to retrieve the top 10 cm of the soil core samples for two subsamples. One subsample was used for the soil bulk density, water, and organic matter content analysis [13,29], while the other was used for the salinity measurement. These subsamples were transferred into 50-mL centrifuge tubes, stored in a portable cooler, and then transported to the laboratory for further analysis. The subsamples were stored in a -20 °C freezer and were analyzed within two weeks at the laboratory. At the laboratory, the pore water was derived from the soil subsample with a syringe, and the salinity was then measured using a portable refractometer (Refractometer FG-201, Hangzhou Chincan Trading Co., Ltd., Hangzhou, Zhejiang Province, China).

2.4. Statistical Analyses

As the Shapiro–Wilk test results demonstrated that the CH₄ emissions and soil property datasets were nonnormally distributed (p-value < 0.05), the nonparametric Kruskal– Wallis test was utilized to determine the differences in CH₄ emissions and soil properties among the studied sites and habitat types. When the results showed a significant difference (*p*-value <0.05), Dunn's test was implemented as a post hoc analysis to determine which sites, habitat types, or levels differed. Stepwise multiple regression analysis

was used to evaluate the effects of the soil properties on the CH₄ emissions across the studied sites in the mangrove ecosystems for both species. R software (Version 3.6.1, https://www.r-project.org/) [30] and SigmaPlot 14.0 (Systat Software, San Jose, CA, USA) were applied for the statistical analyses, and p < 0.05 was considered statistically significant in this study.

3. Results

3.1. CH₄ Emissions and Soil Properties

In the mangroves and adjoining mudflats, CH₄ emissions were significantly different among the studied sites (Figure 3, and Tables 2 and 3). The mean CH₄ fluxes from the mangrove soils ranged from 0.8 to 94.1 µmol-CH₄ m⁻² h⁻¹. Higher CH₄ emissions were observed in the soils of the *Avicennia marina* mangroves (Figure 3 and Table 2). Compared with the *Kandelia obovata* mangroves (-1.7 to 16.6 µmol-CH₄ m⁻² h⁻¹) and mudflats (-0.7 to 7.6 µmol-CH₄ m⁻² h⁻¹), CH₄ emissions were significantly greater in the *A. marina* mangroves (2.1 to 765.9 µmol-CH₄ m⁻² h⁻¹; Figure 4). Soil properties other than the soil temperature varied distinctly among the mangroves (Table 2). However, only the soil bulk density, organic matter, and water content differed distinctly among the mudflats.



Figure 3. CH₄ emissions from the mangrove soils: A—Wazihwei (WZ); B—Zhuwei (ZW); C—Xinfeng (XF); D—Zhunan (ZN); E1—Fangyuan *Kandelia obovata* (FY-K); E2—Fangyuan *Avicennia marina* (FY-A); F—Budai (BD); G—Beimen (BM); H—Chiku (CK). The same letters over different bars suggest no significant differences among sites according to the Kruskal–Wallis test and Dunn's test.



Figure 4. CH₄ emissions from the *A. marina* and *K. obovata* mangroves and the adjoining mudflats soils. Different letters represent significant differences among habitats with the Kruskal–Wallis test and Dunn's test.

Mangrove Site	CH ₄ Emission	Temperature	ORP	лU	Salinity	Bulk Density	Water Content	Organic Matter
	$(\mu mol-CH_4 m^{-2} h^{-1})$	(°C)	(mV)	рп	(psu)	(g cm ⁻³)	(%)	(%)
А	2.4 ± 0.3 ab	25.4 ± 1.2	$10.7\pm9.9~\rm{bc}$	$6.7\pm0.1~\mathrm{d}$	$2.6\pm0.2~\mathrm{ab}$	$1.1\pm0.0~{ m de}$	$32.4\pm0.8~\mathrm{ab}$	3.6 ± 0.1 a
В	1.3 ± 0.3 a	26.2 ± 1.3	$-82.4\pm14.6~\mathrm{ab}$	$6.6\pm0.1~{ m cd}$	$4.0\pm0.1~\mathrm{c}$	$0.9\pm0.0~{ m bc}$	$42.8\pm0.6~bcd$	$5.4\pm0.1~{ m bcd}$
С	$4.2\pm1.0~\mathrm{ab}$	23.0 ± 0.9	$166.5 \pm 13.1 \text{ d}$	$6.3\pm0.0~\mathrm{ab}$	1.1 ± 0.1 a	$1.0\pm0.0~{ m cd}$	$30.7\pm0.6~\mathrm{a}$	5.5 ± 0.2 bc
D	$0.8\pm0.2~\mathrm{a}$	22.7 ± 1.0	$109.3\pm16.0~\text{cd}$	$6.7\pm0.1~\mathrm{d}$	$3.0\pm0.1~{ m bc}$	$1.2\pm0.0~\mathrm{e}$	$28.0\pm0.7~\mathrm{a}$	$4.1\pm0.1~\mathrm{ab}$
E1	1.2 ± 0.3 a	24.9 ± 1.4	$131.0\pm8.0~cd$	$6.7\pm0.1~\mathrm{d}$	$4.5\pm0.5bc$	$0.8\pm0.0~\mathrm{ab}$	$43.5\pm1.0~\text{cd}$	$11.8\pm0.5~\mathrm{de}$
E2	$14.2\pm4.9~\mathrm{bc}$	24.9 ± 1.1	$-48.5\pm16.3\mathrm{b}$	$6.9\pm0.1~\mathrm{d}$	3.1 ± 0.2 bc	$1.2\pm0.0~{ m de}$	$27.3\pm0.8~\mathrm{a}$	3.2 ± 0.1 a
F	$29.6\pm5.7~\mathrm{c}$	26.0 ± 0.7	-283.1 ± 13.1 a	$6.6\pm0.0~\mathrm{abc}$	$4.6\pm0.4~\mathrm{c}$	$0.6\pm0.0~\mathrm{ab}$	$53.1\pm1.8~\mathrm{d}$	$7.3\pm0.3~\mathrm{cde}$
G	$63.5\pm26.0~\mathrm{c}$	25.5 ± 0.8	$-74.7\pm25.2\mathrm{b}$	$6.7\pm0.1~\mathrm{d}$	$4.3\pm0.3~\mathrm{c}$	$1.0\pm0.0~{ m cd}$	$34.5\pm1.1~\mathrm{abc}$	3.3 ± 0.1 a
Н	$94.1\pm41.9~\mathrm{c}$	24.3 ± 0.8	$8.9\pm31.6~\mathrm{bc}$	5.9 ± 0.2 a	$11.5\pm0.5~\mathrm{d}$	0.4 ± 0.0 a	$62.3\pm1.1~\mathrm{d}$	$15.2\pm0.5~\mathrm{e}$

Table 2. CH₄ emissions and soil characteristics (mean ± standard error) of the mangroves at A—Wazihwei (WZ); B—Zhuwei (ZW); C—Xinfeng (XF); D—Zhunan (ZN); E1—Fangyuan *Kandelia obovata* (FY-K); E2—Fangyuan *Avicennia marina* (FY-A); F—Budai (BD); G—Beimen (BM); H—Chiku (CK). Different letters represent significant site differences according to the Kruskal–Wallis test and Dunn's test at the significance level. ORP—redox potential.

Table 3. CH₄ emissions and soil characteristics (mean ± standard error) of the mudflats at C—Xinfeng (XF); D—Zhunan (ZN); E—Fangyuan (FY); F—Budai (BD); G—Beimen (BM). Different letters represent significant site differences according to the Kruskal–Wallis test and Dunn's test at the significance level. ORP—redox potential.

Mudflat Site	CH ₄ Emission	Temperature	ORP	" U	Salinity	Bulk Density	Water Content	Organic Matter
	$(\mu mol-CH_4 m^{-2} h^{-1})$	(°C)	(mV)	рп	(psu)	(g cm ⁻³)	(%)	(%)
С	1.1 ± 0.3 a	24.1 ± 1.3	17.3 ± 28.4	7.0 ± 0.1	2.7 ± 0.2	$1.0\pm0.0~\mathrm{a}$	$35.2\pm0.8~\text{b}$	3.6 ± 0.2 d
D	$3.4\pm0.5b$	23.0 ± 1.5	-93.8 ± 24.3	7.0 ± 0.1	3.1 ± 0.4	$1.1\pm0.0~\mathrm{ab}$	$34.4\pm0.9~\text{b}$	$3.5\pm0.3~\text{cd}$
E2	$0.5\pm0.1~\mathrm{a}$	26.3 ± 1.3	-58.7 ± 15.3	7.2 ± 0.0	3.1 ± 0.1	$1.2\pm0.0~\mathrm{b}$	$32.4\pm0.9~\text{b}$	$1.9\pm0.1~{ m bc}$
F	$0.5\pm0.2~\mathrm{a}$	28.5 ± 1.5	-17.7 ± 25.3	7.1 ± 0.1	2.8 ± 0.5	$1.4\pm0.0~{\rm c}$	$20.0\pm1.0~\text{a}$	$1.0\pm0.1~\mathrm{a}$
G	$1.8\pm0.5~\mathrm{ab}$	26.3 ± 1.2	-137.7 ± 56.0	7.0 ± 0.1	3.6 ± 0.8	$1.3\pm0.0~{ m c}$	$24.6\pm1.6~\mathrm{a}$	$1.6\pm0.1~\mathrm{ab}$

3.2. Effects of Soil Properties and Pneumatophores on Methane Emissions in Mangrove Ecosystems

The results of the multiple regressions demonstrated that the soil pH and salinity exerted significant negative effects on CH₄ emissions (CH₄ flux = $-3.19 \times \text{pH} - 0.50 \times \text{salinity} + 24.69$; *p*-value < 0.01; $R^2 = 0.43$) in the *K. obovata* mangroves. There was an exponential relation between salinity and CH₄ flux, but a linear relationship between pH and CH₄ flux (Figure 5). However, nonsignificant correlations were found between the soil properties and CH₄ emissions in the *A. marina* mangroves. In the mudflats, the CH₄ emissions were negatively related to the soil ORP, but positively related to the organic matter content (CH₄ flux = $-0.01 \times \text{ORP} + 0.65 \times \text{organic matter content} - 0.45$, *p*-value < 0.01, $R^2 = 0.57$) (Figure 6). The results demonstrate that the CH₄ flux ranged from 4.8 to 161.3 µmol-CH₄ m⁻² h⁻¹ with 57 to 1814 pneumatophores m⁻², and greater numbers of pneumatophores produced higher CH₄ emissions in the *A. marina* mangroves (Figure 7).



Figure 5. The relationship between soil salinity, pH, and CH₄ flux in the two mangrove species: (**a**,**c**) *K*. *obovata* (n = 20) and (**b**,**d**) *A*. *marina* (n = 16).



Figure 6. The relationships between the soil (a) ORP and (b) organic matter with CH_4 flux in the mudflats (n = 20).



Figure 7. The relationships between the pneumatophore density and CH₄ flux for the *A. marina* mangroves: E2—Fangyuan (FY); G—Beimen (BM).

4. Discussion

Large variations in CH₄ emissions were observed at the nine mangroves (-1.7 to 765.9 µmol-CH₄ m⁻² h⁻¹; Figure 4) as a result of spatial and habitat differences. However, compared with other studies, CH₄ emissions in the studied mangrove ecosystems were still within the range of previous estimates (*Kandelia obovata*, 0.8 to 72.5 µmol-CH₄ m⁻² h⁻¹, Chen et al. [31]; *Avicennia marina*, 0.2 to 1087.5 µmol-CH₄ m⁻² h⁻¹, Allen et al. [21]; mudflat, 5.6 to 87.5 µmol-CH₄ m⁻² h⁻¹, Xiang et al. [32]). As a result, the studied mangrove soils were significant sources of CH₄ emissions, which should be accounted for in the carbon budgets of mangrove ecosystems.

The current study found that CH₄ emissions in the *A. marina* mangroves were approximately 50- to 100-fold those of the *K. obovata* mangroves and adjoining mudflats (Figure 4). The CH₄ emissions in vegetated soils were generally higher than those in unvegetated soils (mudflats), as more labile organic compounds originating from plants were provided for methanogenic communities [32–34]. However, this observation was not necessarily recapitulated in the *K. obovata* mangroves in this study. This suggests that differences in mangrove species and root structure may lead to various patterns of GHG emissions.

As GHGs were generated mainly as a result of microbial activities that were greatly affected by soil characteristics, GHG emissions were expected to be regulated by the soil properties [31]. Indeed, the multiple regression analyses indicated that the soil salinity and pH in the K. obovata mangroves, and the soil redox potential and organic matter content in the mudflats were the main soil properties influencing CH₄ emissions. Previous findings have reported salinity to be inversely related to CH₄ emissions in mangroves, with relationships illustrated by either linear [35] or logarithmic regressions [18]. Sulfate is among the most abundant ions in seawater. In high salinity environments, the higher availability of sulfate ions enhanced the activities of sulfate-reducing bacteria, which might inhibit methanogenic bacteria obtaining organic substrates; thus, less CH₄ emissions were produced [19,36–39]. Methanogens have been found to be sensitive to soil pH, and demonstrated better growth in the pH range of 6 to 8 [40,41]. It appears that the soil pH in the *K. obovata* mangroves was favorable for methanogenesis. The soil organic matter content exhibited a significantly positive correlation with CH₄ emissions, as high levels of organic matter provide additional carbon sources for methanogens, generating a greater quantity of CH₄ [14,23,42]. In addition, methanogenic bacteria are highly active in lower redox potential conditions [26,30,43]. As a result, higher CH₄ emissions were observed from anaerobic soils with a high organic matter in the mudflats.

Compared with the *K. obovata* mangroves and mudflats, however, the multiple regression results demonstrated that none of the soil properties explained the large proportion of variation in CH₄ emissions from the *A. marina* mangroves. Similar results were also observed by Lin et al. [13]. As the pneumatophores provided gas exchange conduits

between soils and the atmosphere, CH_4 was likely emitted through the pneumatophores from the deep soil [19,25,26]. Our results showed that the density of pneumatophores in the *A. marina* mangroves explained approximately 48% of the variation in CH_4 emissions (Figure 7). Livesley et al. [26] reported that 24% of the variation in CH_4 flux resulted from pneumatophores. Thus, the significance of pneumatophores in transporting CH_4 from the soil to the atmosphere in mangroves cannot be neglected. In summary, the soil properties and pneumatophores were the primary factors affecting CH_4 emissions in *K. obovata* and *A. marina* mangroves, respectively.

To further evaluate the effects of pneumatophore density on CH_4 emissions in different climatic regions in *A. marina* mangroves, our results were compared with other data derived from previous research [25,26,36,44]. The linear regression lines of CH_4 emissions on the pneumatophore density presented in previous studies were transformed into the same units (µmol- CH_4 m⁻² h⁻¹) and were redrawn in this study (Figure 8). Even though the sampling times were different between the studies (Figure 8), the results indicate that the slopes of the regression lines were always steeper in tropical regions than in subtropical or temperate regions, despite the high variation in slopes within tropical regions. As higher temperatures facilitate methanogen activity in soils [18,21], these comparisons suggest that with the same density of pneumatophores, more CH_4 is emitted from *A. marina* mangroves in tropical regions. In addition, CH_4 emissions were positively correlated with pneumatophore density in *A. marina* mangroves across all climate regions.



Figure 8. Comparisons of linear regression lines of CH_4 emissions on pneumatophore density in *A. marina* mangroves in different climatic regions. The numbers in color frames represent the latitudes of the studied sites. Tropical 1: Purvaja et al. [36]; tropical 3: Krithika et al. [25]; subtropical: Kreuzwieser et al. [44]; temperate: Livesley et al. [26]. Sampling time: tropical 1: pre-monsoon, monsoon, post-monsoon, and summer; tropical 3: dry and wet; subtropical: spring and winter; temperate: spring, summer, fall, and winter.

5. Conclusions

In this study, CH₄ emissions and soil characteristics were determined in multiple mangroves of Taiwan, including in the *Kandelia obovata* (subtropical zone) and *Avicennia marina* (tropical zone) mangroves. Our results showed that CH₄ emissions in the *A. marina* mangroves were significantly greater than those in the *K. obovata* mangroves and the adjoining mudflats. The multiple regression analyses indicated that the soil salinity and pH in the *K. obovata* mangroves, and the soil redox potential and organic matter content in the mudflats, were the main soil properties affecting CH₄ emissions across the studied mangroves. However, this study also showed that pneumatophore density alone in *A. marina* mangroves explained approximately 48% of the variation in CH_4 emissions. Thus, compared with the assessed soil properties, the contribution of pneumatophores to the transportation of CH_4 from the soils was more significant. In addition to the soil properties, our results demonstrated that the root structure may also affect GHG emissions in mangroves.

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