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Tidal influence on carbon dioxide and methane fluxes from tree stems and soils in mangrove forests

Zhao-Jun Yong[1], Wei-Jen Lin[1], Chiao-Wen Lin[2], Hsing-Juh Lin[1*]
[1]Department of Life Sciences and Innovation and Development Center of Sustainable Agriculture, National Chung Hsing University, Taichung 40227, Taiwan
[2]Department of Marine Environment and Engineering and The Center for Water Resources Studies, National Sun Yat-sen University, Kaohsiung 80424, Taiwan

Correspondence to: Hsing-Juh Lin (hjlin@dragon.nchu.edu.tw)

Abstract. Mangroves are critical blue carbon ecosystems. Measurements of methane (CH_4) emissions from mangrove tree stems have the potential to reduce the uncertainty in the capacity of carbon sequestration. This study is the first to simultaneously measure the CH_4 fluxes from both stems and soils throughout tidal cycles. We quantified carbon dioxide (CO_2) and CH_4 fluxes from mangrove tree stems of *Avicennia marina* and *Kandelia obovata* during tidal cycles, which have distinct root structures. The mangrove tree stems served as both net CO_2 and CH_4 sources. Compared to those of the soils, the mangrove tree stems exhibited markedly lower CH_4 fluxes, but no difference in CO_2 fluxes. *A. marina* (with pneumatophores) exhibited significantly higher CO_2 and CH_4 fluxes than *K. obovata*. The stems of *A. marina* exhibited an increasing trend in the CO_2 flux from low to high tides, while the CH_4 flux showed high temporal variability, with this species functioning as a sink before tidal inundation and becoming a source during low tides after ebbing. In contrast, the stems of *K. obovata* showed no consistent pattern of the CO_2 or CH_4 flux. Based on our findings, sampling only during low tides might overestimate the stem CO_2 and CH_4 fluxes on a diurnal scale. The stem CO_2 and CH_4 fluxes of *A. marina* could be 55% and 194% less when considering tidal influence, as opposed to ignoring tidal influence. This study highlights species distinctness in the greenhouse gas (GHG) fluxes and the necessity of considering tidal influence when quantifying GHG fluxes from mangrove tree stems.

1 Introduction

Global methane (CH_4) emissions have reached a record high level (Saunois et al., 2020). Currently, there are two primary methods utilized for assessing global CH_4 emissions: the bottom-up method and the top-down method. The bottom-up method relies on compiling data from greenhouse gas (GHG) inventories and biogeochemical models to infer the sources of emissions. On the other hand, the top-down method involves measuring atmospheric CH_4 concentrations and utilizing transport models to infer the sources of emissions in order to estimate and assess CH_4 emissions on a global scale. CH_4 emissions estimated by the bottom-up method are significantly higher than those estimated by the top-down method, indicating a high degree of uncertainty and suggesting that some sources may be overlooked or not well understood (Jackson et al., 2020). CH_4 generated in wetlands can be released into the atmosphere not only through diffusion, bubbles, and transport mediated by herbaceous plants but also through the stems of woody plants (Gauci et al., 2010; Terazawa et al., 2007). Pangala et al. (2017) demonstrated that the difference between the top-down and bottom-up estimates of CH_4 emissions could be accounted for by the upscaled CH_4 flux from tree stems, emphasizing the necessity of considering this pathway in carbon budgets (Carmichael et al., 2014). Furthermore, forest wetlands account for approximately 60% of the global wetland area, highlighting the potential contribution of woody stems to the global GHG emissions (Barba et al., 2019a; Covey and Megonigal, 2019). While carbon dioxide (CO_2) exchange at the stem–atmosphere interface has been examined (Teskey et al., 2008), little is known regarding the sources and mechanisms of CH_4 emissions originating from tree stems relative to those originating from other pathways. CH_4 emitted by tree stems may originate from microorganisms or cryptogams within the stem bark (Jeffrey et al., 2021; Lenhart et al., 2015) or from the soil, where it is produced and enters the roots before being transported in liquid or gaseous form through xylem aerenchyma tissue (Kutschera et al., 2016; Vroom et al., 2022).

GHG emissions from tree stems exhibit temporal and spatial variations with different influencing mechanisms in various studies: i) the tree stem GHG flux tends to be higher during the growing season and lower during the dormant season, but there may also be no significant differences among seasons (Barba et al., 2019b; Köhn et al., 2021; Pangala et al., 2015; Pitz et al., 2018; Wang et al., 2016; Zhang et al., 2022); ii) significant variations in the GHG fluxes from tree stems have been observed at different heights above ground level, with a decreasing trend along the tree trunk height (Moldaschl et al., 2021; Pangala et al., 2013, 2014, 2015; Sjögersten et al., 2020), although some studies have not reported this phenomenon (Machacova et al., 2021; Wang et al., 2016); iii) the tree stem GHG emissions may be regulated by various environmental factors such as temperature, moisture, and redox potential (Barba et al., 2019b; Gao et al., 2021; Jeffrey et al., 2019; Pitz et al., 2018; Schindler et al., 2020, 2021; Sjögersten et al., 2020; Terazawa et al., 2015); iv) tree physiological factors such as lenticel density, wood density, and water content may also influence the GHG fluxes originating from tree stems (Pangala et al., 2013, 2014, 2015; Wang et al., 2016; Zhang et al., 2022).

However, most related studies have focused on freshwater wetlands and upland forests, while relatively limited research has focused on mangrove forests. Jeffrey et al. (2019) reported that dead mangrove trees may contribute approximately 26% to the CH_4 emissions in mangrove ecosystems. He et al. (2019) reported inconsistent results, revealing a relatively small contribution from tree stems. The contribution of tree stems to the total GHG flux in ecosystems is generally less than that in soil (Gao et al., 2021; He et al., 2019; Jeffrey et al., 2019) but still has the potential to exceed 50% (Zhang et al., 2022). Additionally, the GHG fluxes from mangrove tree stems vary among tree species (Zhang et al., 2022) and may even differ within a single tree species (Gao et al., 2021), highlighting the uncertainty in the GHG emissions from mangrove tree stems and emphasizing the need for further investigation.

Mangroves are primarily distributed in tropical and subtropical coastal regions and are regarded as critical ecosystems with a high capacity for sequestering blue carbon (Li et al., 2018; Duarte de Paula Costa and Macreadie, 2022). The anaerobic conditions resulting from tidal inundation, along with the abundant organic matter, turn mangrove soil into a substantial source of CH_4 emissions (Lin et al., 2020). This, in turn, impacts their role in mitigating global warming. Moreover, prior studies have demonstrated the influence of tides on the emission of GHGs in coastal wetlands (Lin et al., 2023). In both seagrass meadows and tidal marshes, the CH_4 flux tends to peak before the rising tide when tidal water reaches the sampling site (Bahlmann et al., 2015; Capooci and Vargas, 2022). The sudden release of CH_4 can occur through physical force under the influence of tidal movement (Li et al., 2021), resulting in the advective exchange of groundwater or soil pore water with the overlying surface water (Billerbeck et al., 2006; Rosentreter et al., 2018). CH_4 emissions during tidal inundation may be higher if tidal water contains high concentrations of dissolved CH_4 and nitrous oxide (N_2O), which can increase the emissions of CH_4 and N_2O through diffusion due to the concentration gradient (Sturm et al., 2017; Tong et al., 2013). Yamamoto et al. (2009) reported a positive correlation between the water table and GHG fluxes in the flooded littoral zone with vegetation, suggesting that the water pressure rather than gas diffusion primarily affects the emissions of CO_2 and CH_4 across the water–atmosphere interface by ejecting gases from pore spaces. This finding is contrary to previous results in which lower CH_4 fluxes were observed during high tides, which may be caused by the higher water pressure limiting CH_4 diffusion in soil pore spaces filled with water and plant-mediated transport (Tong et al., 2010; Tong et al., 2013). Additionally, CH_4 may be oxidized during diffusion in water (Tong et al., 2013). Furthermore, if the dissolved oxygen concentration, sulfate concentration, and salinity are high in tidewater, this may inhibit CH_4 production and/or promote CH_4 oxidation (Huang et al., 2019), resulting in lower CH_4 emissions during high tides. The variation in the CH_4 flux across the water–atmosphere interface during tidal inundation could be driven by current or wind-induced turbulence (Sturm et al., 2017). CH_4 emissions even exhibited different trends during spring and neap tides (Huang et al., 2019; Tong et al., 2013). However, to our knowledge, there is only one study on the GHG fluxes from mangrove tree stems (Epron et al., 2023).

This study aimed to quantify the CO_2 and CH_4 emissions from the tree stems of *K. obovata* and *A. mariana*, which are the dominant mangrove species with distinct root structures distributed on the northern and southern coasts of Taiwan, respectively. We investigated the temporal variations in the stem GHG fluxes during tidal cycles and assessed the influence of tides on the upscaled flux. We also simultaneously measured the GHG emissions from mangrove soil, even during tidal inundation, to compare the temporal dynamics of GHG fluxes between the tree stems and soil. We hypothesized that the GHG fluxes from mangrove tree stems and soil exhibit synchronized temporal and species variation during the tidal cycle and that the tidal cycle may exert a significant impact on GHG emissions on a larger scale.

2 Materials and Methods

2.1 Site description

This study focused on the mangroves at four sites along the western coast of Taiwan (Fig. 1). The dominant mangrove species in Wazihwei (K-WZW; 25°10′N, 121°25′E) and Xinfeng (K-XF; 24°55′N, 120°58′E) is *Kandelia obovata*, while *Avicennia marina* is the dominant species in Fangyuan (A-FY; 23°56′N, 120°19′E) and Beimen (A-BM; 23°17′N, 120°6′E). K-WZW and K-XF are situated in northern Taiwan, a subtropical region, with average annual precipitation values of 2023 and 1537 mm, respectively. A-FY and A-BM are located in southern Taiwan, a tropical region, with average annual precipitation values of 1162 and 1603 mm, respectively. The tides were semidiurnal in all sites. The soil texture at all sites is silt, with an average grain size of 0.046 mm. During the summer season (the study period), the average air temperature was 28.4 °C for *K. obovata* and 29.4 °C for *A. marina* (Lin et al., 2023). The sampling campaign was conducted during the summer season, from 1 June 2022 to 29 July 2022, with each site sampled for 3 days throughout the campaign (Table 1). This period was chosen mainly because there is a higher GHG flux in summer than during the other seasons, as indicated by preliminary studies conducted at the same site (Lin et al., 2020).

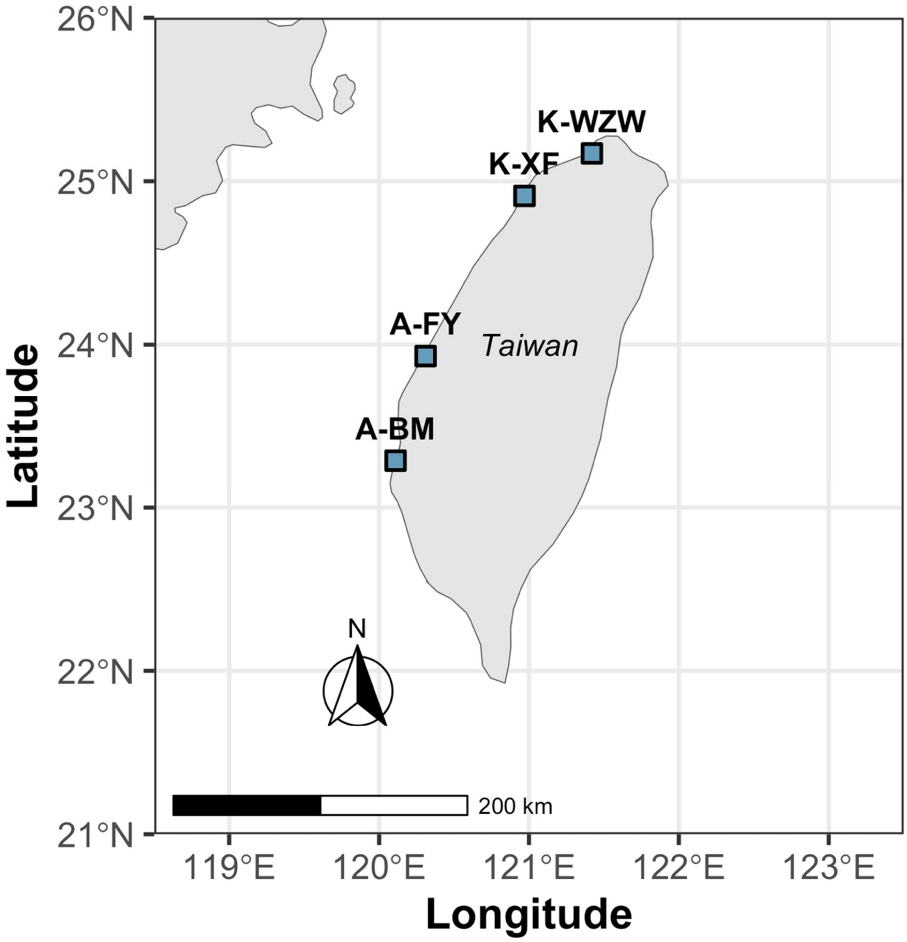

Figure 1. Sample sites along the western coast of Taiwan. K-WZW: Wazihwei; K-XF: Xinfeng; A-FY: Fangyuan; A-BM: Beimen. The dominant mangrove species in K-WZW and K-XF is *Kandelia obovata*, while *Avicennia marina* is the dominant species in A-FY and A-BM (map sources: Natural Earth).

2.2 Flux measurement

At each sampling site, a mangrove tree was selected for the tree stem CO_2 and CH_4 flux measurements at approximately 110 cm above the ground. Due to the differences in the stem morphology, two distinct stem chambers—a semirigid chamber and a cylindrical chamber—were used in this study to measure the GHG emissions of *K. obovata* and *A. marina*, respectively (Fig. S1).

The semirigid chamber was modified from Siegenthaler et al. (2016) and was constructed from transparent recycled polyethylene terephthalate (rPET) bottles. A plastic sheet measuring 14 cm in length and 11 cm in width was cut from a bottle, and 2 cm wide and 1.5 cm thick chloroprene (CR) foam tape was attached around the edges and center of the plastic sheet, with two holes drilled and fitted with adapters for connecting the tubing. The chamber was installed on the tree stem with a strap prior to the measurement and subsequently removed. The cylindrical chamber was constructed from a 0.2 L white polypropylene (PP) bottle, a 16 cm^2 square was cut from the lid, and two small holes were drilled at the bottom of the bottle; these holes were fitted with adapters to connect the tubing. The lid was fixed to the stem and sealed with silicone prior to the measurement. After the measurement, the chamber was removed, but the lid remained on the trunk (Fig. S1).

Two soil surfaces within 2 m of the sampled tree were selected for soil and water–atmosphere interface CH_4 and CO_2 flux measurements during the tidal cycle using a static chamber (Lee et al., 2011) and the floating chamber method, respectively. The soil chamber comprised a semicircular transparent polymethyl methacrylate (PMMA) cover (diameter of 30 cm) and a stainless steel ring (height of 16 cm and diameter of 30 cm) with an adapter on the cover for connecting the tubing. The ring was pressed into the soil before placing the cover over it, and a long-tailed clip was used to secure and cover the steel ring tightly to achieve an airtight seal (Fig. S1).

In this study, a portable gas analyzer (LI-7810, LI-COR Bioscience, NE, USA) was used to simultaneously measure CO_2 and CH_4 fluxes. The chamber was connected to the analyzer through tubing, and the gas inside the chamber was drawn into the analyzer with a pump, with each measurement lasting approximately five and seven minutes for the stem and soil, respectively. During the tidal cycle, tree stems and soil GHG flux were measured consistently, with approximately 3-minute intervals, to allow the GHG concentration within the chamber to stabilize. The water level adjacent to the sampled trees was measured simultaneously at the beginning of the flux measurement. Sampling was mainly conducted during daylight hours. Soil GHG flux data were mainly derived from Lin et al. (unpublished). The GHG flux was calculated based on the slope obtained from the linear regression of GHG concentration changes over time, a more detailed description of the GHG flux calculation process can be found in Lin et al. (2020) and Lin et al. (2021).

2.3 Statistical analysis

All the statistical analyses were performed in R 4.2.2 software. All the data were assessed for a normal distribution using the Shapiro–Wilk test. The nonparametric Wilcoxon rank sum test was used to evaluate the differences in the CO_2 and CH_4 fluxes between the species. The relationships between the CO_2 and CH_4 fluxes during rising and falling tides were analyzed via a simple linear regression model. The results were considered statistically significant when the p value was lower than 0.05.

3 Results

During the study period, the mangrove tree stems served as both net CO_2 and CH_4 sources, but there was distinct species variation (Fig. 2). The CO_2 fluxes from mangrove tree stems during tidal cycles averaged 1.13 ± 0.17 mmol m^{-2} h^{-1} and 14.22 ± 8.21 mmol m^{-2} h^{-1} for *K. obovata* and *A. marina*, respectively (Fig. 2a). The CH_4 fluxes from the tree stems averaged 0.04 ± 0.05 μmol m^{-2} h^{-1} and 0.27 ± 1.05 μmol m^{-2} h^{-1} for *K. obovata* and *A. marina*, respectively (Fig. 2b). Compared to those of the tree stems, the soils of *K. obovata* and *A. marina* mangroves exhibited markedly higher CH_4 fluxes, averaging 7.59 ± 8.74 μmol m^{-2} h^{-1} and 42.23 ± 62.95 μmol m^{-2} h^{-1}, respectively. The CO_2 flux from the soil averaged 1.73 ± 2.31 mmol m^{-2} h^{-1} in *K. obovata* mangroves and 3.42 ± 3.36 mmol m^{-2} h^{-1} in *A. marina* mangroves but did not differ significantly from that from the tree stems.

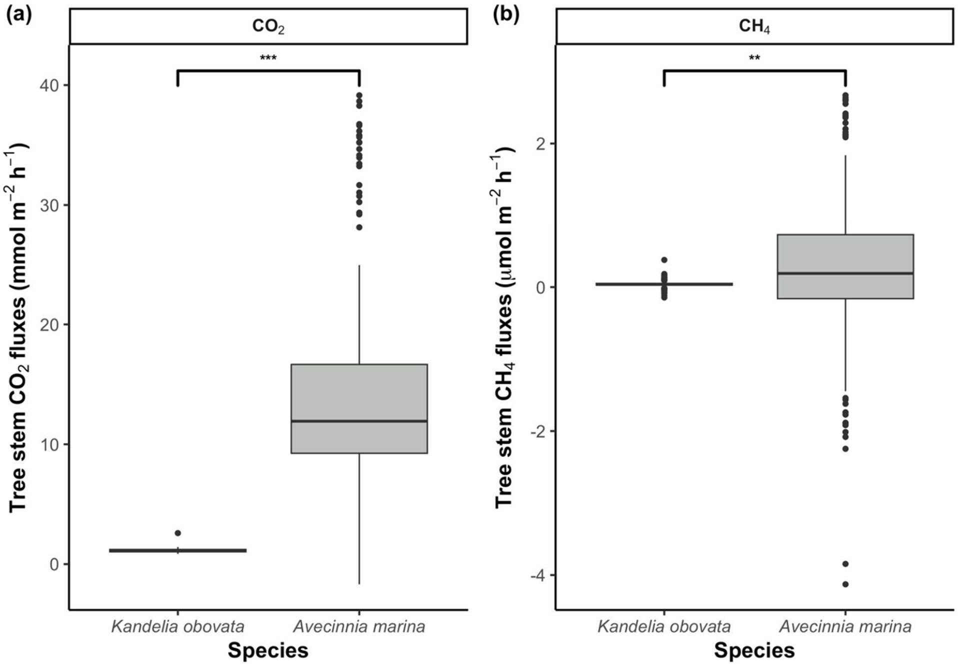

Figure 2. Difference in tree stem (a) CO_2 and (b) CH_4 fluxes between *Kandelia obovata* and *Avicennia marina*. Each data point represents a flux measurement during tidal cycles (*K. obovata*: 170 replicates; *A. marina*: 227 replicates). The label (*) indicates a

statistically significant difference between the species, as determined by the nonparametric Wilcoxon rank sum test (*: *p*<0.05; **: *p*<0.01; *: *p*<0.001).**

The mean inundation time and largest tidal height at each sampling site are provided in Table 1. During tidal cycles, the CO_2 fluxes from mangrove tree stems exhibited different trends depending on the species (Fig. 3). The emissions remained relatively constant during tidal cycles, ranging from 1.01 to 1.43 mmol m^{-2} h^{-1} and from 0.85 to 2.59 mmol m^{-2} h^{-1} at the K-WZW and K-XF sites, respectively (Fig. 3a). However, a sharp emission peak (2.59 mmol m^{-2} h^{-1}) was observed at the K-XF site on Day 2 when the tide was falling, which was threefold higher than the lowest flux (0.85 mmol m^{-2} h^{-1}) measured on the same day (Fig. 3a). Similar to that of *K. obovata*, the CO_2 flux of *A. marina* generally showed an increasing trend from low to high tides, ranging from 4.54 to 14.00 mmol m^{-2} h^{-1} and from -1.68 ± 39.15 mmol m^{-2} h^{-1} at the A-FY and A-BM sites, respectively (Fig. 3a). However, this trend was observed at the A-FY site only on Day 1, when there was a distinct temporal trend in the increase in the CO_2 flux relative to that at the A-BM site. Specifically, the former started to increase before the flood current entered and stabilized after the high tide, reaching a peak flux (10.36 mmol m^{-2} h^{-1}) at the end of the measurement. Conversely, the latter showed no significant change during rising tides, followed by a steep rise toward high tides and a slight decrease during falling tides; however, the CO_2 flux still remained higher than that during preflood tide, ranging from -1.68 to 33.24 mmol m^{-2} h^{-1} during rising tides and from 8.74 to 39.15 mmol m^{-2} h^{-1} during falling tides (Fig. 3a).

Table 1. Comparison of the upscaling methods with and without considering tidal influences on the CO_2 and CH_4 fluxes of mangroves.

		K-WZW	K-XF	A-FY	A-BM
Sampling date		2022-07-14/2022-07-16	2022-06-15/2022-06-17	2022-06-01/2022-06-02, 2022-06-18	2022-07-27/2022-07-29
Sampling time		08:00/15:00	08:30/15:00	10:00/16:30	04:30/15:00
Inundation time (h)		6.69	6.69	5.19	15.33
Highest tidal height (cm)		60.0	73.5	62.0	83.0
Stem CO_2 flux (mmol m^{-2} d^{-1})	Tide	29.00	25.43	250.39	323.52
	None	29.35	25.13	254.80	570.42
	Difference (%)	1.20	1.19	1.75	55.24
Stem CH_4 flux (µmol m^{-2} d^{-1})	Tide	1.10	0.89	-4.31	0.40
	None	1.13	0.91	-4.11	24.47
	Difference (%)	2.69	2.22	4.75	193.57
Stem lenticel density (lenticels cm^{-2})		0.08	0.05	1.83	2.96

Tide: The average fluxes during low and high tides were added after multiplication with the corresponding time length. None: The average fluxes during a tidal cycle were multiplied by 24 hours. The sampling date and time are in ISO 8601 format.

The CO_2 flux pattern observed during tidal cycles differed between the tree stems and soils. Generally, the soil CO_2 flux peaked before and after high tide at all sites, either during rising or falling tides, with the flood current just entering or leaving the sampling site (Fig. 3b).

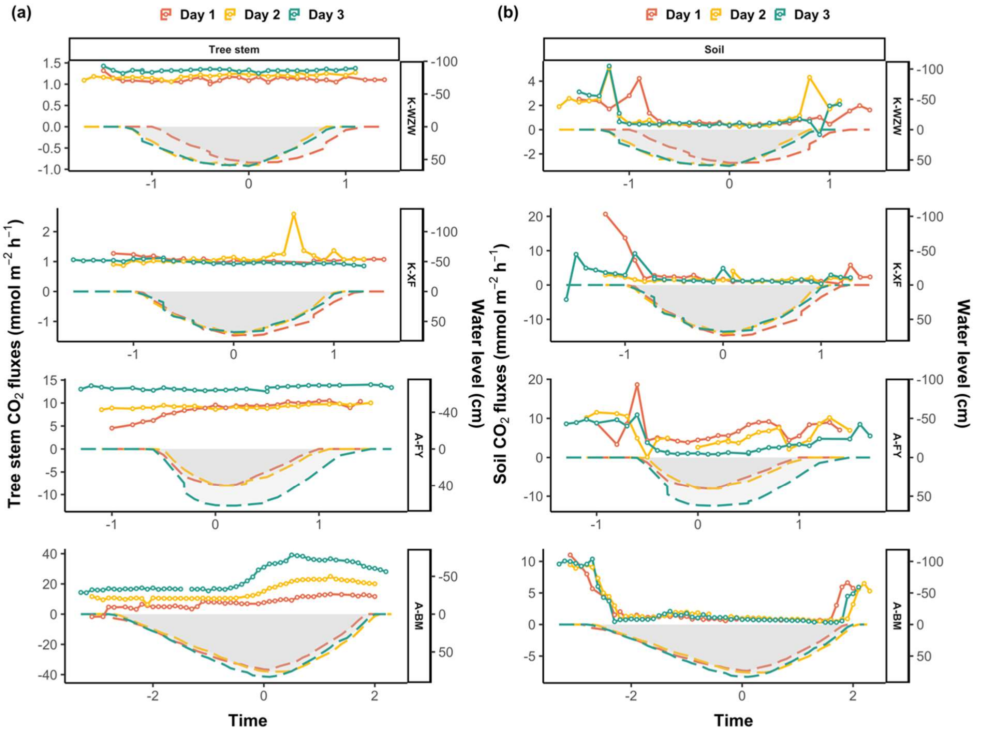

Figure 3. Variations in (a) the tree stem CO_2 fluxes and (b) soil CO_2 fluxes during tidal cycles. The time was standardized based on the time of the highest water level during the high-tide period (set as 0), then adjusted by decrementing the time by 0.1 for every 10-minute interval prior to the peak and incrementing by 0.1 for every 10-minute interval after the peak. The average values of the flux (soild lines) and water level (dashed lines) were calculated when falling within each standardized time interval. The shaded area denotes the water level at the sampled tree. On Days 1, 2, and 3, the plant data were arranged chronologically according to the sampling date.

Similar to those in the CO_2 flux, the CH_4 fluxes of *K. obovata* and *A. marina* exhibited distinct temporal trends during tidal cycles (Fig. 4). In the *K. obovata* mangrove forest, there was significant variation in the stem CH_4 flux during tidal cycles, ranging from -0.14 to 0.38 μmol m^{-2} h^{-1} (0.05 ± 0.06 μmol m^{-2} h^{-1}) and from -0.05 to 0.18 μmol m^{-2} h^{-1} (0.04 ± 0.04 μmol m^{-2} h^{-1}) at K-WZW and K-XF, respectively, while no consistent pattern was detected on each sampling campaign (Fig. 4a). The stem CH_4 flux of *A. marina* increased from low to high tides, ranging from -1.92 to 0.55 μmol m^{-2} h^{-1} (-0.17 ± 0.52 μmol m^{-2} h^{-1}) and from -4.13 to 2.67 μmol m^{-2} h^{-1} (0.48 ± 1.17 μmol m^{-2} h^{-1}) at A-FY and A-BM, respectively. Specifically, the tree stems of *A. marina* functioned as CH_4 sinks before tidal inundation (-0.58 ± 1.14 μmol m^{-2} h^{-1}), but the CH_4 flux gradually increased thereafter, eventually becoming a CH_4 source during low tides (0.60 ± 0.74 μmol m^{-2} h^{-1}). However, this pattern was not observed across all sampling campaigns (Fig. 4a).

For both mangrove species, the soil CH_4 flux during high tides (21.65 ± 45.29 μmol m^{-2} h^{-1}) was lower than that during low tides (47.70 ± 63.27 μmol m^{-2} h^{-1}) (Fig. 4b). Furthermore, there was a peak in the soil CH_4 flux during both tidal increase and decrease on all three sampling days, similar to the soil CO_2 flux (Fig. 3b; Fig. 4b).

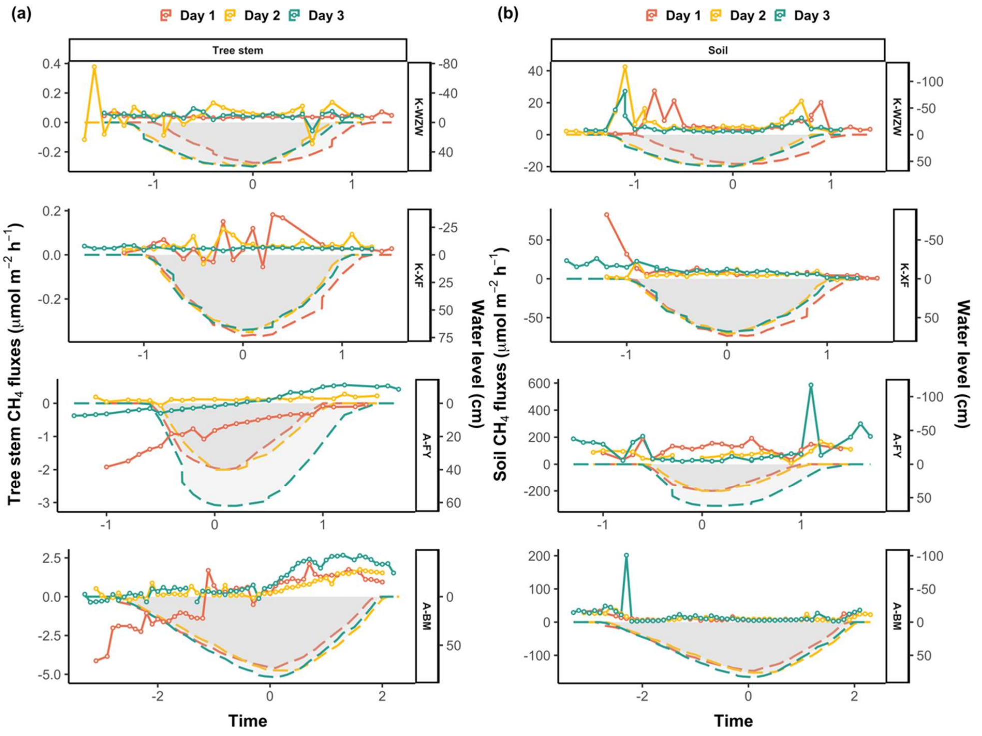

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Figure 4. Variations in (a) the tree stem CH_4 fluxes and (b) soil CH_4 fluxes during the tidal cycle. The time was standardized based on the time of the highest water level during the high-tide period (set as 0), then adjusted by decrementing the time by 0.1 for every 10-minute interval prior to the peak and incrementing by 0.1 for every 10-minute interval after the peak. The average values of the flux (solid lines) and water level (dashed lines) were calculated when falling within each standardized time interval. The shaded area denotes the water level at the sampled tree. On Days 1, 2, and 3, the plant data were chronologically arranged according to the sampling date.

During tidal cycles, the CO_2 flux from the mangrove tree stems was positively correlated with the CH_4 flux during both rising and falling tides. However, a significant relationship was detected only for *A. marina* (Fig. 5a; $p<0.001$). The CO_2 and CH_4 fluxes from both the stems and soils were simultaneously measured, and a negative correlation between the stem and soil fluxes was observed across the two mangrove species. However, a significant relationship was detected only for *A. marina* during falling tides (Fig. 5b, 5c; $p<0.001$).

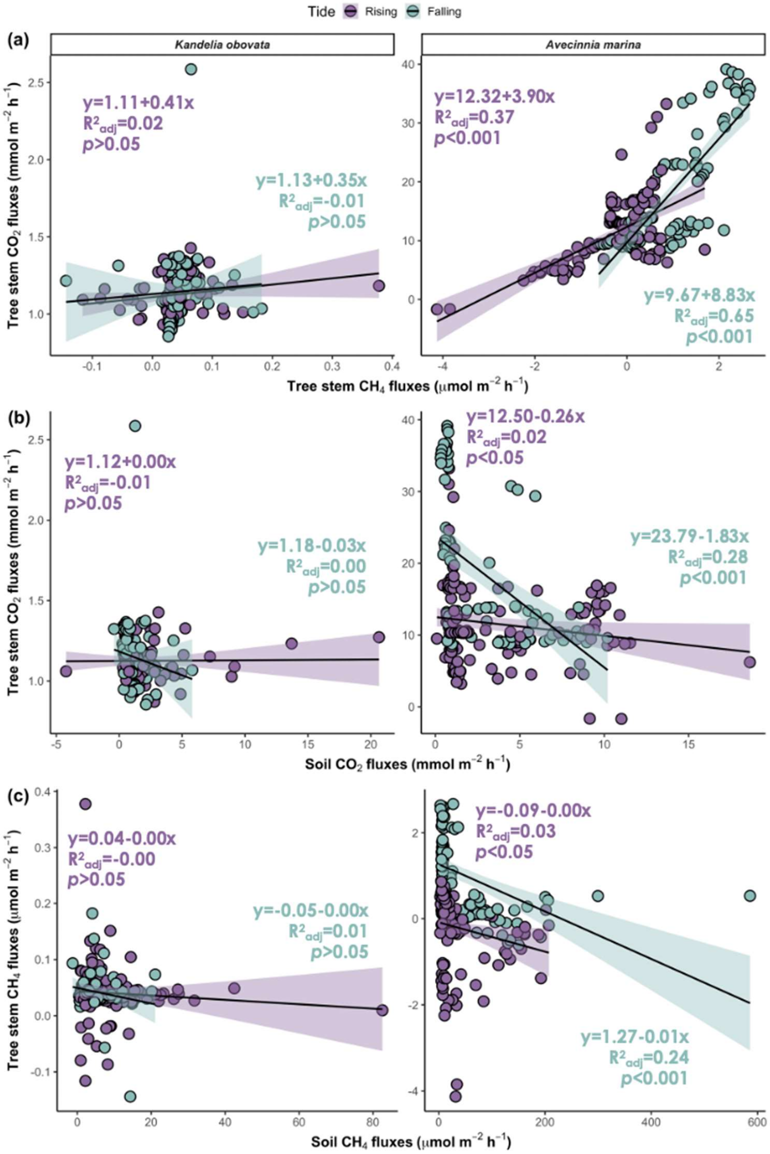

Figure 5. Relationships between (a) the tree stem CO_2 and CH_4 fluxes, (b) tree stem CO_2 fluxes and soil CO_2 fluxes, and (c) tree stem CH_4 fluxes and soil CH_4 fluxes. The shaded areas denote the 95% confidence intervals of the regression lines.

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Since the tides at the sampling sites exhibited a primarily semidiurnal pattern, the average inundation time per day was calculated from the average time of high tides (when the water level was higher than 0 cm) on each sampling event multiplied by 2. The A-BM site exhibited the longest inundation time of 15.33 hours, while the inundation time during the sampling campaign was 6.69 hours at the K-WZW and K-XF sites and 5.19 hours at the A-FY site. The largest tidal height (determined by the distance between the soil and water surface during the high tide) was 60 cm at K-WZW, 74 cm at K-XF, 62 cm at A-FY, and 83 cm at A-BM. Different upscaling methods were applied to determine the tidal influence on the diurnal variation in the fluxes, where "tide" denotes the sum of the average fluxes during low and high tides after multiplication with the corresponding time length, and "none" denotes the average flux during the low tide multiplied by 24 hours. The GHG fluxes exhibited notable differences when tidal influence was considered (Table 1). Based on our findings, sampling only during low tides could overestimate the stem CO_2 and CH_4 fluxes on a diurnal scale. The differences in the stem CO_2 and CH_4 fluxes of *K. obovata* between the two upscaling methods were smaller than those in the fluxes of *A. marina*, ranging from 1.19 to 2.69% (Table 1). However, the stem CO_2 flux of *A. marina* varied by 55% when considering tidal influence, as opposed to ignoring tidal influence (Table 1). Tidal influence also imposed a significant effect on the stem CH_4 flux of *A. marina*, resulting in the highest variation of 194% relative to not accounting for tidal influence (Table 1).

4 Discussion

This study revealed distinct species variations in the CO_2 and CH_4 fluxes originating from tree stems and soils. Specifically, *A. marina* exhibited significantly higher CO_2 and CH_4 fluxes than *K. obovata*, suggesting that *A. marina* may play a more prominent role in GHG dynamics than *K. obovata*. The temporal dynamics during tidal cycles also differed between the two mangrove species. Regarding *K. obovata*, the stem CO_2 and CH_4 fluxes lacked a consistent pattern among each sampling campaign. In contrast, *A. marina* exhibited an increasing trend in the CO_2 flux from low to high tide throughout the tidal cycle, whereas the CH_4 flux exhibited high temporal variability, functioning as a sink before tidal inundation and becoming a source during low tide. Therefore, our results indicate that the different mangrove species, in this case, *K. obovata* and *A. marina*, may provide varying capacities for CO_2 and CH_4 exchange with the atmosphere through the tree stems during tidal cycles.

In terms of biological factors, *A. marina* contains pneumatophores, while *K. obovata* does not. Pneumatophores may facilitate the transport of oxygen to the rhizosphere and increase the oxidation–reduction potential, thereby inhibiting the methanogenesis process (Dušek et al., 2021). However, they can also serve as pathways for deep soil layer CH_4 emissions, facilitating CH_4 transport (He et al., 2019; Lin et al., 2021). In this study, pneumatophores were not intentionally avoided during the measurement. Therefore, the presence of pneumatophores may contribute to the increased soil CH_4 flux in the *A. marina* mangroves.

The GHG emissions of the stem, whether originating from the soil or the stem itself, require radial diffusion through the bark or lenticel to reach the atmosphere (Barba et al., 2019a). Radial diffusion is primarily influenced by biological factors such as wood density, wood moisture content, and lenticel density (Covey and Megonigal, 2019). A higher lenticel density, in particular, creates more pathways for GHG emissions, resulting in increased emissions (Zhang et al., 2022). Based on visual observation *in situ*, we found that *A. marina* exhibited a significantly higher lenticel density than *K. obovata* (Table 1). Therefore, it is speculated that the higher lenticel density of *A. marina* facilitates the emission of GHGs from the stem, resulting in a higher stem GHG flux.

Previous studies on GHG emissions originating from mangrove tree stems were mostly conducted during low tide and under daylight conditions. Gao et al. (2021) showed that the stems of *Kandelia obovata* can both absorb and release CH_4, with average fluxes of -5.69 and 1.84 μmol m^{-2} h^{-1}, respectively. Zhang et al. (2022) reported higher CH_4 emissions from *K. obovata* stems (7.04 μmol m^{-2} h^{-1}), which dominated the ecosystem CH_4 flux of mangroves without pneumatophores. This contradicts the findings of this study, where the CH_4 emissions of *K. obovata* stems contributed less than the soil emissions. In the case of *A. marina*, the stem CH_4 fluxes were 1.56 μmol m^{-2} h^{-1} (Jeffrey et al., 2019) and 2.79 μmol m^{-2} h^{-1} (Zhang et al., 2022) at mangrove sites located in Australia and China, respectively. Regarding other mangrove species, *Kandelia candel* exhibited a stem CH_4 flux of -1.81 μmol m^{-2} h^{-1}, while *Sonneratia apetala*, *Laguncularia racemosa*, and *Bruguiera gymnorhiza-Bruguiera sexangula*, which have the same specialized root structure as that of *A. marina*, provided stem CH_4 fluxes of 2.62, 0.87, and -0.49 μmol m^{-2} h^{-1}, respectively (He et al., 2019). Epron et al. (2023) measured the CH_4 flux of the stems of *Bruguiera gymnorrhiza* throughout a 24-hour cycle, ranging from 0.02 to 2.63 μmol m^{-2} h^{-1}. In this study, the CH_4 fluxes of the stems of *A. marina* and *K. obovata* ranged from -0.14 to 0.38 μmol m^{-2} h^{-1} and from -4.13 to 2.67 μmol m^{-2} h^{-1}, respectively. Herein, *K. obovata* and *A. marina* served as net CH_4 sources rather than sinks, while both species exhibited lower CH_4 emissions than those obtained in previous studies focused on the same species. *A. marina* also exhibited higher variability and a higher capacity for CH_4 sequestration.

The tree stem CO_2 and CH_4 fluxes exhibited similar temporal patterns during tidal cycles. A significant positive relationship was also found between these fluxes, indicating that CO_2 and CH_4 emitted by mangrove tree stems may originate from the same source or be influenced by the same mechanism during tidal cycles. According to previous studies, CO_2 emissions primarily occur through root respiration and stem respiration, as well as internal plant metabolism and transport from soils (Teskey et al., 2008). In contrast, CH_4 may be emitted or absorbed by methanogens and methanotrophs present in tree bark or heartwood (Feng et al., 2022; Jeffrey et al., 2021). CH_4 emitted by tree stems may also originate from the soil, where the CH_4 produced in the soil enters the root system, enters the tree aerenchyma tissues or xylem, and is subsequently directly released into the atmosphere through the lenticel or tree stems (Barba et al., 2019a; Covey and Megonigal, 2019). Therefore, the emission and absorption of CO_2 and CH_4 by the tree stem may originate from the tree stem itself or from the soil. In this study, the transformation of tree stems from CH_4 sinks to CH_4 sources was observed in *A. marina* mangroves. This observation indicates that CH_4 emitted by tree stems may be affected by different sources during different periods of tidal cycles.

The transport mechanism of GHGs in the stem is similar to that of herbaceous plants, occurring mainly by diffusion or evaporation, either jointly or individually. The diffusion direction mainly depends on the CH_4 concentration gradient. For example, if the gas concentration in the rhizosphere is high, GHGs can enter the plant root system either in gaseous or liquid form, thus entering the aerenchyma or xylem tissue (Vroom et al., 2022). Aerenchyma is a specialized tissue found in many mangrove tree species (Evans, 2004). It comprises air-filled spaces that create gas transport pathways within the plant. Aerenchyma facilitates gas movement, including CO_2 and CH_4, within stems. Within the aerenchyma, CO_2 and CH_4 can diffuse or passively flow along concentration gradients. This transport pathway allows gases to move vertically within the plant, from the roots through the stem and ultimately into the atmosphere. Aerenchyma tissue is particularly important for CH_4 transport because CH_4 is produced in oxygen-limited soils or in the rhizosphere by methanogens. The aerenchyma provides a direct pathway for CH_4 to move upward through the stems to be emitted into the atmosphere (Yáñez-Espinosa and Angeles, 2022). CO_2 and CH_4 can also dissolve during dilution and be transported within the xylem via sap flux (Takahashi et al., 2022).

This study reveals the transition of mangrove tree stems from CH_4 sinks to CH_4 sources within a tidal cycle, which has not been observed in other studies, even with a high measurement frequency of upland tree stems at one-hour intervals (Barba et al., 2019b). We speculate that the tree stem of *A. marina* may absorb CH_4 through the presence of methanotrophs during low tide (Jeffrey et al., 2021). During inundation, the diffusion of CH_4 produced in the deep soil layer may be restricted by the water pressure (Tong et al., 2013) since the pore spaces are filled with water. Tong et al. (2010) also reported a significantly lower CH_4 flux during inundation than during low tide. Therefore, we hypothesize that CH_4 produced in the soil during inundation periods may be primarily emitted into the atmosphere through tree stems (Vroom et al., 2022; Yáñez-Espinosa and Angeles, 2022) rather than being emitted across the water–atmosphere interface via diffusion or ebullition (Li et al., 2021), resulting in the observed gradual increase in the CH_4 flux throughout the tidal cycle. This hypothesis was also supported by the negative relationship between the soil and stem CH_4 fluxes during rising and falling tides observed in this study. However, the CH_4 flux of the tree stems of *Bruguiera gymnorrhiza* peaked after the tide receded (Epron et al., 2023), which does not support this hypothesis. It is critical to note that the specific mechanisms driving the observed peaks may vary depending on factors such as mangrove species, environmental conditions, tidal dynamics, and site-specific characteristics. Further research is necessary to fully comprehend the underlying mechanisms.

To our knowledge, this study is the first to simultaneously measure the CH_4 fluxes of both stems and soils throughout a tidal cycle, even during tidal inundation. When quantifying the GHG emissions of mangrove tree stems, the discrete and continuous methods are two common measurement approaches. Discrete measurements involve sampling at specific time points with a lower temporal resolution but are practical and cost effective. Continuous measurements provide real-time monitoring with a high temporal resolution, accurately capturing short-term fluctuations and peak emissions but requiring specialized equipment and technical expertise. When considering tidal influence through continuous measurements, the GHGs emitted by mangrove tree stems were significantly lower, with differences of up to 60% and 194% for the stem CO_2 and CH_4 fluxes, respectively. In tidal salt marshes, the CH_4 flux, accounting for tides, was also lower (Huang et al., 2019). When quantifying the GHG emissions of mangrove tree stems, discrete measurements are commonly used due to sampling difficulty at night and high tide. Although discrete measurements can still provide reliable estimates of the average emission rate over a specific period, they are useful only for broader-scale quantification and carbon and CH_4 budgeting models. This study highlights the need for continuous measurements of the GHG fluxes in coastal ecosystems, which can provide a more detailed understanding of emission patterns, aid in overall emission quantification, help individuals identify key drivers and mechanisms, reduce the uncertainty in GHG emissions, and facilitate the assessment of the impacts of specific events or environmental variables (Capooci and Vargas, 2022). However, when comparing practical, feasible, and cost-effective discrete measurements, continuous measurements require specialized equipment, technical expertise and intensive labor. It should also be noted that considerable differences were mainly observed at the A-BM site, with the longest inundation and highest water table.

5 Conclusion

This study reveals distinct species variations in the CO_2 and CH_4 fluxes of the tree stems of *A. marina* and *K. obovata*. The results demonstrate that *A. marina* exhibited significantly higher emissions of both CO_2 and CH_4 than *K. obovata*, indicating its greater potential contribution to the assessment of the carbon budget. The temporal variation during tidal cycles also differed, with *K. obovata* lacking a consistent pattern, and the CH_4 emissions of *A. marina* stems suggesting a transition from a sink to a source, indicating the influence of different sources and mechanisms. When considering tidal influence, the stem CH_4 flux could vary up to 194% for *A. marina*. This study highlights the need to consider tidal influence when quantifying the GHG fluxes of mangrove tree stems and the potential limitations of discrete measurements relative to continuous measurements. However, further research is needed to fully understand the underlying mechanism driving the observed flux variation and to improve our understanding and reduce the uncertainty in GHG dynamics in mangrove ecosystems.

Data availability. The original contributions presented in the study are included in the article. We encourage prospective data users to contact us before embarking on any analysis.

Author contributions. Zhao-Jun Yong: Methodology, Investigation, Visualization, Writing - Original Draft. Wei-Jen Lin: Methodology, Investigation, Visualization, Chiao-Wen Lin: Methodology, Investigation, Visualization. Hsing-Juh Lin: Conceptualization, Supervision, Writing – Review & Editing, Funding acquisition.

Competing interests. None of the authors declare any conflict of interest.

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