



Review

Dynamics of Methane in Mangrove Forest: Will It Worsen with Decreasing Mangrove Forests?

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Abstract: Mangrove forests sequester a significant amount of organic matter in their sediment and are recognized as an important carbon storage source (i.e., blue carbon, including in seagrass ecosystems and other coastal wetlands). The methane-producing archaea in anaerobic sediments releases methane, a greenhouse gas species. The contribution to total greenhouse gas emissions from mangrove ecosystems remains controversial. However, the intensity CH₄ emissions from anaerobic mangrove sediment is known to be sensitive to environmental changes, and the sediment is exposed to oxygen by methanotrophic (CH₄-oxidizing) bacteria as well as to anthropogenic impacts and climate change in mangrove forests. This review discusses the major factors decreasing the effect of mangroves on CH₄ emissions from sediment, the significance of ecosystem protection regarding forest biomass and the hydrosphere/soil environment, and how to evaluate emission status geospatially. An innovative “digital-twin” system overcoming the difficulty of field observation is required for suggesting sustainable mitigation in mangrove ecosystems, such as a locally/regionally/globally heterogeneous environment with various random factors.

Keywords: geospatial; greenhouse gas; carbon storage; CH₄; microbial activities



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1. Introduction

The carbon (C) sequestered in the biomass and deep sediment of vegetated coastal ecosystems, including mangroves, seagrass beds, and tidal marshes, has been called “blue carbon” [1,2]. Although vegetated coastal habitats cover a relatively small area (<2%) of the coastal ocean, they have C burial rates that are 40 times higher than tropical rainforests and account for more than half of the C burial in marine sediment [3].

Although the global area of vegetated ecosystems is one to two orders of magnitude smaller than that of terrestrial forests, the contribution of vegetated coastal habitats per unit area to long-term C sequestration is much greater, which is in part because of their efficiency in trapping suspended matter and associated organic C during tidal inundation [1]. Among vegetated ecosystems, mangroves have been well highlighted as among the major sources of organic matter in tropical areas because they occupy a large part of the tropical coastal area [4]. Additionally, organic C production is more rapid in these areas than for other estuarine and marine primary producers [3,5].

Mangrove forests have gained attention because of their high C productivity [6,7] and because they are among the most C-rich ecosystems in the world [8,9]. The total net primary production of mangroves is approximately 200 Tg C year⁻¹ [10,11], but most of this C is lost or recycled via CO₂ flux to the atmosphere (34.1 Tg C year⁻¹, ~20%) or is exported as particulate organic C, dissolved organic C, and dissolved inorganic C to the ocean (117.9 Tg C year⁻¹; ~60%) [11,12]. Of the remaining C, burial accounts for 18.4 to

34.4 Tg C year⁻¹ [1,9,10,13,14], and this blue C is considered to represent a significant long-term storage of atmospheric CO₂ [13,15]. The global C sequestration rate in mangrove wetlands is 174 g C m⁻² year⁻¹, on average, corresponding to about 10% to 15% of global coastal ocean C [9]. Organic-rich soils dominate in mangrove C storage, accounting for 49% to 98% of C stocks in mangrove wetlands [8,16].

Global mangroves are mainly distributed along tropical and subtropical coastlines, covering 137,760 km². The world's largest mangrove areas are in low latitudinal regions, such as Indonesia (22.6% of the global total), Australia (7.1%), and Brazil (7.0%) [17]. The world's best developed mangrove forests can be found in the Sundarbans, the Mekong Delta, the Amazon, Madagascar, and Southeast Asia [17]. Furthermore, Indonesia has the highest mangrove species diversity (48 species [15]) and exceptionally high C stocks in mangrove sediment [15]. Because the economic/population growth in those area is also substantial, the loss of mangrove forest due to anthropogenic impacts is substantial globally [15,18,19]. Loss rates vary greatly between countries, ranging from 1% to 20% of the total mangrove forest area, so predicting global mangrove forest changes in the future is difficult [20]. Loss of mangroves by clearing, conversion to industrial estates/aquaculture, and changes in drainage patterns lead to striking changes in soil chemistry and usually result in rapid emission rates of greenhouse gases [21–23].

The rapid loss of vegetated coastal ecosystems due to land-use changes has occurred for centuries and has accelerated in recent decades [2]. Duke et al. [24] predicted a mangrove loss rate of 1% to 3% per year. Recent anthropogenic activities in mangrove forests have led to the loss of habitats, including shrimp cultures (percentage of total anthropogenic impact (PAI): 38%), increased forest use (PAI: 26%), the loss of fish cultures (PAI: 14%), the diversion of freshwater (PAI: 11%), and land reclamation (PAI: 5%) as well as issues due to herbicides, agriculture, salt ponds, etc. [18], the conversion to open water due to accelerated sea-level rise and subsidence as well as natural disasters such as tsunamis [1,18,23–29]. Particularly, sea-level rise caused by global warming is suggested to be the biggest threat to mangroves [13,19,30]. Estimates of cumulative loss over the last 50 to 100 years range from 25% to 50% of the total global area for each ecosystem type [1]. This decline continues today, with estimated losses of 0.5% to 3% annually, depending on ecosystem type, amounting to ~8000 km² lost each year [2,18,20,29,31–33]. At current conversion rates, 30% to 40% of tidal marshes and seagrasses [2] and nearly 100% of mangroves [24] could be lost in the next 100 years.

Inundated natural wetland soils preserving C as organic matter are prone to releasing a certain amount of methane (CH₄) into the atmosphere. The emission rate is sensitive to a few environmental condition changes [34–36]. As a greenhouse gas, methane is 34 times stronger than CO₂ in terms of mass (i.e., methane's global warming potential is 34 times stronger than CO₂ based on mass basis) [37]. The gas species has become the second most important greenhouse gas in the atmosphere, contributing approximately 20% to global warming since the pre-industrial era [38]. The risk of further methane emission is due to mangrove sediment exposed to the above-mentioned anthropogenic impacts by stimulating related methanogens (i.e., CH₄-producing microorganisms) and/or by inhibiting methanotroph (i.e., CH₄-oxidizing microorganisms that contribute to lower the emission from the ecosystem) activity [39–41].

This review discusses the major factors decreasing the effect of mangroves on CH₄ emission from sediment, the significance of the ecosystem protection regarding forest biomass and the hydrosphere/soil environment, and how to evaluate the geospatially emission status.

2. Methane Flux from Mangrove Forests

2.1. Significance of Methane Emission from Mangrove Forests

The magnitude of CH₄ flux in mangrove forests and its relative contribution to global warming compared to CO₂ flux remains controversial. The global scale practice of the mangrove C budget has shown that CH₄ emissions from soil are 2 Tg C year⁻¹ [9]. Consid-

ering its global warming potential, the contribution of CH₄ emissions is comparable to the above-mentioned rate of C burial (18–34 Tg C year⁻¹) and C emission by soil respiration (34 Tg C year⁻¹) [1,9,10,13,14]. Recent studies have reported a significant amount of CH₄ flux from mangrove sediment [42–49] and have claimed that the contribution of CH₄ flux to global warming was non-negligible in estuarine mangrove forests, which could account for 18% to 22% of blue C burial rates [13] and 9% to 33% of plant CO₂ sequestration [50]. However, observed CH₄ flux from mangrove soils is mostly negligible compared to CO₂ emissions from sediment but is highly variable [38–41,51–58], particularly for non-polluted mangrove sediment [21,49,59–62]. To confirm this observation, the authors compared incubation experiments with mangrove sediment collected from the Vietnamese Mekong delta and the Indian Sundarbans forest [39]. CH₄ production was equivalent to only 0.05 to 0.27% of the CO₂ production under aerobic incubation or 0.05 to 0.22% under anaerobic incubation conditions, even when considering the potential difference caused by ($n = 30$ in each incubation experiments).

2.2. Factors Associated with Methane Emission

2.2.1. Soil Conditions

Low CH₄ production and emission in mangrove sediment compared to in interior wetland soils is mainly due to the high presence of sulphate in mangrove sediment, which allows sulphate-reducing bacteria to outcompete CH₄-producing archaea (i.e., methanogens) [40,55–57]. However, soil salinity and sulphate concentration show a low negative relationship with methane-producing activities, which suggests that both forms of methanogenesis are not completely inhibited by sulphate reducers with increasing sulphate concentrations [55]. A significant increase in CH₄ production activity caused by the dilution of seawater was also reported [39]. Therefore, mangrove sediment CH₄ production activity is highly and non-linearly sensitive to its specific soil pH/electrical conductivity by being affected by different freshwater intrusion intensities. Despite few studies on the impact of freshwater intrusion on CH₄ emission, it is still important to evaluate because rice paddies/agricultural fields are often found adjacent to protected mangrove zones (Figure 1). Regardless of a significant correlation between salinity/sulphate concentration in sediment and CH₄ emissions [39,55,63] CH₄ production activity can be significantly increased by the dilution of seawater concentration [39].



Figure 1. Reforestation zone in Sundarbans mangrove area in India (a), protected mangrove forest adjacent to rice paddies (b), and vegetable-growing field adjacent to mangrove forests (c) in Soc Trang, Vietnam.

Another reason for decreased CH₄ production is that compared to herbaceous organic matter, woody organic matter derived from mangrove trees is relatively recalcitrant to methanogens using it as a substrate [58]. Additionally, mangrove ecosystems are inundated by irregular periodic tides affected by the tidally mediated exchange of porewater between sediment and surface water via the ebb and flow of tides [10,59,60]. The tidally mediated exchange of porewater between sediment and surface water occurs via the ebb and flow

of tides (i.e., tidal pumping [64–67]). Tidal pumping is a potential source of solutes to mangrove water and causes ebullition, but the process has only recently been quantified and directly linked to the export of C and nutrients [67,68]. In addition to the spatio-temporal heterogeneity caused by irregular tidal pumping, CH₄ flux is spatio-temporally heterogeneous and is highly variable because of the heterogenic spatial distribution of aerial mangrove tree roots [69] and burrows created by crabs/goby fish. Such activity enhances hydraulic connectivity and increases the surface area of the sediment–water interface [70] where the exchange of the by-products of subterranean respiration can occur during tidal inundation [71–76]. Owing to the difficulty of observing CH₄ flux precisely, CH₄ data for mangrove forests are limited compared to data observing interior wetlands and underestimate the global emission [13,60].

2.2.2. Methanogenic and Methanotrophic Communities

Although CH₄ flux micrometeorological observation data are limited [76], recent studies on the community structures of methanogens and methanotrophs have revealed the biological processes common to interior wetlands and as unique characteristics in coastal wetlands. Previous studies on CH₄ metabolism have indicated that CH₄ emission in natural ecosystems is largely driven by microorganisms, especially methanogens and methanotrophs [34,77–80]. Highly diverse methanogenic and methanotrophic communities can promote CH₄ production and oxidation [81,82]. However, different types of methanogens and methanotrophs have preferable growing conditions, which further affect CH₄ emissions in natural ecosystems [77,83,84]. Methanogens include hydrogenotrophic, acetoclastic, and methylotrophic methanogens [84,85]. Methanotrophs exist under both aerobic and anaerobic conditions. Aerobic methanotrophs are phylogenetically divided into two main groups: type I (*Gammaproteobacteria*, e.g., *Methylococcaceae*) and type II (*Alphaproteobacteria*, e.g., *Methylocystaceae*) [86–89], nitrate- or nitrite-dependent [90,91] and metal-dependent [92] CH₄ oxidizers, respectively. Type I methanotrophs tend to be dominant in natural environments with sufficient nutrients and substrates (i.e., relatively high O₂ concentration, low CH₄ concentration) [39,58,93], whereas type II methanotrophs tend to be abundant in resource-limited environments with a high affinity for their nutrients and substrates (i.e., relatively low O₂ concentration, high CH₄ concentration) [84,87,94,95]. Of note, methanogens and methanotrophs in coastal wetland soils have unique characteristics that are rarely found in interior wetland soils. Hydrogenotrophic and acetoclastic methanogens are considered dominant in natural freshwater wetland soils. However, methylotrophic methanogens are dominant in hypersaline and sulphate-rich environments including coastal wetlands, and they make different contributions to CH₄ production [82,96,97]. In coastal wetlands, anaerobic methanotrophs include sulphate-dependent methanotrophs [39,98], which might have an important role in controlling low coastal CH₄ fluxes. Furthermore, several reports have described the possibility of active CH₄ production under aerobic conditions in mangrove forests based on laboratory incubation experiments and field observations [39,99].

2.2.3. Mangrove Species

The above-mentioned studies have mainly focused on CH₄ emissions from water and sediment in mangrove forests, and CH₄ emission through stems, leaves, and pneumatophores from mangroves is poorly understood [41]. A positive correlation between the density of pneumatophores and CH₄ flux is often found in various mangrove forest sediment [39,49,51,100]. However, some specific mangrove forest tree species such as *Sonneratia apetala* decrease CH₄ flux [41]. The presence of pneumatophores increased soil redox potential (Eh) and sulphate concentration in sediment in a Tanzanian mangrove forest, which suggests the inhibition effect of pneumatophores on CH₄ emission [101]. Pneumatophores of different mangrove species might have different roles in CH₄ flux from sediment [41]. The number of pneumatophores can vary seasonally in some mangrove forests, which could be an important factor in the long-term seasonal dynamics of methanogen activity [49].

The contribution of CH₄ emissions from mangrove tree stems without passing through sediment has been reported. Jeffrey et al. [102] reported that the direct CH₄ emission from living tree stems was 2.3% to 6.7% of the total net ecosystem flux and a significant amount came from dead trees, with emissions contributing to 6.6% to 46.1% of the total net ecosystem flux. These results indicate that the health status of the mangrove tree and the canopy structure of forests also have a substantial effect on CH₄ flux.

2.2.4. Invasive Plant Species

Vegetation invasion is often found to increase regional CH₄ emissions in coastal wetlands because most invasive plant species have higher net primary productivity than native plants and supply a greater amount of fresh organic matter to sediment [41,96]. Furthermore, the vegetation change in coastal wetlands occasionally shifts the major methane-producing process in the sediment from a hydrogenotrophic process to a methylotrophic or acetoclastic process [97]. Soil salinity or sulphate concentration shows a low positive relationship with methane-producing activities, which suggests that both forms of methanogenesis are not completely inhibited by sulphate reducers with increasing sulphate concentrations [39,55,97]. Apart from sulphate supply, fresh organic matter supply was often found to be strongly correlated with methane-producing activities [39]. Consistently, several reports have described that surface layer sediment has greater methane-producing activity and contains higher soil organic matter content compared to other sediment [101,103]. However, the substrate supply in sediment is spatio-temporally heterogeneous because it is affected by tidal pumping, crab/goby burrowing, and the structural complexity of aerial mangrove tree roots [60]. Recent studies are starting to report a significant enhancement in CH₄ emission caused by invading alien species and mangrove trees planted for reforestation, which are more prone to providing greater amounts of fresh organic matter as substrates for methanogens in sediment than native plants and enhance the amount of emission [41,96,97]. Because the invasion/reforestation status of plant species is sensitive, particularly in lawn zones [104,105], and the accumulation zone of substrate for methane production is relatively dense in hollow zones, microscale land surface structure needs to be carefully considered. Although CH₄ flux from the entire of mangrove ecosystem is highly correlated with micro-meteorological properties such as sensible heat flux [76,106], finer spatial resolution evaluation (e.g., chamber-based method) would also be important for considering the interaction between the pollution/invasion status and such geophysical characteristics in local/regional scales.

3. Anthropogenic Effects on Decreasing Mangrove Forests with Increasing Methane Emission

Causes of mangrove habitat conversion vary globally and include mechanical destruction (mariculture/aquaculture ponds), forest over-exploitation, land-use changes for urbanization, industrial use, chemical spills, upstream dams, dredging, eutrophication of overlying waters, urban development, and conversion to open water due to accelerated sea-level rise and subsidence [1,18,23–29]. As mentioned above, these mangrove forest-decreasing factors with high PAI (26% for forestry use, 14% for fish culture, 11% for freshwater diversion, 5% for land reclamation [18]) not only decrease mangrove forests but also enhance CH₄ emission/production. Particularly, with sea-level rise/increasing temperatures, CO₂ emission caused by anthropogenic global warming is suggested to be the biggest threat to mangroves in future decades [13,19,30]. Consistently, these global-scale factors are also recognized as CH₄ emission-enhancing factors, as they accelerate C cycles in wetland soils [107,108]. Even though the contribution of CH₄ emissions from mangrove ecosystems to the total global warming potential is still not clear, various reports have suggested significant impacts on CH₄ emission from mangrove forests [40–42,47]. Mangrove ecosystems cleared for aquaculture or that are polluted by organic waste show significantly more methanodynamic activities (i.e., CH₄ production and oxidation activities) and emissions [47,48,109]. A recent estimate of global CH₄ emissions per area of coastal aquaculture farms is equivalent to 7–430 times higher than emissions from general coastal

habitats, including from mangrove forests, salt marshes, or seagrasses [110]. Enhancing CH₄ emissions through the aquacultural land-use adjacent to the mangrove ecosystem and external species invasion also needs continuous monitoring with high spatial resolution.

Fortunately, satellite remote-sensing technologies to observe these factors have been advancing. Most major studies targeting mangrove forests aim to quantify biomass or canopy height based on synthetic aperture RADAR (SAR) observation (e.g., polarimetric interferometry [111] and SAR-tomography [112]). However, various technologies to detect changes in these factors include aquacultural pond detection in mangrove forest ecosystems by optical sensor data classification with object-based image analysis [113], SAR shadowing-effect analysis for deforestation detection [114], and hyperspectral-sensor data analysis for mangrove tree species identification and for salinity and vegetation stress [115,116]. Particularly, technologies that can detect soil inundation even with soil covered by cloud/vegetation have been well developed. They involve analysing the contribution of double-bounce intensity to the total back-scattering intensity of the L/P band SAR data used for regionalizing CH₄ emissions in various wetland studies [117–122].

For the next phase, we now need to integrate these remote-sensing technologies with biogeochemistry models that consider the above complex factors controlling CH₄ emissions from mangrove soils. Anthropogenic factors monitored by remote-sensing technology are expected to help support decision-making for efficient mangrove forest protection. High CH₄ emission risk is accompanied by a reduction in mangrove forest area, so sophisticated regional evaluation with high transparency and an inter-disciplinary approach is desirable for further development. To realize this, we need to start creating operational applications by developing new processes based on C cycle models that explicitly simulate CH₄ emissions considering the unique behavior of methanogens/methanotrophs in mangrove soils; these applications can realistically represent anthropogenic impacts by using satellite data as input data (i.e., forcing data) or “observation data” for data assimilation [121–123].

Although reports on CH₄ emission simulation studies in coastal catchment areas have been increasing recently, most of the model still does not consider the unique behavior of methanogens in mangrove ecosystems to explicitly solve the above-mentioned distinctive CH₄ production/emissions from the sediment. Among emission studies, most of the reports and validation data for the simulation are derived from tidal marshes, and contributions from mangrove ecosystems are still limited [124,125]. Such an innovative “digital-twin” system overcoming the difficulty of field observation is required in order to suggest sustainable mitigation in mangrove ecosystems, such as a locally/regionally/globally heterogeneous environment with various random factors.

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