Aquatic Botany 184 (2023) 103596

Contents lists available at ScienceDirect

Aquatic Botany

journal homepage: www.elsevier.com/locate/aquabot

The importance of plants for methane emission at the ecosystem scale☆

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ARTICLE INFO

Keywords:
Methane
Greenhouse gas flux
Primary producers
Ecosystem
Vegetation
Plants

ABSTRACT

Methane (CH_4), one of the key long-lived atmospheric greenhouse gases, is primarily produced from organic matter. Accordingly, net primary production of organic matter sets the boundaries for CH_4 emissions. Plants, being dominant primary producers, are thereby indirectly sustaining most global CH_4 emissions, albeit with delays in time and with spatial offsets between plant primary production and subsequent CH_4 emission. In addition, plant communities can enhance or hamper ecosystem production, oxidation, and transport of CH_4 in multiple ways, e.g., by shaping carbon, nutrient, and redox gradients, and by representing a physical link between zones with extensive CH_4 production in anoxic sediments or soils and the atmosphere. This review focuses on how plants and other primary producers influence CH_4 emissions with the consequences at ecosystem scales. We outline mechanisms of interactions and discuss flux regulation, quantification, and knowledge gaps across multiple ecosystem examples. Some recently proposed plant-related ecosystem CH_4 fluxes are difficult to reconcile with the global atmospheric CH_4 budget and the enigmas related to these fluxes are highlighted. Overall, ecosystem CH_4 emissions are strongly linked to primary producer communities, directly or indirectly, and properly quantifying magnitudes and regulation of these links are key to predicting future CH_4 emissions in a rapidly changing world.

1. Introduction

Methane (CH_4), one of the most important greenhouse gases (GHGs), is currently under scrutiny because of its high global warming potential in combination with uncertainties in the CH_4 budget (Kirschke et al., 2013; Saunois et al., 2020). Major sources of atmospheric CH_4 are both anthropogenic and natural and include extraction and handling of fossil fuels, combustion processes, landfills, ruminants, rice cultivation, and emissions from wildfires. Other key CH_4 sources are wetlands, marine- and freshwater environments (lakes, reservoirs, ponds, and streams) (Saunois et al., 2020). The two main CH_4 sinks are considered to be upland soil microbial methane oxidation (ca. 10 %), and abiotic atmospheric oxidation (ca. 90 %). Terrestrial upland vegetation has also been suggested to be important for atmospheric CH_4 exchange, although not always being mentioned in global CH_4 budgets (Carmichael et al., 2014).

The atmospheric CH_4 levels have sharply increased since pre-industrial times, but in contrast to the other long-lived GHGs (carbon dioxide and nitrous oxide), the increase has been irregular with variable growth rates among years and decades for reasons not yet fully understood (Dlugokencky et al., 2011). Several non-exclusive explanations for this variability have been proposed and one of them emphasise the potentially important role of wetland emissions (Nisbet et al., 2014; Lan et al., 2021). Moreover, the recent discovery of large CH_4 emissions from inland waters, including lakes, ponds, reservoirs, and running water environments, resulted in a situation where the atmospheric CH_4 growth

☆ Solicited review for special issue of Aquatic Botany edited by Pascal Bodmer and Sarian Kosten.

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https://doi.org/10.1016/j.aquabot.2022.103596
Received 30 June 2022; Received in revised form 29 September 2022; Accepted 3 November 2022
Available online 5 November 2022
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rates are considerably smaller than expected by summing estimated contributions from various sources, referred to as a mismatch between global top-down and bottom-up CH_4 emission estimates, respectively (Kirschke et al., 2013; Saunois et al., 2020). The temporal irregularities in atmospheric CH_4 growth rates and the mismatch between top-down and bottom-up flux estimates jointly highlight the current knowledge gaps regarding CH_4 emission rates and source attribution. Although emission uncertainties exist for all types of fluxes, the large biogenic ecosystem CH_4 fluxes, both natural and related with land use, have been considered the most uncertain (Saunois et al., 2020).

It was recently suggested that up to half of the global CH_4 emissions depend on fluxes from wet ecosystems, including various types of wetlands, lakes, ponds, reservoirs, running water, ocean and coastal areas, and rice cultivation (Rosentreter et al., 2021). These fluxes are closely linked to mechanisms controlled by plant communities in or upstream of the aquatic environments. Regardless of where in the landscape CH_4 fluxes occur, primary production sets the boundaries for overall carbon cycling, and thereby for the CH_4 production, and plants are the main primary producers in most ecosystems. In other words, the net ecosystem production by plants or other primary producers is a major indirect factor regulating ecosystem CH_4 production.

Human land use, including increased anthropogenic input of nutrients to ecosystems, as well as climate change, profoundly impacts plant communities around the world. There is already evidence of changes in growing season lengths, net primary productivity, plant biomass stocks, and plant community composition, exemplified by observations of global greening (Piao et al., 2020). There are also specific observations of rapid changes of e.g., aquatic macrophyte distribution in the arctic that can cause large perturbations of ecosystem CH_4 emissions (Andresen et al., 2017). Consequently, a better understanding of present and future CH_4 emissions is dependent on improved knowledge about plant community dynamics and particularly of the links between plant communities and ecosystem CH_4 fluxes.

This review will first briefly summarize key processes controlling ecosystem CH_4 emissions, which is needed as a background for the subsequent discussion on how plants influence ecosystem CH_4 fluxes. The aims are to (1) provide fundamental understanding on how plants play multiple important roles for ecosystem CH_4 emissions, and (2) give examples from selected ecosystem types. The words "emission" and "flux" are used in similar contexts to make the language more varied, but with an important distinction: "Emission" is unidirectional and regards flux to the atmosphere, while "flux" is omnidirectional and regards transport from one location to another in any direction.

2. Fundamental processes shaping ecosystem CH_4 emissions

2.1. CH_4 production

Biogenic CH_4 is a major final degradation product from anaerobic organic matter decomposition, formed by methanogenic *Archaea* where or when alternative terminal electron acceptors such as nitrate, manganese (IV), iron (III), and sulfate are low in abundance (Segers, 1998; Garcia et al., 2000). Freshwater aquatic systems, and some saline systems where salinity is caused by high carbonate levels, have low availability of such alternate electron acceptors, and anoxic CH_4 production can be extensive throughout all parts of the sediment or water saturated soils devoid of molecular oxygen (O_2) (Bastviken, 2022). In marine systems, anoxic CH_4 production is dominant deeper in the sediments, at depths where the alternative electron acceptors have been depleted by other organic matter degradation processes. CH_4 production in anoxic waters are rarely considered and substantial anoxic CH_4 production seems largely associated with sediments, soils, or particle-rich fluids (Bastviken, 2022).

In addition to the anoxic CH_4 production, CH_4 formation can occur under oxic conditions. Stress on foliage from incoming light including ultraviolet radiation, rising temperature, and physical injury, has been reported to trigger oxic CH_4 formation associated with terrestrial vegetation – in many cases from non-enzymatic processes and with suggested influence from reactive oxygen species and with variability among plant species (Liu et al., 2015; Martel and Qaderi, 2017; Ernst et al., 2022). In addition, oxic CH_4 formation in surface water has been attributed to e.g., cyanobacterial photosynthesis with methylphosphonates and trimethylamine as precursors in surface lake water (Bižić et al., 2020). Overall, anoxic CH_4 production is believed to dominate while the magnitudes of the oxic production may be considerable but are still uncertain (Carmichael et al., 2014; Günthel et al., 2019; Peeters et al., 2019).

2.2. CH_4 oxidation

The oxidation of CH_4 in ecosystems is primarily performed by microbes, while plants can substantially influence where conditions are suitable for this microbial CH_4 oxidation and the extent to which CH_4 can bypass oxidation (discussed in Sections 2.3 and 3 below after describing fundamentals about the oxidation process here). Microbial oxidation of CH_4 is a source of energy and carbon to microorganisms in habitats where CH_4, being the most reduced organic compound, coexists with suitable electron acceptors. CH_4 oxidizing bacteria (MOB) are phylogenetically diverse (Smith and Wrighton, 2019) and are well-known to be able to rapidly consume large amounts of CH_4 in the presence of O_2 (Bastviken, 2022). Upon oxidation, CH_4 is transformed to CO_2 and H_2O. Similarly, other microorganisms, often found to act in syntrophic consortia, can oxidize CH_4 under anaerobic conditions in the presence of e.g., nitrate, manganese (IV), iron (III), and sulfate (Kallistova et al., 2017). The oxidation process is often most active where the abundance or re-supply rates of both CH_4 and suitable electron acceptors are high enough, which is typically at redox transition zones in sediments, soils, or water. The ecosystem balance between CH_4 production and oxidation sets the limits for how much CH_4 can be emitted, and zones with microbial CH_4 oxidation can act as important biofilters preventing large amounts of emissions. It has been estimated that CH_4 oxidation removes 45 % to almost 100 % of the produced CH_4 in lake ecosystems and 20–40 % in wetland soils before emission (Whalen, 2005; Bastviken et al., 2008; Bastviken, 2022).

2.3. CH_4 transport processes

The processes controlling CH_4 transport through the ecosystems – from locations of CH_4 production towards the atmosphere – determine the residence times in different ecosystem habitats (e.g. oxic and anoxic zones), and thereby the extent to which oxidation can consume CH_4 before it is emitted. Hence, the different transport processes are of great importance for overall ecosystem CH_4 emissions. This section therefore briefly outlines major transport types because they are important for the understanding of how plants can influence ecosystem fluxes.

The movements of dissolved CH_4 in soil, sediment, and surface water can occur in two fundamental ways. If there is a net water movement over significant distances, dissolved CH_4 follows moving water, i.e., is transported by advection. If the movement of the water itself is small over larger distances, the transport can be better described as Fickian transport, i.e., transport of dissolved compounds from locations with higher concentrations towards locations with lower concentrations in ways that can be described by Fick's Law (Hemond and Fechner, 2015).

The Fickian transport includes molecular diffusion and eddy diffusion where turbulence eddies greatly speed up the transport rates (Hemond and Fechner, 2015). The Fickian transport rates are determined by the concentration gradient representing the change in concentration with distance, and the diffusion coefficient describing the transport rate given the physical conditions. In the absence of turbulence, the slow molecular diffusion limits transport. This can happen in deep undisturbed sediment or soil pore waters with little subsurface water flow, or across the diffusive boundary layers, including the water

surface diffusive boundary layer at the water-air interface. Where there is turbulence in the water, the Fickian transport is dominated by the faster eddy diffusion, often represented by greater diffusion coefficients (Hemond and Fechner, 2015). During advective transport with the water flow, Fickian transport occur simultaneously and distribute the solutes within the flowing water volume. In sediments or soils, particles can influence this process by dispersion (Hemond and Fechner, 2015).

Accordingly, CH_4 produced in anoxic soils or sediments and dissolved in the pore water may move slowly by Fickian transport or faster by advection via ground water movement. When reaching the air-filled pores in soil, gas exchange occurs if the CH_4 concentrations in the water and air are not at equilibrium. The CH_4 exchanged into the gas phase is further transported by advection or Fickian transport at rates given by the local air movement or diffusion coefficient. In aquatic environments, solutes reaching the top of the sediment will be transported through the water column by advective transport or eddy diffusion depending on local hydrodynamic conditions. Thermo- or halocline stratifications can greatly reduce the diffusion coefficients and thereby effectively limit transport rates across such gradients. Finally, when dissolved CH_4 reaches the water surface, the diffusive boundary layer at the interface between water and air is the final limiting step for the emission of dissolved CH_4 to the atmosphere – often termed diffusive emission. CH_4 formed under oxic conditions in surface water, an additional source of dissolved CH_4, can also be emitted via diffusive emission.

The dissolved CH_4 often has a relatively long residence time of CH_4 in the ecosystem (days or more; Bastviken et al., 2008), in turn allowing anaerobic and aerobic CH_4 oxidation to consume large amounts of the CH_4 before being emitted. However, upon episodes of high turbulence and extensive mixing, emission by diffusive flux can be rapid. One example is water column turnover in stratified lakes where bottom waters develop anoxia during the stratification, and therefore can store and subsequently release large amounts of CH_4. In such cases the turnover generates a very steep CH_4 gradient across the air-water interface that can drive large and rapid emissions (Johnson et al., 2022).

Because CH_4 has a low solubility in water, bubbles often form in sediments and where CH_4 formation rates are high enough. These bubbles will grow and if the sediments are sufficiently loose or have pore space allowing bubble migration towards the surface, and they are eventually released and rapidly rise to the atmosphere by ebullition. In many aquatic environments with open water surfaces, ebullition is a dominant flux pathway (Bastviken et al., 2004, 2011). Within such ecosystems, ebullition seems most prominent at shallow waters and/or where the sediment organic matter accumulation is high (e.g., accumulation bottoms, river/stream inlet areas, or near littoral areas with high primary productivity) (DelSontro et al., 2011; Sobek et al., 2012; Natchimuthu et al., 2016). Ebullition can also be a dominant emission mechanism in peatlands (Christensen et al., 2003). Ebullition release is too rapid to be directly influenced by CH_4 oxidation as the bubbles pass too quickly through the oxic sediment zone or water column, but ebullition from deep sediments can lead to substantial dissolution of CH_4 from the rising bubbles into the water (McGinnis et al., 2006), and this dissolved CH_4 can be oxidized as described in Section 2.2.

Vascular plants represent important conduits for CH_4 from the root zone to the atmosphere (Fig. 1). For more details about this topic please see (Vroom et al., 2022). Briefly, many plants with roots in water-saturated soils or sediments have internal gas transport systems for supplying root cells with O_2 (Joabsson et al., 1999; Laanbroek, 2010). This is particularly prominent in many aquatic macrophytes with aerenchyma tissue specially adapted for gas transport. To maintain pressure, the aerenchyma tissue transports gases both downwards and upward in the plant between roots and leaf stomata, or stem lenticels on trees, where the gas is exchanged with the atmosphere. Accordingly, gases entering roots may rapidly be transported via the aerenchyma to the atmosphere (Yavitt and Knapp, 1998). At least two types of transport via plants have been suggested – molecular diffusion (passive) and convective flow (active) (Kim et al., 1998). The convective flow is driven

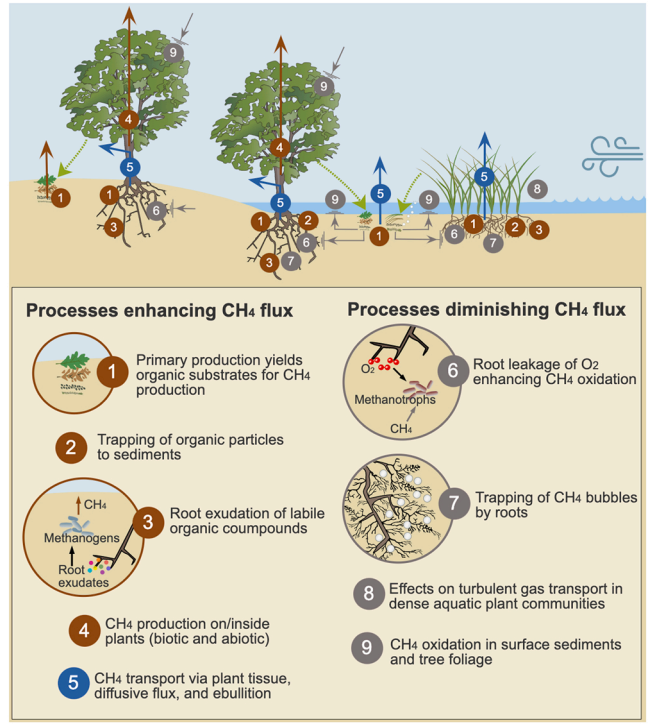

Fig. 1. Examples of how plants and other primary producers can influence terrestrial and aquatic ecosystem CH_4 fluxes. The colours on numbers and arrows represent CH_4 production (brown), transport (blue), oxidation (grey), and source of organic substrate (green). Plant drawings are generic to vascular non-woody and woody plants but are intended to represent all primary producers, although not all illustrated mechanisms are relevant for non-vascular plants. This figure represents a simplification (for a more extensive list of mechanisms and their global implications please see e.g., Carmichael et al., 2014; Liu et al., 2015; Bodmer et al., 2021).

by a pressure gradient in the plant and the interplay between molecular flux and convective flux has been suggested responsible for diel variability in the plant-mediated fluxes (Bendix et al., 1994; Brix et al., 1996; Whiting and Chanton, 1996; Kim et al., 1998; Kaki et al., 2001; Ding et al., 2004; Juutinen et al., 2004; Duan et al., 2005). However, some studies over multiple day-night cycles indicate negligible diel flux variability from areas dominated by vascular plants in high-latitude wetlands (Bäckstrand et al., 2008; Milberg et al., 2017). Beyond the explicit diel day-night variability in the plant-mediated flux, temporal variability in CH_4 flux is linked with multiple factors including temperature, light, humidity, and plant biomass (Chanton et al., 1993; Brix et al., 1996; Hirota et al., 2004; Juutinen et al., 2004; Duan et al., 2005; Kankaala et al., 2005; Wang and Han, 2005; Bergstrom et al., 2007; Milberg et al., 2017). The plant-mediated flux regulation may be strongly dependent on plant species (Armstrong and Armstrong, 1991; Chanton and Whiting, 1996; Joabsson et al., 1999). However, there are also observations of similar long-term mean emissions per m^2 from nearby plant species, suggesting little importance of specific species for long-term mean areal fluxes (Milberg et al., 2017). Additionally, transport of CH_4 via tree stems has relatively recently been demonstrated to be important (Barba et al., 2019).

Overall, plant mediated emissions allow CH_4 formed in sediments to bypass pore water or water column oxidation before emission. This type of transport can dominate CH_4 emissions in habitats with emergent aquatic macrophytes (Juutinen et al., 2003; Larmola et al., 2004; Bergstrom et al., 2007; Pangala et al., 2017). There are indications of a possible trade-off with reduced ebullition from areas with substantial plant-mediated emission (Noyce et al., 2014; Aben et al., 2022).

3. Mechanisms by which plants can influence ecosystem CH_4 emission

Terrestrial and aquatic plants and other primary producers can stimulate CH_4 emissions in many ways at ecosystem scales (Fig. 1). Examples include:

+ Primary production provides the primary substrates for both anoxic and oxic CH_4 formation in most environments. For e.g., wetland and standing water environments, higher CH_4 emissions are commonly observed under conditions and locations with higher primary production (see examples in Section 4 below).
+ Plants can provide favourable sites for CH_4 formation inside or on the plants themselves (Covey and Megonigal, 2019). At the larger scale the foliage of vegetation (both terrestrial and aquatic) represents a large surface area for abiotic CH_4 production (Keppler et al., 2006; Carmichael et al., 2014).
+ Plant communities in aquatic environments contribute to trapping of particulate organic matter to the sediment where stands of plants reduce turbulence (Braskerud, 2001; Duarte et al., 2013; Bodmer et al., 2021; Work et al., 2021) increasing the potential for sediment CH_4 production
+ Plant mediated transport by rooted vascular plants substantially enhance emissions by speeding up transport and reducing exposure to CH_4 oxidation (Vroom et al., 2022).

Plants can also hamper CH_4 emissions in several ways:

- Rooted vascular plants transport O_2 down to the root zone leading to O_2 leakage into the sediment or soil, which can favour CH_4 oxidation there and reduce emissions (King et al., 1998).
- Plants, including trees and mosses, can offer large surface areas for CH_4 oxidizing microorganisms in ecosystems (Sundh et al., 1995; Basiliko et al., 2004; Kip et al., 2010; Sundqvist et al., 2012; Stępniewska et al., 2018).
- Dense floating vegetation can also trap bubbles temporarily before they reach the atmosphere, which increases the CH_4 residence time in the system, favouring CH_4 oxidation (Bartlett et al., 1988; Kosten et al., 2016; Oliveira Junior et al., 2021).
- Dense aquatic vegetation stands can influence turbulence and thereby the transport of dissolved CH_4 towards and across the atmospheric interface in several ways. Dense floating macrophyte populations can reduce the wind-induced turbulence in the water, in turn reducing gas exchange rates, and increasing the potential for oxidation before emission (Kosten et al., 2016; Oliveira Junior et al., 2021). Diel differences in temperature between open water and floating plant mats, together with basin scale water movements, can cause lateral advection so that dissolved gases from vegetated areas are exported and emitted elsewhere (Amaral et al., 2022). In flooded forests, where winds are also reduced, turbulence-driven gas exchange rates can be regulated by a combination of shear from wind-driven water movements induced outside the forest and from convection associated with nocturnal cooling (MacIntyre et al., 2019). Accordingly, dense aquatic vegetation can not only influence gas exchange directly, but also the relative importance of different processes regulating transport and emissions of dissolved CH_4 (Oliveira Junior et al., 2021).

Other plant effects on fluxes can be logically inferred or hypothesized although hitherto seemingly not being studied or quantified:

- Roots of aquatic macrophytes may stabilize sediments, preventing the release of sediment bubbles and reducing ebullition rates.
- In dryer environments, transpiration by rooted vegetation can lower the soil water level, increasing the depth of the aerated CH_4 oxidation zone in the upper soil – reducing emissions.

Further studies are needed to fully explore the quantitative importance of these potential plant-related effects on CH_4 emissions across different ecosystems.

4. Interactions between vegetation and CH_4 emission in example ecosystems

4.1. General primary producer influences on ecosystem CH_4 cycling

Given the many and complex processes by which plants influence ecosystem carbon fluxes as outlined in Section 3 above and in Fig. 1, it is difficult to quantitatively assess the total plant contributions to total CH_4 flux, and such knowledge is missing in many ecosystems. Accordingly, the sections below should be seen as attempts to integrate existing conceptual knowledge with available scattered quantitative information on the importance of plants for CH_4 fluxes in example ecosystems (some of them illustrated in Fig. 2).

Common to all ecosystems is that primary productivity controls the availability of substrates for CH_4 production over time. Increasing amounts of evidence indicate that CH_4 production and emissions are stimulated by the production of labile organic matter and by high primary production (Whiting and Chanton, 1993; Bellisario et al., 1999; King and Reeburgh, 2002; King et al., 2002; Bäckstrand et al., 2008; Bastviken et al., 2008; Davidson et al., 2015; West et al., 2015; Grasset et al., 2018; Kuhn et al., 2021; Aben et al., 2022). The link between primary production and CH_4 production and emission can be delayed (example at the end of Section 4.4 below), and for full consideration integration across long enough time periods is necessary. The indirect influence of plant communities on CH_4 fluxes has been acknowledged in many ecosystem models where ecosystem primary productivity proxies are used as an important emission driver (Wania et al., 2013).

Several links between whole-ecosystem carbon cycling and CH_4 have been made for lakes, ponds, or wetlands, including:

- Anaerobic CH_4 production was estimated to 13 % of primary production (Rudd and Taylor, 1980) and 20–56 % of organic matter respiration across multiple ecosystems (Capone and Kiene, 1988; Kuivila et al., 1988; Bédard and Knowles, 1991; Mattson and Likens,

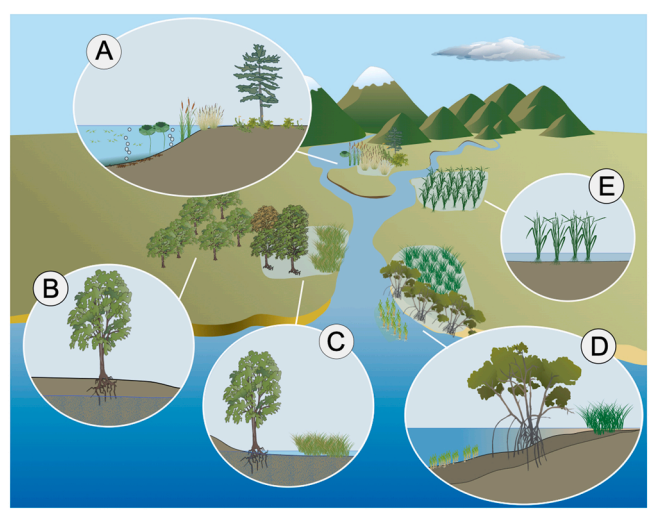

Fig. 2. Examples of ecosystems where plant influences are important for total net CH_4 emissions: A) Lentic open water (lakes, ponds, and reservoirs) and freshwater marsh, bog, and fen ecosystems along a hydrological gradient characteristic of higher latitudes; B) upland forests; C) floodplain forests and wetlands exemplifying lower latitudes; D) coastal vegetated areas (salt marshes, mangroves, and seagrass meadows); E) rice fields. See Fig. 1 and text for illustration of mechanisms by which the plant communities influence CH_4 fluxes in the respective ecosystems.

1993; Boon and Mitchell, 1995; Hamilton et al., 1995; Ford et al., 2002).

- Oxic CH_4 oxidation can be similar to primary production rates during limited time periods in aquatic ecosystems (Rudd and Taylor, 1980; Kankaala et al., 2006).
- The production of CH_4 oxidizing bacteria was found to be 0.3 to > 10 % of primary productivity and their biomass constituted 1.4–41 % of total bacterial biomass in lakes of different types (Utsumi et al., 1998; Bastviken et al., 2003; Eller et al., 2005; Sundh et al., 2005).
- CH_4 emissions have been reported to correspond to 24–37 % of summer productivity in a small shallow hypereutrophic lake (Strayer and Tiedje, 1978), and plant-mediated CH_4 fluxes from stands of *Typha* sp. and *Cladium jamaicense* in the Everglades were 3–14 % of net ecosystem production (Chanton et al., 1993).

Collectively, these findings illustrate the large general importance of plant primary production for CH_4 production, and a large quantitative importance of CH_4 in relation to overall carbon cycling in aquatic ecosystems.

Aerobic CH_4 production associated with surfaces of terrestrial upland vegetation or litter has been comprehensively reviewed (Carmichael et al., 2014; Liu et al., 2015). Experimental studies observed CH_4 production on upland plants that if extrapolated would result in > 200 Tg CH_4 per year (up to 36 % of the total global CH_4 budget), while other experiments showed much smaller or negligible production (Carmichael et al., 2014). Most of this information rely on small-scale incubation studies and field-scale observations of associated fluxes are rare. Given the large vegetation and litter surface area, potential associated ecosystem fluxes could be important as discussed further in Section 4.6 below. Other interactions between terrestrial upland vegetation includes the supply organic substrates for microbial CH_4 production in soil. However, most of this upland soil CH_4 may be oxidized in aerated top soils (Saunois et al., 2020), unless high soil moisture lead to emissions (Lohila et al., 2016) or lateral export with soil and ground water lead to emissions in recipient streams (Natchimuthu et al., 2017; Lupon et al., 2019).

There can be important, yet complex interactions between plants and temporal variability of CH_4 emissions. There is growing support for a positive exponential relationship between ecosystem CH_4 emissions and temperature (Yvon-Durocher et al., 2014; Aben et al., 2017). This temperature regulation interacts with supply rates of organic substrates for CH_4 production from plant primary production, and with the other plant effects on CH_4 dynamics, including availability of plant-mediated transport pathways (Fig. 1). Accordingly, there can be plant-induced enhancement of ecosystem CH_4 emissions in synergy with the direct temperature effect, by increased plant productivity, biomass, or prolonged plant growing seasons (Andresen et al., 2017). For example, synergies between nutrient additions and temperature treatments have been confirmed in experimental studies with submerged or floating macrophytes (*Elodea canadensis*, *Potamogeton crispus, Ceratophyllum demersum, Myriophyllum spicatum, and Azolla filiculoides*) (Davidson et al., 2018), and in some cases plant productivity and composition effects have been found more important for CH_4 emissions than temperature changes (Davidson et al., 2015, 2018; Aben et al., 2022). Another study in less productive nitrogen limited boreal lakes found weak influence of whole lake nitrogen additions on CH_4 emissions (Klaus et al., 2018), indicating that the importance of plant-effects versus effects of other factors for CH_4 emissions may differ among ecosystem types.

4.2. High latitude wetlands

In high latitude wetlands, the water table position and nutrient status determine the plant community composition that then affects CH_4 flux through influence on production, oxidation, and transport as has been comprehensively discussed in earlier reviews on wetland methane emissions (Bartlett and Harriss, 1993; Bubier and Moore, 1994; Blodau, 2002; Whalen, 2005; Lai, 2009; Bridgham et al., 2013; Abdalla et al., 2016; Kuhn et al., 2021). Early studies on CH_4 fluxes showed the correlation between water table position and daily flux, where water tables near the surface had the highest emissions and correlated with vegetation composition and moss types (Bubier, 1995). Further research demonstrated the role of vascular plants in controlling CH_4 emissions from high latitude wetlands by influencing both substrate availability through recent photosynthates, oxidation and the transport pathways (Joabsson et al., 1999). However, time lags between photosynthesis and CH_4 production as well as the storage of CH_4 in sediments can mask the relationship between primary productivity and emissions, which may become clearer when integrated over seasonal to annual time scales (Blodau, 2002).

Recent syntheses have shown that broader wetland classes can be used to predict fluxes because these capture the mean water table position and dominant vegetation types (Olefeldt et al., 2013; Turetsky et al., 2014; Treat et al., 2018; Kuhn et al., 2021). The major classes have been defined broadly as freshwater marshes, fens with sedges and mosses, and bogs with *Sphagnum* mosses (Table 1). CH_4 emissions are variable within and across these classes, with highest emissions from marshes, followed by fens and bogs, respectively (Table 1). The presence of permafrost is also a key control on CH_4 emissions; emissions from permafrost wetlands are on average 60 % lower than from northern wetlands without permafrost (Treat et al., 2018). Coastal tidal-influenced and saline marshes have generally been considered separately but observations are limited for many northern regions (Poffenbarger et al., 2011). Other northern ecosystems such as upland tundra and boreal forests can also emit CH_4 (Lohila et al., 2016; Zona et al., 2016). While these wetland or land cover classes show considerable variability within each class, likely because these classes include the variability among the plot and community scale vegetation composition discussed above, these are useful categories because there are significant differences in CH_4 flux among them (Table 1). Furthermore, often they can be distinguished with some success from remote sensing observations or machine learning analysis (Webster et al., 2018; Matthews et al., 2020; Olefeldt et al., 2021). Until now, uncertainties in the distribution of different wetland types and water bodies have prevented comparisons between high latitude emissions from models that prescribe wetland emissions based on area coverage (Melton et al., 2013) and observations (Olefeldt et al., 2013; Turetsky et al., 2014; Treat et al., 2018; Kuhn et al., 2021).

Temperature provides another broad control on CH_4 flux across high latitude wetlands by controlling the timing and length of the growing season (also influenced by radiation) and by influencing the soil temperature. Generally, annual CH_4 fluxes increase with annual temperature in wetlands (Delwiche et al., 2021), with temperate wetlands having higher annual emissions (median: 13.3 g CH_4 m^{-2} yr^{-1}) than similar types of wetlands in boreal (7.2 g CH_4 m^{-2} yr^{-1}) or Arctic regions (6.2 g CH_4 m^{-2} yr^{-1}; (Treat et al., 2018). This is likely due to the direct influence of temperature on rates of microbial CH_4 production (Dunfield et al., 1993; Yavitt et al., 1997; Treat et al., 2015), but also the indirect effects of vegetation productivity. In northern soils where freezing is common, peak temperatures in soils lag peak air temperatures. This causes a delay in peak CH_4 emissions relative to the peak season GPP that can range from nearly simultaneous to as much as 60 days (Delwiche et al., 2021). Due to these warm soil temperatures into the fall, as well as CH_4 storage in sediments, emissions outside of the growing season can account for a substantial portion (13–47 %) of annual emissions (Treat et al., 2018). Thus, even in the absence of vegetation activity, CH_4 emissions can occur in northern wetlands (Mastepanov et al., 2008; Zona et al., 2016).

Questions remain about the response of CH_4 flux in northern wetlands to disturbance, including permafrost thaw, fire, flooding, and other extreme events, such as excessive heat and drought. However, there are only a few sites with long enough records of CH_4 fluxes to be

Table 1
Examples of net CH_4 emission ranges observed in ecosystem habitats with different primary producer communities. Flux denotes range as measured by min-max or IQR (interquartile range). Global CH_4 budget estimates are provided at the lower part of the Table to enable easy comparisons.

Biome and ecosystem	Habitat	Flux range (mg CH_4 m^{-2} d^{-1})	Global flux (Tg CH_4 yr^{-1}) (seasonally integrated)	Refs.
High-latitude wetlands	Bog[b]	-4.3 to 278; 7–57 (IQR)	9 (permafrost region)	(Bao et al., 2021; Kuhn et al., 2021; Treat et al., 2021)
	Fen[a]	-30 to 371; 20–107 (IQR)	21.5 (permafrost region)	
	Marsh[c]	-38 to 761; 71–200 (IQR)	2.6 (permafrost region)	
Rice fields			25–38	(Saunois et al., 2020)
Lakes, reservoirs, and ponds	Open water emission	0.1–2497; 9–153 (IQR)	31–73	Measured fluxes: (Rosentreter et al., 2021). Seasonally integrated global flux; (Johnson et al., 2021, 2022).
	Littoral with emergent plants	8–1392	6–15[d]	(Juutinen et al., 2003, 2004; Kankaala et al., 2003; Duan et al., 2005; Bastviken et al., 2011; Milberg et al., 2017; Kyzivat et al., 2022)
Tropical floodplain forests	Global flooded tree flux		37.1 (stem flux)	(Pangala et al., 2017; Gauci et al., 2022)
	Non-flooded tree flux		6.4 (stem flux)	(Gauci et al., 2022)
	Amazonian flooded forest	1–6504 (stem m^2)	12.7–21.1 (stem flux)	(Pangala et al., 2017; Gauci et al., 2022)
	Aquatic diffusive flux	2.5–50.5		(Barbosa et al., 2020) (data from flooded forest only)
	Aquatic ebullition	45–168		(Barbosa et al., 2021) (data from flooded forest only) (Barbosa et al., 2020)
	Amazon aquatic total flux	36–617	9.7 ± 5.2	(Pangala et al., 2017) (Amazon flooded forest)
Global forests	Stem flux in upland and wetland forests	-14 to 6504 (stem m^2)	60	(Covey and Megonigal, 2019)
	Abiotic CH_4 production on plant and litter surfaces		8–176	(Carmichael et al., 2014; Liu et al., 2015)
Coastal vegetation	Mangroves	-1.1 to 1169	1.5–4.0	(Al-Haj and Fulweiler, 2020; Rosentreter et al., 2021).
	Salt marshes	-1.5 to 1510	1.1–2.0	
	Seagrass meadows	0.02–6.4	0.5–1.0	
Global CH_4 flux estimates for 2008–2017 extracted from Saunois et al. (2020) ***for comparison***				
Flux category		*Tg CH_4 yr^{-1} (mean and range; bottom-up estimates)*		
Total global emissions (top-down)			*576 [550–594]*	(Saunois et al., 2020)
Total global emissions (bottom-up)			*737 [594–881]*	
Fossil fuel production and use			*128 [113–154]*	
griculture and waste			*206 [191–223]*	
Biomass and biofuel burning			*30 [26–40]*	
Wetlands			*149 [102–182]*	
Other natural emissions (total)			*222 [143–306]*	
	Freshwater		*159 [117–212]*	
	Biogenic open ocean and coastal		*6 [4–10]*	

[a] Variable hydrological connectivity and productivity; Sphagnum, sedges, shrubs.
[b] Ombrotrophic; low productivity; Sphagnum-dominated.
[c] Minerotrophic, high productivity; emergent macrophytes, sedges, often in standing water.
[d] Based on estimates of 10 Tg CH_4 yr^{-1} or 21 % of open water emissions (see references).

able to discern these types of events, and due to lag times between production and emission, measurements should continue beyond the growing season into the shoulder seasons and winter.

4.3. Rice paddies

Rice probably represents the plant genus responsible for most plant-mediated CH_4 emissions. Rice field emissions are estimated to be 24–40 Tg CH_4 yr^{-1} (Bridgham et al., 2013; Saunois et al., 2020). The CH_4 production in rice paddies is stimulated by the release of labile organic matter synthetized by photosynthesis via the roots. More than 50 % of the rice CH_4 emission is generated from the root exudates or decomposed plant material (Lu and Conrad, 2005). Rice production demands the establishment and maintenance of flooded conditions that reduce the presence of oxygen and other electron acceptors (e.g., nitrate or sulfate) favouring CH_4 production. The high sediment CH_4 production rates result in high CH_4 emissions via rice aerenchyma to the atmosphere, bypassing the sediment oxic-anoxic interface.

Most of the global production of rice happens at lower latitudes where the temperatures and also CH_4 production rates are high (Fernando, 1993), and the rice paddies act as landscape emission hotspots. Considering that CH_4 production is positively correlated with temperatures (Yvon-Durocher et al., 2014), increasing global temperatures may trigger an increase in overall rice-mediated CH_4 fluxes. Furthermore, given the predicted increase in global world population from the present 8 to > 10 billion by 2100 (Ezeh et al., 2012), the growing demand for food will likely increase rice paddy cultivation and increase CH_4 fluxes from rice paddies in the future.

Several management approaches have been tested in order to minimize the CH_4 emissions from rice paddies, with the application of gypsum and phosphogypsum, and the application of sulfate with N fertilizer (e.g., ammonium sulfate) being the most common practices (Liu et al., 2018). Sulfate reduction is an anaerobic process energetically more favourable than methanogenesis and therefore sulfate addition decreases CH_4 production and emissions without affecting the rice growth or yield. Other strategies have focused on management of the flooding regime or straw amendment (Belenguer-Manzanedo et al., 2022). Genetic modifications have also been successful in regulating CH_4 emissions, e.g., the addition of a transcription barley gene SUSIBA2 to experimental rice strains, promoted a shift in rice carbon flow decreasing its CH_4 emissions (Su et al., 2015). A decrease in 50 % CH_4 emission with the *SUSIBA2 japonica* and *SUSIBA2 indica* rice types have been reported, due to a decrease in organic carbon to the soil, without decreasing rice yield (Du et al., 2021). We do not intend to claim that genetically modified rice strains should indiscriminately replace non-modified rice types, and this controversial topic is out of the scope of this study. More relevant in the frameworks of this review is that these findings exemplify how plant physiology and genetic traits of plant communities can influence ecosystem CH_4 cycling.

4.4. Lakes, reservoirs, and ponds

Substrates for CH_4 production in lakes, reservoirs, and ponds (standing water systems collectively referred to as lentic waters) include organic matter from plant primary production in upstream catchments and littoral zones, and from phytoplankton and periphyton production. The catchment organic matter contributions can fuel substantial CH_4 emission also in systems with low internal primary production. Positive relationships between in-system primary productivity (aquatic plants, periphyton, and phytoplankton supplying the most labile organic material) and CH_4 production have also been suggested (Bastviken et al., 2008; Duc et al., 2010; Davidson et al., 2015; West et al., 2015; Grasset et al., 2018).

Most available CH_4 emission measurements from lentic ecosystems consider fluxes from the open water surface, where diffusive flux and ebullition dominates. From a mechanistic point of view, such emissions are not directly linked to primary productivity or CH_4 production rates, and instead represent a balance between multiple processes, including CH_4 production, different transport pathways, and CH_4 oxidation. However, for reservoirs, a recent meta-analysis found a clear relationship between open water fluxes and chlorophyll-a levels, representing a proxy for in-system phytoplankton primary productivity (Deemer and Holgerson, 2021). If the recently suggested oxic surface water CH_4 production is primarily linked with planktonic photosynthesis, this adds a direct link between phytoplankton metabolism and CH_4 emissions (Bižić et al., 2020; Günthel et al., 2020). A whole-lake experiment where the primary producers were ^{13}C-labelled by adding ^{13}C-bicarbonate to two lakes provides relevant information to evaluate this possibility. The experiment showed that the dissolved surface water CH_4 responded most strongly to the ^{13}C addition approximately one month after the ^{13}C signal reached the particulate organic carbon (Bastviken et al., 2008). This indicates a delayed link between dissolved CH_4 and lake primary production (Fig. 3). Accordingly, this whole-lake C tracer experiment points towards the importance of the longer, indirect link between primary production and epilimnetic CH_4 via anoxic sediment CH_4 production, rather than direct, oxic surface water CH_4 production linked to photosynthesis in the studied small lakes. However, conditions may differ among systems and the debate about the ecosystem implications of oxic surface water CH_4 production (Günthel et al., 2019; Peeters et al., 2019; Hartmann et al., 2020) requires additional consideration.

Littoral zones include areas with submerged, floating-leaved (rooted or non-rooted), and emergent vegetation. Few field studies have focused on submerged macrophytes but their potential importance was recently highlighted (Hilt et al., 2022), and experimental studies with submerged plants have indicated high importance for system CH_4 dynamics and emissions in interaction with nutrient concentrations (see Section 4.1) (Davidson et al., 2015, 2018; Aben et al., 2022). Free-floating plants can also have important effects on CH_4 fluxes by providing substrates for CH_4 production while also influencing CH_4 transport, as outlined in Section 3 and being detailed elsewhere (Kosten et al., 2016; Oliveira Junior et al., 2021). In a field study of a tropical floodplain lake, open water fluxes within 0–20 m of dense floating macrophyte populations (*Eichhornia* sp.) was shown > 2-fold greater than from areas being > 45 m away from such vegetation belts with no depth difference among locations (Peixoto et al., 2015). This indicates substantial local contributions of decaying plant biomass for ebullition.

A number of field studies in littoral zones have focused on emissions from emergent vascular aquatic macrophytes (Juutinen et al., 2003; Larmola et al., 2004; Bergstrom et al., 2007). Littoral flux measurements and regulation seem largely consistent with wetland observations (see Sections 2.3 and 4.2 above). It has been suggested that the littoral zones with plant mediated fluxes can contribute a large share of the total flux (the sum of vegetated and open water fluxes) if the vegetated area is extensive enough. Littoral vegetated zones contributed 66–77 % of the ice-free period integrated CH_4 fluxes from three Finnish lakes (Juutinen et al., 2003). In a Canadian lake, a detailed study showed that 26 % of the area covered by emergent macrophytes contributed 80 % of the mean daily CH_4 flux during the ice-free season, and that 34 % of the flux from the vegetated area was emitted via plant mediated flux while 62 % was emitted by ebullition among the plants (Desrosiers et al., 2022). This study also showed that plant community composition was important for determining the predominant flux pathway.

In some cases, littoral plant-mediated CH_4 emissions are large

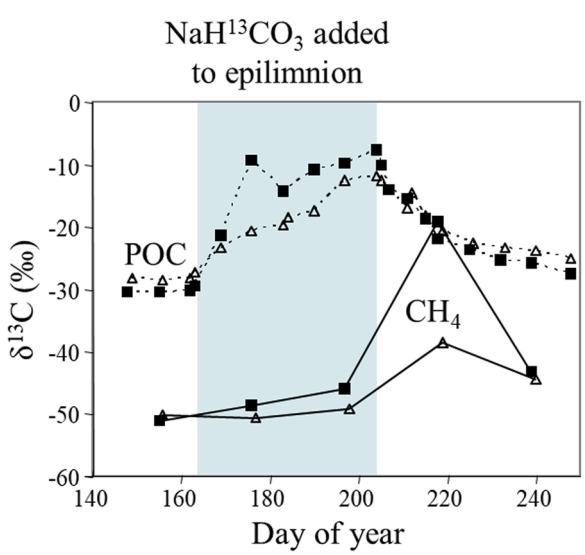

Fig. 3. Results from a whole-lake experiment where ^{13}C-labelled sodium bicarbonate were added to the epilimnion to act as ^{13}C tracer of primary production in the ecosystem (Pace et al., 2004). The shaded area denotes the time period of ^{13}C addition. The response of epilimnetic particulate organic carbon (POC; including phytoplankton) and CH_4 is shown and were offset in time. Black squares and open triangles are Paul and Peter Lake, respectively, Wisconsin, USA. Results illustrate a clear but delayed link between recent primary production and dissolved CH_4 in a whole-lake context.
(Modified from Bastviken et al., 2008.).

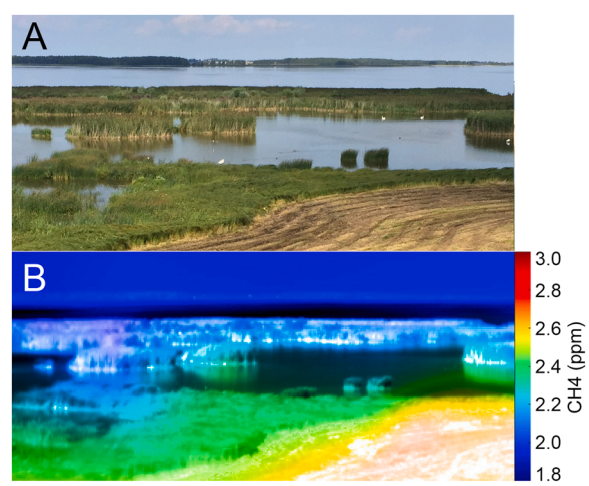

Fig. 4. Image of a lake shore with a hyperspectral camera optimized for sensitive detection of CH_4 (Gålfalk et al., 2016). Panel A shows the visible light image of the scene and Panel B shows mean CH_4 mixing ratio along each line of sight from the camera to the background. The wind comes from the lake towards the shore which moves emitted CH_4 towards the lower parts of the image. Some CH_4 emissions from the outer reed belts (*Phragmites australis*) are visible via slightly elevated nearby mixing ratio with a somewhat patchy appearance depending on local wind mixing. Larger CH_4 emissions from the near-shore sedge vegetation are clearly visible. For methods behind the imaging, see Gålfalk et al. (2017).

enough to create CH_4 flux gradients along lake shores (Fig. 4). Recent airborne imaging spectroscopy has identified hot spot zones within 40 m from standing water, possibly indicating the importance of combined emissions from open water and littoral zones (Elder et al., 2020). Recent mapping of > 4500 arctic-boreal lakes showed that the area with emergent vegetation comprised 16 % of the lake area and including CH_4 fluxes from this area was suggested to increase estimates of total lake CH_4 emissions by 18–25 % (Kyzivat et al., 2022). One challenge is ensuring that regional scaling of CH_4 fluxes does not double-count lake littoral zones as both a part of the lake CH_4 emission estimate and as a part of the wetland CH_4 emission estimate.

The issue of double-counting CH_4 emissions from lakes and wetlands are further discussed elsewhere (Thornton et al., 2016). Fundamentally, this is a question about matching land cover categories with flux measurements. There may be a mismatch between the traditional definition of lakes including their littoral zones versus a more "methanocentric" land cover categorization based on underlying mechanisms and regulation. The latter leads to a potential conclusion that all vegetated aquatic environments – also in lakes, ponds, and reservoirs – are better categorized as wetlands of different types, while open water, being more easily distinguished by remote sensing and being dominated by other CH_4 flux pathways and other flux regulation, represents another main land cover category. Such a methanocentric land cover categorization may have many advantages for CH_4 emission extrapolation but require replacing traditional ecosystem definitions with land cover categories based on predominant biogeochemical processes. Overall, littoral zones require additional attention to properly quantify lentic CH_4 emissions, and efforts developing a clear distinction of how all CH_4 emitting land cover types are classified and combined with the most relevant flux observations are critically needed (Kuhn et al., 2021; Olefeldt et al., 2021).

Most examples above from lentic systems indicates that presence of plants increases CH_4 emissions. However, in hypereutrophic aquatic systems which emit large amounts of CH_4, such as agricultural dams (Grinham et al., 2018; Ollivier et al., 2019), there are observations that increased presence of vegetation can result in less nitrogen and phosphorous in the water, more dissolved oxygen, and lower methane emissions (Malerba et al., 2022). Speculated reasons could include combinations of factors mentioned above such as root zone oxygenation and trapping of bubbles along with more surfaces suitable for CH_4 oxidisers, and possibly also reduced phytoplankton production if there was light competition.

4.5. Amazon floodplain forests

The Amazonian lowland basin forest is an example of a vast tropical floodplain forest (Melack and Hess, 2011; Hess et al., 2015). It represents a highly diverse, yet unique environment constituted by a rich mosaic of terrestrial, aquatic and transitional ecosystems subjected to seasonal and permanent waterlogging (Junk et al., 2011). The Amazon River flows 4000 km from the Andes to the Atlantic, carrying more water than any other river. The basin includes an extensive system of riverine flooded forests, which in some cases are flooded on a seasonal basis and in other cases are flooded all through the year. Hot tropical temperatures, extensive tree cover with continuous supply of fresh carbon substrates and anoxia due to flooding create favourable conditions for CH_4 production and emission(Wassmann et al., 1992). Therefore, it is not surprising when this region alone is responsible for emitting ~ 8 % (46.2 ± 10.3 Tg CH_4 yr^{-1}) (Basso et al., 2021) of the global CH_4 emissions estimated to 576 Tg CH_4 yr^{-1} (Saunois et al., 2020).

The floodplain forests experience extensive flooding, and the flooding depth and duration is linked to the type of forest (low várzea, high várzea or chavascal), location (upstream or downstream of the river) and draining catchment characteristics (Junk et al., 2011). Since the late 1980s, attempts have been made to quantify different CH_4 sources of tropical floodplain forests and significant CH_4 emissions are reported from the flooded forest soils, floating and rooted macrophytes, aquatic sources within the flooded forest and adjoining open waters of lakes and rivers (example data in Table 1) (Bartlett et al., 1988; Devol et al., 1988; Bastviken et al., 2010; Sawakuchi et al., 2014; Barbosa et al., 2020, 2021). The trees are adapted to anoxic environment through morphological and physiological traits, including gas transport to supply root cells with O_2, to survive flooding (Junk et al., 2010; Parolin and Wittmann, 2010). As other woody plants experiencing flooding, they have lenticels on the stems for such gas exchange and the gas exchange contribute to an extensive recently discovered plant mediated CH_4 flux from tree stems (Gauci et al., 2010).

Large seasonal variation in inundation period and areas is a key challenge to identifying the variability in space and time of CH_4 emissions from the Amazon flooded forests (Barbosa et al., 2021). This is further complicated when new CH_4 emissions pathways such as those from flooded trees are discovered, when regionalization of emissions from previously known CH_4 sources in the Amazon basin is already a challenging task (Melack et al., 2022). In recent years, flooded trees are not only known to influence CH_4 dynamics through their fresh carbon supply stimulating methanogenesis and root-zone O_2 leakage stimulating CH_4 oxidation - they are also known to emit CH_4 (Pangala et al., 2017). Further, stem flux from flooded trees were estimated to contribute nearly half the regional Amazon basin CH_4 emissions (Pangala et al., 2017). Apart from the tree-mediated flux of CH_4 from the root zone to the atmosphere, enhanced by morphological adaptations in flooded trees, recent studies now suggest that trees themselves can produce CH_4 within their tree stems albeit at lower rates (Covey et al., 2012; Covey and Megonigal, 2019).

CH_4 emissions from 13 forested floodplains along the Amazon River in Brazil were measured, attempting to capture spatial variability (Pangala et al., 2017). The measurements were made during a single high-water event leading to uncertainty in extrapolations over time. In a recent study, tree stem CH_4 emissions were reported to continue throughout all four hydrological distinct seasons (rising, flooded, receding and low water period), albeit at lower rates (Gauci et al., 2022). The study also found a strong relationship between water table depth below the surface and tree CH_4 emission and highlighted that riparian floodplain margins with water table below-ground contribute an additional 2.3–3.9 Tg CH_4 yr^{-1} to the atmosphere. Applying this to global tropical wetlands yield a non-flooded riparian tree CH_4 emission estimate of 6.4 Tg CH_4 yr^{-1} with recognition that the area-related extrapolation is uncertain (Gauci et al., 2022).

While studies so far suggest CH_4 emissions from the floodplain forest are significant, the variability and regulation remains largely unknown, including the extent to which the spatial variability is driven by soil dynamics, climate, flooding regime, or tree species traits. For instance, white-water (carrying sediments from the Andes), clear-water (draining the ancient shields) and black-water (draining white sand areas and soils with humic substances) are known to emit different quantities of CH_4 (Pangala et al., 2017), thereby greatly influencing the rates and overall regional annual CH_4 estimates in synergy with ecosystem processes including plant influences on CH_4 fluxes (Fig. 1). The nutrients associated with water types strongly determine the floodplain forest ecology and species composition. While studies in other forested wetlands highlight a link between tree traits and tree CH_4 flux (Barba et al., 2019; Covey and Megonigal, 2019), the Amazonian flooded forest tree species influence on CH_4 flux remains unclear.

In recent years there has been a renewed threat to Amazon forests from the expansion of cattle ranching, low-productivity agriculture, dams, mining, fire, deforestation and intensified flooding and prolonged dry period, changing the face of the flooded forests at an alarming rate. How CH_4 emissions, particularly from flooded trees, respond to such change is still unclear. Amazonian tree mortality rates are already increasing in many intact forests and Amazonian forest species composition has been affected by flooding and recent droughts. The mortality

of wet-affiliated Amazonian tree genera has increased in places where the dry season has intensified (Aleixo et al., 2019) or where the hydrology was changed by damming (Assahira et al., 2017). Such changes may have profound impact on the CH_4 dynamics from flooded forests and on future tropical CH_4 emissions.

4.6. Vegetation-related CH_4 emissions in other forests

Beyond the Amazon floodplain, the number of CH_4 flux measurements from tree stems growing on temperate and tropical peatlands, in upland forest ecosystems and in riparian forests has been increasing. Temperate ecosystems growing in both riparian lowland ecosystems and peatlands have demonstrated CH_4 emissions from both ash trees (*Fraxinus mandschurica*; (Terazawa et al., 2007), alder (*Alnus glutinosa;* (Gauci et al., 2010; Pangala et al., 2015) and birch (*Betula pubescens*; (Pangala et al., 2015). All trees tended to demonstrate a decrease in stem emissions with distance from the forest floor as found in many other studies of wetland tree emissions. The two species birch and alder measured in a UK alder carr ecosystem, tended to operate differently in terms of their seasonal CH_4 emissions with birch giving a large range of emissions depending on season of up to ~ 200 μg m^{-2} h^{-1} in summer and as low as ~ 50 μg m^{-2} h^{-1} in winter. This is in contrast to alder, where emissions ranged between ~ 100 μg m^{-2} h^{-1} in winter and around ~ 180 μg m^{-2} h^{-1} in summer (Pangala et al., 2015) suggesting differences in the CH_4 transport mechanisms from soil to emission, between the tree species. More controlled mesocosm experiments with alder saplings gave further insights into factors controlling the size of emissions (Pangala et al., 2014) with pore water CH_4 concentrations and stem lenticel density exhibiting a major control over emissions.

Further controls over tree stem emissions have been found for Southeast Asian peat swamp forests where a large range of CH_4 fluxes measured from 10 peatland tree species (zero to ~ 200 μg m^{-2} h^{-1}) seemed to be controlled by wood specific density (with the higher the wood density, the lower the emission), soil pore water CH_4 concentrations and stem diameter (Pangala et al., 2014). Cumulatively, emissions from tree stems in these ecosystems, as with those from the Amazon floodplain, dominated ecosystem emissions when scaled. This is in contrast to emissions from trees in neotropical peatlands in Panama where trees contributed ~ 30 % of total ecosystem emissions where factors such as species identity, stem diameter, water level and soil temperature explained much of the observed variance in tree stem emission (Sjögersten et al., 2020). Fluxes, were, however larger than those from SE Asian peat swamps with individual stem fluxes, particularly near the stem base in the range 1–30 mg m^{-2} d^{-1}. While palm emissions in these Panamanian peat swamps tended to be negligible, confining tree-stem emissions solely to hard wood trees, in Peruvian peatlands palm stems tended to emit substantial quantities of CH_4 (Soosaar et al., 2022).

In upland ecosystems, trees inhabit areas of lower water availability given free draining soils and substrates and so there is less soil CH_4 being produced in relatively sparse anaerobic microsites. That said, emissions are still observed, particularly at the stem bases (30 cm above the forest floor) in Panamanian upland trees where emissions at around ~ 100 μg m^{-2} h^{-1} were comparable to those observed in Borneo peat swamps and temperate alder carr. Other results, tend to conflict with some trees demonstrating some emission, but with no clear vertical pattern of exchange and with high variability (Pitz et al., 2018; Barba et al., 2019, 2021) though net uptake has been observed in other studies (Machacova et al., 2021; Gauci et al., 2022).

While trees are clearly capable of emitting soil-derived CH_4 at their stem bases, uptake of CH_4 further up the tree stem has been suggested (Jeffrey et al., 2020; Gauci et al., 2022). In parallel, there is a growing literature regarding abiotic oxic CH_4 production at plant and litter surfaces generating emissions (reviewed by Carmichael et al., 2014; Liu et al., 2015). This literature is based on observations of CH_4 release from plant tissue enclosed in CH_4-free vials or chambers. Mechanisms are discussed and plant produced molecules with detachable methyl groups are potential precursors. The CH_4 release seem enhanced by UV-light, increasing temperature, reactive oxygen species and other types of plant stress. Measured CH_4 production rates are often low in absolute numbers in the experimental settings but scaling to large plant surface areas results in global emission estimates in the order of 8–176 Tg CH_4 y^{-1} (Carmichael et al., 2014; Liu et al., 2015) to a large extent from forests, or 1–31 % of the global CH_4 emissions (using a global top-down estimate of 576 Tg CH_4 yr^{-1}; Table 1). Because of the high uncertainty in extrapolation of small-scale incubation studies and limited field scale observations, this flux was not yet specifically considered in recent global CH_4 budgets (Saunois et al., 2020), and large emissions from aerobic CH_4 production on plants and forests are challenging to reconcile with in-situ observations at present. There may be some bias in in-situ flux measurements if not properly capturing UV-effects, but top-down inversion estimates based on atmospheric concentration gradients in space and time should capture all emissions. Hence, overall tree and vegetation emissions at ecosystem scales remain enigmatic and represent an important challenge to constrain and predict the global CH_4 budget.

4.7. Coastal ecosystems

Globally, vegetated coastal areas including salt marshes, mangroves and seagrass meadows are estimated to emit 3.6–6.2 Tg CH_4 yr^{-1}, with the highest fluxes observed in salt marshes followed by mangroves and seagrass meadows (Table 1) (Al-Haj and Fulweiler, 2020; Rosentreter et al., 2021). As previously described in other environments, the roots can transport CH_4 from the sediments directly to the atmosphere bypassing the CH_4 oxidation in the sediments. In an Australian mangrove, tree emissions from pneumatophores (roots growing upwards into the air for gas exchange increasing root system O_2 access) accounted for ~ 26 % of the mangrove emissions (Jeffrey et al., 2019). Although no direct evidence of plant-mediated emissions from seagrass have been found in the literature, it has been suggested that dead seagrass or detached parts deposited in the sediment can provide methylated compounds that can sustain CH_4 production for a long time (Schorn et al., 2022). As in other freshwater environments, plants and cyanobacteria have a key role as suppliers of organic matter. A main difference from freshwater environments is that coastal environments tend to be sulfate-rich areas, and sulfate-reducing microorganisms outcompete methanogens for organic substrates limiting CH_4 production (Oremland and Polcin, 1982; Schorn et al., 2022). Zhuang et al. (2018) observed that methylotropic methanogenesis contributed to 43–87 % of the total CH_4 production in the sulfate reduction zone at the top layer of the sediment, and the remaining produced by hydrogenotrophic methanogenesis. The lower layers of the sediment, where sulfate was depleted, 67–98 % of the CH_4 was produced by hydrogenotrophic methanogenesis. Acetoclastic methanogenesis contributed a maximum of 31 % of the CH_4 production in organic-rich sediment (Zhuang et al., 2018). Due to the thicker sediment redox gradient where sulfate metabolism dominates, CH_4 production is confined to deeper sediment layers than in freshwaters. Therefore, plant mediated CH_4 emissions in coastal areas may be more extensive via plants with deeper roots. Despite this limitation, methylotropic methanogenesis can still maintain significant CH_4 production, sustaining a sediment-water flux of approximately 1.7 mg CH_4 m^{-2} d^{-1} in seagrass sediments (Schorn et al., 2022). Coastal environments are estimated to account for up to ~ 1 % of the global CH_4 budget and contribute more than 60 % of the marine CH_4 emission (Al-Haj and Fulweiler, 2020).

Sulfate reduction is associated with anaerobic oxidation of CH_4 (AOM), which can significantly influence the fluxes of CH_4 from the sediment to the water column in coastal areas (Egger et al., 2018). In addition to AOM, rooted plants transport oxygen to the root zone and sediment, where aerobic methane oxidation can occur. Fluxes from deforested mangroves and cut seagrass indicate an increase in CH_4

emissions that was attributed to cessation of the O_2 transport and oxidation in the sediment (Giani et al., 1996).

As in any other aquatic ecosystem, plants have a major role as source of organic substrates. Therefore, CH_4 emissions from coastal environments may increase with intensified land-use and eutrophication of coastal areas leading to greater primary production and organic matter sediment load (Rosentreter et al., 2021).

5. Conclusions and need for future studies

Overall, primary production is indirectly the foundation for all contemporary non-fossil CH_4 emissions, corresponding to approximately 80 % of the annual atmospheric CH_4 budget, or 431–671 Tg CH_4 yr^{-1} including fluxes from agriculture, forestry, other land use, biomass burning, and from the waste sector (Saunois et al., 2020; bottom-up fluxes 2008–2017 used). In addition, plants can influence the extent and dynamics of ecosystem CH_4 fluxes in many ways (Fig. 1). Importantly, plant communities respond rapidly to environmental change. Therefore, adequate understanding and predictions of relevant plant community features are key to adequate assessments of future landscape CH_4 emissions. To approach such understanding, improved quantitative knowledge on CH_4 fluxes from plant habitats under varying conditions are needed. This leads to several demands on future ecosystem-level research of vegetation-related CH_4 fluxes including:

- All CH_4 sources and sinks associated with vegetation need to be properly identified and quantified, and fluxes with different regulation need to be distinguished.
- Flux variability should be examined across spatial and temporal scales of relevance for local habitat/vegetation communities to distinguish short-term local variability from long-term large-scale trends.
- Comprehensive long-term ecosystem CH_4 flux assessments are needed, simultaneously quantifying plant-related emissions and other major types of emissions, along with careful characterization of properties and processes in studied ecosystems that can provide regulatory or predictive understanding. This should be done at sites representative of different vegetation types, to support dynamic ecosystem scale modelling of CH_4 flux.
- Tropical ecosystems need increased scientific attention, given their great importance for contemporary and future CH_4 emissions.
- For flux extrapolation, more accurate areal distributions of key ecosystems and habitats based on criteria optimized for estimating CH_4 emissions are needed. This includes, e.g., distinguishing different types of vegetated wetlands, such as the respective areas of bogs, fens and marshes in precise and dynamic ways that capture changes over time (Melack and Hess, 2022).

Addressing these key knowledge gaps effectively would greatly benefit from improvements in the methodologies to assess greenhouse gas emissions, vegetation dynamics, and potential driver variables at high resolution across landscapes (Bastviken et al., 2022). Because plant communities can change quickly in response to land use, hydrology, and climate, an appropriate understanding of present and future plant community dynamics are essential to predict CH_4 emissions in a rapidly changing world.

CRediT authorship contribution statement

DB: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **CT, SRP, VG, AEP:** Data curation, Investigation, Formal analysis, Writing – original draft, Writing – review & editing. **MK:** Investigation, Validation, Writing – review & editing. **MG:** Software, Formal analysis, Visualization. **MBR:** Formal analysis, Visualization. **HOS:** Data curation, Investigation, Formal analysis, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data are available via already published literature.

Acknowledgements

DB, MK, MG, and HOS acknowledge the European Research Council (ERC H2020 Grant no. 725546 METLAKE), and the Swedish Research Councils VR (Grant no. 2016-04829) and Formas (Grant nos. 2018-01794 and 2018-00570). CT was supported by ERC H2020 Grant no. 851181 FluxWIN and the Helmholtz Impulse and Networking Fund. VG acknowledges support from the UK NERC (Grants nos. NE/J010928/1 and NE/N015606/1 as part of The Global Methane Budget MOYA consortium), the AXA Research Fund 426, and the Royal Society. SRP acknowledges support from the Royal Society Dorothy Hodgkin Research Fellowship (Grant no. DH160111). AEP acknowledges funding from the Swedish Research Council Formas (Grant no. 2021-02429).

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