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Review

Plant-mediated CH_4 exchange in wetlands: A review of mechanisms and measurement methods with implications for modelling

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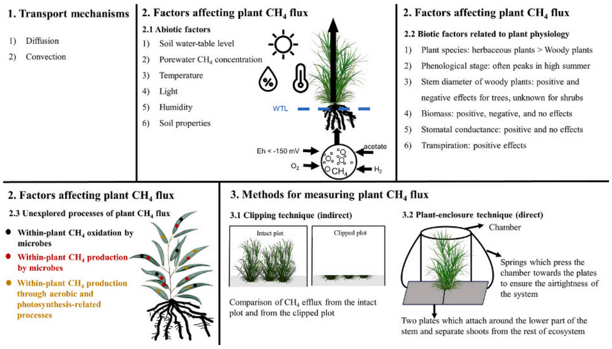
HIGHLIGHTS

- Abiotic and biotic factors, and their interactions affect plant-mediated CH_4 transport (PMT).
- Plant-mediated CH_4 exchange (PME) include PMT, within-plant CH_4 production and oxidation.
- PME can be measured by the clipping technique and plant-enclosure technique.
- Spatial and temporal variation, plant traits, and data-model fusion method should be considered for assessing ecosystem PMT.

GRAPHICAL ABSTRACT



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ABSTRACT

Plant-mediated CH_4 transport (PMT) is the dominant pathway through which soil-produced CH_4 can escape into the atmosphere and thus plays an important role in controlling ecosystem CH_4 emission. PMT is affected by abiotic and biotic factors simultaneously, and the effects of biotic factors, such as the dominant plant species and their traits, can override the effects of abiotic factors. Increasing evidence shows that plant-mediated CH_4 fluxes include not only PMT, but also within-plant CH_4 production and oxidation due to the detection of methanogens and methanotrophs attached to the shoots. Despite the inter-species and seasonal differences, and the probable contribution of within-plant microbes to total plant-mediated CH_4 exchange (PME), current process-based ecosystem models only estimate PMT based on the bulk biomass or leaf area index of aerenchymatous plants. We highlight five knowledge gaps to which more research efforts should be devoted. First, large between-species

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variation, even within the same family, complicates general estimation of PMT, and calls for further work on the key dominant species in different types of wetlands. Second, the interface (rhizosphere-root, root-shoot, or leaf-atmosphere) and plant traits controlling PMT remain poorly documented, but would be required for generalizations from species to relevant functional groups. Third, the main environmental controls of PMT across species remain uncertain. Fourth, the role of within-plant CH_4 production and oxidation is poorly quantified. Fifth, the simplistic description of PMT in current process models results in uncertainty and potentially high errors in predictions of the ecosystem CH_4 flux. Our review suggest that flux measurements should be conducted over multiple growing seasons and be paired with trait assessment and microbial analysis, and that trait-based models should be developed. Only then we are capable to accurately estimate plant-mediated CH_4 emissions, and eventually ecosystem total CH_4 emissions at both regional and global scales.

1. Introduction

Methane (CH_4) is a powerful greenhouse gas with a global warming potential more than 30 times higher than that of carbon dioxide (Saunois et al., 2016). Despite covering only around 5 % of the global land surface (Mitsch and Gosselink, 2000; Prigent et al., 2007), wetlands are the largest individual source of atmospheric CH_4 (Saunois et al., 2020), offering anoxic soil conditions favourable for methanogenesis (Garnett et al., 2020; Lai, 2009). However, the uncertainty in estimating wetland CH_4 emissions is still large (Saunois et al., 2020), partly due to the large differences in CH_4 emissions from different wetland ecosystems and latitudinal patterns (Bao et al., 2021; Gauci et al., 2022; Johnson et al., 2022; Pangala et al., 2017; Treat et al., 2021). For example, the wet and nutrient-rich fens often have high CH_4 emissions (Bao et al., 2021; Bellisario et al., 1999), while CH_4 emissions from the ombrotrophic raised bogs (Bubier, 1995) and marine coastal wetlands are often small (Noyce and Megonigal, 2021).

Recent studies have suggested that increasing wetland CH_4 emissions are partly responsible for the global atmospheric CH_4 growth in 2020 (Peng et al., 2022; Zhang et al., 2023), highlighting the importance of understanding the wetland processes responsible for CH_4 emissions. CH_4 transport is a critical component of wetland CH_4 emissions as it regulates the fraction and the rate of soil-produced CH_4 being released into the atmosphere (Walter and Heimann, 2000). Soil-produced CH_4 can be transported to the atmosphere through diffusion, ebullition, and through vascular plants (King et al., 1998; Yang et al., 2022).

To cope with the anoxic environment, wetland plants have developed aerenchymatous tissues to transport oxygen from shoots to roots. Through the same pathway but a reversed direction, soil-produced CH_4 can be transported to the atmosphere, bypassing oxidation in the oxic surface layer. In wetlands, plant-mediated CH_4 transport (PMT), a low-resistance pathway for CH_4 emissions, can account for over 90 % of total ecosystem CH_4 emissions (Dorodnikov et al., 2011; Ge et al., 2023a; Riutta et al., 2020; Villa et al., 2020; Yang et al., 2022). The effect of PMT is so strong that it can deplete porewater CH_4 concentration, and it significantly increases ecosystem CH_4 emissions (Dise, 1993; Noyce et al., 2014; Shannon et al., 1996a; Van Der Nat and Middelburg, 2000).

The pioneer work of PMT was conducted by Sebacher et al. (1985), who confirmed that aquatic plants play a crucial role in exchanging gases between wetlands and the atmosphere through surveying CH_4 emissions from 22 common wetland species. After that, PMT has been investigated for almost four decades across a range of rice paddies, tropical and temperate wetlands, and boreal peatlands (Aulakh et al., 2000a, 2000b; Ding et al., 2005; Ge et al., 2023a, 2023b; Holzapfel-Pschorn and Seiler, 1986; Hu et al., 2016; Koelbener et al., 2010; Nouchi et al., 1990; Pangala et al., 2017; Pangala et al., 2015; Shannon et al., 1996; Yang et al., 2022). These efforts have led to understanding of species differences, temporal and spatial variations and drivers on total emissions, summarized in several reviews (Bridgham et al., 2013; Gong et al., 2020; Olefeldt et al., 2013; Turetsky et al., 2014). Surprisingly, only a limited number of studies have directly investigated the drivers controlling PMT (Ge et al., 2023a, 2023b; Korrensalo et al., 2021). Besides, plant species and traits have been found to explain herbaceous PMT better than any abiotic factors (Korrensalo et al., 2021). However, to our knowledge, none of the existing studies combine herbaceous PMT measurements and traits analysis to reveal which proxy should be used to predict PMT at an ecosystem level.

Since Schütz et al. (1989) first reported that stems of trees can emit CH_4, many mesocosm experiments and field studies have confirmed this phenomenon (Pangala et al., 2017; Pangala et al., 2015). More recent studies have also detected CH_4 emissions from tree branches and canopy (Machacova et al., 2016; Tenhovirta et al., 2022), revealing potentially important new sources of CH_4 in forest ecosystems. There is growing evidence that regardless of the growing habitat in wetland or upland forests, trees may contribute significantly to ecosystem CH_4 flux (Pangala et al., 2015; Wang et al., 2016). These results and processes of tree CH_4 flux dynamics in forest ecosystems have been summarized in several recent reviews (Barba et al., 2019; Covey and Megonigal, 2019) and are outside the scope of this review.

Instead, for shrubs, common in many wetland types, mechanisms and factors controlling the CH_4 flux have been poorly studied. In some studies, the presence of shrubs has been found to attenuate ecosystem CH_4 flux (Halmeenmäki et al., 2017; Ge et al., 2023a, 2023b). Halmeenmäki et al. (2017) found in a mesocosm experiment that all the studied shrubs increased the amount of methanotrophic bacteria in the rhizosphere, which was further reflected in higher soil CH_4 consumption compared to a bare soil. These studies call for further assessment of the interactive effects of shrubs with soil and eventually of their effects on wetland CH_4 dynamics.

The review by Vroom et al. (2022) thoroughly discusses the physiological processes controlling CH_4 transport through different wetland plants, including trees, emergent and floating plants, as well as submerged plants. However, they and none of the previous reviews discusses the impacts of traits and phenology of wetland plants on PMT or the production/oxidation of CH_4 within plants. Furthermore, the earlier reviews lack discussion on the formulation of PMT in the existing process models. We are focusing this review accordingly, and avoid, to the extent feasible, repeating the contents of the previous reviews.

In most empirical studies, PMT has been estimated by comparing CH_4 flux from intact plant plots to those clipping plots where plants had been clipped (Ding et al., 2005; Garnett et al., 2020; Whiting and Chanton, 1992). This method is called the clipping technique, whose reliability has been challenged by the residual effect, the peak of releasing substrate due to the gradual death of an unnatural number of roots after clipping shoots (Noyce, 2009; Riutta et al., 2020). The clipping technique can also terminate the substrate provision and oxygen transport by the clipped shoots. These interfering effects can be avoided if CH_4 fluxes from plants are directly measured by creating a sealed mesocosm enclosing the shoots, which does not disturb the roots. This is known as the plant-enclosure technique (Dorodnikov et al., 2011). However, both techniques have their own advantages and shortcomings that warrant a review to support future efforts for empirical PMT studies.

A lack of a thorough synthesis also hinders modelling of PMT. PMT along with the other CH_4 transport processes is included in process-based models that are used to predict wetland CH_4 emissions, but the simplistic description of PMT and lack of empirical data about the process have been identified as significant sources of uncertainty in these models (Ma et al., 2022; Wania et al., 2010). Furthermore, besides plants acting as conduits for CH_4 produced in the peat, laboratory and field studies show that CH_4 emissions from plants may also involve within-plant CH_4 production and oxidation (Keppler et al., 2006; Larmola et al., 2010) (Fig. 1). While Sphagna and the associated CH_4 oxidation have been widely studied (Kip et al., 2010; Kox et al., 2020; Liebner et al., 2011; Petro et al., 2023), for herbaceous and woody species, field-scale information of within-plant processes has just started to emerge (Ge et al., 2023a; Tenhovirta et al., 2022). Consequently, we introduce a novel term, plant-mediated CH_4 exchange (PME), which may include PMT as well as production and oxidation of CH_4 occurring in the shoots of plants.

Our aim is to synthesize information needed to understand and describe PMT and PME, to propose research needs of PME based on identified current gaps, and to provide guidelines for improving models of PMT and PME. We first summarize gas transport mechanisms in plants, including ventilation mechanisms and key interfaces (transition/transport zones in Fig. 1) restricting the transport. Second, we discuss biotic and abiotic drivers controlling PME. Third, we discuss and compare the current methods for measuring PME. Fourth, we report how PMT has been included in existing ecosystem process models and suggest ways to improve ecosystem CH_4 modelling.

To give the reader a perspective of the increasing body of literature on PME, a search in Web of Science produced over 1000 papers with the key word 'plant CH_4 emission' since 1985 when Sebacher et al. (1985) published the pioneer work of PMT. To filter through this large body of literature, we focused on articles investigating PMT as well as within-plant CH_4 production and oxidation in herbaceous plants, and we excluded the processes and fluxes linked to peatland mosses which have been widely studied (Larmola et al., 2010; Putkinen et al., 2014) and trees that have been reviewed before (Barba et al., 2019; Covey and Megonigal, 2019; Putkinen et al., 2021).

2. Transport mechanisms

Soil-produced CH_4 escapes into the atmosphere by three main mechanisms: passive diffusion, ebullition, and plant-mediated CH_4 transport (PMT). Diffusion of gases in water is slow. Accordingly, in wetlands, up to 90 % of soil-derived CH_4 is oxidized in the oxic soil layers before reaching the atmosphere through passive diffusion (Tveit et al., 2019). Ebullition can occur when dissolved CH_4 is supersaturated in porewater, causing bubble formation and forcing their way to the surface (Schütz et al., 1989; Strack et al., 2005). Due to the low solubility of CH_4 in water (23–40 mg l^{-1} at 0–20 °C), ebullition can be an important pathway from wetland surfaces without plants or during the early growing season when plant biomass is low, but its contribution diminishes as plants mature (Chanton and Dacey, 1991). Ebullition also requires a direct path between the pores where bubbles form and the

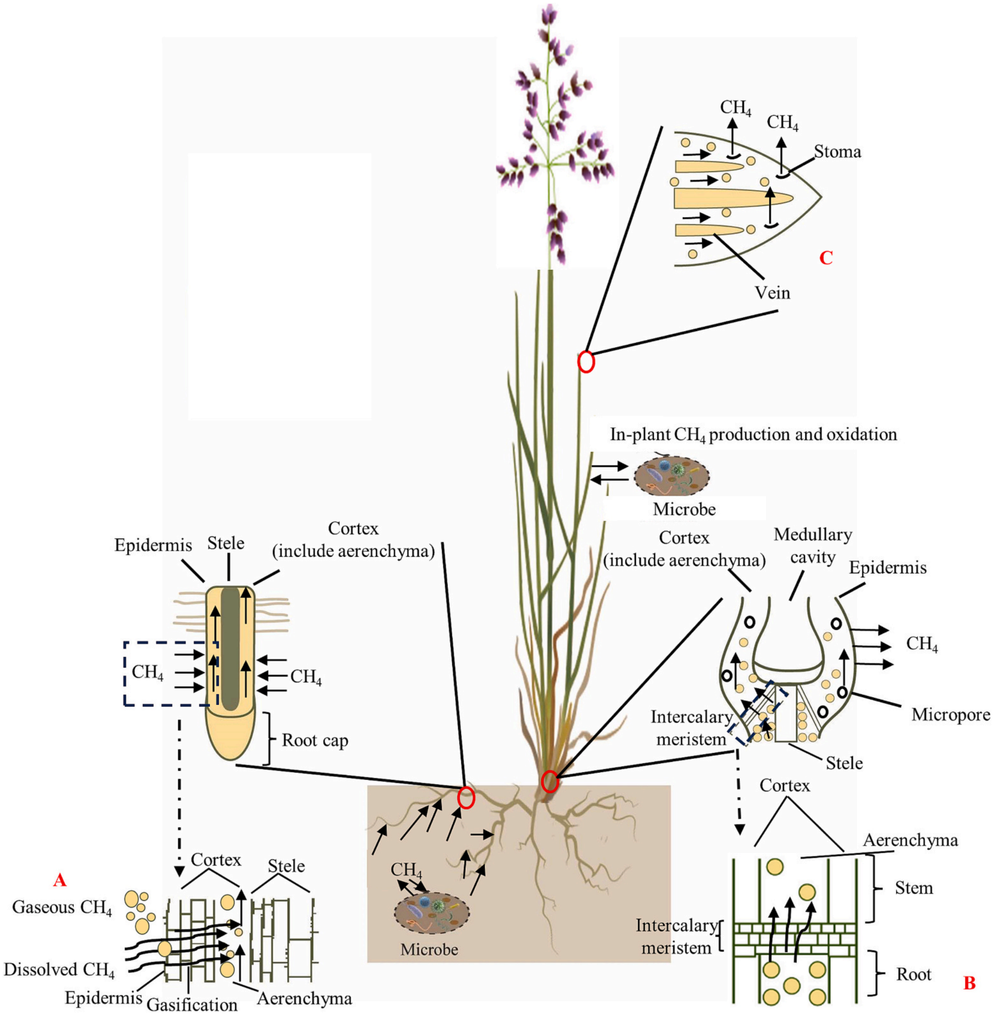


Fig. 1. Schematic of plant-mediated CH_4 exchange (PME) in wetlands, including plant-mediated transport (PMT) and production and oxidation of CH_4 occurring in the shoots of plants. The amount of PMT depends on the rates at which soil-produced CH_4 enters the roots (A), moves through the interface between the roots and shoots (B), and moves out of micropores in the stem or stomata in the leaves (C). Red circles denote the key interfaces restricting PMT. Modified from Dou et al. (2017).

atmosphere. Plants with aerenchymatous tissues offer a path of less resistance for CH_4 transport compared to diffusion and ebullition and, consequently, provide a significant pathway to the atmosphere (Garnett et al., 2020; Korrensalo et al., 2021; Shannon et al., 1996). PMT involves plant-mediated diffusion as well as convective transport.

2.1. *Plant-mediated diffusion*

Diffusive CH_4 transport within aerenchyma occurs whenever a concentration gradient exists between the soil and plant air spaces, and between the plant air spaces and the atmosphere. Respiration consumes oxygen (O_2) from roots, leading to a concentration gradient that facilitates O_2 diffusion from shoots to roots, and finally from roots to the rhizosphere. When rhizospheric CH_4 concentration is higher than the atmospheric CH_4 concentration, the outflux of O_2 from roots is accompanied by an influx of CH_4, which subsequently diffuses upward in the aerenchyma and eventually escapes into the atmosphere. Thus, plants can be viewed as an extension of the atmosphere into the anoxic CH_4-producing soil. Diffusive transport is the dominant ventilation method for smaller monocotyledonous plants which seldom grow in deep water (Korrensalo et al., 2021; Moore et al., 2011).

Plants can release CH_4 into the atmosphere from micropores in the stem, and from stomata or intercellular spaces on leaves (Morrissey et al., 1993; Nouchi et al., 1990; Shannon et al., 1996). If stomata are the major CH_4 release site, their closure also controls diffusive CH_4 transport through plants, which could be expected to result in diurnal or seasonal variations in CH_4 flux and vary over time of the day and season. If stomata are not the major CH_4 release site, CH_4 may also be released through the micropores or intercellular spaces in some plants (Schimel, 1995; Shannon et al., 1996). In such plants, CH_4 flux would be expected to show little variation over shorter time scales (e.g., diurnally) due to the long-time scale of changes in the CH_4 concentration gradient in the soil-plant-atmosphere-continuum (days and weeks) (Ding et al., 2004). Besides, seasonal variations in CH_4 flux may be mild as diffusive flux through micropores or intercellular space does not drop significantly when plants are senescing (Noyce et al., 2014; Pangala et al., 2015; Shannon et al., 1996).

The rate of gas diffusion from plants to the atmosphere is lower than would be expected based on the partial pressure of CH_4 around the roots (Den Van Der Gon and Van Breemen, 1993). Thus, besides diffusion, other controls play a role too. These include the rates at which CH_4 is transported into the root aerenchyma, transported through the interface between the roots and shoots, and then released through the interface between plant and the atmosphere (Fig. 1). These controls for CH_4 transport have been most extensively studied in rice. PMT in rice has been found to decrease significantly after root cutting, and to increase along with increasing temperature in the root zone, suggesting that it is determined by the processes involved in CH_4 passing through the roots (Hosono and Nouchi, 1997). Using scanning electron microscopy (SEM), Butterbach-Bahl et al. (2000) observed that PMT in rice was restricted by the root-shoot interface with parenchymatical cell layers. The same conclusion was also reached by Groot et al. (2005) by measuring the gas conductance of the root-shoot interface. Moreover, SEM also indicated that CH_4 was released from micropores on the leaf sheaths (Butterbach-Bahl et al., 2000; Nouchi et al., 1990). Wang et al. (1997) further concluded that rice leaf is only important for releasing CH_4 in the early growing stage when stems are small and the number of nodes is limited. All these facts suggest that the key interface controlling CH_4 transport in rice is either the interface between the rhizosphere and roots, or between the roots and shoots.

Of wetland plant species that diffusively transport gas, the key interface controlling PMT has been thoroughly examined in *Juncus effusus* through a series of manipulation experiments with results showing that the lateral roots and the root tips are important for gas movement (Henneberg et al., 2012). *Carex aquatilis* is another wetland species addressed by several studies in the past 30 years, yet the rate-limiting step for it still remains an open question. Morrissey et al. (1993) concluded that the leaves and stomata restrain gas transport through *C. aquatilis* based on the observation that CH_4 flux decreased significantly following stomatal closure induced by the application of an antitranspirant to the plant surface or by enclosure in an opaque chamber. In support for the stomatal control for CH_4 transport, Schimel (1995) observed a substantial increase in CH_4 flux through *C. aquatilis* after clipping the shoots. Yet, Kelker and Chanton (1997) observed no such increase in CH_4 flux through *C. aquatilis* after clipping shoots and thus concluded that the highest resistance occurred at the rhizosphere-root or root-shoot interfaces. Through a clipping experiment and SEM of fine roots, rhizome, and culm, Kutzbach et al. (2004) further narrowed down the rate-limiting step for *C. aquatilis* to the dense root exodermis. However, they did not use SEM to examine the root-shoot interface, which could potentially override the root exodermis as the most restrictive zone for transport. Although so few plant species have been examined for their species-specific PMT rate-limiting plant part, the existing literature points out that the same plant part does not seem to be the main restriction across species in the same genus. Identifying the exact plant part that has the largest control on PMT is a complicated task requiring investigation of plant morphology and anatomy of different plant parts accompanied with systematically designed manipulative experiments. Conducting such thorough investigations across a larger range of aerenchymous species remains a challenge.

2.2. *Convective transport*

Convective transport of gases is defined as their movement from a high-pressure area to a low-pressure area (Brix et al., 1992). Thus, it occurs if partial pressure gradients between the inside and outside of a plant are large enough to impact the total pressure in the plant (Armstrong et al., 1992). One mechanism of convective transport is thermo-osmotic pressurization, which means that a temperature difference between the inside and outside of a plant leads to the diffusion of gases from the colder exterior to the warmer interior, which can increase internal pressure (Armstrong and Armstrong, 1990). Another mechanism is humidity-induced pressurization (Armstrong et al., 1992; Brix et al., 1996), in which the high humidity inside a plant dilutes internal O_2 and nitrogen (N_2) concentrations and, thus, O_2 and N_2 are transported along the concentration gradient from the atmosphere into the leaves. This eventually increases the internal pressure (Van Den Berg et al., 2020). Because of these two mechanisms, a pressure difference between leaf and root is built up, resulting in convective transport of gases from the site of high pressure (leaves) to the site of low pressure (root) (Brix et al., 1992; Van Den Berg et al., 2020). From the roots, gases either enter the soil or escape into the atmosphere through rhizomes connected to older leaves (Brix et al., 1992). Generally, pressurization and convection stop at night when stomata close and atmospheric humidity approaches 100 % (Armstrong and Armstrong, 1991; Armstrong et al., 1992). Thus, the interior of plants accumulates soil-derived gases which are then flushed out by convection after sunrise when stomata open (Armstrong and Armstrong, 1991). This can lead to convective transport displaying strong diurnal variation and the maximum flux strongly and only correlating with shoot CH_4 concentration measured before the onset of the gas flow (Yavitt and Knapp, 1998).

Moreover, convective transport is an important adaptation to growth in anoxic conditions and offers competitive advantages over plants with diffusive transport (Armstrong et al., 1992; Brix et al., 1996). Many wetland plants (e.g., *Phragmites*, *Typha*, and *Nuphar* (Armstrong et al., 1988; Brix et al., 1992)) with cylindrical culm and linear leaves have a pressurized transport system (Brix et al., 1992; Käki et al., 2001; Sorrell and Brix, 2003) and usually grow in deeper water (Bendix et al., 1994; Dacey, 1981; Van Den Berg et al., 2020). Yet, these plants vary remarkably in how effectively they convert internal pressurization into convection due to different internal resistance to airflow (Brix et al., 1992). For most species with pressurized transport systems, the most restrictive zone for airflow is the interface between the root and shoot that contains compact meristematic tissue (Brix et al., 1992). Interestingly, recent studies provide compelling evidence that trees in forested wetlands might also have pressurized transport systems (Pangala et al., 2015; Pitz and Megonigal, 2017; Rice et al., 2010).

3. Factors affecting plant CH_4 emissions

A mechanistic understanding of how plants regulate ecosystem CH_4 emissions through the conduit effect would significantly improve the predictions of future CH_4 emissions under a changing climate. For this, we need to improve our understanding of key controls on PMT. Overall, PMT is affected by both abiotic and biotic factors, and their interactions. The changing climate will lead to changes in abiotic factors, e.g., temperature and soil moisture, and successional changes in vegetation, all of which eventually affect PMT and ecosystem CH_4 emissions.

3.1. Abiotic factors

3.1.1. Water-table level

A temporarily rising soil water-table level (WTL) can increase PMT by exposing more roots to anoxic conditions with higher CH_4 concentration, resulting in more CH_4 entering roots (Ding et al., 2002; Moore et al., 2011; Noyce et al., 2014). Yet when WTL is above the soil surface, it can also reduce PMT by blocking CH_4 fluxes from plant shoots into the atmosphere (Hirota et al., 2004; Nouchi et al., 1990; Wang et al., 1997). Some studies report that temporary variations in WTL do not affect PMT if WTL varies only slightly and/or the dominant plant species are deep-rooted (Andresen et al., 2017; Bellisario et al., 1999; Bhullar et al., 2013a; Schimel, 1995). All these results imply that the effects of WTL on PMT can be site/species-specific.

WTL affects PMT also indirectly. Over longer terms (years), WTL controls the vegetation types. Sites with persistently high WTL and shallow if any oxic soil layer are often dominated by deep-rooted graminoid species, especially *Carex* and *Eriophorum*, that have a high gas transport capacity (Bubier et al., 2005; Bubier et al., 1995; Bubier et al., 1993), whereas drier sites with oxic conditions extending deeper into the soil are often dominated by shallow-rooted shrubs with a low gas transport capacity (Bubier, 1995; Shannon et al., 1996b). In addition, WTL affects the rates of CH_4 production and oxidation (Ding et al., 2003; Ding et al., 2005; Schimel, 1995; Bastviken et al., 2023) as well as the amount of peat volume where oxidation can happen (Riutta et al., 2020), both of which can determine the CH_4 supply to roots and indirectly affect the PMT (Turetsky et al., 2014). Higher WTL can stimulate methanogenesis in the short- to mid-term by increasing the amount of substrate available in or being produced directly into the inundated, anoxic soil layers (Ding et al., 2003; Knox et al., 2021), but it can also inhibit methanogenesis in the long term due to reduced vascular plant biomass and substrate input to soil (Turetsky et al., 2014). Clearly, depending on the temporal scale of changes, the effects of WTL on PMT can vary in both magnitude and direction.

3.1.2. Porewater CH_4 concentration

As an indicator of CH_4 supply to roots, porewater CH_4 concentration ($[CH_4]_{pw}$) can positively affect PMT (Ding et al., 2004; Nouchi and Mariko, 1993; Pangala et al., 2014; Pangala et al., 2015). However, some studies also found no relationship between $[CH_4]_{pw}$ and PMT, which might be owing to at least three potential reasons (Aulakh et al., 2000a, 2000b; Ge et al., 2023a; Käki et al., 2001; Van Der Nat et al., 1998). Firstly, the response of PMT to the $[CH_4]_{pw}$ may generally be saturating; yet species vary in how fast they reach their maximum PMT as the $[CH_4]_{pw}$ rises. For instance, rice plants showed such saturation at 14 μmol l^{-1} (Aulakh et al., 2000a, 2000b), whereas no sign of saturation was observed at 284 μmol l^{-1} for *C. rostrata* (Ge et al., 2023b). Second, the effects of $[CH_4]_{pw}$ can be masked by other controls, e.g., temperature and phenology (Ge et al., 2023a). Third, CH_4 stored in the intercellular airspace of plants might be the source of daytime CH_4 efflux, in addition to dissolved CH_4 in the porewater (Yavitt and Knapp, 1998).

$[CH_4]_{pw}$ can be used to calculate plant CH_4 transport efficiency (flux through plants per unit of $[CH_4]_{pw}$, (Ge et al., 2023a)) which describes to what extent PMT may respond to changes in the $[CH_4]_{pw}$. Even though this parameter is not yet commonly used, based on the results of Schimel (1995) it can be estimated that the transport efficiency of *Carex aquatilis* is higher than that of *Eriophorum angustifolium*, indicated by the greater flux through *C. aquatilis* than through *E. angustifolium* even though their roots were exposed to the same bulk of soil CH_4 supply. Correspondingly, Ge et al. (2023a) observed significantly higher transport efficiency for *Carex rostrata* than for other species (*Betula nana*, *Salix lapponum, Equisetum fluviatile* and *Comarum palustre*) that coexisted with it in the same subsite.

In an ecosystem with a single dominant species, seasonal changes in $[CH_4]_{pw}$ at the dominant rooting zone together with changes in PMT of the dominant species can provide clues about how the plant community controls ecosystem CH_4 flux (Chanton and Dacey, 1991; Dise, 1993; Shannon et al., 1996; Verville et al., 1998; Frenzel and Karofeld, 2000; Van Der Nat and Middelburg, 2000; Joabsson and Christensen, 2001; Noyce et al., 2014). A sharp decrease of $[CH_4]_{pw}$ and simultaneous increase of PMT indicate the importance of transport (Bansal et al., 2020). An increase in CH_4 oxidation or a decrease in CH_4 production could also explain the depletion of $[CH_4]_{pw}$, but they cannot to lead to an increase in PMT of the dominant species and ecosystem flux. Thus, it is necessary to measure $[CH_4]_{pw}$ together with plant traits and flux measurements to get a holistic picture of PMT and improve ecosystem modelling.

3.1.3. Temperature

The effects of temperature on ecosystem CH_4 flux have been well studied (Whiting and Chanton, 1993; Shannon et al., 1996; Kim et al., 1999; Joabsson and Christensen, 2001; Chen et al., 2020a, 2020b; Qian et al., 2022; Knox et al., 2021). Temperature can affect ecosystem CH_4 flux through microbial processes that are temperature dependent (Ueyama et al., 2020; Zhu et al., 2021). Considerably fewer studies have focused on the effects of temperature on PMT. Temperature, and the temperature difference between soil and the atmosphere can affect PMT as the temperature difference is a driver for pressurization and convection and, thus, regulates convective gas transport (Armstrong and Armstrong, 1991; Bendix et al., 1994; Knapp and Yavitt, 1995). Moreover, temperature is also expected to regulate passive diffusion by affecting diffusion coefficients or plant physiology, e.g., root permeability, stomatal conductance, photosynthesis and transpiration (Hosono and Nouchi, 1997; Li et al., 2019); yet, the effects of temperature on them are nonlinear and may be opposite. For example, temperature has a positive effect on photosynthesis activity until it reaches the thermal optimum, above which photosynthesis decreases (Yamasaki et al., 2002). High temperature can make the plants close their stomata to minimize water losses (Okamoto et al., 2022). Rising temperature also increases the diffusion coefficient, which directly influences diffusive CH_4 fluxes. However, the thermal optimum for photosynthesis and stomatal conductance is species-specific and, thus, more studies should be directed to assess the thermal optimum of at least the key species in each ecosystem. On the other hand, higher temperature also reduces the solubility of CH_4 in porewater and, thus, can decrease the amount of CH_4 entering into roots (Ge et al., 2023a). In the long-term, warming can cause changes in plant species cover and trait composition (Alkama et al., 2022; Laine et al., 2019; Zhang et al., 2022). However, it is unknown whether the change in PMT resulting from altered vegetation properties is significant for the ecosystem flux and to what extent the plasticity of traits within the existing species could impact PMT and thus ecosystem flux.

3.1.4. Light and humidity

Light is an important control for convective transport, which is fast on sunny and warm days with low relative humidity, and typically higher in daytime than in night-time when relative humidity can reach 100 % (Bendix et al., 1994). Under direct sunlight, the temperature inside of the plant increases faster than outside. This can affect the convective transport by several mechanisms. These include an increase in evaporation or humidity, which eventually increase leaves to air water-vapor pressure difference and drives more gas entering into plants, i.e., thermally enhanced humidity-induced diffusion (Armstrong and Armstrong, 1990). Also, as relative humidity is often being reduced in light conditions mainly due to rising air temperature, this offers less resistance for humidity-induced convection (Armstrong and Armstrong, 1991), and further increases the tendency of cooler gases to enter the plants by thermal transpiration (Grosse et al., 1991). On the other hand, light can also enhance convective transport by stimulating stomatal conductance (White and Ganf, 2000), which has also been found in plants that diffusively transport gas but release gas through stomata (Morrissey et al., 1993). Some diffusively transporting species that release CH_4 through stomata could be expected to respond to light and humidity; however, there is not enough evidence to assess how important this control is.

3.1.5. *Soil properties*

Soil properties, e.g., acidity, porosity, nutrient status, structure, and carbon content may affect PMT in direct and indirect ways. They can directly impact PMT by regulating plant traits, e.g., the development of aerenchyma in roots and shoots, root porosity and length, and root/shoot ratio (Kludze et al., 1993; Singh et al., 1998; Visser et al., 2000). Soil properties such as organic matter and nutrient content and environmental conditions such as redox potential also strongly affect the microbial community and CH_4 production and oxidation processes in the soil (Al-Haj and Fulweiler, 2020; Bastviken, 2022), which consequently control the supply of CH_4 to plant roots. For example, a nutrient-rich fertile environment stimulates plant growth and increases leaf chlorophyll concentration (Evans, 1989) (Shangguan et al., 2000), leading to a higher photosynthesis rate and a greater substrate supply to the soil via root exudation. This may further stimulate soil CH_4 production and oxidation, with feedbacks to the porewater CH_4 concentration that directly affects PMT, as described in Section 3.1.2.

Salinity has also been found to increase the chlorophyll content and photosynthetic efficiency of plants (Yang et al., 2020) which eventually increases the substrate supply to the soil. Yet, the effects soil parameters and interactions with plants can be complex, e.g., salinity may stimulate the connections of airspace in leaf, stem, and root and thus enhance gas transport, while it can also restrain gas transport by reducing the aerenchyma development near the root tip and root-shoot interface (Akhtar et al., 1998), or by hastening the death of leaves (Munns, 1993). Soil structure such as macropores and pore connectedness affect the vertical and lateral movement of gases in the soil (Christophersen and Kjeldsen, 2001; Kiuru et al., 2022a, 2022b). A peat layer with large pores, such as recently formed, little decomposed peat, or a degraded, thick peat with a tendency to form cracks (Liu et al., 2016), could therefore promote ebullition and thus discourage PMT. While the effects of soil properties on soil CH_4 fluxes have been rather well studied in upland and wetland ecosystems (Poffenbarger et al., 2011; Sun et al., 2016; Van Der Gon and Neue, 1995; Yang et al., 2023), the effects of soil properties on PMT are still poorly understood.

3.2. *Biotic factors related to the plant properties and physiology*

3.2.1. *Plant species*

Previous studies have confirmed that different plant species strongly differ in how they affect ecosystem CH_4 emissions (Bubier et al., 1995; Christensen et al., 2003; Ding et al., 2005; Joabsson and Christensen, 2001; Mueller et al., 2020; Bao et al., 2021; Bezabih Beyene et al., 2022). Different species produce different kind of substrate and thus, affect methanogenesis (Joabsson and Christensen, 2001). However, the mechanism that affects ecosystem emissions and is more important but has not been studied so much is the species-specific rate of PMT (Bhullar et al., 2013a; Koelbener et al., 2010; Korrensalo et al., 2021). Firstly, plants, within the same functional type and even within the same genus, vary in their transport mechanisms and responses to changes in environmental conditions (Korrensalo et al., 2021; Pangala et al., 2015). Species with pressurized transport systems can transport gas more efficiently than species relying on diffusion, and the former are more sensitive to changes in light, water vapor, and temperature (Armstrong and Armstrong, 1991; Käki et al., 2001; Yavitt and Knapp, 1998). Secondly, plant species vary in morphology, anatomy, and physiology, resulting in different amounts of CH_4 entering their roots and different rates at which CH_4 is transported through and out of the plants. Species with favourable traits, e.g., deep-penetrating and highly permeable roots with high porosity, large aerenchyma in roots and shoots, the lack of diaphragm, no compact meristematic tissue, soft epidermal layers and outer stem cells, often offer little resistance for gas movement and show high transport capacity (Andresen et al., 2017; Brix et al., 1992; Ding et al., 2005; Greenup et al., 2000; Sebacher et al., 1985). Thirdly, plants differ in rhizospheric CH_4 production and oxidation and thus the supply of CH_4 to roots (Aben et al., 2022; Kankaala et al., 2005; Ström et al., 2005).

Species has such a strong effect on CH_4 transport that it can even override the impacts of abiotic factors in certain ecosystems such as peatlands (Ge et al., 2023a; Korrensalo et al., 2021). Apart from the different traits that we discussed above, plant species also have niches along the gradients of environmental conditions (e.g., nutrient availability, temperature, and WTL) and, thus, they carry information on those abiotic factors which affect the CH_4 emissions. The ongoing climate change and the associated successional change in plant species dominance (Zhang et al., 2020) can cause a considerable shift in CH_4 emissions. To predict such effects, more species should be measured due to the species-level differences in CH_4 transport. However, considering the large number of different species often present in even a single wetland, including species-specific CH_4 transport in ecological modelling might be unfeasible. Similarly, it would be inefficient to aim at measuring the transport of all the species; instead, finding the traits which determine the transport characteristics of a given plant species would be a better solution.

3.2.2. *Phenological stage*

Plant phenology, i.e., seasonal development and senescence, is commonly denoted by leaf area index (LAI) in the process-based models. Plant phenology can affect ecosystem CH_4 flux by changing the availability of plant-produced substrates available to methanogens (Helfter et al., 2022; Lai et al., 2014a). This effect is, however, subject to a lag depending on the season, as during spring the methanogen community may not immediately be large enough after winter to use up the increased substrate (Chang et al., 2021). Phenology also affects PMT by impacting the mode of ventilation (Askaer et al., 2011; Kim et al., 1999), releasing sites (micropores or stomata) (Wang et al., 1997; Yavitt and Knapp, 1998), morphology (e.g., size and proportion of aerenchyma (Askaer et al., 2011; Kim et al., 1999), root permeability and length (Fagerstedt, 1992; Nouchi et al., 1994), root biomass (Kankaala et al., 2005), and leaf area), and physiology (transpiration, stomatal conductance, and senescence (Morrissey et al., 1993; Pangala et al., 2015)). Plant phenology can also indirectly affect PMT by regulating plant-associated CH_4 oxidation and production in the rhizosphere (Kankaala and Bergström, 2004; Lai et al., 2014b; Van Der Nat et al., 1998), and thus the amount of CH_4 entering the roots.

Phenology has been found to be a universal parameter affecting PMT (Ge et al., 2023b) but its dynamics and effects can be altered by climate change (Inouye, 2022; Numata et al., 2022). Thus, it is crucial to find a quasi-continuous proxy (e.g., vegetation greenness index from phenology camera or satellite image) for phenology when predicting PMT at the ecosystem scale. Besides, PMT measurements should be conducted over multiple growing seasons to cover the variation in phenological cycles and further investigate its impacts on PMT. Comparing PMT measurement results with historic measurements conducted at the same site can also offer useful information of the phenological changes and their impacts on PMT.

3.2.3. *Stem diameter of woody plants*

Stem diameter is a crucial factor affecting CH_4 emissions from trees (Pangala et al., 2015). The correlation between stem emissions and stem diameter varies among ecosystems: trees in wetlands display negative correlations (Pangala et al., 2017), and trees in uplands show positive correlations (Pitz et al., 2018; Wang et al., 2016). These contrasting results may result from sampling limitations such as species, a small range of diameters, small sample sizes, or the complex nature of field conditions that conflate many biotic and abiotic factors. The sources for the CH_4 can also be different, i.e., trees can transport soil-produced CH_4 in wetlands (Vainio et al., 2022) but CH_4 can be produced in stems themselves in uplands (Wang et al., 2016). Nevertheless, stem diameter can affect diffusion processes (Barba et al., 2019), and stem pH, also covarying with age of trees, driving changes in microbial communities within plants (Yip et al., 2019), which eventually impact stem CH_4 emissions. Despite the abundance of shrubs in many peatlands, the effect of stem diameter on shrub-mediated CH_4 flux is so far unknown. Future plant flux studies should consider including woody species with different stem diameters since the estimation error is unavoidable if measurements are based primarily on specimens with either small or large diameters.

3.2.4. *Biomass*

Shoot biomass of herbaceous plants is a surrogate for the plant conduit potential (Whiting and Chanton, 1993) due to its close relationship with stem cross-sectional area and root biomass (Gross et al., 1991; Whigham and Simpson, 1978), parameters crucial for gas transport. As shoot biomass often correlates with PMT (Ding et al., 2005; Wang et al., 1997), it is commonly used for normalizing the fluxes, i.e., expressing the CH_4 flux per unit of shoot biomass (mg CH_4 g^{-1} h^{-1}) (Korrensalo et al., 2021; Shannon et al., 1996). However, poor correlations have also been found in several species where the belowground parts of plants regulate the flux (Ge et al., 2023b; Hu et al., 2016; Kelker and Chanton, 1997).

Increasing belowground biomass may enhance PMT by offering more surface for soil-derived CH_4 entering plants (Bhullar et al., 2013b; Hu et al., 2016). However, greater belowground biomass may also reduce PMT by releasing more oxygen to the soil and thus stimulating rhizospheric CH_4 oxidation, which eventually reduces the amount of soil-derived CH_4 entering roots (Koelbener et al., 2010; Korrensalo et al., 2021; Münchberger et al., 2019). Therefore, it could be hypothesized that belowground biomass has an optimum level where it enhances PMT without enhancing CH_4 oxidation too much, and that this nonlinear relationship between belowground biomass and PMT would be further modulated by the other species-specific anatomical features. However, establishing such relationships across species would require laborious studies including measures of root characteristics.

Notably, belowground biomass or root biomass may also be poor predictors of gas transport (Joabsson and Christensen, 2001; Reid et al., 2015). PMT may be restricted by other plants traits, including other root parameters (length, surface area, porosity and permeability, fine and coarse root ratio) (Andresen et al., 2017; Bhullar et al., 2013a; Colmer., 2003; Henneberg et al., 2012; Li et al., 2022), the existence of compact meristematic tissues at the root-shoot interface (Aulakh et al., 2000b; Butterbach-Bahl et al., 2000; Den Van Der Gon and Van Breemen, 1993), and stomatal conductance (Joabsson and Christensen, 2001; Morrissey et al., 1993). Also, within-plant CH_4 production and oxidation that affect the amount of CH_4 coming out of the plants (Putkinen et al., 2021) may confound the effect. To date, the correlation between biomass and PMT has not been thoroughly examined, neither the effect of the specific anatomical and morphological factors on PMT, probably due to the complicated measurement setups required for this type of study.

3.2.5. *Stomatal conductance*

Increasing stomatal conductance can stimulate photosynthesis of wetland plants (Lawson and Vialet-Chabrand, 2019) which in turn affects CH_4 production and oxidation in the rhizosphere, regulated by substrate supply and oxygen supply (Ding et al., 2005; Whiting and Chanton, 1992). Stomatal conductance can also directly affect PMT if plants release CH_4 through stomata (Chanton et al., 1993; Morrissey et al., 1993; Schimel, 1995; Thomas et al., 1996).

Photosynthetically active radiation (PAR) can regulate stomatal conductance and thus correlate with PMT. However, PAR also drives some plants to aerobically form CH_4 (Keppler et al., 2006; Tenhovirta et al., 2022), making it difficult to tell whether increasing PAR enhances emissions via increasing stomatal conductance, aerobic CH_4 production, or the combination of both. This suggests that merely using traditional methods like clipping or shading to investigate the importance of stomatal control is insufficient (Joabsson and Christensen, 2001; Shannon et al., 1996), as these treatments change not only stomatal conductance but also light conditions and the amounts of precursors for aerobic CH_4 production (e.g., pectin (Bruhn et al., 2009), lignin, cellulose (Vigano et al., 2008), and methionine (Althoff et al., 2014)). Thus, other methods should be used for studying the importance of stomata in releasing CH_4, such as (i) spraying an antitranspirant that only blocks stomata but does not affect light conditions and precursor chemicals (Morrissey et al., 1993), (ii) conducting leaf incubation experiments under aerobic conditions to check for the presence of aerobic CH_4 production in leaves (Wang et al., 2011), or (iii) using scanning electron microscopy (SEM) to check whether the studied species have micropores on the stem or leaf sheath. If a species has micropores, it is unlikely to release CH_4 from stomata (Wang et al., 1997).

Notably, the importance of stomata for the transport mediated by *Carex aquatilis*, one of the most well-studied species in northern peatlands, shows site-dependent variation (Table 1). The causes underlying this are unclear. It might be due to variations in leaf sheath/bundle morphology in different ecosystems (Kelker and Chanton, 1997) but additional study of this regional variability and its causes is needed. To date, the importance of stomatal control has been widely studied for large emergent plants with the pressurized gas transport system that grow along the banks of marshes, ponds, lakes, and rivers (Armstrong and Armstrong, 1991; Armstrong et al., 1992; Brix et al., 1992); however, it is unclear for other wetland species, even for the most studied ones like *Carex* spp..

3.2.6. *Transpiration*

Almost all soil water in wetlands contains dissolved CH_4, and plants take up a large amount of water each day through roots and transport it to leaves via xylem (McGuire et al., 2007). Thus, if the water taken up by the roots contains dissolved CH_4, and if the CH_4 is not oxidized in the plants, then CH_4 must be released by transpiration. The possible pathway for transpiration-driven CH_4 emissions is: CH_4 is produced in soils, dissolved into water, absorbed by roots, gasified in the plants, and eventually emitted through plant surfaces (Kelker and Chanton, 1997; Kutzbach et al., 2004; MacDonald et al., 1998; Nouchi et al., 1990). The importance of transpiration-driven emission can be indicated by: (i)

Table 1
Results of stomatal control on *Carex aquatilis*-mediated CH_4 transport.

Ecosystem	Stomatal control observed	Reference
Arctic tundra and boreal taiga wetlands	Yes	Morrissey et al. (1993)
Arctic wet meadow tundra	Yes	Schimel (1995)
Arctic wet polygonal tundra	No	Kutzbach et al. (2004)
Boreal fen	No	Kelker and Chanton (1997)

plants with greater sap flow rate and stem CH_4 storage showing higher emissions (Gartner et al., 2009); (ii) whole plants displaying an order of magnitude greater emissions than detached leaves because the latter would not be replenished with water (Nisbet et al., 2009); (iii) a sudden drop of emissions during the night and leafless periods (Nisbet et al., 2009; Pangala et al., 2015).

Due to the low solubility of CH_4, dissolved CH_4 would easily escape from the sap flow to the air spaces in the plants, from where it can diffuse radially to the atmosphere (Anttila et al., 2023; Vainio et al., 2022). Thus, CH_4 cannot travel long distances, e.g., more than a few meters above the ground, driven by transpiration. This implies that whereas the CH_4 flux in the canopy of tall trees cannot be soil-derived CH_4, in low herbaceous vegetation the flux can consist of soil-derived CH_4. Still, we do not know what the fraction of transpiration-driven CH_4 emissions is, and assessing this can be challenging. Firstly, wetland herbs can absorb gaseous CH_4 from soil without water uptake (Nouchi et al., 1990). Secondly, CH_4 produced in the plants can also be dissolved into the sap (Anttila et al., 2023) and disturb the estimation. The importance of transpiration as a control or facilitator of CH_4 transport might be solved by providing labelled CH_4 as the source and quantifying carbon isotopes in transpiration.

3.3. *Previously unexplored processes of plant CH_4 emission*

3.3.1. *Microbial processes*

Microbes in the soil are the main facilitators of CH_4 production and oxidation, which determine porewater CH_4 concentration and thus are a major biotic factor affecting PMT. However, based on the recent studies, also within-plant microbes may have an impact on the plant-derived CH_4 emissions. Microbes on the surface or inside of trees can potentially produce CH_4 (Putkinen et al., 2021). Both shrubs and herbs can also potentially produce CH_4 through microbial processes as methanogens dwell in their shoots (Ge et al., 2023b), but that has not been quantified thus far. This is partly due to the difficulty of verifying within-plant microbial CH4 production which can be easily shrouded by PMT that can be active simultaneously. Further Recent field and laboratory studies have already observed CH_4 consumption by the shoots of plants belonging to different PFTs (tree, shrub, and herb) (Ge et al., 2023a; Ge et al., 2023b; Sundqvist et al., 2012). Accordingly, methanotrophs with both high and low affinity have been detected in the stem and leaves of trees (Covey et al., 2012; Doronina et al., 2004; Iguchi et al., 2012), *Sphagnum* mosses (Larmola et al., 2010; Putkinen et al., 2014), and different shrubs and herbs (Ge et al., 2023b). This contradicts the earlier idea of plants acting as passive “CH_4 straws” merely transporting CH_4 produced in the soil into the atmosphere in the case of herbs (Hu et al., 2016; Koelbener et al., 2010), or only affecting the ecosystem CH_4 flux by affecting the soil chemistry and microbial population in the case of shrubs (Cao et al., 2008; Halmeenmäki et al., 2017; Riutta et al., 2020). Instead, it is possible that also wetland plants can directly participate in CH_4 production and consumption. Notably, when conducting within-plant microbial analysis, different spatiotemporal aspects should be considered since Putkinen et al. (2021) reported that microbes in trees can differ significantly between young and old specimens, between heights of the same tree, and between the seasons.

3.3.2. *Non-microbial processes*

By using purified plant compounds and plant parts, laboratory measurements have demonstrated that precursor compounds (e.g., pectin (Keppler et al., 2006), cellulose, lignin (Vigano et al., 2008), or methionine (Althoff et al., 2014) can aerobically form CH_4. Such aerobic CH_4 formation is driven by radical oxygen species (ROS), a normal by-product of aerobic plant metabolism (i.e., aerobic respiration and photosynthesis) or induced by environmental stressors (e.g., ultraviolet radiation (Vigano et al., 2008), heat (Qaderi and Reid, 2009), or physical cutting (Wang et al., 2009)). Ernst et al. (2022) further concluded that aerobic CH_4 production can be found across all living organisms.

However, to date only a few studies confirm aerobic CH_4 production in the field and only in boreal trees (Machacova et al., 2016; Tenhovirta et al., 2022). Testifying aerobic CH_4 emissions from wetland herbs in situ seems impossible as they mostly grow in wet conditions and cannot cut off the supply of soil-derived CH_4. Yet, even if such emission exists, it can be assumed to be a quantitatively unimportant process in the ecosystem scale in wetlands, where CH_4 production in the soil is high and serves as the major source of CH_4. For woody species that can survive both in oxic and anoxic conditions, in situ measurements are possible, but need to be carefully designed and consider following points. Firstly, when measuring shoot emissions from woody species, they should grow in oxic soils to cut off soil-derived CH_4 supply. Secondly, soil incubation measurement should be included to show the possibility of oxic soils to produce CH_4. Thirdly, microbe analysis should also be included to demonstrate whether soil and plant specimens have methanogens and clarify the occurrence of methanogenesis. Fourth, CH_4 fluxes from stems and shoots should be measured simultaneously since higher fluxes can be observed in shoots if aerobic CH_4 production exists. Fifth, ancillary measurements such as observations of PAR, temperature, driving forces of aerobic CH_4 emission, should also be included. Only with thorough measurement set-ups can aerobic CH_4 production be testified in situ. Nevertheless, the detection of aerobic CH_4 production suggest the overlooked ways in which plants can affect the flow of CH_4 through them, usually as a side effect of some other process or feature.

4. Methods for estimating plant CH_4 emission

The estimated plant-mediated CH_4 emissions in wetlands substantially vary from 30 % to over 90 % of the total ecosystem emissions (Dorodnikov et al., 2011; Ge et al., 2023a; Noyce et al., 2014; Whiting and Chanton, 1992; Yang et al., 2022). Although the above-mentioned studies did not investigate the same species, the large variation can also partly be due to differences in measurement methods. Thus, it is important to evaluate the common measurement methods and to identify their advantages and pitfalls under certain situations.

4.1. *Clipping technique*

Most studies so far have indirectly estimated herbaceous plant-mediated CH_4 transport (PMT) using the clipping technique (Fig. 2). That involves comparing total ecosystem CH_4 emissions (soil and plant surface) from plots with intact plant communities to those from plots where plants responsible for emissions have been clipped off just above soil surface (Ding et al., 2003; Ding et al., 2005; Noyce et al., 2014; Whiting and Chanton, 1992). The clipping technique allows the use of the same chamber design in the intact and clipped plots. It is may then be assumed that the measurement artefacts are the same for both plots when partitioning the proportion of PMT to the total CH_4 emissions.

After the clipping treatment, the total CH_4 flux can decrease. This is because the reduction in exudates decreases the soil CH_4 production when the microbes run out of labile carbon, and also the end of transpiration decreases the transport of CH_4 dissolved in water. On the other hand, clipping shoots causes the gradual death of belowground parts and thus creates unnatural amounts of fresh root necromass, leading to a pulse of substrate release known as the residual effect (Dorodnikov et al., 2011; Riutta et al., 2020). If methanogenesis at the study site is substrate-limited, higher fluxes can initially be observed in clipped plots than in plots with intact plants. The duration of the residual effect depends on the plant species. Due to a high lignin content, the decomposition of shrub litter takes a longer time than that of herbaceous litter. However, much of the root biomass of shrubs will decompose under oxic conditions in the top layers of peat, and thus they don’t provide much fresh litter to the methanogen community (Murphy et al., 2009). A substantial fraction of herbaceous roots may decompose under anoxic conditions since they extend deeper into the soil than shrub roots (Saarinen, 1996). Taken together, when using clipping technique to quantify the contribution of plant-mediated CH_4 flux, multiple-year measurements should be conducted and it should be carefully considered which year's data should be used.

Another method for estimating herbaceous PMT indirectly involves measuring total CH_4 emissions from vegetated soil surface and subtracting CH_4 emissions from nearby bare soil (Askaer et al., 2011; Schimel, 1995). However, this method may not be applicable on sites with dense vegetation. Also, the CH_4 emissions from bare soil surfaces may not be similar to the soil emissions of vegetated surfaces that have more substrate available for methanogenesis and thus, some bias may be introduced by such variation. It further may not be always assumed that overall, the conditions in unvegetated plots are the same as in vegetated ones; there is usually a reason why plants did not colonize the unvegetated areas (Fig. 2).

4.2. Plant-enclosure technique

Herbaceous and woody PMT can also be directly measured by the plant-enclosure technique, which allows measurement of gas exchange of individual shoots, excluding other gas-exchanging surfaces (Dorodnikov et al., 2011; Frenzel and Rudolph, 1998; Ge et al., 2023a; Korrensalo et al., 2021; Kutzbach et al., 2004; Schimel, 1995). Notably, when measuring CH_4 flux from trees growing in wetland forests, plant-enclosure technique is also suitable but only a small part of stems and/or branches are enclosed in the chamber.

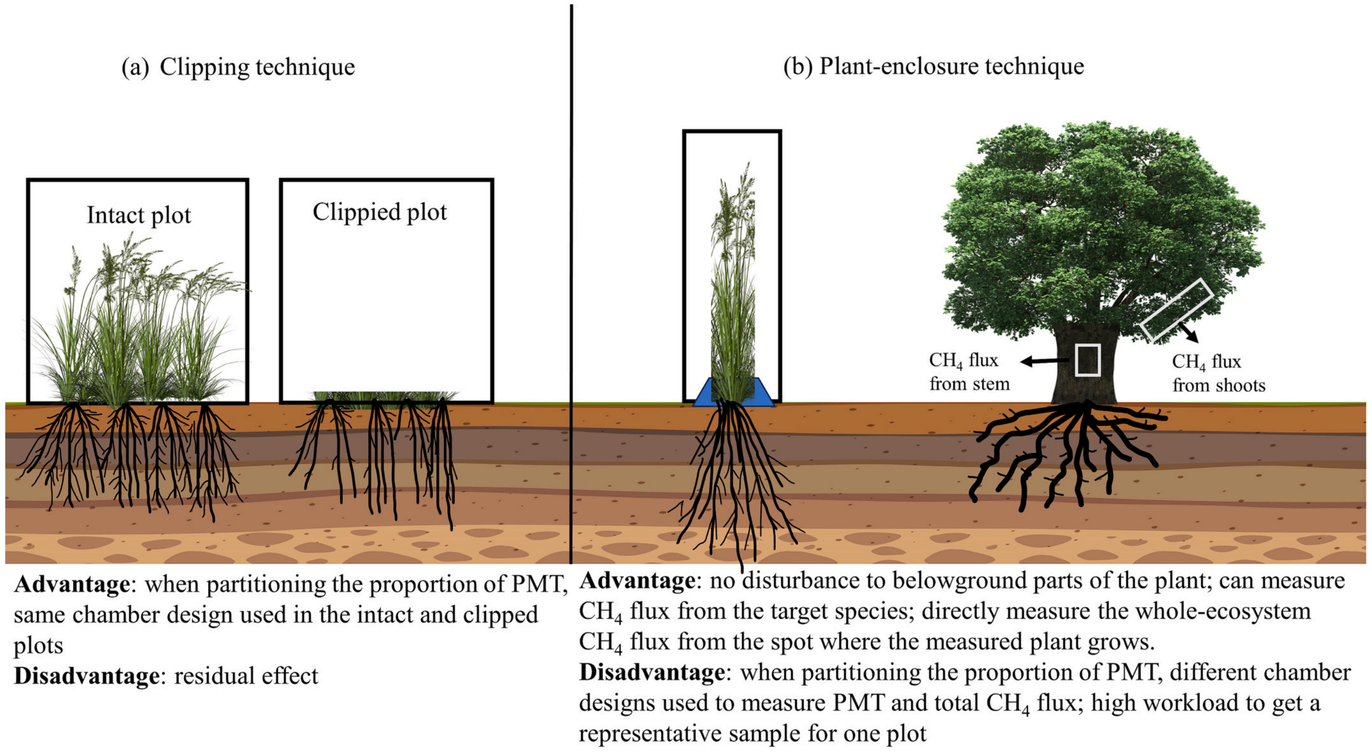
Unlike the clipping technique, the plant-enclosure technique does not affect roots or stop the supply of fresh photosynthates into the roots and soil and, thus, causes little disturbance to the measurement plot. Because of this, when investigating the effects of, e.g., temperature, precipitation, or nitrogen addition on PMT on the manipulation plot, the plant-enclosure technique is recommended. Besides, the plant-enclosure technique allows measuring plant CH_4 flux and its contribution to total flux of an individual plant species growing in a mixed stand. In contrast, separate plots are necessary for the clipping method. Thus, when investigating CH_4 flux from a specific species, the plant-enclosure technique is more convenient than the clipping technique.

Notably, the enclosure method measures the net effect of the plant on the system. By using this method while measuring PMT, we also include the substrate effect and effect of O_2 transport into the rhizosphere. While plant clipping stops all this, enclosure includes all this. We are still left unsure, what is the effect of CH_4 transport alone. Besides, the enclosure technique involves potentially large uncertainties when upscaling from individual shoot to ground area, and the work load is high because a large number of individual measurements are needed to get a representative sample for one plot.

5. Modelling implications

Many of the publications testing, developing or reviewing process-based models in wetlands identify the simplistic description of plant gas transport (PMT) as one of the most important sources of uncertainty in the current model predictions (Riley et al., 2011; Ueyama et al., 2023; Xu et al., 2016). In some models, it is treated as gaseous diffusion which is driven by the concentration gradient between the studied soil layer and the atmosphere (e.g., Riley et al., 2011). On the other hand, most models estimate PMT based on plant aerenchyma factors, which usually include the following aspects: vegetation type, plant density (LAI), root distribution and in-plant diffusivity (Kaiser et al., 2017; Raivonen et al., 2017; Salmon et al., 2022; Walter and Heimann, 2000). At least five perspectives in PMT identified in this review could be considered in the improvement of mechanistic CH_4 modelling.

First, the current process-based models lack description of spatial variability in PMT. Most current transport models are one-dimensional descriptions on the depth axis, and consider all properties homogeneous along the peatland area (Raivonen et al., 2017; Wania et al., 2010). However, soil properties (e.g., soil salinity, redox potential, nitrogen content, frozen depth) and root characteristics (e.g., root permeability, root length, proportion of root aerenchyma) usually vary



Advantage: when partitioning the proportion of PMT, same chamber design used in the intact and clipped plots
Disadvantage: residual effect

Advantage: no disturbance to belowground parts of the plant; can measure CH_4 flux from the target species; directly measure the whole-ecosystem CH_4 flux from the spot where the measured plant grows.
Disadvantage: when partitioning the proportion of PMT, different chamber designs used to measure PMT and total CH_4 flux; high workload to get a representative sample for one plot

Fig. 2. Illustration of clipping and plant-enclosure techniques. By using the clipping technique (a), herbaceous plant-mediated CH_4 flux is the net result of CH_4 flux from the intact plot (soil and plant surface combined) minus CH_4 flux from the clipped plot (only soil). By using the plant enclosure technique, herbaceous and woody plant-mediated CH_4 flux is the flux from the sealing chamber which separates the shoots or the stem of the plant from the rest of ecosystem.

at different soil layers and they all have impact on PMT. Therefore, utilizing different plant transport coefficients at different layers would be a straightforward solution for improving the predictability of plant transport CH_4 modelling. The approach of one-dimensional descriptions on the depth axis also omits any lateral gas transport in the soil, which might be important considering the high spatial variability in observed CH_4 fluxes (Christophersen and Kjeldsen, 2001). Lateral gas transport can be promoted by macropores (Liu et al., 2016; Kiuru et al., 2022a, 2022b). A model with a full set of soil spatial parameters would open the way into studying the causes of spatial variability, with plant roots being one possible contributing factor and the pore network another.

Second, the current process-based models also lack description of temporal variability in PMT. PMT has been observed to show seasonal variability between the phenological phases (Ge et al., 2023a) and even senesced plants may transport small quantities of CH_4 (Korrensalo et al., 2021). Including phenology-dependent effects would be much more challenging, involving detailed descriptions of plant physiology in the model, and parameterization with laboratory experiments involving several plant species, but may nevertheless have an impact on the model outcomes. Furthermore, the current process-based models also miss the potential effect of time lag between CH_4 substrate supply, production and transport. If the water table is at or above soil surface, CH_4 can reach the atmosphere immediately in a single time step by PMT (Zhuang et al., 2004). However, in reality, there are hysteretic responses between microbial and abiotic controls of CH_4 (Chang et al., 2021), meaning that the maxima of methanogen biomass, production of CH_4, and temperature have a time-lag between each other. That is a general pattern, not only specifically for PMT, but is relevant for all CH_4 transport processes.

Third, some process-based models group plants according to the traditionally-used plant functional types (PFTs, e.g., shrubs, sedges and forbs) which aim at grouping plant species with similar properties from the perspective of ecosystem functioning (Frolking et al., 2010; Wullschleger et al., 2014). PFTs can be an efficient way to count for variations in PMT, at least between plants with or without aerenchyma, since plants with aerenchyma transport much more CH_4 than those without. However, empirical research has demonstrated that species within the same “traditional” PFT can vary markedly in their CH_4 transport capacity and response to environmental drivers (Bhullar et al., 2013a; Korrensalo et al., 2021; Ström et al., 2005). Alternatively, specific PFTs based on CH_4 transport capacity should be created, or, preferably, a trait-based approach should be developed. There is currently an ongoing shift towards modelling plants through continuous traits rather than PFTs with ecosystem processes (Wullschleger et al., 2014), and such trait-based approach has been found to improve predictability of the model (Verheijen et al., 2012). Accounting for variation in traits (e.g., shoot/root ratio (Jackson, 1994), aerenchyma size (Garnet et al., 2005), and diameter of shoot base (Jackson, 1989), root length (Raivonen et al., 2017) and permeability (Beckett et al., 2001; Henneberg et al., 2012)) could be beneficial for predicting PMT.

Fourth, data-model fusion approach could provide insight into processes that are so far less known. For example, at the root-soil interface, dissolved CH_4 readily enters plant roots with water uptake, but it is less clear to what extent gaseous CH_4 may enter or exit the root. Furthermore, it is not clear if gaseous transport within aerenchyma is entirely diffusive, or if there is an advective component, driven by e.g., temperature differences. Such processes can be constrained based on observations using inverse modelling and data assimilation techniques (Peng et al., 2011).

Last but not least, the modelling community should follow closely the empirical work related to CH_4 production and oxidation inside the shoots and if this process seems like a relevant component in the ecosystem scale, then attempt to include it in the models.

6. Conclusions

Modelling CH_4 emissions from different ecosystem requires information of the abiotic and biotic factors mention above. Of particular importance is identifying the most restricting processes (e.g., belowground or aboveground parts of the plants) of CH_4 transport. The growing body of literature on plant-derived CH_4 flux show that plant CH_4 exchange processes are far more complex than merely transporting soil-produced CH_4. Plants can produce CH_4 through microbial and non-microbial processes. The methanotrophs attached to the shoots can also oxidize CH_4 produced by soils and plant themselves. These overlapping processes, their seasonality and drivers are critically important in process modelling to estimate ecosystem CH_4 fluxes in current and in future climates. We recommend multifaceted experiments which aim to investigate plant-derived flux, alongside its main source, environmental variables, plant morphology and physiology, microbes attached to different parts of plants. This may require the combination of flux measurement, labelling experiment, microbial and plant traits analysis. Only then, we can better quantify magnitudes, explain patterns, and reveal mechanisms and eventually lead to accurate predictions at ecosystem scale.

CRediT authorship contribution statement

Mengyu Ge: Writing – review & editing, Writing – original draft, Visualization. **Aino Korrensalo:** Writing – review & editing, Writing – original draft. **Raija Laiho:** Writing – review & editing, Visualization. **Lukas Kohl:** Writing – review & editing, Visualization. **Annalea Lohila:** Writing – review & editing. **Mari Pihlatie:** Writing – review & editing. **Xuefei Li:** Writing – review & editing, Writing – original draft. **Anna M. Laine:** Writing – review & editing. **Jani Anttila:** Writing – review & editing, Writing – original draft. **Anuliina Putkinen:** Writing – review & editing. **Weifeng Wang:** Writing – review & editing. **Markku Koskinen:** Writing – review & editing, Writing – original draft, Visualization.

Declaration of competing interest

The authors declare no conflicts of interest associated with this manuscript.

Data availability

No data was used for the research described in the article.

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