

**This is an electronic reprint of the original article.**

**This reprint *may differ* from the original in pagination and typographic detail.**

**Author(s):** Mengyu Ge, Aino Korrensalo, Raija Laiho, Lukas Kohl, Annalea Lohila, Mari Pihlatie, Xuefei Li, Anna M. Laine, Jani Anttila, Anuliina Putkinen, Weifeng Wang & Markku Koskinen

**Title:** Plant-mediated CH<sub>4</sub> exchange in wetlands: A review of mechanisms and measurement methods with implications for modelling

**Year:** 2024

**Version:** Published version

**Copyright:** The Authors 2024

**Rights:** CC BY-NC-ND 4.0

**Rights url:** <http://creativecommons.org/licenses/by-nc-nd/4.0/>

**Please cite the original version:**

Ge, M., Korrensalo, A., Laiho, R., Kohl, L., Lohila, A., Pihlatie, M., Li, X., Laine, A. M., Anttila, J., Putkinen, A., Wang, W., & Koskinen, M. (2024). Plant-mediated CH<sub>4</sub> exchange in wetlands: A review of mechanisms and measurement methods with implications for modelling. *Science of The Total Environment*, 914, 169662. <https://doi.org/10.1016/j.scitotenv.2023.169662>

All material supplied via *Jukuri* is protected by copyright and other intellectual property rights. Duplication or sale, in electronic or print form, of any part of the repository collections is prohibited. Making electronic or print copies of the material is permitted only for your own personal use or for educational purposes. For other purposes, this article may be used in accordance with the publisher's terms. There may be differences between this version and the publisher's version. You are advised to cite the publisher's version.



## Review

# Plant-mediated CH<sub>4</sub> exchange in wetlands: A review of mechanisms and measurement methods with implications for modelling

Mengyu Ge<sup>a,b,\*</sup>, Aino Korrensalo<sup>c,d</sup>, Raija Laiho<sup>d</sup>, Lukas Kohl<sup>a,b,c</sup>, Annalea Lohila<sup>e</sup>, Mari Pihlatie<sup>a,b,f</sup>, Xuefei Li<sup>b</sup>, Anna M. Laine<sup>g</sup>, Jani Anttila<sup>d</sup>, Anuliina Putkinen<sup>a,b</sup>, Weifeng Wang<sup>h</sup>, Markku Koskinen<sup>a,b</sup>

<sup>a</sup> Department of Agricultural Sciences, University of Helsinki, PO Box 56, Helsinki 00014, Finland

<sup>b</sup> Institute for Atmospheric and Earth System Research (INAR)/Forest Sciences, University of Helsinki, PO Box 56, Helsinki 00014, Finland

<sup>c</sup> Department of Environmental and Biological Sciences, University of Eastern Finland, PO Box 111, Kuopio 80101, Finland

<sup>d</sup> Natural Resources Institute Finland, Latokartanonkaari 9, Helsinki 00790, Finland

<sup>e</sup> Finnish Meteorological Institute, Erik Palménin aukio 1, Helsinki 00560, Finland

<sup>f</sup> Department of Agricultural Sciences, Viikki Plant Science Centre (ViPS), University of Helsinki, PO Box 56, 00014 Helsinki, Finland

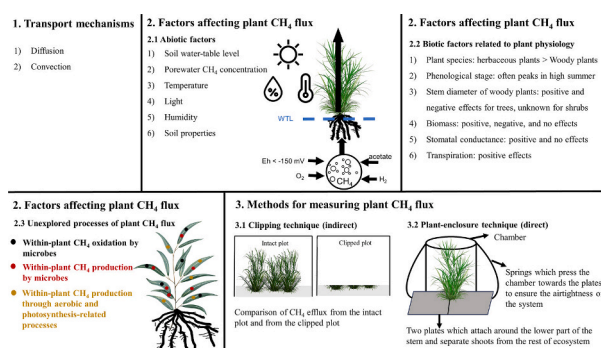
<sup>g</sup> Geological Survey of Finland, PO Box 1237, 70211 Kuopio, Finland

<sup>h</sup> College of Biology and the Environment, Nanjing Forestry University, 210037 Nanjing, China

## HIGHLIGHTS

- Abiotic and biotic factors, and their interactions affect plant-mediated CH<sub>4</sub> transport (PMT).
- Plant-mediated CH<sub>4</sub> exchange (PME) include PMT, within-plant CH<sub>4</sub> 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



## ARTICLE INFO

Editor: Jan Vymazal

## Keywords:

Plant CH<sub>4</sub> transport  
Mechanisms  
Drivers  
Processes  
Modelling  
Wetland plants

## ABSTRACT

Plant-mediated CH<sub>4</sub> transport (PMT) is the dominant pathway through which soil-produced CH<sub>4</sub> can escape into the atmosphere and thus plays an important role in controlling ecosystem CH<sub>4</sub> 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<sub>4</sub> fluxes include not only PMT, but also within-plant CH<sub>4</sub> 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<sub>4</sub> 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

\* Corresponding author at: Department of Agricultural Sciences, University of Helsinki, PO Box 56, Helsinki 00014, Finland.

E-mail address: [mengyu.ge@helsinki.fi](mailto:mengyu.ge@helsinki.fi) (M. Ge).

<https://doi.org/10.1016/j.scitotenv.2023.169662>

Received 3 July 2023; Received in revised form 22 December 2023; Accepted 22 December 2023

Available online 28 December 2023

0048-9697/© 2023 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

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<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> emissions, and eventually ecosystem total CH<sub>4</sub> emissions at both regional and global scales.

## 1. Introduction

Methane (CH<sub>4</sub>) 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<sub>4</sub> (Saunois et al., 2020), offering anoxic soil conditions favourable for methanogenesis (Garnett et al., 2020; Lai, 2009). However, the uncertainty in estimating wetland CH<sub>4</sub> emissions is still large (Saunois et al., 2020), partly due to the large differences in CH<sub>4</sub> 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<sub>4</sub> emissions (Bao et al., 2021; Bellisario et al., 1999), while CH<sub>4</sub> 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<sub>4</sub> emissions are partly responsible for the global atmospheric CH<sub>4</sub> growth in 2020 (Peng et al., 2022; Zhang et al., 2023), highlighting the importance of understanding the wetland processes responsible for CH<sub>4</sub> emissions. CH<sub>4</sub> transport is a critical component of wetland CH<sub>4</sub> emissions as it regulates the fraction and the rate of soil-produced CH<sub>4</sub> being released into the atmosphere (Walter and Heimann, 2000). Soil-produced CH<sub>4</sub> 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<sub>4</sub> can be transported to the atmosphere, bypassing oxidation in the oxic surface layer. In wetlands, plant-mediated CH<sub>4</sub> transport (PMT), a low-resistance pathway for CH<sub>4</sub> emissions, can account for over 90 % of total ecosystem CH<sub>4</sub> 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<sub>4</sub> concentration, and it significantly increases ecosystem CH<sub>4</sub> 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<sub>4</sub> 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 (Bridgman 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<sub>4</sub>, 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<sub>4</sub> emissions from tree branches and canopy (Machacova et al., 2016; Tenhoviirta et al., 2022), revealing potentially important new sources of CH<sub>4</sub> 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<sub>4</sub> flux (Pangala et al., 2015; Wang et al., 2016). These results and processes of tree CH<sub>4</sub> 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<sub>4</sub> flux have been poorly studied. In some studies, the presence of shrubs has been found to attenuate ecosystem CH<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> dynamics.

The review by Vroom et al. (2022) thoroughly discusses the physiological processes controlling CH<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> transport processes is included in process-based models that are used to predict wetland CH<sub>4</sub> 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  $\text{CH}_4$  produced in the peat, laboratory and field studies show that  $\text{CH}_4$  emissions from plants may also involve within-plant  $\text{CH}_4$  production and oxidation (Keppler et al., 2006; Larmola et al., 2010) (Fig. 1). While *Sphagnum* and the associated  $\text{CH}_4$  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; Tenhoviirta et al., 2022). Consequently, we introduce a novel term, plant-mediated  $\text{CH}_4$  exchange (PME), which may include PMT as well as production and oxidation of  $\text{CH}_4$  occurring in the shoots of plants.

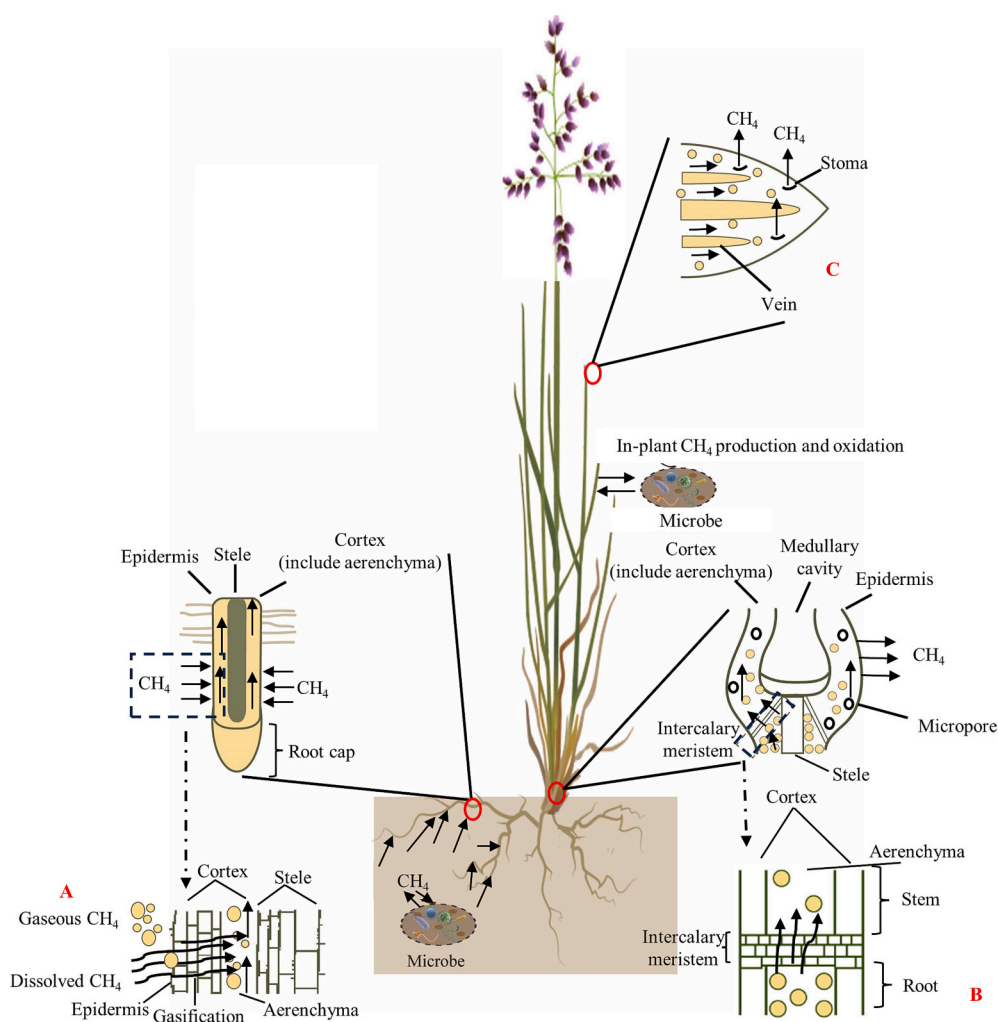
Our aim is to synthesize information needed to understand and describe PMT and PME, to propose research needs of PME based on identified current gaps, and to provide guidelines for improving models of PMT and PME. We first summarize gas transport mechanisms in plants, including ventilation mechanisms 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  $\text{CH}_4$  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  $\text{CH}_4$  emission’ since 1985 when Sebach 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  $\text{CH}_4$  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  $\text{CH}_4$  escapes into the atmosphere by three main mechanisms: passive diffusion, ebullition, and plant-mediated  $\text{CH}_4$  transport (PMT). Diffusion of gases in water is slow. Accordingly, in wetlands, up to 90 % of soil-derived  $\text{CH}_4$  is oxidized in the oxic soil layers before reaching the atmosphere through passive diffusion (Tveit et al., 2019). Ebullition can occur when dissolved  $\text{CH}_4$  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  $\text{CH}_4$  in water (23–40  $\text{mg l}^{-1}$  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  $\text{CH}_4$  exchange (PME) in wetlands, including plant-mediated transport (PMT) and production and oxidation of  $\text{CH}_4$  occurring in the shoots of plants. The amount of PMT depends on the rates at which soil-produced  $\text{CH}_4$  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<sub>4</sub> 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<sub>4</sub> 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<sub>2</sub>) from roots, leading to a concentration gradient that facilitates O<sub>2</sub> diffusion from shoots to roots, and finally from roots to the rhizosphere. When rhizospheric CH<sub>4</sub> concentration is higher than the atmospheric CH<sub>4</sub> concentration, the outflux of O<sub>2</sub> from roots is accompanied by an influx of CH<sub>4</sub>, 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<sub>4</sub>-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<sub>4</sub> 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<sub>4</sub> release site, their closure also controls diffusive CH<sub>4</sub> transport through plants, which could be expected to result in diurnal or seasonal variations in CH<sub>4</sub> flux and vary over time of the day and season. If stomata are not the major CH<sub>4</sub> release site, CH<sub>4</sub> may also be released through the micropores or intercellular spaces in some plants (Schimel, 1995; Shannon et al., 1996). In such plants, CH<sub>4</sub> 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<sub>4</sub> concentration gradient in the soil-plant-atmosphere-continuum (days and weeks) (Ding et al., 2004). Besides, seasonal variations in CH<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> 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 parenchymatous 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<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> transport, Schimel (1995) observed a substantial increase in CH<sub>4</sub> flux through *C. aquatilis* after clipping the shoots. Yet, Kelker and Chanton (1997) observed no such increase in CH<sub>4</sub> 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 aerenchymatous 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 thermodynamic 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<sub>2</sub> and nitrogen (N<sub>2</sub>) concentrations and, thus, O<sub>2</sub> and N<sub>2</sub> 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<sub>4</sub> 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<sub>4</sub> emissions

A mechanistic understanding of how plants regulate ecosystem CH<sub>4</sub> emissions through the conduit effect would significantly improve the predictions of future CH<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> concentration, resulting in more CH<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> concentration

As an indicator of CH<sub>4</sub> supply to roots, porewater CH<sub>4</sub> concentration ([CH<sub>4</sub>]<sub>pw</sub>) 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<sub>4</sub>]<sub>pw</sub> 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<sub>4</sub>]<sub>pw</sub> may generally be saturating; yet species vary in how fast they reach their maximum PMT as the [CH<sub>4</sub>]<sub>pw</sub> rises. For instance, rice plants showed such saturation at 14  $\mu\text{mol l}^{-1}$  (Aulakh et al., 2000a, 2000b), whereas no sign of saturation was observed at 284  $\mu\text{mol l}^{-1}$  for *C. rostrata* (Ge et al., 2023b). Second, the effects of [CH<sub>4</sub>]<sub>pw</sub> can be masked by other controls, e.g., temperature and phenology (Ge et al., 2023a). Third, CH<sub>4</sub> stored in the intercellular

airspace of plants might be the source of daytime CH<sub>4</sub> efflux, in addition to dissolved CH<sub>4</sub> in the porewater (Yavitt and Knapp, 1998).

[CH<sub>4</sub>]<sub>pw</sub> can be used to calculate plant CH<sub>4</sub> transport efficiency (flux through plants per unit of [CH<sub>4</sub>]<sub>pw</sub>, (Ge et al., 2023a)) which describes to what extent PMT may respond to changes in the [CH<sub>4</sub>]<sub>pw</sub>. 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<sub>4</sub> 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 co-existed with it in the same subsite.

In an ecosystem with a single dominant species, seasonal changes in [CH<sub>4</sub>]<sub>pw</sub> 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<sub>4</sub> 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<sub>4</sub>]<sub>pw</sub> and simultaneous increase of PMT indicate the importance of transport (Bansal et al., 2020). An increase in CH<sub>4</sub> oxidation or a decrease in CH<sub>4</sub> production could also explain the depletion of [CH<sub>4</sub>]<sub>pw</sub>, but they cannot lead to an increase in PMT of the dominant species and ecosystem flux. Thus, it is necessary to measure [CH<sub>4</sub>]<sub>pw</sub> 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<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> in porewater and, thus, can decrease the amount of CH<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> production and oxidation processes in the soil (Al-Haj and Fulweiler, 2020; Bastviken, 2022), which consequently control the supply of CH<sub>4</sub> 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<sub>4</sub> production and oxidation, with feedbacks to the porewater CH<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> 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; Kåki et al., 2001; Yavitt and Knapp, 1998). Secondly, plant species vary in morphology, anatomy, and physiology, resulting in different amounts of CH<sub>4</sub> entering their roots and different rates at which CH<sub>4</sub> 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<sub>4</sub> production and oxidation and thus the supply of CH<sub>4</sub> to roots (Aben et al., 2022; Kankaala et al., 2005; Ström et al., 2005).

Species has such a strong effect on CH<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> emissions. To predict such effects, more species should be measured due to the species-level differences in CH<sub>4</sub> transport. However, considering the large number of different species often present in even a single wetland, including species-specific CH<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> can also be different, i.e., trees can transport soil-produced CH<sub>4</sub> in wetlands (Vainio et al., 2022) but CH<sub>4</sub> 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<sub>4</sub> emissions. Despite the abundance of shrubs in many peatlands, the effect of stem diameter on shrub-mediated CH<sub>4</sub> 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<sub>4</sub> flux per unit of shoot biomass (mg CH<sub>4</sub> g<sup>-1</sup> h<sup>-1</sup>) (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<sub>4</sub> 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<sub>4</sub> oxidation, which eventually reduces the amount of soil-derived CH<sub>4</sub> 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<sub>4</sub> 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 plant 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<sub>4</sub> production and oxidation that affect the amount of CH<sub>4</sub> 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 Violet-Chabrand, 2019) which in turn affects CH<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> (Keppler et al., 2006; Tenhovirta et al., 2022), making it difficult to tell whether increasing PAR enhances emissions via increasing stomatal conductance, aerobic CH<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub>, 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<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub>, 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<sub>4</sub>, and if the CH<sub>4</sub> is not oxidized in the plants, then CH<sub>4</sub> must be released by transpiration. The possible pathway for transpiration-driven CH<sub>4</sub> emissions is: CH<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub>, dissolved CH<sub>4</sub> 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<sub>4</sub> cannot travel long distances, e.g., more than a few meters above the ground, driven by transpiration. This implies that whereas the CH<sub>4</sub> flux in the canopy of tall trees cannot be soil-derived CH<sub>4</sub>, in low herbaceous vegetation the flux can consist of soil-derived CH<sub>4</sub>. Still, we do not know what the fraction of transpiration-driven CH<sub>4</sub> emissions is, and assessing this can be challenging. Firstly, wetland herbs can absorb gaseous CH<sub>4</sub> from soil without water uptake (Nouchi et al., 1990). Secondly, CH<sub>4</sub> 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<sub>4</sub> transport might be solved by providing labelled CH<sub>4</sub> as the source and quantifying carbon isotopes in transpiration.

### 3.3. Previously unexplored processes of plant CH<sub>4</sub> emission

#### 3.3.1. Microbial processes

Microbes in the soil are the main facilitators of CH<sub>4</sub> production and oxidation, which determine porewater CH<sub>4</sub> 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<sub>4</sub> emissions. Microbes on the surface or inside of trees can potentially produce CH<sub>4</sub> (Putkinen et al., 2021). Both shrubs and herbs can also potentially produce CH<sub>4</sub> 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 CH<sub>4</sub> production which can be easily shrouded by PMT that can be active simultaneously. Further Recent field and laboratory studies have already observed CH<sub>4</sub> 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<sub>4</sub> straws” merely transporting CH<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub>. Such aerobic CH<sub>4</sub> 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<sub>4</sub> production can be found across all living organisms.

However, to date only a few studies confirm aerobic CH<sub>4</sub> production in the field and only in boreal trees (Machacova et al., 2016; Tenhoviirta et al., 2022). Testifying aerobic CH<sub>4</sub> 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<sub>4</sub>. Yet, even if such emission exists, it can be assumed to be a quantitatively unimportant process in the ecosystem scale in wetlands, where CH<sub>4</sub> production in the soil is high and serves as the major source of CH<sub>4</sub>. 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<sub>4</sub> supply. Secondly, soil incubation measurement should be included to show the possibility of oxic soils to produce CH<sub>4</sub>. Thirdly, microbe analysis should also be included to demonstrate whether soil and plant specimens have methanogens and clarify the occurrence of methanogenesis. Fourth, CH<sub>4</sub> fluxes from stems and shoots should be measured simultaneously since higher fluxes can be observed in shoots if aerobic CH<sub>4</sub> production exists. Fifth, ancillary measurements such as observations of PAR, temperature, driving forces of aerobic CH<sub>4</sub> emission, should also be included. Only with thorough measurement set-ups can aerobic CH<sub>4</sub> production be testified in situ. Nevertheless, the detection of aerobic CH<sub>4</sub> production suggest the overlooked ways in which plants can affect the flow of CH<sub>4</sub> through them, usually as a side effect of some other process or feature.

## 4. Methods for estimating plant CH<sub>4</sub> emission

The estimated plant-mediated CH<sub>4</sub> 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<sub>4</sub> transport (PMT) using the clipping technique (Fig. 2). That involves comparing total ecosystem CH<sub>4</sub> 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 may then be assumed that the measurement artefacts are the same for both plots when partitioning the proportion of PMT to the total CH<sub>4</sub> emissions.

After the clipping treatment, the total CH<sub>4</sub> flux can decrease. This is because the reduction in exudates decreases the soil CH<sub>4</sub> production when the microbes run out of labile carbon, and also the end of transpiration decreases the transport of CH<sub>4</sub> 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  $\text{CH}_4$  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  $\text{CH}_4$  emissions from vegetated soil surface and subtracting  $\text{CH}_4$  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  $\text{CH}_4$  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  $\text{CH}_4$  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  $\text{CH}_4$  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

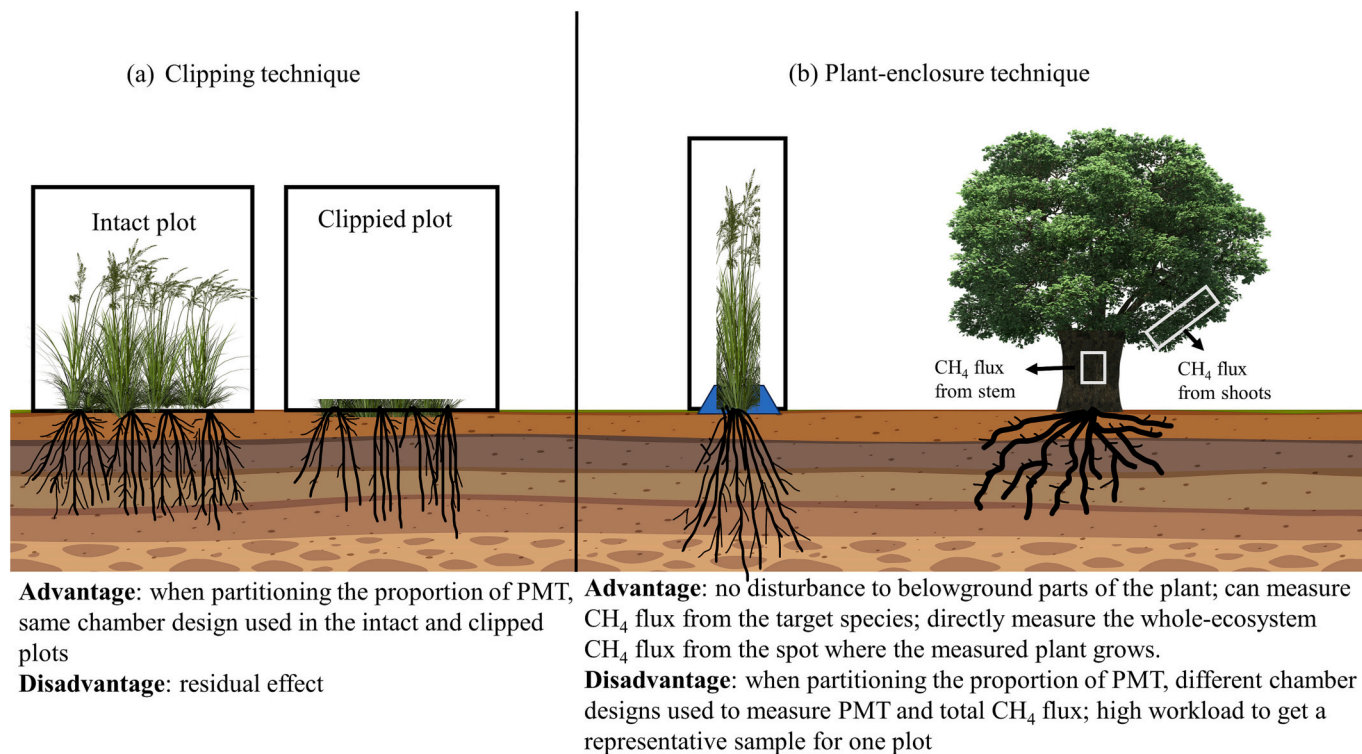
investigating  $\text{CH}_4$  flux from a specific species, the plant-enclosure technique is more convenient than the clipping technique.

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  $\text{O}_2$  transport into the rhizosphere. While plant clipping stops all this, enclosure includes all this. We are still left unsure, what is the effect of  $\text{CH}_4$  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  $\text{CH}_4$  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



**Fig. 2.** Illustration of clipping and plant-enclosure techniques. By using the clipping technique (a), herbaceous plant-mediated  $\text{CH}_4$  flux is the net result of  $\text{CH}_4$  flux from the intact plot (soil and plant surface combined) minus  $\text{CH}_4$  flux from the clipped plot (only soil). By using the plant enclosure technique, herbaceous and woody plant-mediated  $\text{CH}_4$  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<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> (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<sub>4</sub> substrate supply, production and transport. If the water table is at or above soil surface, CH<sub>4</sub> 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<sub>4</sub> (Chang et al., 2021), meaning that the maxima of methanogen biomass, production of CH<sub>4</sub>, 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<sub>4</sub> 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; Wulfschlegel 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<sub>4</sub> than those without. However, empirical research has demonstrated that species within the same “traditional” PFT can vary markedly in their CH<sub>4</sub> 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<sub>4</sub> 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 (Wulfschlegel 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<sub>4</sub> readily enters plant roots with water uptake, but it is less clear to what extent gaseous CH<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub> transport. The growing body of literature on plant-derived CH<sub>4</sub> flux show that plant CH<sub>4</sub> exchange processes are far more complex than merely transporting soil-produced CH<sub>4</sub>. Plants can produce CH<sub>4</sub> through microbial and non-microbial processes. The methanotrophs attached to the shoots can also oxidize CH<sub>4</sub> produced by soils and plant themselves. These overlapping processes, their seasonality and drivers are critically important in process modelling to estimate ecosystem CH<sub>4</sub> 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.

## Acknowledgement

This work was supported by the China Scholarship Council (CSC), the Academy of Finland (338980, 315415, 339489), the H2020 Marie Skłodowska-Curie Actions (843511), the H2020 European Research Council (757695) and the Academy of Finland Flagship funding for ACCC (337550). Finally, we thank Zhiying Yang for drawing Fig. 1.

## References

- Aben, R.C.H., Oliveira Junior, E.S., Carlos, A.R., van Bergen, T.J.H.M., Lamers, L.P.M., Kosten, S., 2022. Impact of plant species and intense nutrient loading on CH<sub>4</sub> and N<sub>2</sub>O fluxes from small inland waters: an experimental approach. *Aquat. Bot.* 180, 103527.
- Akhtar, J., Gorham, J., Qureshi, R., Aslam, M., 1998. Does tolerance of wheat to salinity and hypoxia correlate with root dehydrogenase activities or aerenchyma formation? *Plant Soil* 201, 275–284.
- Al-Haj, A.N., Fulweiler, R.W., 2020. A synthesis of methane emissions from shallow vegetated coastal ecosystems. *Glob. Chang. Biol.* 26, 2988–3005.
- Althoff, F., Benzing, K., Comba, P., McRoberts, C., Boyd, D.R., Greiner, S., et al., 2014. Abiotic methanogenesis from organosulphur compounds under ambient conditions. *Nat. Commun.* 5, 1–9.
- Alkama, R., Forzieri, G., Duveiller, G., Grassi, G., Liang, S., Cescatti, A., 2022. Vegetation-based climate mitigation in a warmer and greener world. *Nat. Commun.* 13, 606.
- Andresen, C.G., Lara, M.J., Tweedie, C.E., Loughheed, V.L., 2017. Rising plant-mediated methane emissions from arctic wetlands. *Glob. Chang. Biol.* 23, 1128–1139.



- Anttila, J., Tikkasalo, O.P., Hölttä, T., Lintunen, A., Vainio, E., Leppä, K., et al., 2023. Model of methane transport in tree stems: Case study of sap flow and radial diffusion. *Plant Cell Environ.* 47, 140–155.
- Armstrong, J., Armstrong, W., 1990. Light-enhanced convective throughflow increases oxygenation in rhizomes and rhizosphere of *Phragmites australis* (Cav.) Trin. *Ex Steud.* New Phytol. 114, 121–128.
- Armstrong, J., Armstrong, W., 1991. A convective through-flow of gases in *Phragmites australis* (Cav.) Trin. *Ex Steud.* Aquat. Bot. 39, 75–88.
- Armstrong, J., Armstrong, W., Beckett, P., 1988. *Phragmites australis*: a critical appraisal of the ventilating pressure concept and an analysis of resistance to pressurized gas flow and gaseous diffusion in horizontal rhizomes. *New Phytol.* 110, 383–389.
- Armstrong, J., Armstrong, W., Beckett, P., 1992. *Phragmites australis*: Venturi- and humidity-induced pressure flows enhance rhizome aeration and rhizosphere oxidation. *New Phytol.* 120, 197–207.
- Askaer, L., Elberling, B., Friberg, T., Jørgensen, C.J., Hansen, B.U., 2011. Plant-mediated CH<sub>4</sub> transport and C gas dynamics quantified in-situ in a *Phalaris arundinacea*-dominant wetland. *Plant Soil* 343, 287–301.
- Aulakh, M., Bodenbender, J., Wassmann, R., Rennenberg, H., 2000a. Methane transport capacity of rice plants. I. Influence of methane concentration and growth stage analysed with an automated measuring system. *Nutr. Cycl. Agroecosyst.* 58, 357–366.
- Aulakh, M., Wassmann, R., Rennenberg, H., Fink, Biology S.J.P., 2000b. Pattern and amount of aerenchyma relate to variable methane transport capacity of different rice cultivars. *Plant Biol.* 2, 182–194.
- Bansal, S., Johnson, O.F., Meier, J., Zhu, X., 2020. Vegetation affects timing and location of wetland methane emissions. *J. Geophys. Res. Biogeosci.* 125, e2020JG005777.
- Bao, T., Jia, G., Xu, X., 2021. Wetland heterogeneity determines methane emissions: a pan-arctic synthesis. *Environ. Sci. Technol.* 55, 10152–10163.
- Barba, J., Bradford, M.A., Brewer, P.E., Bruhn, D., Covey, K., van Haren, J., Megonigal, J. P., Mikkelsen, T.N., Pangala, S.R., Pihlatie, M., et al., 2019. Methane emissions from tree stems: a new frontier in the global carbon cycle. *New Phytol.* 222, 18–28.
- Bastviken, D., 2022. Methane. Elsevier, Oxford, pp. 136–154.
- Bastviken, D., Treat, C.C., Pangala, S.R., Gauci, V., Enrich-Prast, A., Karlson, M., et al., 2023. The importance of plants for methane emission at the ecosystem scale. *Aquat. Bot.* 184, 103596.
- Beckett, P.M., Armstrong, W., Armstrong, J., 2001. Mathematical modelling of methane transport by *Phragmites*: the potential for diffusion within the roots and rhizosphere. *Aquat. Bot.* 69, 293–312.
- Bellisario, L.M., Bubier, J.L., Moore, T.R., Chanton, J.P., 1999. Controls on CH<sub>4</sub> emissions from a northern peatland. *Glob. Biogeochem. Cycles* 13, 81–91.
- Bendix, M., Tornbjerg, T., Brix, H., 1994. Internal gas transport in *Typha latifolia* L. and *Typha angustifolia* L. 1. Humidity-induced pressurization and convective throughflow. *Aquat. Bot.* 49, 75–89.
- Bezabih Beyene, B., Li, J., Yuan, J., Dong, Y., Liu, D., Chen, Z., et al., 2022. Non-native plant invasion can accelerate global climate change by increasing wetland methane and terrestrial nitrous oxide emissions. *Glob. Chang. Biol.* 28, 5453–5468.
- Bhullar, G.S., Edwards, P.J., Olde, Venterink H., 2013a. Variation in the plant-mediated methane transport and its importance for methane emission from intact wetland peat mesocosms. *J. Plant Ecol.* 6, 298–304.
- Bhullar, G.S., Irvani, M., Edwards, P.J., Olde, Venterink H., 2013b. Methane transport and emissions from soil as affected by water table and vascular plants. *BMC Ecol.* 13, 1–9.
- Bridgman, S.D., Cadillo-Quiroz, H., Keller, J.K., Zhuang, Q., 2013. Methane emissions from wetlands: biogeochemical, microbial, and modeling perspectives from local to global scales. *Glob. Chang. Biol.* 19, 1325–1346.
- Brix, H., Sorrell, B.K., Orr, P.T., 1992. Internal pressurization and convective gas flow in some emergent freshwater macrophytes. *Limnol. Oceanogr.* 37, 1420–1433.
- Brix, H., Sorrell, B.K., Schierup, H.H., 1996. Gas fluxes achieved by in situ convective flow in *Phragmites australis*. *Aquat. Bot.* 54, 151–163.
- Bruhn, D., Mikkelsen, T.N., Øbro, J., Willats, W., Ambus, P., 2009. Effects of temperature, ultraviolet radiation and pectin methyl esterase on aerobic methane release from plant material. *Plant Biol.* 11, 43–48.
- Bubier, J., Moore, T., Savage, K., Crill, P., 2005. A comparison of methane flux in a boreal landscape between a dry and a wet year. *Glob. Biogeochem. Cycles* 19, 1–11.
- Bubier, J.L., 1995. The relationship of vegetation to methane emission and hydrochemical gradients in northern peatlands. *J. Ecol.* 83, 403.
- Bubier, J.L., Moore, T.R., Roulet, N.T., 1993. Methane emissions from wetlands in the midboreal region of northern Ontario, Canada. *Ecology* 74, 2240–2254.
- Bubier, J.L., Moore, T.R., Bellisario, L., Comer, N.T., Crill, P.M., 1995. Ecological controls on methane emissions from a Northern Peatland Complex in the zone of discontinuous permafrost, Manitoba, Canada. *Glob. Biogeochem. Cycles* 9, 455–470.
- Butterbach-Bahl, K., Papen, H., Rennenberg, H.J.P., 2000. Scanning electron microscopy analysis of the aerenchyma in two rice cultivars. *Phyton* 40, 43–55.
- Cao, G., Xu, X., Long, R., Wang, Q., Wang, C., Du, Y., Zhao, X., 2008. Methane emissions by alpine plant communities in the Qinghai-Tibet Plateau. *Biol. Lett.* 4, 681–684.
- Chang, K.Y., Riley, W.J., Knox, S.H., Jackson, R.B., McNicol, G., Poulter, B., Aurela, M., Baldocchi, D., Bansal, S., Bohrer, G., 2021. Substantial hysteresis in emergent temperature sensitivity of global wetland CH<sub>4</sub> emissions. *Nat. Commun.* 12, 2266.
- Chanton, J., Dacey, J., 1991. Effects of vegetation on methane flux, reservoirs, and carbon isotopic composition. In: Sharkey, T.D., Holland, E.A., Mooney, H.A. (Eds.), *Trace Gas Emissions by Plants*. Academic, San Diego, Calif., USA.
- Chanton, J.P., Whiting, G.J., Happell, J.D., Gerard, G., 1993. Contrasting rates and diurnal patterns of methane emission from emergent aquatic macrophytes. *Aquat. Bot.* 46, 111–128.
- Chen, H., Xu, X., Fang, C., Li, B., Nie, M., 2020a. Differences in the temperature dependence of wetland CO<sub>2</sub> and CH<sub>4</sub> emissions vary with water table depth. *Nat. Clim. Chang.* 11, 766–771.
- Chen, H., Zhu, T., Li, B., Fang, C., Nie, M., 2020b. The thermal response of soil microbial methanogenesis decreases in magnitude with changing temperature. *Nat. Commun.* 11, 5733.
- Christensen, T.R., Panikov, N., Mastepanov, M., Joabsson, A., Stewart, A., Öquist, M., Sommerkorn, M., Reynaud, S., Svensson, B.J.B., 2003. Biotic controls on CO<sub>2</sub> and CH<sub>4</sub> exchange in wetlands—a closed environment study. *Biochemistry* 64, 337–354.
- Christophersen, M., Kjeldsen, P., 2001. Lateral gas transport in soil adjacent to an old landfill: factors governing gas migration. *Waste Manag. Res.* 19, 579–594.
- Colmer, 2003. Long-distance transport of gases in plants: a perspective on internal aeration and radial oxygen loss from roots. *Plant Cell Environ.* 26, 17–36.
- Covey, K.R., Megonigal, J.P., 2019. Methane production and emissions in trees and forests. *New Phytol.* 222, 35–51.
- Covey, K.R., Wood, S.A., Warren, R.J., Lee, X., Bradford, M.A., 2012. Elevated methane concentrations in trees of an upland forest. *Geophys. Res. Lett.* 39, 1137–1147.
- Den Van Der Gon, H.A., Van Breemen, N., 1993. Diffusion-controlled transport of methane from soil to atmosphere as mediated by rice plants. *Biogeochemistry* 21, 177–190.
- Ding, W., Cai, Z., Tsuruta, H., Li, X.J.A.E., 2002. Effect of standing water depth on methane emissions from freshwater marshes in northeast China 36, 5149–5157.
- Ding, W., Cai, Z., Tsuruta, H., Li, X., 2003. Key factors affecting spatial variation of methane emissions from freshwater marshes. *Chemosphere* 51, 167–173.
- Ding, W., Cai, Z., Tsuruta, H., 2004. Diel variation in methane emissions from the stands of *Carex lasiocarpa* and *Deyeuxia angustifolia* in a cool temperate freshwater marsh. *Atmos. Environ.* 38, 181–188.
- Ding, W., Cai, Z., Tsuruta, H., 2005. Plant species effects on methane emissions from freshwater marshes. *Atmos. Environ.* 39, 3199–3207.
- Dise, N.B., 1993. Methane emission from Minnesota peatlands: spatial and seasonal variability. *Glob. Biogeochem. Cycles* 7, 123–142.
- Dorodnikov, M., Knorr, K.H., Kuzyakov, Y., Wilmking, M.J.B., 2011. Plant-mediated CH<sub>4</sub> transport and contribution of photosynthates to methanogenesis at a boreal mire: a <sup>14</sup>C pulse-labeling study. *Biogeosciences* 8, 2365–2375.
- Doronina, N., Ivanova, E., Suzina, N., Trotsenko, Y.A., 2004. Methanotrophs and methylobacteria are found in woody plant tissues within the winter period. *Microbiology* 73, 702–709.
- Dou, B., Xue, D., Wang, Y., Wang, Z., 2017. Research advancement in the processes and mechanisms of transporting methane by emerged herbaceous plants and hygrophytes. In *Chinese J. Plant Ecol.* 41, 1208–1218.
- Ernst, L., Steinfeld, B., Barayeu, U., Klitzsch, T., Kurth, M., Grimm, D., Dick, T.P., Rebelein, J.G., Bischofs, I.B., Keppler, F., 2022. Methane formation driven by reactive oxygen species across all living organisms. *Nature* 603, 482–487.
- Evans, J.R., 1989. Photosynthesis and nitrogen relationships in leaves of C3 plants. *Oecologia* 78, 9–19.
- Fagerstedt, K.V., 1992. Development of aerenchyma in roots and rhizomes of *Carex rostrata* (Cyperaceae). *Nord. J. Bot.* 12, 115–120.
- Frenzel, P., Karofeld, E.J.B., 2000. CH<sub>4</sub> emission from a hollow-ridge complex in a raised bog: the role of CH<sub>4</sub> production and oxidation. *Biogeochemistry* 51, 91–112.
- Frenzel, P., Rudolph, J., 1998. Methane emission from a wetland plant: the role of CH<sub>4</sub> oxidation in Eriophorum. *Plant Soil* 202, 27–32.
- Frolking, S., Roulet, N.T., Tuittila, E., Bubier, J.L., Quillet, A., Talbot, J., Richard, P., 2010. A new model of Holocene peatland net primary production, decomposition, water balance, and peat accumulation. *Earth Syst. Dynam.* 1, 1–21.
- Garnet, K.N., Megonigal, J.P., Litchfield, C., Taylor, G.E., 2005. Physiological control of leaf methane emission from wetland plants. *Aquat. Bot.* 81, 141–155.
- Garnett, M.H., Hardie, S.M.L., Murray, C., 2020. Radiocarbon analysis reveals that vegetation facilitates the release of old methane in a temperate raised bog. *Biogeochemistry* 148, 1–17.
- Gartner, K., Nadezhzhina, N., Englisch, M., Čermak, J., Leitgeb, E.J.F.E., Management., 2009. Sap flow of birch and Norway spruce during the European heat and drought in summer 2003. *For. Ecol. Manag.* 258, 590–599.
- Gauci, V., Figueiredo, V., Gedney, N., Pangala, S.R., Stauffer, T., Weedon, G.P., et al., 2022. Non-flooded riparian Amazon trees are a regionally significant methane source. *Philos. Trans. R. Soc.* 380, 20200446.
- Ge, M., Korrensalo, A., Laiho, R., Lohila, A., Makiranta, P., Pihlatie, M., Tuittila, E.S., Kohl, L., Putkinen, A., Koskinen, M., 2023a. Plant phenology and species-specific traits control plant CH<sub>4</sub> emissions in a northern boreal fen. *New Phytol.* 238, 1019–1032.
- Ge, M., Korrensalo, A., Putkinen, A., Laiho, R., Kohl, L., Pihlatie, M., et al., 2023. CH<sub>4</sub> transport in wetland plants under controlled environmental conditions: untangling the impacts of phenology. *bioRxiv*, 2023.10.08.561392.
- Gong, Y., Wu, J.H., Vogt, J., Ma, W.W., 2020. Greenhouse gas emissions from peatlands under manipulated warming, nitrogen addition, and vegetation composition change: a review and data synthesis. *Environ. Rev.* 28, 428–437.
- Greenup, A., Bradford, M., McNamara, N., Ineson, P., Lee, J., 2000. The role of Eriophorum vaginatum in CH<sub>4</sub> flux from an ombrotrophic peatland. *Plant Soil* 227, 265–272.
- Groot, T., Van Bodegom, P., Meijer, H., Harren, F., 2005. Gas transport through the root-shoot transition zone of rice tillers. *Plant Soil* 277, 107–116.
- Gross, M.F., Hardisky, M.A., Wolf, P.L., Klemas, V., 1991. Relationship between aboveground and belowground biomass of *Spartina alterniflora* (smooth cordgrass). *Estuaries* 14, 180–191.



- Grosse, W., Bernhard Büchel, H., Tiebel, H., 1991. Pressurized ventilation in wetland plants. *Aquat. Bot.* 39, 89–98.
- Halmmeenmäki, E., Heinonsalo, J., Putkinen, A., Santalahti, M., Fritze, H., Pihlatie, M., 2017. Above- and belowground fluxes of methane from boreal dwarf shrubs and *Pinus sylvestris* seedlings. *Plant Soil* 420, 361–373.
- Helfter, C., Gondwe, M., Murray-Hudson, M., Makati, A., Lunt, M.F., Palmer, P.I., et al., 2022. Phenology is the dominant control of methane emissions in a tropical non-forested wetland. *Nat. Commun.* 13, 133.
- Henneberg, A., Sorrell, B.K., Brix, H., 2012. Internal methane transport through *Juncus effusus*: experimental manipulation of morphological barriers to test above- and below-ground diffusion limitation. *New Phytol.* 196, 799–806.
- Hirota, M., Tang, Y.H., Hu, Q.W., Hirata, S., Kato, T., Mo, W.H., Cao, G.M., Mariko, S., 2004. Methane emissions from different vegetation zones in a Qinghai-Tibetan Plateau wetland. *Biochemistry* 36, 737–748.
- Holzapfel-Pschorn, A., Seiler, W., 1986. Methane emission during a cultivation period from an Italian rice paddy. *J. Geophys. Res.* 91, 11803.
- Hosono, T., Nouchi, I., 1997. The dependence of methane transport in rice plants on the root zone temperature. *Plant Soil* 191, 233–240.
- Hu, Q., Cai, J., Yao, B., Wu, Q., Wang, Y., Xu, X., 2016. Plant-mediated methane and nitrous oxide fluxes from a *Carex* meadow in Poyang Lake during drawdown periods. *Plant Soil* 400, 367–380.
- Iguchi, H., Sato, I., Sakakibara, M., Yurimoto, H., Sakai, Y., 2012. Distribution of methanotrophs in the phyllosphere. *Biosci. Biotechnol. Biochem.* 120281.
- Inouye, D.W., 2022. Climate change and phenology. *Wiley Interdisciplinary Reviews: Climate Change* 13, e764.
- Jackson, M.B., 1989. Regulation of aerenchyma formation in roots and shoots by oxygen and ethylene. *Cell Separ. Plants* 263–274.
- Jackson, M.B., 1994. Root-to-shoot communication in flooded plants: involvement of abscisic acid, ethylene, and 1-aminocyclopropane-1-carboxylic acid. *Agron. J.* 86, 775–782.
- Joabsson, A., Christensen, T.R., 2001. Methane emissions from wetlands and their relationship with vascular plants: an Arctic example. *Glob. Chang. Biol.* 7, 919–932.
- Johnson, M.S., Matthews, E., Du, J., Genovesi, V., Bastviken, D., 2022. Methane emission from global lakes: new spatiotemporal data and observation-driven modeling of methane dynamics indicates lower emissions. *J. Geophys. Res. Biogeosci.* 127, e2022JG006793.
- Kaiser, S., Göckede, M., Castro-Morales, K., Knoblauch, C., Ekici, A., Kleinen, T., Zubrzycki, S., Sachs, T., Wille, C., Beer, C., 2017. Process-based modelling of the methane balance in periglacial landscapes (JSBACH-methane). *Geosci. Model Dev.* 10, 333–358.
- Käki, T., Ojala, A., Kankaala, P., 2001. Diel variation in methane emissions from stands of *Phragmites australis* (Cav.) Trin. ex Steud. and *Typha latifolia* L. in a boreal lake. *Aquat. Bot.* 71, 259–271.
- Kankaala, P., Bergström, I., 2004. Emission and oxidation of methane in *Equisetum fluviatile* stands growing on organic sediment and sand bottoms. *Biogeochemistry* 67, 21–37.
- Kankaala, P., Käki, T., Mäkelä, S., Ojala, A., Pajunen, H., Arvola, L., 2005. Methane efflux in relation to plant biomass and sediment characteristics in stands of three common emergent macrophytes in boreal mesoeutrophic lakes. *Glob. Chang. Biol.* 11, 145–153.
- Kelker, D., Chanton, J., 1997. The effect of clipping on methane emissions from *Carex*. *Biogeochemistry* 39, 37–44.
- Kepler, F., Hamilton, J.T., Braß, M., Röckmann, T., 2006. Methane emissions from terrestrial plants under aerobic conditions. *Nature* 439, 187–191.
- Kim, J., Verma, S.B., Billesbach, D.P., 1999. Seasonal variation in methane emission from a temperate *Phragmites*-dominated marsh: effect of growth stage and plant-mediated transport. *Glob. Chang. Biol.* 5, 433–440.
- King, J.Y., Reeburgh, W.S., Regli, S.K., 1998. Methane emission and transport by arctic sedges in Alaska: results of a vegetation removal experiment. *J. Geophys. Res. Atmos.* 103, 29083–29092.
- Kiuru, P., Palviainen, M., Marchionne, A., Grönholm, T., Raivonen, M., Kohl, L., Laurén, A., 2022a. Pore network modeling as a new tool for determining gas diffusivity in peat. *Biogeosciences* 19, 5041–5058.
- Kiuru, P., Palviainen, M., Grönholm, T., Raivonen, M., Kohl, L., Gauci, V., Urzainki, I., Laurén, A., 2022b. Peat macropore networks – new insights into episodic and hotspot methane emission. *Biogeosciences* 19, 1959–1977.
- Kip, N., Van Winden, J.F., Pan, Y., Bodrossy, L., Reichart, G.-J., Smolders, A.J., et al., 2010. Global prevalence of methane oxidation by symbiotic bacteria in peat-moss ecosystems. *Nat. Geosci.* 3, 617–621.
- Kludze, H., DeLaune, R.D., Patrick, W.H., 1993. Aerenchyma formation and methane and oxygen exchange in rice. *Soil Sci. Soc. Am. J.* 57, 386–391.
- Knapp, A.K., Yavitt, J.B., 1995. Gas exchange characteristics of *Typha latifolia* L. from nine sites across North America. *Aquat. Bot.* 49, 203–215.
- Knox, S.H., Bansal, S., McNicol, G., Schafer, K., Sturtevant, C., Ueyama, M., et al., 2021. Identifying dominant environmental predictors of freshwater wetland methane fluxes across diurnal to seasonal time scales. *Glob. Chang. Biol.* 27, 3582–3604.
- Koelbener, A., Ström, L., Edwards, P.J., Venterink, H.O., 2010. Plant species from mesotrophic wetlands cause relatively high methane emissions from peat soil. *Plant Soil* 326, 147–158.
- Korrensalo, A., Mammarella, I., Alekseychik, P., Vesala, T., Tuittila, E.S., 2021. Plant mediated methane efflux from a boreal peatland complex. *Plant Soil* 471, 375–392.
- Kox, M.A.R., van den Elzen, E., Lamers, L.P.M., Jetten, M.S.M., van Kessel, M.A.H.J., 2020. Microbial nitrogen fixation and methane oxidation are strongly enhanced by light in *Sphagnum* mosses. *AMB Express* 10, 61.
- Kutzbach, L., Wagner, D., Pfeiffer, E.M., 2004. Effect of microrelief and vegetation on methane emission from wet polygonal tundra, Lena Delta, northern Siberia. *Biogeochemistry* 69, 341–362.
- Lai, D.Y.F., 2009. Methane dynamics in northern peatlands: a review. *Pedosphere* 19, 409–421.
- Lai, D.Y.F., Moore, T.R., Roulet, N.T., 2014a. Spatial and temporal variations of methane flux measured by autochambers in a temperate ombrotrophic peatland. *J. Geophys. Res. Biogeosci.* 119, 864–880.
- Lai, D.Y.F., Roulet, N.T., Moore, T.R., 2014b. The spatial and temporal relationships between CO<sub>2</sub> and CH<sub>4</sub> exchange in a temperate ombrotrophic bog. *Atmos. Environ.* 89, 249–259.
- Laine, A.M., Makiranta, P., Laiho, R., Mehtatalo, L., Penttilä, T., Korrensalo, A., et al., 2019. Warming impacts on boreal fen CO<sub>2</sub> exchange under wet and dry conditions. *Glob. Chang. Biol.* 25, 1995–2008.
- Larmola, T., Tuittila, E.S., Tirola, M., Nykänen, H., Martikainen, P.J., Yrjölä, K., Tuomivirta, T., Fritze, H.J.E., 2010. The role of *Sphagnum* mosses in the methane cycling of a boreal mire. *Ecology* 91, 2356–2365.
- Lawson, T., Violet-Chabrand, S., 2019. Speedy stomata, photosynthesis and plant water use efficiency. *New Phytol.* 221, 93–98.
- Li, S., Jiang, H., Wang, J., Wang, Y., Pan, S., Tian, H., Duan, M., Wang, S., Tang, X., Mo, Z., 2019. Responses of plant growth, physiological, gas exchange parameters of super and non-super rice to rhizosphere temperature at the tillering stage. *Sci. Rep.* 9, 10618.
- Li, S., Chen, L., Han, X., Yang, K., Liu, K., Wang, J., et al., 2022. Rice cultivar renewal reduces methane emissions by improving root traits and optimizing photosynthetic carbon allocation. *Agriculture* 12, 2134.
- Liebner, S., Zeyer, J., Wagner, D., Schubert, C., Pfeiffer, E.M., Knoblauch, C., 2011. Methane oxidation associated with submerged brown mosses reduces methane emissions from Siberian polygonal tundra. *J. Ecol.* 99, 914–922.
- Liu, H., Janssen, M., Lennartz, B., 2016. Changes in flow and transport patterns in fen peat following soil degradation. *Eur. J. Soil Sci.* 67, 763–772.
- Ma, S., Jiang, L., Wilson, R.M., Chanton, J.P., Bridgman, S., Niu, S., Iversen, C.M., Malhotra, A., Jiang, J., Lu, X., 2022. Evaluating alternative ebullition models for predicting peatland methane emission and its pathways via data-model fusion. *Biogeosciences* 19, 2245–2262.
- MacDonald, J., Fowler, D., Hargreaves, K., Skiba, U., Leith, I., Murray, M.J.A.E., 1998. Methane emission rates from a northern wetland; response to temperature, water table and transport. *Atmos. Environ.* 32, 3219–3227.
- Machacova, K., Bäck, J., Vanhatalo, A., Halmmeenmäki, E., Kolari, P., Mammarella, I., Pumpanen, J., Acosta, M., Urban, O., Pihlatie, M., 2016. *Pinus sylvestris* as a missing source of nitrous oxide and methane in boreal forest. *Sci. Rep.* 6, 23410.
- McGuire, M., Cerasoli, S., Teskey, R., 2007. CO<sub>2</sub> fluxes and respiration of branch segments of sycamore (*Platanus occidentalis* L.) examined at different sap velocities, branch diameters, and temperatures. *J. Exp. Bot.* 58, 2159–2168.
- Mitsch, W.J., Gosselink, J.G., 2000. *Wetlands* John Wiley & sons Inc. New York, New York.
- Moore, T.R., De Young, A., Bubier, J.L., Humphreys, E.R., Lafleur, P.M., Roulet, N.T., 2011. A multi-year record of methane flux at the Mer Bleue Bog, southern Canada. *Ecosystems* 14, 646–657.
- Morrissey, L., Zobel, D., Livingston, G.J.C., 1993. Significance of Stomatal Control on Methane Release From *Carex*-dominated Wetlands, 26, pp. 33–355.
- Mueller, P., Mozdzer, T.J., Langley, J.A., Aoki, L.R., Noyce, G.L., Megonigal, J.P., 2020. Plant species determine tidal wetland methane response to sea level rise. *Nat. Commun.* 11, 5154.
- Münchberger, W., Knorr, K.H., Blodau, C., Pancotto, V.A., Kleinebecker, T., 2019. Zero to moderate methane emissions in a densely rooted, pristine Patagonian bog—biogeochemical controls as revealed from isotopic evidence. *Biogeosciences* 16, 541–559.
- Munns, R., 1993. Physiological processes limiting plant growth in saline soils: some dogmas and hypotheses. *Plant Cell Environ.* 16, 15–24.
- Murphy, M., Laiho, R., Moore, T.R., 2009. Effects of water table drawdown on root production and aboveground biomass in a boreal bog. *Ecosystems* 12, 1268–1282.
- Nisbet, R.E.R., Fisher, R., Nimmo, R., Bendall, D., Crill, P., Gallego-Sala, A.V., Hornibrook, E., López-Juez, E., Lowry, D., Nisbet, E.G., 2009. Emission of methane from plants. *Proc. R. Soc. B Biol. Sci.* 276, 1347–1354.
- Nouchi, I., Mariko, S., 1993. Mechanism of methane transport by rice plants. In: *Biogeochemistry of Global Change: Radiatively Active Trace Gases Selected Papers from the Tenth International Symposium on Environmental Biogeochemistry*, pp. 336–352.
- Nouchi, I., Mariko, S., Aoki, K., 1990. Mechanism of methane transport from the rhizosphere to the atmosphere through rice plants. *Plant Physiol.* 94, 59–66.
- Nouchi, I., Hosono, T., Aoki, K., Minami, K., 1994. Seasonal variation in methane flux from rice paddies associated with methane concentration in soil water, rice biomass and temperature, and its modelling. *Plant Soil* 161, 195–208.
- Noyce, G.L., 2009. Effect of *Carex rostrata* Removal on CH<sub>4</sub> Emissions From a Temperate Peatland. Master thesis, University of New Hampshire, Durham, New Hampshire, USA.
- Noyce, G.L., Megonigal, J.P., 2021. Biogeochemical and plant trait mechanisms drive enhanced methane emissions in response to whole-ecosystem warming. *Biogeosciences* 18, 2449–2463.
- Noyce, G.L., Varner, R.K., Bubier, J.L., Frolking, S.J., 2014. Effect of *Carex rostrata* on seasonal and interannual variability in peatland methane emissions. *J. Geophys. Res. Biogeosci.* 119, 24–34.
- Numata, S., Yamaguchi, K., Shimizu, M., Sakurai, G., Morimoto, A., Alias, N., et al., 2022. Impacts of climate change on reproductive phenology in tropical rainforests of Southeast Asia. *Commun. Biol.* 5, 311.

- Okamoto, A., Koyama, K., Bhusal, N., 2022. Diurnal change of the photosynthetic light-response curve of Buckbean (*Menyanthes trifoliata*) an emergent aquatic plant. *Plants* 11, 174.
- Olefeldt, D., Turetsky, M.R., Crill, P.M., McGuire, A.D., 2013. Environmental and physical controls on northern terrestrial methane emissions across permafrost zones. *Glob. Chang. Biol.* 19, 589–603.
- Pangala, S.R., Gowing, D.J., Hornibrook, E.R.C., Gauci, V., 2014. Controls on methane emissions from *Alnus glutinosa* saplings. *New Phytol.* 201, 887–896.
- Pangala, S.R., Hornibrook, E.R.C., Gowing, D.J., Gauci, V., 2015. The contribution of trees to ecosystem methane emissions in a temperate forested wetland. *Glob. Chang. Biol.* 21, 2642–2654.
- Pangala, S.R., Enrich-Prast, A., Basso, L.S., Peixoto, R.B., Bastviken, D., Hornibrook, E.R.C., Gatti, L.V., Marotta, H., Calazans, L.S.B., Sakuragui, C.M., Bastos, W.R., Malm, O., Gloor, E., Miller, J.B., Gauci, V., 2017. Large emissions from floodplain trees close the Amazon methane budget. *Nature* 552, 230–234.
- Peng, C., Guot, J., Wu, H., Jiang, H., Luo, Y., 2011. Integrating models with data in ecology and palaeoecology: advances towards a model–data fusion approach. *Ecol. Lett.* 14, 522–536.
- Peng, S., Lin, X., Thompson, R.L., Xi, Y., Liu, G., Hauglustaine, D., Lan, X., Poulter, B., Ramonet, M., Saunio, M., et al., 2022. Wetland emission and atmospheric sink changes explain methane growth in 2020. *Nature* 612, 477–482.
- Petro, C., Carrell, A.A., Wilson, R.M., Duchesneau, K., Noble-Kuchera, S., Song, T., et al., 2023. Climate drivers alter nitrogen availability in surface peat and decouple N<sub>2</sub> fixation from CH<sub>4</sub> oxidation in the Sphagnum moss microbiome. *Glob. Chang. Biol.* 29, 3159–3176.
- Pitz, S., Megonigal, J.P., 2017. Temperate forest methane sink diminished by tree emissions. *New Phytol.* 214, 1432–1439.
- Pitz, S.L., Megonigal, J.P., Chang, C.-H., Szalavec, K., 2018. Methane fluxes from tree stems and soils along a habitat gradient. *Biogeochemistry* 137, 307–320.
- Poffenbarger, H.J., Needelman, B.A., Megonigal, J.P., 2011. Salinity influence on methane emissions from tidal marshes. *Wetlands* 31, 831–842.
- Prigent, C., Papa, F., Aires, F., Rossow, W.B., Matthews, E., 2007. Global inundation dynamics inferred from multiple satellite observations, 1993–2000. *J. Geophys. Res. Atmos.* 112.
- Putkinen, A., Larmola, T., Tuomivirta, T., Siljanen, H.M., Bodrossy, L., Tuittila, S., et al., 2014. Peatland succession induces a shift in the community composition of *Sphagnum*-associated active methanotrophs. *FEMS Microbiol. Ecol.* 88, 596–611.
- Putkinen, A., Siljanen, H.M., Laiho, A., Paasisto, I., Porkka, K., Tirola, M., Haikarainen, I., Tenhoviirta, S., Pihlatie, M., 2021. New Insight to the Role of Microbes in the Methane Exchange in Trees: Evidence From Metagenomic Sequencing, 231, pp. 524–536.
- Qaderi, M.M., Reid, D.M., 2009. Methane emissions from six crop species exposed to three components of global climate change: temperature, ultraviolet-B radiation and water stress. *Physiol. Plant.* 137, 139–147.
- Qian, H., Zhang, N., Chen, J., Chen, C., Hungate, B.A., Ruan, J., et al., 2022. Unexpected parabolic temperature dependency of CH<sub>4</sub> emissions from rice paddies. *Environ. Sci. Technol.* 56, 4871–4881.
- Raivonen, M., Smolander, S., Backman, L., Susiluoto, J., Aalto, T., Markkanen, T., Mäkelä, J., Rinne, J., Peltola, O., Aurela, M.J.G.M.D., 2017. HIMMELI v1.0: Helsinki Model of Methane build-up and emission for Peatlands, 10, pp. 4665–4691.
- Reid, M.C., Pal, D.S., Jaffé, P.R., 2015. Dissolved gas dynamics in wetland soils: root-mediated gas transfer kinetics determined via push-pull tracer tests. *Water Resour. Res.* 51, 7343–7357.
- Rice, A.L., Butenhoff, C.L., Shearer, M.J., Teama, D., Rosenstiel, T.N., MAK, Khalil, 2010. Emissions of anaerobically produced methane by trees. *Geophys. Res. Lett.* 37.
- Riley, W., Subin, Z., Lawrence, D., Swenson, S., Torn, M., Meng, L., Mahowald, N., Hess, P., 2011. Barriers to predicting changes in global terrestrial methane fluxes: analyses using CLM4Me, a methane biogeochemistry model integrated in CESM. *Biogeosciences* 8, 1925–1953.
- Riutta, T., Korrensalo, A., Laine, A.M., Laine, J., Tuittila, E.S., 2020. Interacting effects of vegetation components and water level on methane dynamics in a boreal fen. *Biogeosciences* 17, 727–740.
- Saaren, T., 1996. Biomass and production of two vascular plants in a boreal mesotrophic fen. *Canad. J. Bot.* 74, 934–938.
- Salmon, E., Jégou, F., Guenet, B., Jourdain, L., Qiu, C., Bastrikov, V., Guimbaud, C., Zhu, D., Ciais, P., Peylin, P., et al., 2022. Assessing methane emissions for northern peatlands in ORCHIDEE-PEAT revision 7020. *Geosci. Model Dev.* 15, 2813–2838.
- Saunio, M., Bousquet, P., Poulter, B., Peregon, A., Ciais, P., Canadell, J.G., et al., 2016. The global methane budget 2000–2012. *Earth Syst. Sci. Data* 8, 697–751.
- Saunio, M., Stavert, A.R., Poulter, B., Bousquet, P., Canadell, J.G., Jackson, R.B., Raymond, P.A., Dlugokencky, E.J., Houweling, S., Patra, P., et al., 2020. The global methane budget 2000–2017. *Earth Syst. Sci. Data* 12, 1561–1623.
- Schimel, J.P., 1995. Plant transport and methane production as controls on methane flux from arctic wet meadow tundra. *Biogeochemistry* 28, 183–200.
- Schütz, H., Seiler, W., Conrad, R., 1989. Processes involved in formation and emission of methane in rice paddies. *Biogeochemistry* 7, 33–53.
- Sebacher, D.I., Harris, R.C., Bartlett, K.B., 1985. Methane emissions to the atmosphere through aquatic plants. *J. Environ. Qual.* 14, 40–46.
- Shangguan, Z., Shao, M., Dyckmans, J., 2000. Effects of nitrogen nutrition and water deficit on net photosynthetic rate and chlorophyll fluorescence in winter wheat. *J. Plant Physiol.* 156, 46–51.
- Shannon, R.D., White, J.R., Lawson, J.E., Gilmour, B.S., 1996. Methane efflux from emergent vegetation in peatlands. *J. Ecol.* 84, 239.
- Singh, S., Kashyap, A.K., Singh, J.S., 1998. Methane flux in relation to growth and phenology of a high yielding rice variety as affected by fertilization. *Plant Soil* 201, 157–164.
- Sorrell, B.K., Brix, H., 2003. Effects of water vapour pressure deficit and stomatal conductance on photosynthesis, internal pressurization and convective flow in three emergent wetland plants. *Plant and Soil* 253, 71–79.
- Strack, M., Kellner, E., Waddington, J.M., 2005. Dynamics of biogenic gas bubbles in peat and their effects on peatland biogeochemistry. *Global Biogeochem. Cycles* 19.
- Ström, L., Mastepanov, M., Christensen, T.R., 2005. Species-specific effects of vascular plants on carbon turnover and methane emissions from wetlands. *Biogeochemistry* 75, 65–82.
- Sun, B., Hong, Z., Lü Y, Fei L, Wang X., 2016. The effects of nitrogen fertilizer application on methane and nitrous oxide emission/uptake in Chinese croplands. *J. Integr. Agric.* 15, 440–450.
- Sundqvist, E., Crill, P., Mölder, M., Vestin, P., Lindroth, A., 2012. Atmospheric methane removal by boreal plants. *Geophys. Res. Lett.* 39.
- Tenhoviirta, S.A.M., Kohl, L., Koskinen, M., Patama, M., Lintunen, A., Zanetti, A., Lilja, R., Pihlatie, M., 2022. Solar radiation drives methane emissions from the shoots of scots pine. *New Phytol.* 235, 66–77.
- Thomas, K.L., Benstead, J., Davies, K.L., Lloyd, D., 1996. Role of wetland plants in the diurnal control of CH<sub>4</sub> and CO<sub>2</sub> fluxes in peat. *Soil Biol. Biochem.* 28, 17–23.
- Treat, C.C., Jones, M.C., Brosius, L., Grosse, G., Anthony, K.W., Frohling, S., 2021. The role of wetland expansion and successional processes in methane emissions from northern wetlands during the Holocene. *Quat. Sci. Rev.* 257, 106864.
- Turetsky, M.R., Kotowska, A., Bubier, J., Dise, N.B., Crill, P., Hornibrook, E.R.C., Minkinen, K., Moore, T.R., Myers-Smith, I.H., Nykänen, H., et al., 2014. A synthesis of methane emissions from 71 northern, temperate, and subtropical wetlands. *Glob. Chang. Biol.* 20, 2183–2197.
- Tveit, A.T., Hestnes, A.G., Robinson, S.L., Schintmeister, A., Dedysh, S.N., Jehmlich, N., Von Bergen, M., Herbold, C., Wagner, M., Richter, A., 2019. Widespread soil bacterium that oxidizes atmospheric methane. *Proc. Natl. Acad. Sci.* 116, 8515–8524.
- Ueyama, M., Yazaki, T., Hirano, T., Futakuchi, Y., Okamura, M., 2020. Environmental controls on methane fluxes in a cool temperate bog. *Agric. For. Meteorol.* 281, 13.
- Ueyama, M., Knox, S.H., Delwiche, K.B., Bansal, S., Riley, W.J., Baldocchi, D., Hirano, T., McNicol, G., Schafer, K., Windham-Myers, L., et al., 2023. Modeled production, oxidation, and transport processes of wetland methane emissions in temperate, boreal, and Arctic regions. *Glob. Chang. Biol.* 29, 2313–2334.
- Vainio, E., Haikarainen, I.P., Machacova, K., Putkinen, A., Santalahti, M., Koskinen, M., Fritze, H., Tuomivirta, T., Pihlatie, M., 2022. Soil-tree-atmosphere CH<sub>4</sub> flux dynamics of boreal birch and spruce trees during spring leaf-out. *Plant Soil* 478, 391–407.
- Van Den Berg, M., Van Den Elzen, E., Ingwersen, J., Kosten, S., Lamers, L.P., Streck, T., 2020. Contribution of plant-induced pressurized flow to CH<sub>4</sub> emission from a Phragmites fen. *Sci. Rep.* 10, 1–10.
- Van Der Gon, H.D., Neue, H.U., 1995. Methane emission from a wetland rice field as affected by salinity. *Plant Soil* 170, 307–313.
- Van Der Nat, F.F.W., Van Meteren, D., Wielema, A.J.B., 1998. Diel methane emission patterns from *Scirpus lacustris* and *Phragmites australis*. *Biogeochemistry* 41, 1–22.
- Van Der Nat, F.J., Middelburg, J.J., 2000. Methane emission from tidal freshwater marshes. *Biogeochemistry* 49, 103–121.
- Verheijen, L.M., Brovkin, V., Aerts, R., Bonisch, G., Cornelissen, J.H.C., Kattge, J., Reich, P.B., Wright, I.J., Van Bodegom, P.M., 2012. Impacts of trait variation through observed trait–climate relationships on performance of an earth system model: a conceptual analysis. *Biogeosciences* 10, 18907–18950.
- Verville, J., Hobbie, S., Chapin, F.S., Hooper, D.U., 1998. Response of tundra CH<sub>4</sub> and CO<sub>2</sub> flux to manipulation of temperature and vegetation. *Biogeochemistry* 41, 215–235.
- Vigano, I., Van Weelden, H., Holzinger, R., Keppler, F., McLeod, A., Röckmann, T., 2008. Effect of UV radiation and temperature on the emission of methane from plant biomass and structural components. *Biogeosciences* 5, 937–947.
- Villa, J.A., Ju, Y., Stephen, T., Rey-Sanchez, C., Wright, K.C., Bohrer, G., 2020. Plant-mediated methane transport in emergent and floating-leaved species of a temperate freshwater mineral-soil wetland. *Limnol. Oceanogr.* 65, 1635–1650.
- Visser, E.J.W., Bögemann, G.M., Van De Steeg, H.M., Pierik, R., Blom, C.W.P.M., 2000. Flooding tolerance of *Carex* species in relation to field distribution and aerenchyma formation. *New Phytol.* 148, 93–103.
- Vroom, R., Van Den Berg, M., Pangala, S., Van Der Scheer, O., Sorrell, B., 2022. Physiological processes affecting methane transport by wetland vegetation—a review. *Aquat. Bot.*, 103547.
- Walter, B.P., Heimann, M., 2000. A process-based, climate-sensitive model to derive methane emissions from natural wetlands: application to five wetland sites, sensitivity to model parameters, and climate. *Glob. Biogeochem. Cycles* 14, 745–765.
- Wang, B., Neue, H.U., Samonte, H.P., 1997. Role of rice in mediating methane emission. *Plant Soil* 189, 107–115.
- Wang, Z.P., Gullledge, J., Zheng, J.Q., Liu, W., Li, L.H., Han, X.G., 2009. Physical injury stimulates aerobic methane emissions from terrestrial plants. *Biogeosciences* 6, 615–621.
- Wang, Z.P., Xie, Z.Q., Zhang, B.C., Hou, L.Y., Zhou, Y.H., Li, L.H., Han, X.G., 2011. Aerobic and anaerobic nonmicrobial methane emissions from plant material. *Environ. Sci. Technol.* 45, 9531–9537.
- Wang, Z.P., Gu, Q., Deng, F.D., Huang, J.H., Megonigal, J.P., Yu, Q., Lü, X.T., Li, L.H., Chang, S., Zhang, Y.H., et al., 2016. Methane emissions from the trunks of living trees on upland soils. *New Phytol.* 211, 429–439.
- Wania, R., Ross, I., Prentice, I.J.G.M.D., 2010. Implementation and evaluation of a new methane model within a dynamic global vegetation model: LPJ-WHyMe v1. 3.1. *Geosci. Model Dev.* 3, 565–584.

- Whigham, D.F., Simpson, R.L., 1978. The relationship between aboveground and belowground biomass of freshwater tidal wetland macrophytes. *Aquat. Bot.* 5, 355–364.
- White, S.D., Ganf, G.G., 2000. Influence of stomatal conductance on the efficiency of internal pressurisation in *Typha domingensis*. *Aquat. Bot.* 67, 1–11.
- Whiting, G.J., Chanton, J.P., 1992. Plant-dependent CH<sub>4</sub> emission in a subarctic Canadian fen. *Glob. Biogeochem. Cycles* 6, 225–231.
- Whiting, G.J., Chanton, J.P., 1993. Primary production control of methane emission from wetlands. *Nature* 364, 794–795.
- Wulfschleger, S.D., Epstein, H.E., Box, E.O., Euskirchen, E.S., Goswami, S., Iversen, C.M., Kattge, J., Norby, R.J., van Bodegom, P.M., Xu, X., 2014. Plant functional types in earth system models: past experiences and future directions for application of dynamic vegetation models in high-latitude ecosystems. *Ann. Bot.* 114, 1–16.
- Xu, X., Yuan, F., Hanson, P.J., Wulfschleger, S.D., Thornton, P.E., Riley, W.J., Song, X., Graham, D.E., Song, C., Tian, H., 2016. Reviews and syntheses: four decades of modeling methane cycling in terrestrial ecosystems. *Biogeosciences* 13, 3735–3755.
- Yamasaki, T., Yamakawa, T., Yamane, Y., Koike, H., Satoh, K., Katoh, S., 2002. Temperature acclimation of photosynthesis and related changes in photosystem II electron transport in winter wheat. *Plant Physiol.* 128, 1087–1097.
- Yang, W., Hu, Y., Yang, M., Wen, H., Jiao, Y., 2023. Methane uptake and nitrous oxide emission in saline soil showed high sensitivity to nitrogen fertilization addition. *Agronomy* 13, 473.
- Yang, P., Lai, D.Y.F., Yang, H., Lin, Y., Tong, C., Hong, Y., et al., 2022. Large increase in CH<sub>4</sub> emission following conversion of coastal marsh to aquaculture ponds caused by changing gas transport pathways. *Water Res.* 222, 118882.
- Yang, Z., Li, J.-L., Liu, L.-N., Xie, Q., Sui, N., 2020. Photosynthetic regulation under salt stress and salt-tolerance mechanism of sweet sorghum. *Front. Plant Sci.* 10, 1722.
- Yavitt, J.B., Knapp, A.K., 1998. Aspects of methane flow from sediment through emergent cattail (*Typha latifolia*) plants. *New Phytol.* 139, 495–503.
- Yip, D.Z., Veach, A.M., Yang, Z.K., Cregger, M.A., Schadt, C.W., 2019. Methanogenic Archaea dominate mature heartwood habitats of eastern cottonwood (*Populus deltoides*). *New Phytol.* 222, 115–121.
- Zhang, H., Välranta, M., Piilo, S., Amesbury, M.J., Aquino-López, M.A., Roland, T.P., et al., 2020. Decreased carbon accumulation feedback driven by climate-induced drying of two southern boreal bogs over recent centuries. *Glob. Chang. Biol.* 26, 2435–2448.
- Zhang, Y., Piao, S., Sun, Y., Rogers, B.M., Li, X., Lian, X., Liu, Z., Chen, A., Peñuelas, J., 2022. Future reversal of warming-enhanced vegetation productivity in the northern hemisphere. *Nat. Clim. Chang.* 12, 581–586.
- Zhang, Z., Poulter, B., Feldman, A.F., Ying, Q., Ciais, P., Peng, S., Li, X., 2023. Recent intensification of wetland methane feedback. *Nat. Clim. Chang.* 1–4.
- Zhu, D., Wu, N., Bhattarai, N., Oli, K.P., Chen, H., Rawat, G.S., et al., 2021. Methane emissions respond to soil temperature in convergent patterns but divergent sensitivities across wetlands along altitude. *Glob. Chang. Biol.* 27, 941–955.
- Zhuang, Q., Melillo, J.M., Kicklighter, D.W., Prinn, R.G., McGuire, A.D., Steudler, P.A., Felzer, B.S., Hu, S., 2004. Methane fluxes between terrestrial ecosystems and the atmosphere at northern high latitudes during the past century: a retrospective analysis with a process-based biogeochemistry model. *Glob. Biogeochem. Cycles* 18.