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Physiological processes affecting methane transport by wetland vegetation – A review

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ABSTRACT

Wetland plants transport oxygen to belowground tissues to survive in anoxic sediments, and simultaneously conduct methane (CH_4) from the sediment to the atmosphere. Although plant-mediated transport is the main CH_4 emission pathway in vegetated wetlands, the contribution of vegetated areas to total emissions in wetlands remains uncertain. To accurately quantify these emissions, understanding the physiological processes driving plant-mediated CH_4 transport is crucial. This review describes the state of the art understanding of CH_4 transport through trees, emergent, floating-leaved, and submerged freshwater macrophytes. Gas transport mechanisms in plants include diffusion, pressurized flow, and transpiration-driven flow. Pressurized flow in the gas-filled aerenchyma leads to higher gas transport rates than diffusion, and mostly occurs in plants standing in deeper water. Transpiration-driven flow occurs in the xylem tissue of trees, whereby dissolved CH_4 is transported by sap flow. Pressurized flow and transpiration-driven flow both result in diel cycles in CH_4 emission, with higher emissions during the day than at night. The total CH_4 emission through a wetland plant depends on its growth stage, transport mechanisms and the balance between sediment and in-plant CH_4 production and oxidation. Although plants contribute substantially to total CH_4 emissions, soil carbon content, soil temperature, nutrient availability, and water depth are often stronger driving factors than plant species. Nevertheless, accurate quantification of emissions from vegetated wetlands requires standardization of measurement protocols which capture diurnal and seasonal variation in emissions. Knowledge on CH_4 transport through trees and submersed and free-floating macrophytes is scarce and warrants further research.

1. Introduction

Despite being critical global carbon sinks, wetlands are an important source of tropospheric methane (CH_4), the second-most important biogenic greenhouse gas, with a 27 times higher global warming potential than CO_2 on a 100-year time horizon (IPCC, Canadell et al., 2021). A recent meta-analysis has estimated that half of the global CH_4 emissions arise from aquatic ecosystems, with anthropogenic impacts increasing their emissions (Rosentreter et al., 2021).

The three main CH_4 emission pathways in wetlands are diffusion through the water column, gas bubble release (ebullition), and plant-mediated transport (Bastviken, 2009). Wetland plants facilitate gas transport between the atmosphere and the soil because their internal anatomy features large intercellular air spaces, the function of which is aeration of belowground tissues and oxidation of the rhizosphere (Armstrong, 1979; Colmer, 2003). As a result of plant-mediated gas transport, CH_4 formed in the anoxic sediment can be conducted to the atmosphere, bypassing the oxic water and sediment layers where oxidation can occur (Dacey and Klug, 1979; Sebacher et al., 1985). Many studies have found that the dominant pathway of wetland CH_4 release in vegetated soils is plant transport (e.g., Whiting and Chanton, 1992; Brix et al., 2001; Hendriks et al., 2010), with ebullition much reduced because of plant transport depleting soil CH_4 reservoirs (Sorrell and Boon, 1994; van der Nat et al., 1998a; van den Berg, et al. 2020). The net effect of vegetation on the total emission will also depend on how much oxygen (O_2) is released into the anoxic soil by roots, which increases CH_4

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oxidation (van der Nat and Middelburg, 1998a; Le Mer and Roger, 2001). Due to the different magnitude of these processes, the extent to which plant-mediated CH_4 transport contributes to total wetland emissions is highly variable (Carmichael et al., 2014; Rosentreter et al., 2021). Due to this high variability and a lack of data, the effect of plant-mediated CH_4 transport is often omitted in models used to compute emissions (e.g. Kleinen et al., 2012; Hayman et al., 2014), or only is partially included (e.g. no pressurized flow) (Riley et al., 2011). This creates substantial uncertainties in global CH_4 budgets, including those of the IPCC (Canadell et al., 2021) and the Global Carbon Project (Saunois et al., 2020). Carmichael et al. (2014) estimated that herbaceous vegetation may contribute from 28% to > 90% to total ecosystem CH_4 emissions. CH_4 transport through woody plants is much less studied, but tree stems may account for 0–25% of temperate and 2.6–87% of tropical wetland CH_4 emissions (Carmichael et al., 2014; Covey and Megonigal, 2019). Although these estimates have a large degree of uncertainty, these contributions are of a magnitude that cannot be ignored.

The magnitude of CH_4 transport through a given plant species differs considerably due to different plant growth forms, morphologies, and gas transport mechanisms. Three main gas transport mechanisms can be distinguished: diffusion, pressurized mass flow, and transpiration-driven flow. In the first two cases, gases from the atmosphere (including O_2) are transported towards the roots and rhizosphere, and soil gases (CO_2 and CH_4) are transported in the opposite direction. Pressurized flow can deliver a fivefold higher O_2 flux to belowground tissues than diffusion (Brix et al., 2001).

The earliest pioneering studies that measured plant-mediated gas transport in the mid-19th century focussed mostly on the gas pressures and flow rates in rooted floating-leaved plants, and the understanding of the physical mechanisms of this pressurisation (Grosse et al., 1996). After the first recognition of gas transport through plants, later research emphasised the effects of O_2 transport on roots and soil. The effects of plant-mediated gas transport on CH_4 oxidation, transport and emission have only been studied more recently (Dacey and Klug, 1979) and to a lesser extent, but quantifying it is essential for estimating greenhouse gas budgets for wetlands.

In this review, we revisit the physiological processes involved in plant gas transport, and place them into the modern context and understanding of plant-mediated CH_4 emissions. We focus mainly on freshwater macrophytes and trees that occur in wetlands, but also include studies from other freshwater bodies, such as streams and lakes. We highlight the anatomical features and physiological mechanisms involved in wetland plant CH_4 transport. We then compare and contrast state-of-the-art knowledge on CH_4 transport through different wetland plant types: trees, emergent plants, floating plants, and submerged plants. Finally, we propose research needs in the field of plant-mediated CH_4 transport for accurately modelling greenhouse gas balances in wetlands.

2. Flooding tolerance of wetland vegetation

In terrestrial plants, tissues are aerated by radial diffusion of external O_2 into stems and roots from the atmosphere and soil (Armstrong and Beckett, 1987). In unsaturated soils, gas phase diffusion in the small intercellular air spaces that occur in all plants is sufficient to maintain aerobic metabolism in most cells (Armstrong, 1979). For aquatic habitats, diffusion in the liquid phase, which is up to 10,000 times slower than in the gas phase, cannot sustain the O_2 demand of the saturated soil (Armstrong, 1979). The soil then becomes hypoxic or anoxic and the external O_2 supply is inadequate or non-existent for aeration (Bailey--Serres and Voesenek, 2008). Therefore, the sole supply is by axial O_2 transport from the aerial tissues. This requires a low-resistance gas phase pathway capable of providing sufficient O_2 flux rates to sustain aerobic metabolism, especially in the apical meristems, which are the most distal parts of the transport pathway and where metabolic rates and O_2 demands are very high (Armstrong and Armstrong, 1991; Sorrell et al., 2000). Aerenchyma, a specialized tissue with enlarged gas spaces, is a solution to this transport requirement. The very high porosity conferred by aerenchyma development provides a much lower resistance to diffusion and O_2 fluxes can thereby sustain tissue aerobiosis (Visser et al., 2000). Fluxes are usually high enough to result in significant radial O_2 loss from roots. Radial oxygen loss (ROL) creates the oxidized rhizosphere of aquatic plant roots (Scholz et al., 2019), which is important in protecting plants from phytotoxins generated by anaerobic processes in the soil (Armstrong and Armstrong, 2001). Furthermore, ROL may speed up decomposition processes and alter nutrient availability by supplying O_2 to belowground microbial communities (Lamers et al., 2012; Mueller et al., 2016). The development of aerenchyma in tissues also assists aeration by lowering the O_2 demand, due to the lower fraction of the tissue occupied by live, respiring cells (Justin and Armstrong, 1987). This is especially true in the case of lysigenous aerenchyma, which forms by sacrificing cortical parenchyma cells (Seago et al., 2005). Aerenchyma development occurs in all types of wetland vegetation, including wetland-adapted trees (Kozlowski, 1997).

Although the function of aerenchyma tissues is primarily O_2 transport and aeration, any other gases that occur in aquatic ecosystems will also diffuse in and out of plants and be transported in the gas transport pathway, including CH_4. CH_4 is usually thought to be biologically inert for plants, being neither metabolized nor having any toxic effects on them, although some recent studies suggest it can regulate some growth processes at very high (> 50%) concentrations, at least in vitro (reviewed by Li et al., 2020; Wang et al., 2020). The high rates of CH_4 production in freshwater soils and low rates of diffusion in the aquatic environment generate a steep concentration gradient to the very low CH_4 concentrations in the atmosphere, leading to high rates of vertical transport of CH_4 in the low-resistance plant gas transport pathway (Chanton et al., 1989; Sorrell and Boon, 1994). Plant CH_4 transport is therefore simply an inadvertent by-product of the presence of the gas transport pathway that evolved for aeration.

3. Anatomical and morphological features governing gas transport

3.1. Aerenchyma formation

The porosity of plant tissue is defined by the ratio of the volume of gas to the volume of cellular material in a plant tissue (Armstrong, 1979). The volume of gas includes all intercellular airspaces within a plant. This comprises the constitutive gas-filled spaces between cells found in all plants (Sifton, 1945, 1957), with the addition of aerenchyma (Armstrong, 1979). Aerenchyma in aquatic plants is prevalent in the root cortex (Armstrong, 1979) and is also developed extensively in rhizomes and stems (Armstrong and Armstrong, 1988), and continues at a lower porosity through shoot bases (Jackson, 1989).

Aerenchyma formation occurs by three main mechanisms (Seago et al., 2005). First, aerenchyma can form through schizogeny. In this process, cells within organs with extensive parenchyma tissue start to differentiate their growth patterns (Sifton, 1945). These differentiated cells then separate, creating enlarged air spaces. Second, aerenchyma can form through lysigeny (Seago et al., 2005 There is no difference in growth patterns between cells in this process. Instead, some cells experience programmed cell death, resulting in open air spaces. The third mechanism by which aerenchyma is formed is expansigeny (Seago et al., 2005). In this case, the enlarged air spaces are formed directly by cell division and cell arrangement, without cell separation or programmed cell death.

Trees display stem thickening due to the growth of bark tissues. In wetland-adapted trees, this is accompanied by an increase in the proportion of aerenchyma in vascular tissues and modification in the lower stem and roots to facilitate gas transport to roots. Such changes are well-characterised for flood-tolerant angiosperms and gymnosperms in temperate zones (Kozlowski, 1997) and tropical zones (Parolin and

Wittmann, 2010; Waldhoff and Parolin, 2010).

In most wetland species, multi-perforate diaphragms periodically interrupt the large aerenchyma canals in stems. These are most conspicuous at stem nodes and root-rhizome junctions (Armstrong and Armstrong, 1988), but in some taxa are also found internodally, for example in the petioles of many floating-leaved plants. These diaphragms protect the aerenchyma against flooding; in cases of damage, water can only flow into a small section of the plant (Soukup et al., 2000). The diaphragms have pores to ensure continuity of the gas transport pathway and offer very little resistance to gas diffusion. In the case of pressurized flow, however, the diaphragms create most of the resistance to gas flow (Sorrell and Dromgoole, 1988; Armstrong and Armstrong, 1988; Sorrell et al., 1997).

3.2. Radial oxygen loss

Higher tissue porosity in the root tips increases radial oxygen loss (ROL), making plants better-equipped to handle anoxic conditions (Colmer, 2003; Lemoine et al., 2012). Lemoine et al. (2012) showed that aquatic plants exposed to anaerobic conditions can increase their root porosity and thus their ROL.

To prevent excessive ROL and ensure adequate O_2 supply from the root base to the high O_2 demand of the apical meristem, many wetland plants develop a barrier to ROL in the exodermis (Armstrong, 1979). This barrier arises at the subapical zones of the root, and improves internal aeration efficiency throughout the root, restricting the highest rates of ROL to the elongating root apex. The barrier is formed by a combination of densely packed cells in a hexagonal arrangement, deposition of lignin and/or suberin in the exodermis, and/or a high O_2 demand in the epidermal-hypodermal cylinder (Armstrong, 2000; Colmer, 2003; Soukup et al., 2007). The barrier to ROL may be intersected by thin-walled passage areas (termed 'windows'), from where new lateral roots will emerge (Armstrong, 2000). The 'tightness' of the barrier (i.e., its resistance to gas diffusion), is species-dependent, as are the resulting rates of ROL (Visser et al., 2000; Soukup et al., 2007; Manzur et al., 2015). Within species, the barrier to ROL may also develop differently depending on developmental stage, rooting depth, root diameter and soil redox potential (Visser et al., 2000; Colmer, 2003; Manzur et al., 2015). There is some evidence that the iron plaques that arise from oxidation and precipitation of soluble Fe^{2+} due to ROL may also act as a barrier to ROL (Møller and Sand-Jensen, 2008). A barrier to ROL potentially decreases root permeability not only for O_2, but also water, nutrients and phytotoxins (Armstrong et al., 1996b; Colmer and Bloom, 1998). It is very probable that this barrier also restricts the rate of the transport of CH_4 into and within plant roots, depending, amongst other factors, on its tightness. However, it has never been explicitly investigated whether a barrier to ROL is permeable to CH_4.

3.3. Root morphology

To counteract root mortality in flooded anoxic soils, many wetland plants invest heavily in adventitious root formation (Kozlowski, 1997; Visser and Voesenek, 2004; Voesenek and Bailey-Serres, 2015). Adventitious roots originate from non-root tissues. In the case of flooding, they originate at the stem base or other nodes. Depending on the plant species, adventitious root formation either occurs constitutively or is induced by waterlogging. Adventitious roots generally contain more aerenchyma and are therefore more porous than lateral roots, allowing more gas transport (Colmer, 2003). Thus, the morphology of adventitious roots, including their surface area, depth, thickness, and the number of lateral roots, affect plant gas transport (Sorrell et al., 2000; Colmer, 2003).

Aerenchyma usually terminate a few centimetres before the root tip (Armstrong, 1971). Gases transported through the aerenchyma must also diffuse radially through the cellular tissue of the exodermis and epidermis to reach the rhizosphere (Colmer, 2003). The gas flux towards this outer layer of cells depends largely on the pattern of cell arrangement in the cortex. For example, roots of rice plants with a cuboidal arrangement of cells have a porosity of approximately 9% (Armstrong, 1971), whereas in roots with a hexagonal cell arrangement, and thus more contact between cells, porosity is only 1% (Justin and Armstrong, 1987). Although the effect of cell arrangement on porosity in most tissues is small compared to the effect of aerenchyma development, cell arrangement can play a crucial role in gas transport processes at the root tips (Colmer, 2003). The relation between root morphology and the balance of CH_4 transport and oxidation, has rarely been investigated in detail (Henneberg et al., 2012).

4. Mechanisms of CH_4 transport

4.1. Molecular diffusion

The most common gas transport mechanism in vascular plants is molecular diffusion along concentration gradients (e.g. Barber et al., 1962; Sorrell and Brix, 2015). In this way, O_2 is transported from the atmosphere to the roots, where it is either used for respiration or released into the rhizosphere by ROL. CH_4 diffuses in the opposite direction, from high concentrations in the soil to low concentrations in the atmosphere (Chanton and Dacey, 1991; Colmer, 2003).

High rates of ROL can limit CH_4 diffusion into the roots, as more ROL leads to enhanced rhizosphere CH_4 oxidation. This results in a concentration gradient which varies within and among roots, depending on root and soil respiration, the presence of a barrier to ROL, root porosity and soil CH_4 concentrations (Colmer, 2003). For instance, in *Juncus effusus*, where gas transport takes place solely by diffusion, the gas-permeable root surface area was the most limiting factor for CH_4 transport (Henneberg et al., 2012). The laterals of its fine roots and tips of coarser roots that both lacked a barrier to ROL were the most permeable for CH_4. Since O_2 release and CH_4 uptake both occur at the most permeable root surfaces, diffusive CH_4 transport will ultimately be determined by soil CH_4 concentrations and the extent of CH_4 oxidation.

Several mathematical models have been developed to describe diffusive gas transport in wetland plant roots. Historically, these focused on O_2 and ROL (e.g., Armstrong and Beckett, 1987), but more recent models also include the transport of CH_4 in the opposite direction (Watson et al., 1997; Beckett et al., 2001). Watson et al. (1997) showed that the distribution of roots within the soil determines the rate of CH_4 transport to the atmosphere. Root tip distributions will affect CH_4 oxidation rates since ROL is highest at the root apices. Beckett et al. (2001) found that CH_4 diffusion into the roots varies along the root length as a function of ROL, leading to CH_4 oxidation in the oxidized rhizosphere. Rhizospheric CH_4 concentrations may even fall to zero due to this oxidation, resulting in zero transport, or CH_4 may diffuse into the root at one point, but diffuse back into the rhizosphere at another point.

Shoot features, in contrast, restrict diffusive CH_4 release rates less, due to the generally high porosity and permeability of shoot tissue. Thus, CH_4 diffusion is rarely affected by stomatal conductance, with release occurring mainly via micropores in stems (Henneberg et al., 2012) or petioles directly at the base of shoots (Harden and Chanton, 1994). Therefore, most diffusive CH_4 release from shoots occurs just above the waterlogged soil, or, in the case of standing water, just above the waterline, and cutting of the aerial shoots has little effect on this release (Kelker and Chanton, 1997; Greenup et al., 2000; Henneberg et al., 2012). In the case of submerged plant tissues, which lack stomata, the surface of the shoots may be sufficiently permeable to allow CH_4 transfer to the water phase (Armstrong, 1979). As CH_4 diffusion is independent of stomatal aperture, there is rarely any strong diel pattern in CH_4 release from plants that only transport CH_4 by diffusion (e.g., *Juncus effusus*, *Peltandra virginica* (Chanton et al., 1992; Whiting and Chanton, 1996)). However, a diel pattern in emission rates may still occur, due to variation in CH_4 production and oxidation when temperatures or rates of photosynthesis change (e.g. Yavitt and Knapp, 1998). In

wetland-adapted trees, diffusion-driven CH_4 transport plays a major role (e.g., *Alnus* species, Amazonian tree species; Rusch and Rennenberg, 1998; Pangala et al., 2015, 2017) but other emission pathways can operate simultaneously (*Betula pubescens*; Pangala et al., 2015). It is not yet clear whether pathways of O_2 and CH_4 transport in wetland trees are coupled or independent, but the absence of diel variability in CH_4 emissions in *Alnus glutinosa*, for example, suggests the dominant role of diffusion-driven CH_4 transport despite the potential for pressurized transport (Covey and Megonigal, 2019).

4.2. Pressurized flow

Pressurized gas flow is a more efficient mechanism than diffusion for wetland plants to transport O_2 from the leaves to the roots and vent soil gases to the atmosphere. This type of gas transport occurs in species of several taxonomically distinct genera, such as *Nymphaea*, *Nuphar*, *Nelumbo*, *Phragmites*, *Typha*, *Eleocharis*, *Equisetum*, *Hydrocleys*, and *Victoria* (Brix et al., 1992; Chanton et al., 1993; Grosse et al., 1996; Vretare Strand, 2002). The pressurization is purely physical, with humidity and temperature gradients between the leaf or shoot aerenchyma and the external atmosphere generating the pressures.

The two mechanisms of pressurization in emergent and rooted floating-leaved species are humidity-induced pressurization and thermal transpiration. Humidity-induced pressurization occurs when gas inside the plant has a higher relative humidity than the external atmosphere. In the internal aerenchyma, the gas composition is similar to that of the atmosphere (mainly N_2 and O_2), but water vapour pressure is higher inside the aerenchyma, due to continuous evaporation of water from the surrounding cells, keeping the air close to water saturation. This difference in water vapour pressure dilutes the concentration of the other internal gases, resulting in diffusion of these gases from the atmosphere into the aerenchyma. Because stomata and the sub-stomatal gas spaces in the pressure-creating leaves have a small diameter, they have a higher resistance to pressurized flow than to diffusion, so that gas diffusion into the leaf leads to a higher pressure (Dacey and Klug, 1982; Armstrong et al., 1996b, 1996c). The higher pressure within the leaf creates an air flow towards areas with lower pressure (rhizomes), and gases are vented out via older leaves or broken stems.

When a pressure gradient is caused by temperature differences, solar heating of the leaf or stem generates a higher temperature inside leaves or stems than outside; the resulting inwards gas flux is called thermal transpiration or thermo-osmosis (Grosse et al., 1991, 1996; Armstrong et al., 1996d). A temperature difference of 5 K can cause a pressure difference up to 100 Pa (Schröder et al., 1986). Thermal transpiration can occur simultaneously with humidity-induced pressurization, increasing the effect. It can also counteract humidity-induced pressure when temperatures are lower inside the plant due to evaporative cooling and heat loss by transpiration.

The dimensions of the intercellular airspaces in the mesophyll tissue and sub-stomatal cavity, and the stomatal conductance contribute to creating a pressure difference with the atmosphere. If the overall effective pore size is too large, there is not enough resistance to mass flow between the external and internal gas to allow a pressure gradient (White and Ganf, 2000). If the pore size is too small, diffusion rates will be too slow to generate pressures. The optimal pore size has a diameter of ca. 0.2 μm for a single layer of cells (Armstrong et al., 1996c), but pressures can be achieved with larger pore sizes in multicellular tissues due to the length and tortuosity of the airspace pathway.

Not only the pressurization, but also the resistance to mass flow within the aerenchyma determines the flow rate. Flow rates can differ among emergent species from 0.2 up to > 10 cm^3 min^{-1} $culm^{-1}$ (Brix et al., 1992). *Phragmites australis* has the optimal pore size of ca. 0.2 μm, and it also has low gas flow resistance due to a large pith cavity and aerenchyma channels, which means that *Phragmites* can create a very high flow rate compared to other wetland plants (Brix et al., 1992; Armstrong et al., 1996d). A higher flow rate is advantageous for plants growing in deeper water (Brix et al., 1992; Tornberg et al., 1994; Vretare Strand, 2002).

The influx and efflux parts of a plant differ depending on the species. In *Nuphar* and most other rooted floating-leaved species, the youngest emerging leaves have a higher ability to create a pressure difference than mature leaves. This means that the influx is in the young leaves and the efflux in the older leaves (Dacey and Klug, 1982). In *Phragmites*, the leaf sheaths around all living stems are responsible for creating the pressure and the efflux occurs from old broken stems that are still connected to the rhizomes. In *Typha*, individual leaves can function as either influx or efflux sites, depending on the relative position in the shoot and along the rhizome (Tornberg et al., 1994). If plants are damaged by physical forces or by herbivory, an artificial efflux can be created before the air reaches the rhizomes. This means that less O_2 can enter the roots and plant vitality will be reduced (Armstrong et al., 1996a). Cutting or bending of dead shoots can also result in lower O_2 concentrations in the rhizomes, reducing above-ground biomass in the next growing season (Jordan and Whigham, 1988).

Because pressurized flow is optimal in high light (stomatal conductance), high temperature and low humidity, the highest flow rate is often reached in the afternoon, and the lowest during the night (Dacey and Klug, 1982; Brix et al., 1992). This also has consequences for the timing of plant-mediated transport of the soil gases CH_4 and CO_2 towards the atmosphere, with a clear diel cycle in CH_4 emissions often seen in plants with pressurized flow (Chanton et al., 1993; Whiting and Chanton, 1996; van der Nat et al., 1998b; van den Berg et al., 2016). Sometimes a CH_4 peak at sunrise is observed, since CH_4 accumulates in the stem at night when there is no gas flow, and is vented out as soon as the pressurized flow starts (Chanton et al., 1993; van der Nat et al., 1998b). Just before sunrise, the internal CH_4 concentration can be up to 1000 times higher than during midday in the stem of *Phragmites* (Chanton et al., 2002).

A pressure gradient can also be caused by wind (venturi-induced convection), which can drive gas flow when solar-driven pressurization does not operate. Venturi-induced flow occurs when wind blows over broken stems, resulting in a pressure reduction that causes an airflow from the rhizome via these stems to the atmosphere. The influx comes from lower broken stems that capture less wind (Armstrong et al., 1992, 1996b). Venturi-induced flow is especially relevant during night and winter when humidity-induced or thermal transpiration is absent. It has been documented in *P. australis* (Armstrong et al., 1992), but, so far, not in other species.

A final mechanism that can create an elevated internal pressure in the plant is driven by direct partitioning of photosynthetically-produced O_2 to the gas spaces. This occurs in fully-submerged plants (Sorrell and Dromgoole, 1988; Schuette and Klug, 1995). However, since submerged plants lack an outflow to the atmosphere, there is no evidence that this leads to an air circulation that can aerate the soil and transport CH_4 upward faster than gas fluxes achieved by diffusion alone. A pressurised air flow occurs only if flowering plant parts are present (submerged or emergent) (Schuette and Klug, 1995; Heilman and Carlton, 2001a). Otherwise, diffusion will likely be the main gas transport mechanism.

4.3. Transpiration-driven flow

Transpiration-driven mass flow in the xylem tissue is now well-established in driving long-distance CH_4 transport in wetland trees (e.g., *Taxodium distichum* (Garnet et al., 2005); *Salix fluviatilis* (Rice et al., 2010); *Betula pubescencs* (Pangala et al., 2015)). CH_4 produced in the soil can dissolve into the soil porewater, be absorbed by the roots, and then transported up the tree through sap flow and emitted via the stem and leaf surfaces (Barba et al., 2019a, 2019b). This pathway will be dominant during the day when the transpiration is at its peak. Hence, the increased emission during the day compared to night-time emission observed for *Betula pubescens* by Pangala et al. (2015) was driven by transpiration-driven CH_4 transport.

5. CH_4 transport through different wetland vegetation types

5.1. Trees

Similar to herbaceous vegetation, trees in wetlands, floodplains and riparian zones also survive anoxic conditions. Their flooding adaptation depends on the flooding depth, flood duration, tree species and tree age (Parolin and Wittmann, 2010). Physiological and morphological adaptations include the formation of lenticels, pneumatophores, knees, adventitious roots, and aerial roots (Kozlowski, 1997). Biochemical processes include switching from aerobic metabolism to fermentation for generating energy and the emission of ethanol and acetaldehyde, reduction in tree carbon fixation (reduced photosynthesis), change in carbon allocation (investing in roots and aerenchyma formation), and reduced hydraulic conductivity (Kozlowski, 1997). These flooding adaptations in trees facilitate O_2 transport from the atmosphere to the anoxic roots and are now also known to allow tree-mediated CH_4 emissions via stem and leaf surfaces, and aerial tree root surfaces, including pneumatophores and knees (Pangala et al., 2015).

In contrast to herbaceous wetland vegetation, the transport of gases in wetland trees is long-distance; CH_4 emission has been detected in tree stems and leaves up to 5 m away from the soil surface (Pangala et al., 2017; Sjögersten et al., 2020; Jeffrey et al., 2020). Despite the long distance, CH_4 transport processes in wetland trees are often thought to operate similarly to herbaceous vegetation: by diffusion and mass flow (albeit driven by a different mechanism), or a combination of the two. Diffusion-driven CH_4 transport is indicated by decreasing stem CH_4 emissions with increasing stem height (Pangala et al., 2013, 2015; Sjögersten et al., 2020), small emissions from young tree leaves and no emissions from mature tree leaves (Pangala et al., 2013, 2017). Additional evidence includes minimal if not negligible differences between day and night-time stem CH_4 emissions (Pangala et al., 2014; Schindler et al., 2021), continued emissions from dead trees (Carmichael et al., 2018; Jeffrey et al., 2019), and sustained emissions from trees in the winter following autumnal leaf senescence (Pangala et al., 2015; Terazawa et al., 2015). Tree species that transport CH_4 via diffusion include *Populus davidiana* (Wang et al., 2016), *Fraxinus mandshurica* (Terazawa et al., 2015), *Alnus incana* (Schindler et al., 2021), and *A. glutinosa* (Pangala et al., 2015).

In contrast to diffusion, transpiration-driven CH_4 transport is characterized by strong diel variability in stem CH_4 emissions (Jeffrey et al., 2020), a drastic decline in stem CH_4 emissions following leaf senescence (Pangala et al., 2015), and a strong relationship between transpiration rates, sap flow and stem CH_4 flux (Barba et al., 2019b; Megonigal et al., 2020). Tree species that transport CH_4 via transpiration include *B. pubescens* (Pangala et al., 2015), *Melaleuca quinquenervia* (Jeffrey et al., 2020), *Liriodendron tulipifera* and *Fagus grandfolia* (Pitz et al., 2018). Transpiration-driven transport could also indirectly enhance diffusion-driven transport as transpiration reduces the internal tree stem water content (Steppe et al., 2015; Megonigal et al., 2020), which acts as a barrier for gas diffusion (Barba et al., 2019a). A recent study using radon measurement has indicated that changes in plant hydraulics affect CH_4 transport within tree stems (Megonigal et al., 2020). Peak CH_4 emissions observed during the daily cycle were related to stem diameter (stem diameter is known to vary through the day), i.e., minimal stem water content, which suggests that stem CH_4 flux is controlled by water content in the tree and not directly by the transpiration rate. As stem water content varies throughout the day (trees are drier during the day than night due to transpiration) and between seasons (trees are drier in the summer than winter), stem hydraulics may play a vital role in the regulation of diel and seasonal variability in stem CH_4 emissions (Megonigal et al., 2020). This is in addition to other biotic and abiotic factors that exert control on CH_4 production and transport in general.

Unlike herbaceous wetland vegetation, where soil-produced CH_4 is primarily the source of the CH_4 released, wetland trees can also act as 'vertical wetlands'. They provide habitat in their tissues not only for methanogens (Wang et al., 2016; Yip et al., 2019; Flanagan et al., 2021) but also methanotrophs (Sundqvist et al., 2012; Jeffrey et al., 2021), thereby making CH_4 emissions more dynamic. CH_4 emitted from tree stem surfaces can be derived from CH_4 produced both in soils and within trees, and the net emissions measured at the stem or leaf surfaces are the product of the balance of in situ CH_4 production and oxidation of CH_4. Jeffrey et al. (2021) found a CH_4 oxidising bacterial community dominated by *Methylomonas* spp. on the bark of *M. quinquenervia*, a tropical tree species. CH_4-oxidising bacteria mitigated around 36% of the CH_4 emitted from tree stems. They suggested that the methanotrophic population might also be ubiquitous across wetlands and therefore exert a major control on the magnitude of emissions of forested wetlands.

A small percentage of measured wetland trees have been reported to produce CH_4 internally within the tree stems (Pangala et al., 2017), with soil-derived CH_4 being the dominant source. However, high rates of CH_4 production within the tree stems are reported for upland trees (Covey et al., 2012; Flanagan et al., 2021), which are responsible for offsetting the soil CH_4 sink (Pitz and Megonigal, 2017). CH_4 production is enhanced by a large stem diameter, an anoxic internal stem environment, higher wood moisture content, heartwood rot (Flanagan et al., 2021) and bacterial infections. With a localised CH_4 source, as in the case of in-tree CH_4 production, radial diffusion of CH_4 becomes a dominant pathway for the CH_4 transport and emission through stem surfaces. The magnitude of radial diffusion is controlled by tree wood density, water content, presence of wet heartwood, lenticel density, and differences in diffusivity of stem tissue types (i.e., heartwood, sapwood, bark) (Zeikus and Ward, 1974; Pangala et al., 2013; Wang et al., 2016; Barba et al., 2019a; Covey and Megonigal, 2019). While radial CH_4 diffusion plays a dominant role in short-distance localised CH_4 transport, vertical molecular diffusion following a diffusion gradient and transpiration-driven transport aided by lateral CH_4 diffusion will likely drive long-distance CH_4 transport from the soil where it is produced to the length of the tree where it is predominantly released via stem surfaces. Radial diffusion alone may play a significant role when in-tree CH_4 production exceeds soil CH_4 production. Therefore, when soil-produced CH_4 is the dominant CH_4 source in wetlands, tree CH_4 emissions display a classic pattern with height. High CH_4 emissions are observed at the base of the tree stem, and emissions decrease with increasing stem height (e.g., Pangala et al., 2015; Terazawa et al., 2015; Ward et al., 2019) with either low or no emissions observed from tree leaves (Pangala et al., 2014, 2017). In contrast, when in-tree derived CH_4 is the dominant or localised CH_4 source, such classic decreasing emissions with increasing stem height become less apparent and a heterogeneous emission pattern is observed along with the height of the tree, as often observed for upland trees (Barba et al., 2019b; Welch et al., 2019).

The CH_4 source (soil vs. in-tree produced) controls the amount of CH_4 available for transport, as evidenced by the linear relationship between stem CH_4 flux and pore water CH_4 concentration (Pangala et al., 2014; Jeffrey et al., 2020) and internal stem CH_4 concentration (Covey et al., 2012; Ward et al., 2019). The different transport mechanisms further attenuate these fluxes and transport them from the source to the exchange surfaces where CH_4 is emitted to the atmosphere. Lenticel density (tree stem CH_4 exit points) controls the amount of CH_4 ultimately released to the atmosphere. A linear relationship has been observed between lenticel density and stem CH_4 flux in *A. glutinosa* saplings (Pangala et al., 2014). The recent discovery of CH_4-oxidising bacteria in wetland tree stems and the growing body of literature on the presence of methanogenesis inside tree stems reaffirms that CH_4 can simultaneously be produced and oxidised within the soil-tree continuum. Thus, only a fraction of CH_4 produced and transported up the tree is ultimately released to the atmosphere.

5.2. Emergent and floating plants

5.2.1. Emergent plants

The term 'emergent aquatic plant' refers to any herbaceous species with belowground tissues in waterlogged, anaerobic soils, and shoots emerging from the water surface into the atmosphere. This includes a wide range of morphologies, including rhizomatous and non-rhizomatous taxa, broad-leaved and narrow-leaved species, and species where the aerial foliage consists of cylindrical, leafless culms rather than shoots with leaves. CH_4 release to the atmosphere has been documented in all of these growth forms (Harden and Chanton, 1994; Calhoun and King, 1997; Sutton-Grier and Megonigal, 2011).

Emergent plants grow in the ecotone between terrestrial and wetland environments, from soil that is only intermittently flooded to a maximum depth of ca. 3 m. The distribution of diffusion and pressurized flow as the predominant gas transport mechanism is a function of depth (Vretare Strand, 2002; Sorrell and Hawes, 2010). In both these studies, species incapable of pressurization were restricted to water shallower than 0.5 m, species with limited pressurization (e.g., *Schoenoplectus lacustris, S. tabernaemontani)* occurred at depths of ca. 1.0 – 1.5 m depth, whereas species with high gas flow rates (e.g., *P. australis* and *Typha* spp.) form the deepest littoral vegetation in lakes.

CH_4 fluxes are not necessarily higher in species with pressurized flow than in species with only diffusion. Although pressurized flow clearly delivers higher internal gas transport rates and much more efficient aeration than diffusion, variation in hydrological regimes, wetting and drying cycles, and different sediment types (Kankaala and Bergström, 2004; Kankaala et al., 2005) can be more important than plant ecophysiology in determining CH_4 fluxes. In northern European lakes, Bergström et al. (2007) found that *P. australis* (with pressurized flow) had similar emissions to *Equisetum fluviatile* (no pressurized flow), both of which were higher than the floating-leaved *Nuphar lutea* (with pressurized flow). In contrast, Kao-Kniffin et al. (2010), in comparing nine species, reported higher CH_4 emission in non-pressurized flow species such as *Carex* and *Scirpus* spp. than in *P. australis* and *T. latifolia*, attributing this to enhanced rhizosphere methanotrophy by the pressurized flow species due to their greater ROL.

5.2.2. Rooted floating-leaved plants

Floating-leaved plants grow in deeper water than emergent plants, as their flexible petioles can better withstand wave action (Etnier and Villani, 2007; Richards et al., 2011), and they have overall higher rates of pressurized flow than emergent plants (Konnerup et al., 2011). They are characteristic of the 1 – 5 m water depth range in wetlands, and pressurized flow is almost ubiquitous in this growth form. Many of the earliest studies of internal gas flow and CH_4 release to the atmosphere were in floating-leaved species such as *N. lutea* (Dacey, 1980, 1981). In contrast to emergent species, only the youngest, recently-emerged leaves of floating-leaved plants can pressurize and function as influx sites, with most of the fully-expanded floating leaves being efflux sites (Dacey and Klug, 1982; Grosse, 1996). In *Nymphoides* species, the influx and efflux sites are in individual leaf whorls (Grosse, 1996). The most specialized gas transport mechanism is that of *Nelumbo nucifera*, in which there is bi-directional flow in individual leaves, with the canals and chambers of the rhizome ensuring that influx flow from a given leaf is ventilated at least two nodes away from the leaf from which it entered (Matthews and Seymour, 2006). Gas fluxes in *N. nucifera* are not only a function of the humidity and temperature driving pressurization, but are also regulated at the efflux site (the central disk of the leaf) by stomatal opening and closing (Matthews and Seymour, 2014).

5.2.3. Free-floating plants

Free-floating macrophytes can extract nutrients from surface waters and do not typically root in anoxic sediments. Nevertheless, the occurrence of ROL has been established in several species, including *Azolla filiculoides*, *Eichornia crassipes* and *Salvinia natans* (Moorhead and Reddy, 1988; Kosten et al., 2016). Furthermore, these plants' roots can support CH_4-oxidizing bacteria, substantially increasing oxidation rates of dissolved CH_4 (Kosten et al., 2016). In eutrophic waterbodies with limited water flow, these species can form dense beds, hampering gas diffusion between water and atmosphere and capturing CH_4 bubbles. On the other hand, shading of the underlying water layer can result in anoxia and enhanced methanogenesis. Due to these complex interactions, both reduction and increase of total CH_4 emissions by free-floating plants have been observed (Kosten et al., 2016).

5.2.4. Contribution to CH_4 emission

The contribution of emergent and floating-leaved plants to CH_4 transport and release from wetlands is highly variable. Early studies emphasized the significance of plant gas transport as a low-resistance pathway that can be responsible for most of the CH_4 release in vegetated sediments (Dacey and Klug, 1979; Chanton et al., 1989; Sorrell and Boon, 1994). However, there is an almost infinite combination of aerobic and anaerobic zones in different species in the soil-plant-atmosphere continuum for CH_4 fluxes, allowing a wide range of scenarios. Falling water levels, for example, can cause unvegetated soils to release more CH_4 by ebullition than the plant-mediated flux in adjacent vegetated soils (Bansal et al., 2020). In ombrotrophic bogs, there are examples of sites with deep, aerenchymatous roots with very high ROL creating sufficiently aerobic conditions to completely inhibit methanogenesis and CH_4 emissions (Fritz et al., 2011). In similar ecosystems, rhizosphere oxidation does little to attenuate emissions, and plants increase emissions as root exudates stimulate methanogenesis more than O_2 can stimulate methanotrophy (Nielsen et al., 2017; Turner et al., 2020). Fluxes from such aerenchymatous bog vegetation can be > 900 μg CH_4 m^{-2} h^{-1} (Frenzel and Rudolph, 1998).

Plant CH_4 fluxes appear to be particularly important for emissions in the emergent marshes of the littoral zones of lakes (Juutinen et al., 2003; Chen et al., 2009), where permanent flooding creates a permanently anaerobic sediment conducive to extensive methanogenesis, and the hydrostatic pressure of deep water inhibits ebullition. The outer, deep margin of the littoral zone is usually a site of peak emissions in lakes, higher than in the pelagic zone or the less anaerobic varial zone where there is wetting and drying (Kankaala and Bergström, 2004). Here, emergents such as *P. australis* have higher fluxes than floating-leaved species like *Nuphar*, with 7% (Kankaala et al., 2003) to 24% of the total annual net primary production converted to CH_4. 'Hotspots' of CH_4 emission also occur where aerenchymatous plants dominate reducing sediments at riparian margins (Audet et al., 2013).

Although several studies have investigated the overall effect of free-floating plants on CH_4 emissions (e.g. Oliveira-Junior et al., 2020; Singh et al., 2000), CH_4 transport and their gas transport mechanism have never been explicitly researched. The observation of enhanced CH_4 emissions in *E. crassipes* when it did root in anoxic sediments (Oliveira-Junior et al., 2018) suggests a CH_4 transport pathway. However, as CH_4 concentrations are generally much lower in surface waters than in underlying sediments, the relevance of this pathway in free-floating plants has yet to be established.

5.3. Submerged plants

In submerged plants, both diffusive transport and pressurized gas flow occur. Pressurized flow can occur along a pressure gradient that is driven by O_2 accumulation in the lacunar system due to photosynthesis. Tissues with higher photosynthetic activity accumulate more O_2, thus creating a pressure gradient from shoot apex to base (Sorrell and Dromgoole, 1988). For this pressure gradient to lead to pressurized gas flow, a venting mechanism is required. There is lack of an outflow in submerged macrophytes, except from floral spikes when anthers dehisce and release their pollen (Verhoeven, 1979). Schuette and Klug (1995) showed that in a natural population of *Myriophyllum heterophyllum* in a freshwater lake, CH_4 was released in a diel pattern. This pattern

coincides with the pressure pattern measured in the lacunar system of the plants, indicating that the increased lacunar pressures indeed caused a CH_4 flow from roots to emergent spikes, where it then was released. Submerged floral spikes also act as a venting mechanism for pressurized flow in *Potamogeton amplifolius*, with the internal pressures causing ebullition of lacunar gas from these spikes (Heilman and Carlton, 2001a). For *Potamogeton angustifolius*, daytime plant-mediated CH_4 release contributed 19 – 29% to the total areal release (plant and sediment emission), making it a significant transport pathway.

Diffusive transport through submerged plants also leads to a diel cycle in CH_4 emissions. CH_4 consumption by methanotrophs living on the stems and leaves of submerged macrophytes causes a decrease in CH_4 concentrations during daytime (Heilman and Carlton, 2001b; Sorrell et al., 2002). At night, higher CH_4 concentrations are observed in e.g. *Myriophyllum exalbescens,* indicating CH_4 diffusion from the soil to the plant and from the plant to the water. Under illumination, photosynthetically-derived O_2 is transported to the root system of the plants, leading to increased methanotrophic activity and low CH_4 transport. In the dark, CH_4 transport increases due to a lack of O_2 supply to the roots and rhizosphere, and thus increased CH_4 concentrations in the sediment.

The amount of CH_4 transport via diffusion depends on the tissue porosity of the plant, gas transport distance, flow rate of the surrounding water, methanotrophy inside the plant, CH_4 concentration in the soil, and O_2 transport to the roots (Sorrell and Downes, 2004). For highly porous submerged plants with low gas transport distances like *Iseotus alpinus*, transport of CH_4 is mainly dependent on the flow rate of the surrounding water, especially if plant-associated methanotrophic activity is negligible. For less porous species like *Potamogeton crispus*, water flow rate has little influence; methanotrophic activity plays a much bigger role for these plants.

Submerged vegetation can act as a CH_4 sink during the day, when methanotrophic activity peaks (Heilman and Carlton, 2001b). However, sub-tropical lakes have shown higher CH_4 emissions from *Hydrilla verticillata* and *Potamogeton malaianus*-dominated submerged vegetation than areas without submerged plants (Zhang et al., 2019). The net CH_4 flux from submerged vegetation is especially high during summer and autumn (Xing et al., 2006; Zhang et al., 2019). On a larger spatial and temporal scale, the inhibition of methanogenesis due to O_2 supply to the sediment combined with increased CH_4 oxidation does not outweigh the supply of readily biodegradable substrate for methanogenesis that the biomass of submerged macrophytes provides (Carpenter et al., 1983; Xing et al., 2006).

Besides the presence of vegetation, wind speed, water turbulence, and sediment temperature correlate positively with emissions in wetland areas with standing water (Xing et al., 2006; Zhang et al., 2019). The positive relation with wind speeds and water turbulence can be explained by the increased CH_4 diffusive emissions from the water surface due to more convective mixing in the water column.

6. Synthesis

6.1. Main controls on plant CH_4 transport

CH_4 transport occurs in all wetland plant types, but the occurrence of pressurized flow is species-specific. Wetland plants that transport gases only through diffusion show no diel pattern in CH_4 transport, although emissions may vary according to CH_4 production and oxidation rates. CH_4 diffusion is mostly dependent on root anatomy, including root porosity, the extent of ROL, the presence of a barrier to ROL, root tip distribution, and the formation of adventitious roots (Fig. 1). In contrast to diffusion, pressurized flow is dependent on shoot properties: stomatal size, pith cavity and aerenchyma diameter, leaf and stem age, and the extent of damage of the stem. In plants that exhibit pressurized gas flow, CH_4 transport is also regulated by external factors including temperature, photosynthetically active radiation, wind speed and humidity – often resulting in diel variation, i.e., high transport rates during the day and low during the night, with a peak at sunrise in some cases. Species that exhibit pressurized flow do not necessarily release more CH_4 than species that only have diffusion, since pressurized flow also results in a higher ROL and, therefore, higher CH_4 oxidation rates in the rhizosphere.

The most important anatomical properties affecting tree CH_4 transport are wood density, stem water content, presence of wet heartwood,

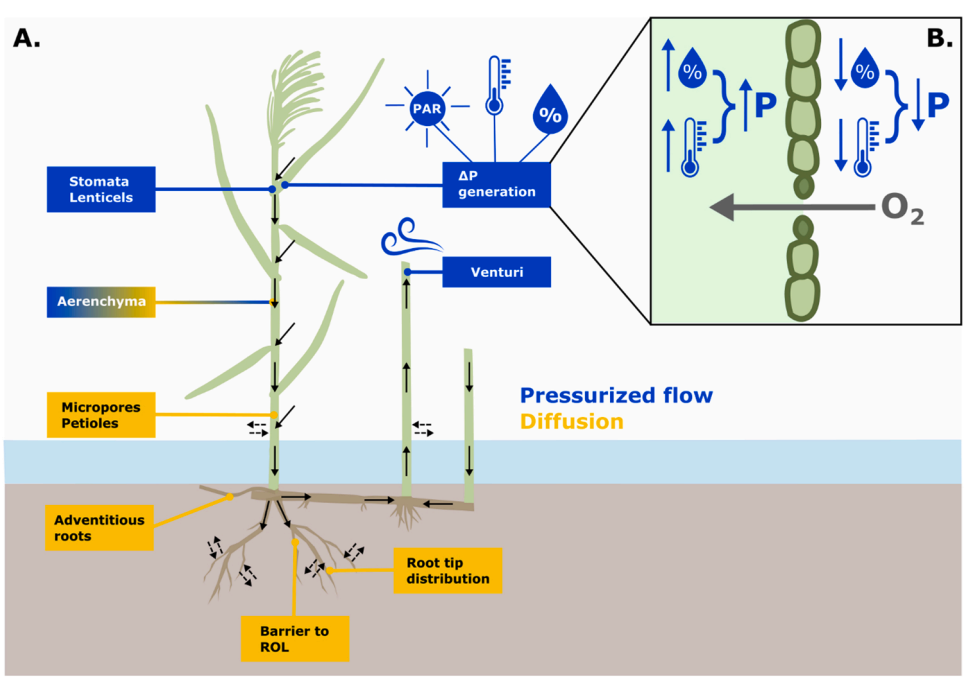

Fig. 1. A. Different anatomical features and environmental drivers for gas diffusion (yellow) and pressurized flow (blue). Black arrows indicate the direction of the gas flow though a wetland plant. B. The establishment of a pressure difference due to higher temperatures and humidity inside the plant results in a pressurized gas flow.

lenticel density and differences in diffusivity of stem tissue types. In trees, a diurnal pattern in CH_4 flux is caused by transpiration-driven flow, leading to higher fluxes during daytime. As well as transporting CH_4 from the soil, within-tree CH_4 can also be produced and oxidized, making trees act as vertical wetlands.

The ecotone between the terrestrial and aquatic habitat is a gradient from aerobic to anaerobic soils, with higher species diversity in the drier soil and the vegetation transitioning to monospecific stands of clonal rhizomatous helophytes, floating and submerged macrophytes in the deepest water. Predominant gas transport mechanisms shift along this gradient (Fig. 2) (Brix et al., 1992; Vretare Strand, 2002). In waterlogged soil without standing water, diffusion is adequate to satisfy most belowground O_2 demands. Species commonly occurring in standing water often have some degree of pressurization and low internal flow rates, restricted by high flow resistances in the aerenchyma. High flow rates that can efficiently aerate belowground tissues occur in the deepest-growing emergent species (Sorrell and Hawes, 2010), such as *Phragmites australis* (Armstrong and Armstrong, 1991), and most *Typha* species (Bendix et al., 1994; White and Ganf, 2000). Pressure is generated by live shoots and gas exits through dead shoots. Rooted floating-leaved plants often have higher rates of pressurized flow than emergent plants. Young leaves generate high pressure and gas exits from the older leaves. Pressurization can also occur in submerged plants, but CH_4 can only exit to the atmosphere when an inflorescence is present. Diffusion can depend on the CH_4 concentration gradient between the soil, plant and surrounding water, and flow rate of the surrounding water. CH_4 transport by submerged macrophytes is also highly dependent on the activity of methanotrophs present on the shoot.

6.2. Contribution of plant CH_4 transport to total wetland CH_4 emissions

The dominant role of plant-mediated CH_4 transport over other mechanisms of CH_4 release in vegetated wetlands has been confirmed in multiple studies in many different types of wetlands. Examples include tropical freshwater marshes such as the Florida Everglades (Whiting and Chanton, 1996), the Amazon basin (Devol et al., 1988; Melack et al., 2004), Australian floodplain ponds (Sorrell and Boon, 1992, 1994; Jeffrey et al., 2019), lake littoral zones (Hyvönen et al., 1998; Milberg et al., 2017), a Botswanan river delta (Helfter et al., 2022) and even lowland streams (Sanders et al., 2007; Wilcock and Sorrell, 2008). In all cases, the low-resistance transport pathway of the aerenchyma provides an effective short-circuit for CH_4 release compared to ebullition or diffusion through water. This confirms the importance of quantifying plant aerenchymatous transport of CH_4 for an accurate estimate of a wetland's CH_4 flux. The importance of any individual species as a CH_4 conduit will be a function of the rates of methanogenesis and CH_4 oxidation in the soil, CH_4 oxidation in the plant tissues, the tissue porosities and hence resistance to gas transport, and whether diffusion or convective flow is the transport mechanism.

Which factors are most important in determining the CH_4 flux from any particular vegetated habitat? In addition to the environmental factors that control pressurized gas flow rates and stomatal opening (air temperature and humidity, and light intensity), factors controlling methanogenesis and CH_4 oxidation appear to be as, or more, important. Fluctuating water levels, allowing occasional soil oxidation, reduce CH_4 emissions greatly in soils colonized by wetland plants (Altor and Mitsch, 2006, 2008; Silvey et al., 2019). Higher CH_4 fluxes in permanently flooded soils can be associated with less CH_4 oxidation, whereas dynamic redox fluctuations in the soil when water levels fluctuate can lower methanogenesis and emissions (Jeffrey et al., 2019). Plant-mediated transport can influence the redox conditions in the rhizosphere by increasing Fe(III) concentrations (depending on the amount of iron in the soil) and thereby reducing methanogenesis (Neubauer et al., 2005; Sutton-Grier and Megonigal, 2011). Another essential factor for methanogenesis is the availability of substrate. The input of easily degradable carbon into the soil is mainly controlled by net primary production. It is estimated that around 3% of the net primary production is emitted back as CH_4 (Whiting and Chanton, 1993).

Soil C content, soil temperature, nutrient availability, and water depth are often stronger driving factors of CH_4 emissions than which plant species are present or their gas transport traits (Smith and Lewis, 1992; Sturtevant et al., 2016; Bansal et al., 2016; Zhu et al., 2020). Soil redox potential and wetland primary production can also be important driving factors (Wang et al., 2006). Turetsky et al. (2014), in a meta-analysis of 71 wetlands, emphasized all of these factors, with plant transport processes being the most important controlling factor in only a few cases.

The total CH_4 emission from a wetland can only be estimated if all transport processes (diffusion, ebullition and plant transport) are considered, since plant transport will cause a shift in the transport

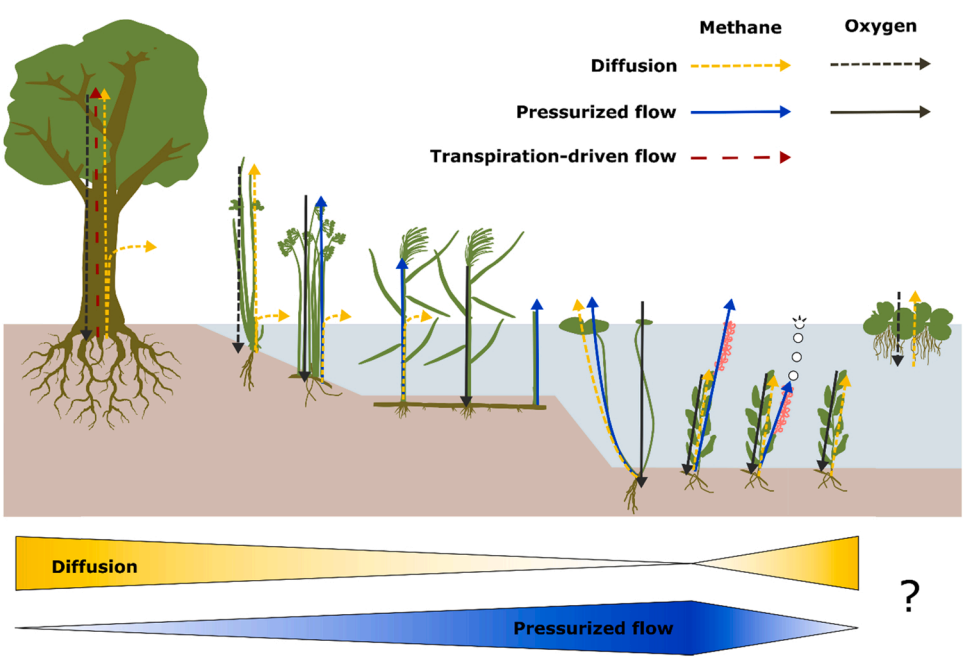

Fig. 2. CH_4 emission pathways for different plant types. From left to right: trees exhibiting diffusion and transpiration driven-flow (e.g. *Alnus* spp.), emergent plants with only diffusion (e.g. *Juncus effusus*), emergent plants that show a small degree of pressurized flow (e.g. some *Schoenoplectus* spp.), emergent plants with efficient pressurized flow (e.g. *Phragmites australis*), rooted floating-leaved plants with efficient pressurized flow (e.g. *Nuphar luteum*), submerged plants with effective pressurized flow, only venting CH_4 through floral spikes, resulting in ebullition when underwater (e.g. *P. amplifolius*), submerged plants with only diffusion (e.g. *I. alpinus*), and free-floating plants for which the importance of pressurized flow remains unclear (e.g. *Salvinia natans*). The effectiveness and importance of pressurized flow increases with increasing water levels. Arrows indicate the direction of the gas flow for O_2 and CH_4.

processes (Bansal et al., 2020).

6.3. Directions for future research

A major challenge in determining the contribution of plant CH_4 transport vs other emission mechanisms is the highly dynamic nature of CH_4 production and release processes on daily, seasonal, and spatial scales. Comparing across studies is difficult when diurnal vs nocturnal shifts in dominant mechanisms are addressed differently. An under-appreciation of hydrodynamic mixing and short-term stratification in shallow wetlands and its enhancement of nocturnal diffusion of CH_4 from the water surface (Ford et al., 2002; Poindexter et al., 2016), may have led to this mechanism being undervalued. Plants with pressurized flow have dramatically different emission rates between night and day, and summer and winter (Morin et al., 2014; van den Berg, 2016), but winter shoots can still be an important emission source (Larmola et al., 2004). The cessation of pressurized flow at night in temperate climates and the tendency of the plant body therefore to act as a nocturnal capacitor for CH_4 (Yavitt and Knapp, 1998), can lead to underestimates of CH_4 release if the high emissions immediately after dawn are not captured. In warm climates, where pressurized flow rates decrease at night but still operate 24 h per day, nocturnal data are essential to capture the daily cycle (Boon and Sorrell, 1995). Furthermore, it is essential to capture a variety of differently aged shoots. In general, standardization of flux measurement techniques and protocols would improve comparisons.

Research on tree-mediated CH_4 emissions in wetlands is only in its infancy, with many unknowns and only a handful of studies. Given that there are over 60,000 tree species in the world and stem CH_4 fluxes not only vary between species but within the same species over relatively small spatial, topographic, and hydrological gradients (Pangala et al., 2017; Jeffrey et al., 2020; Gauci et al., 2022), further research into tree mediated CH_4 emissions across different latitudes will offer much-needed clarity on CH_4 transport processes and dynamics. It is noteworthy that both upland and wetland trees are known to emit CH_4, sometimes independent of soils acting as a source of CH_4, thereby not only making this area of research complex, but also potentially impactful in the global CH_4 budget, as forested ecosystems can switch from CH_4 sinks to sources when tree CH_4 emissions are considered (Pitz and Megonigal, 2017). This is further confounded as trees themselves can act as vertical wetlands by cycling CH_4 within their stem and leaf surfaces (Sundqvist et al., 2012). Unravelling the complex processes that govern wetland tree stem CH_4 cycling is of paramount importance, if we are to accurately account for tree CH_4 emissions in global CH_4 budgets in this rapidly changing world.

The number of studies about CH_4 transport in submerged plants is very limited. All existing system-wide studies have been done in subtropical lakes, leaving a huge knowledge gap for the effect of submerged vegetation in more temperate regions. The large effect of environmental factors that are missing in single-plant experiments further stresses the need for system-wide studies. Whether the pressurized flow during flowering also supports a more active methanotrophic community has not yet been studied. Answering this question is vital to assess the net effect of submerged vegetation on CH_4 emission.

The effects of species diversity in wetland communities on CH_4 emissions remain uncertain and deserve further study. Bouchard et al. (2007) found that an increase in richness of functional plant groups enhanced belowground biomass with a more diverse array of root morphologies, lowering emission presumably by enhancing belowground CH_4 oxidation. This pattern was not observed in a similar study by Schultz and Pett (2018), where particular functional types rather than overall diversity were associated more with low emissions.

Grazing by waterfowl can increase CH_4 fluxes through inhibiting CH_4 oxidation processes by hampering O_2 transport to the soil (Dingemans et al., 2011; Winton and Richardson, 2017). Similar anthropogenic disturbances, such as cutting and harvesting activities, may also enhance emissions (Rietl et al., 2017; Johnson et al., 2021), and by invasion by productive species adding organic C loads (Lawrence et al., 2017). CH_4 emissions are also increasing due to elevated atmospheric CO_2 concentrations increasing primary productivity and providing more organic carbon substrate (Megonigal and Schlesinger, 1997; Yuan et al., 2021), but relatively few studies have addressed this important issue.

Finally, new discoveries about the nature of methanogenesis are challenging our understanding. In particular, the evidence for high rates of aerobic methanogenesis in some wetland soils (Angle et al., 2017) may greatly alter the current picture of how plants function in CH_4 processes. As yet, this has not been noted in many studies, but is a major topic requiring further investigation.

Declaration of Competing Interest

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

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References

Altor, A.E., Mitsch, W.J., 2006. Methane flux from created riparian marshes: relationship to intermittent versus continuous inundation and emergent macrophytes. Ecol. Eng. 28, 224–234. https://doi.org/10.1016/j.ecoleng.2006.06.006.

Altor, A.E., Mitsch, W.J., 2008. Pulsing hydrology, methane emissions and carbon dioxide fluxes in created marshes: a 2-year ecosystem study. Wetlands 28, 423–438. https://doi.org/10.1672/07-98.1.

Angle, J.C., Morin, T.H., Solden, L.M., Narrowe, A.B., Smith, G.J., Borton, M.A., Rey-Sanchez, C., Daly, R.A., Mirfenderesgi, G., Hoyt, D.W., Riley, W.J., Miller, C.S., Bohrer, G., Wrighton, K.C., 2017. Methanogenesis in oxygenated soils is a substantial fraction of wetland methane emissions. Nat. Commun. 8, 1–9. https://doi.org/10.1038/s41467-017-01753-4.

Armstrong, J., Armstrong, W., 1988. *Phragmites australis* - a preliminary study of soil-oxidizing sites and internal gas transport pathways. N. Phytol. 108, 373–382. https://doi.org/10.1111/j.1469-8137.1988.tb04177.x.

Armstrong, J., Armstrong, W., 1991. A convective through-flow of gases in *Phragmites australis* (Cav.) Trin. ex Steud. Aquat. Bot. 39, 75–88. https://doi.org/10.1016/0304-3770(91)90023-X.

Armstrong, J., Armstrong, W., 2001. Rice and *Phragmites*: effects of organic acids on growth, root permeability, and radial oxygen loss to the rhizosphere. Am. J. Bot. 88, 1359–1370. https://doi.org/10.2307/3558443.

Armstrong, J., Armstrong, W., Beckett, P.M., 1992. *Phragmites australis*: Venturi- and humidity-induced pressure flows enhance rhizome aeration and rhizosphere oxidation. N. Phytol. 120, 197–207. https://doi.org/10.1111/j.1469-8137.1992.tb05655.x.

Armstrong, J., Armstrong, W., Armstrong, I.B., Pittaway, G.R., 1996a. Senescence, and phytotoxin, insect, fungal and mechanical damage: factors reducing convective gas-flows in *Phragmites australis*. Aquat. Bot. 54, 211–226. https://doi.org/10.1016/0304-3770(96)82384-9.

Armstrong, J., Armstrong, W., Beckett, P.M., Halder, J.E., Lythe, S., Holt, R., Sinclair, A., 1996b. Pathways of aeration and the mechanisms and beneficial effects of humidity- and Venturi-induced convections in *Phragmites australis* (Cav.) Trin. ex Steud. Aquat. Bot. 54, 177–197. https://doi.org/10.1016/0304-3770(96)01044-3.

Armstrong, W., 1971. Radial oxygen losses from intact rice roots as affected by distance from the apex, respiration and waterlogging. Physiol. Plant. 25, 192–197. https://doi.org/10.1111/j.1399-3054.1971.tb01427.x.

Armstrong, W., 1979. Aeration in higher plants. Adv. Bot. Res. 7, 225–332. https://doi.org/10.1016/S0065-2296(08)60089-0.

Armstrong, W., 2000. Oxygen distribution in wetland plant roots and permeability barriers to gas-exchange with the rhizosphere: a microelectrode and modelling study with *Phragmites australis*. Ann. Bot. 86, 687–703. https://doi.org/10.1006/anbo.2000.1236.

Armstrong, W., Beckett, P.M., 1987. Internal aeration and development of stelar anoxia in submerged roots: a multishelled mathematical model combining axial diffusion of oxygen in the cortex with radial losses to the stele, the wall layers and the rhizosphere. New Phytol. 105, 221–245. https://doi.org/10.1111/j.1469-8137.1987.tb00860.x.

Armstrong, W., Armstrong, J., Beckett, P.M., 1996c. Pressurised ventilation in emergent macrophytes: the mechanism and mathematical modelling of humidity-induced convection. Aquat. Bot. 54, 121–135. https://doi.org/10.1016/0304-3770(96)01040-6.

Armstrong, W., Armstrong, J., Beckett, P.M., 1996d. Pressurised aeration in wetland macrophytes: some theoretical aspects of humidity-induced convection and thermal transpiration. Folia Geobot. 31, 25–36. https://doi.org/10.1007/bf02803991.

Audet, J., Elsgaard, L., Kjaergaard, C., Larsen, S.E., Hoffmann, C.C., 2013. Greenhouse gas emissions from a Danish riparian wetland before and after restoration. Ecol. Eng. 57, 170–182. https://doi.org/10.1016/j.ecoleng.2013.04.021.

Bailey-Serres, J., Voesenek, L., 2008. Flooding stress: acclimations and genetic diversity. Annu Rev. Plant Biol. 59, 313–339. https://doi.org/10.1146/annurev.arplant.59.032607.092752.

Bansal, S., Tangen, B., Finocchiaro, R., 2016. Temperature and hydrology affect methane emissions from prairie pothole wetlands. Wetlands 36, 371–381. https://doi.org/10.1007/s13157-016-0826-8.

Bansal, S., Johnson, O., Meier, J., Zhu, X., 2020. Vegetation affects timing and location of wetland methane emissions. J. Geophys. Res. Biogeosci. 125, 1–14. https://doi.org/10.1002/ESSOAR.10502877.1.

Barba, J., Poyatos, R., Vargas, R., 2019b. Automated measurements of greenhouse gases fluxes from tree stems and soils: magnitudes, patterns and drivers. Sci. Rep. 9, 1–13. https://doi.org/10.1038/s41598-019-39663-8.

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., Poulter, B., Rivas-Ubach, A., Schadt, C.W., Terazawa, K., Warner, D.L., Zhang, Z., Vargas, R., 2019a. Methane emissions from tree stems: a new frontier in the global carbon cycle. New Phytol. 222, 18–28. https://doi.org/10.1111/nph.15582.

Barber, D.A., Ebert, M., Evans, N.T.S., 1962. The movement of 15O through barley and rice plants. J. Exp. Bot. 13, 397–403. https://doi.org/10.1093/jxb/13.3.397.

Bastviken, D., 2009. Methane. In: Likens, G.E. (Ed.), Encyclopedia of Inland Waters. Elsevier, Oxford, pp. 783–805. https://doi.org/10.1016/B978-012374410-4.00385-X.

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. https://doi.org/10.1016/S0304-3770(01)00144-9.

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. https://doi.org/10.1016/0304-3770(94)90030-2.

Bergström, I., Mäkelä, S., Kankaala, P., Kortelainen, P., 2007. Methane efflux from littoral vegetation stands of southern boreal lakes: An upscaled regional estimate. Atmos. Environ. 41, 339–351. https://doi.org/10.1016/j.atmosenv.2006.08.014.

Boon, P.I., Sorrell, B.K., 1995. Methane fluxes from an Australian floodplain wetland: the importance of emergent macrophytes. J. North Am. Benthol. Soc. 14, 582–598. https://doi.org/10.2307/1467543.

Bouchard, V., Frey, S.D., Gilbert, J.M., Reed, S.E., 2007. Effects of macrophyte functional group richness on emergent freshwater wetland functions. Ecology 88, 2903–2914. https://doi.org/10.1890/06-1144.1.

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. https://doi.org/10.4319/lo.1992.37.7.1420.

Brix, H., Sorrell, B.K., Lorenzen, B., 2001. Are *Phragmites*-dominated wetlands a net source or net sink of greenhouse gases? Aquat. Bot. 69, 313–324. https://doi.org/10.1016/S0304-3770(01)00145-0.

Calhoun, A., King, G.M., 1997. Regulation of root-associated methanotrophy by oxygen availability in the rhizosphere of two aquatic macrophytes. Appl. Environ. Microbiol. 63, 3051–3058. https://doi.org/10.1128/aem.63.8.3051-3058.1997.

Canadell, J.G., Monteiro, P.M.S., Costa, M.H., Cunha, L.C., da, Cox, P.M., Eliseev, A.V., Henson, S., Ishii, M., Jaccard, S., Koven, C., Lohila, A., Patra, P.K., Piao, S., Rogelj, J., Syampungani, S., Zaehle, S., Zickfeld, K., 2021. Global carbon and other biogeochemical cycles and feedbacks. In: Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S.L., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L., Gomis, M.I., Huang, M., Leitzell, K., Lonnoy, E., Matthews, J.B.R., Maycock, T.K., Waterfield, T., Yelekçi, O., Yu, R., Zhou, B. (Eds.), Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press.

Carmichael, M.J., Bernhardt, E.S., Bräuer, S.L., Smith, W.K., 2014. The role of vegetation in methane flux to the atmosphere: should vegetation be included as a distinct category in the global methane budget? Biogeochemistry 119, 1–24. https://doi.org/10.1007/s10533-014-9974-1.

Carmichael, M.J., Helton, A.M., White, J.C., Smith, W.K., 2018. Standing dead trees are a conduit for the atmospheric flux of CH_4 and CO_2 from wetlands. Wetlands 38, 133–143. https://doi.org/10.1007/s13157-017-0963-8.

Carpenter, S.R., Elser, J.J., Olson, K.M., 1983. Effects of roots of *Myriophyllum verticillatum* L. on sediment redox conditions. Aquat. Bot. 17, 243–249. https://doi.org/10.1016/0304-3770(83)90060-8.

Chanton, J.P., Dacey, J., 1991. Effects of vegetation on methane flux, reservoirs, and carbon isotopic composition. In: Sharkey, T., Holland, E., Mooney, H. (Eds.), Trace Gas Emissions by Plants. Academic Press, San Diego, California, pp. 65–92.

Chanton, J.P., Martens, C.S., Kelley, C.A., 1989. Gas transport from methane-saturated, tidal freshwater and wetland sediments. Limnol. Oceanogr. 34, 807–819. https://doi.org/10.4319/lo.1989.34.5.0807.

Chanton, J.P., Whiting, G.J., Happell, J.D., Gerard, C., 1993. Contrasting rates and diurnal patterns of methane emission from emergent aquatic macrophytes. Aquat. Bot. 46, 111–128. https://doi.org/10.1016/0304-3770(93)90040-4.

Chanton, J.P., Arkebauer, T.J., Harden, H.S., Verma, S.B., 2002. Diel variation in lacunal CH_4 and CO_2 concentration and $\delta^{13}C$ in *Phragmites australis*. Biogeochemistry 59, 243–249. https://doi.org/10.1023/A:1016067610783.

Chanton, J.P., Martens, C.S., Kelley, C.A., Crill, P.M., Showers, W.J., 1992. Methane transport mechanisms and isotopic fractionation in emergent macrophytes of an Alaskan tundra lake. J. Geophys. Res. 97, 16681–16688. https://doi.org/10.1029/90jd01542.

Chen, H., Wu, N., Gao, Y., Wang, Y., Luo, P., Tian, J., 2009. Spatial variations on methane emissions from Zoige alpine wetlands of Southwest China. Sci. Total Environ. 407, 1097–1104. https://doi.org/10.1016/j.scitotenv.2008.10.038.

Colmer, T.D., 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. https://doi.org/10.1046/j.1365-3040.2003.00846.x.

Colmer, T.D., Bloom, A.J., 1998. A comparison of NH_4^+ and NO_3^- net fluxes along roots of rice and maize. Plant Cell Environ. 21, 240–246. https://doi.org/10.1046/j.1365-3040.1998.00261.x.

Covey, K.R., Megonigal, J.P., 2019. Methane production and emissions in trees and forests. New Phytol. 222, 35–51. https://doi.org/10.1111/nph.15624.

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, 1–6. https://doi.org/10.1029/2012GL052361.

Dacey, J.W.H., 1980. Internal winds in water lilies: an adaptation for life in anaerobic sediments. Science 210, 1017–1019. https://doi.org/10.1126/science.210.4473.1017.

Dacey, J.W.H., 1981. Pressurized ventilation in the yellow waterlily. Ecology 62, 1137–1147. https://doi.org/10.2307/1937277.

Dacey, J.W.H., Klug, M.J., 1979. Methane efflux from lake sediments through water lilies. Science 203, 1253–1255. https://doi.org/10.1126/science.203.4386.1253.

Dacey, J.W.H., Klug, M.J., 1982. Tracer studies of gas circulation in Nuphar: $^{18}O_2$ and $^{14}CO_2$ transport. Physiol. Plant. 56, 361–366. https://doi.org/10.1111/j.1399-3054.1982.tb00353.x.

van den Berg, M., Ingwersen, J., Lamers, M., Streck, T., 2016. The role of *Phragmites* in the CH_4 and CO_2 fluxes in a minerotrophic peatland in southwest Germany. Biogeosciences 13, 6107–6119. https://doi.org/10.5194/bg-13-6107-2016.

van den Berg, M., van den Elzen, E., Ingwersen, J., Kosten, S., Lamers, L.P.M., Streck, T., 2020. Contribution of plant-induced pressurized flow to CH_4 emission from a *Phragmites* fen. Sci. Rep. 10, 12304. https://doi.org/10.1038/s41598-020-69034-7.

van der Nat, F.J.W.A., Middelburg, J.J., 1998a. Seasonal variation in methane oxidation by the rhizosphere of *Phragmites australis* and *Scirpus lacustris*. Aquat. Bot. 61, 95–110. https://doi.org/10.1016/S0304-3770(98)00072-2.

van der Nat, F.J.W.A., Middelburg, J.J., van Meteren, D., Wielemakers, A., 1998b. Diel methane emission patterns from *Scirpus lacustris* and *Phragmites australis*. Biogeochemistry 41, 1–22. https://doi.org/10.1023/A:1005933100905.

Devol, A.H., Richey, J.E., Clark, W.A., King, S.L., Martinelli, L.A., 1988. Methane emissions to the troposphere from the Amazon floodplain. J. Geophys. Res. Atmosph. 93, 183–1592. https://doi.org/10.1029/JD093iD02p01583.

Dingemans, B.J.J., Bakker, E.S., Bodelier, P.L.E., 2011. Aquatic herbivores facilitate the emission of methane from wetlands. Ecology 92, 1166–1173. https://doi.org/10.1890/10-1297.1.

Etnier, S.A., Villani, P.J., 2007. Differences in mechanical and structural properties of surface and aerial petioles of the aquatic plant *Nymphaea odorata* subsp. *tuberosa* (Nymphaeaceae). Am. J. Bot. 94, 1067–1072. https://doi.org/10.3732/ajb.94.7.1067.

Flanagan, L.B., Nikkel, D.J., Scherloski, L.M., Tkach, R.E., Smits, K.M., Selinger, L.B., Rood, S.B., 2021. Multiple processes contribute to methane emission in a riparian cottonwood forest ecosystem. N. Phytol. 229, 1970–1982. https://doi.org/10.1111/nph.16977.

Ford, P.W., Boon, P.I., Lee, K., 2002. Methane and oxygen dynamics in a shallow floodplain lake: the significance of periodic stratification. Hydrobiologia 485, 97–110. https://doi.org/10.1023/A:1021379532665.

Frenzel, P., Rudolph, J., 1998. Methane emission from a wetland plant: the role of CH_4 oxidation in *Eriophorum*. Plant Soil 202, 27–32. https://doi.org/10.1023/A:1004348929219.

Fritz, C., Pancotto, V.A., Elzenga, J.T.M., Visser, E.J.W., Grootjans, A.P., Pol, A., Iturraspe, R., Roelofs, J.G.M., Smolders, A.J.P., 2011. Zero methane emission bogs: Extreme rhizosphere oxygenation by cushion plants in Patagonia. N. Phytol. 190, 398–408. https://doi.org/10.1111/j.1469-8137.2010.03604.x.

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. https://doi.org/10.1016/j.aquabot.2004.10.003.

Gauci, V., Figueiredo, V., Gedney, N., Pangala, S.R., Stauffer, T., Weedon, G.P., Enrich-Prast, A., 2022. Non-flooded riparian Amazon trees are a regionally significant methane source. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences 380 (2215). https://doi.org/10.1098/rsta.2020.0446.

Greenup, A.L., Bradford, M.A., McNamara, N.P., Ineson, P., Lee, J.A., 2000. The role of *Eriophorum vaginatum* in CH_4 flux from an ombrotrophic peatland. Plant Soil 227, 265–272. https://doi.org/10.1023/A:1026573727311.

Grosse, W., Bernhard Büchel, H., Tiebel, H., 1991. Pressurized ventilation in wetland plants. Aquat. Bot. 39, 89–98. https://doi.org/10.1016/0304-3770(91)90024-Y.

Grosse, W., Armstrong, J., Armstrong, W., 1996. A history of pressurised gas-flow studies in plants. Aquat. Bot. 54, 87–100. https://doi.org/10.1016/0304-3770(96)01037-6.
Harden, H.S., Chanton, J.P., 1994. Locus of methane release and mass-dependent fractionation from two wetland macrophytes. Limnol. Oceanogr. 39, 148–154. https://doi.org/10.4319/lo.1994.39.1.0148.
Hayman, G.D., O'Connor, F.M., Dalvi, M., Clark, D.B., Gedney, N., Huntingford, C., Prigent, C., Buchwitz, M., Schneising, O., Burrows, J.P., Wilson, C., Richards, N., Chipperfield, M., 2014. Comparison of the HadGEM2 climate-chemistry model against in situ and SCIAMACHY atmospheric methane data. Atmos. Chem. Phys. 14, 13257–13280 https://doi.org/10.5194/acp-14-13257-2014, 2014.
Heilman, M.A., Carlton, R.G., 2001a. Ebullitive release of lacunar gases from floral spikes of *Potamogeton angustifolius* and *Potamogeton amplifolius*: effects on plant aeration and sediment CH_4 flux. Aquat. Bot. 71, 19–33. https://doi.org/10.1016/S0304-3770(01)00166-8.
Heilman, M.A., Carlton, R.G., 2001b. Methane oxidation associated with submersed vascular macrophytes and its impact on plant diffusive methane flux. Biogeochemistry 52, 207–244. https://doi.org/10.1023/A:1006427712846.
Helfter, C., Gondwe, M., Murray-Hudson, M., Makati, A., Lunt, M.F., Palmer, P.I., Skiba, U., 2022. Phenology is the dominant control of methane emissions in a tropical non-forested wetland. Nat. Commun. 13, 133. https://doi.org/10.1038/s41467-021-27786-4.
Hendriks, D.M.D., van Huissteden, J., Dolman, A.J., 2010. Multi-technique assessment of spatial and temporal variability of methane fluxes in a peat meadow. Agric. . Meteorol. 150, 757–774. https://doi.org/10.1016/j.agrformet.2009.06.017.
Henneberg, A., Sorrell, B.K., Brix, H., 2012. Internal methane transport through *Juncus effusus*: Experimental manipulation of morphological barriers to test above- and belowground diffusion limitation. N. Phytol. 196, 799–806. https://doi.org/10.1111/j.1469-8137.2012.04303.x.
Hyvönen, T., Ojala, A., Kankaala, P., Martikainen, P.J., 1998. Methane release from stands of water horsetail (*E. fluviatile*) in a boreal lake. Freshw. Biol. 40, 275–284. https://doi.org/10.1046/j.1365-2427.1998.00351.x.
Jackson, M.B., 1989. Regulation of aerenchyma formation in roots and shoots by oxygen and ethylene. In: Cell Separation in Plants. Springer Berlin Heidelberg, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-74161-6_25.
Jeffrey, L.C., Maher, D.T., Tait, D.R., Euler, S., Johnston, S.G., 2020. Tree stem methane emissions from subtropical lowland forest (*Melaleuca quinquenervia*) regulated by local and seasonal hydrology. Biogeochemistry 151, 273–290. https://doi.org/10.1007/s10533-020-00726-y.
Jeffrey, L.C., Reithmaier, G., Sippo, J.Z., Johnston, S.G., Tait, D.R., Harada, Y., Maher, D. T., 2019. Are methane emissions from mangrove stems a cryptic carbon loss pathway? Insights from a catastrophic forest mortality. N. Phytol. 224, 146–154. https://doi.org/10.1111/nph.15995.
Jeffrey, L.C., Maher, D.T., Chiri, E., Leung, P.M., Nauer, P.A., Arndt, S.K., Tait, D.R., Greening, C., Johnston, S.G., 2021. Bark-dwelling methanotrophic bacteria decrease methane emissions from trees. Nat. Commun. 12, 1–8. https://doi.org/10.1038/s41467-021-22333-7.
Johnson, M.S., Matthews, E., Bastviken, D., Deemer, B., Du, J., Genovese, V., 2021. Spatiotemporal methane emission from global reservoirs. J. Geophys. Res. Biogeosci. 126. https://doi.org/10.1029/2021JG006305.
Jordan, T.E., Whigham, D.F., 1988. The importance of standing dead shoots of the narrow leaved cattail, *Typha angustifolia* L. Aquat. Bot. 29, 319–328. https://doi.org/10.1016/0304-3770(88)90076-9.
Justin, S.H.F.W., Armstrong, W., 1987. The anatomical characteristics of roots and plant response to soil flooding. N. Phytol. 465–495.
Juutinen, S., Larmola, T., Remus, R., Mirus, E., Merbach, W., Silvola, J., Augustin, J., 2003. The contribution of *Phragmites australis* litter to methane (CH_4) emission in planted and non-planted fen microcosms. Biol. Fertil. Soils 38, 10–14. https://doi.org/10.1007/s00374-003-0618-1.
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. https://doi.org/10.1023/B:BIOG.0000015277.17288.7a.
Kankaala, P., Mäkelä, S., Käki, T., Ojala, A., Pajunin, 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. Change Biol. 11, 145–153. https://doi.org/10.1111/j.1365-2486.2004.00888.x.
Kankaala, P., Mäkelä, S., Huitu, E., Käki, T., Ojala, A., Rantakari, M., Kortlainen, P., Arvola, L., Bergström, I., 2003. Midsummer spatial variation in methane efflux from stands of littoral vegetation in a boreal meso-eutrophic lake. Freshw. Biol. 48, 1617–1629. https://doi.org/10.1046/j.1365-2427.2003.01113.x.
Kao-Kniffin, J., Freyre, D.S., Balser, T.C., 2010. Methane dynamics across wetland plant species. Aquat. Bot. 93, 107–113. https://doi.org/10.1016/j.aquabot.2010.03.009.
Kelker, D., Chanton, J., 1997. The effect of clipping on methane emissions from *Carex*. Biogeochemistry 39 (1), 37–44. 〈http://www.jstor.org/stable/1469071〉.
Kleinen, T., Brovkin, V., Schuldt, R.J., 2012. A dynamic model of wetland extent and peat accumulation: results for the Holocene. Biogeosciences 9, 235–248. https://doi.org/10.5194/bg-9-235-2012.
Konnerup, D., Sorrell, B.K., Brix, H., 2011. Do tropical wetland plants possess a convective gas transport mechanism? N. Phytol. 190, 379–386. https://doi.org/10.1111/j.1469-8137.2010.03585.x.
Kosten, S., Piñeiro, M., de Goede, E., de Klein, J., Lamers, L.P.M., Ettwig, K., 2016. Fate of methane in aquatic systems dominated by free-floating plants. Water Res 104, 200–207. https://doi.org/10.1016/j.watres.2016.07.054.
Kozlowski, T.T., 1997. Responses of woody plants to flooding and salinity. Tree Physiol. 17, 1–28. https://doi.org/10.1093/treephys/17.7.490.
Lamers, L.P., van Diggelen, J.M., Op den Camp, H.J., Visser, E.J., Lucassen, E.C., Vile, M. A., Jetten, M.S., Smolders, A.J., Roelofs, J.G., 2012. Microbial transformations of nitrogen, sulfur, and iron dictate vegetation composition in wetlands: a review. Front. Microbiol. 3, 156. https://doi.org/10.3389/fmicb.2012.00156.
Larmola, T., Alm, J., Juutinen, S., Huttunen, J.T., Martikainen, P.J., Silvola, J., 2004. Contribution of vegetated littoral zone to winter fluxes of carbon dioxide and methane from boreal lakes. J. Geophys. Res. 109, D19102 https://doi.org/10.1029/2004JD004875.
Lawrence, B.A., Lishawa, S.C., Hurst, N., Castillo, B.T., Tuchman, N.C., 2017. Wetland invasion by *Typha* × *glauca* increases soil methane emissions. Aquat. Bot. 137, 80–87. https://doi.org/10.1016/j.aquabot.2016.11.012.
Le Mer, J., Roger, P., 2001. Production, oxidation, emission and consumption of methane by soils: A review. Eur. J. Soil Biol. 37, 25–50. https://doi.org/10.1016/S1164-5563(01)01067-6.
Lemoine, D.G., Mermillod-Blondin, F., Barrat-Segretain, M.-H., Massé, C., Malet, E., 2012. The ability of aquatic macrophytes to increase root porosity and radial oxygen loss determines their resistance to sediment anoxia. Aquat. Ecol. 46, 191–200. https://doi.org/10.1007/s10452-012-9391-2.
Li, L., Wie, S., Shen, W., 2020. The role of methane in plant physiology: a review. Plant Cell Rep. 39, 171–179. https://doi.org/10.1007/s00299-019-02478-y.
Manzur, M., Grimoldi, A., Insausti, P., Striker, G., 2015. Radial oxygen loss and physical barriers in relation to root tissue age in species with different types of aerenchyma. Funct. Plant Biol. 42, 9–17. https://doi.org/10.1071/FP14078.
Matthews, P.G.D., Seymour, R.S., 2006. Anatomy of the gas canal system of *Nelumbo nucifera*. Aquat. Bot. 85, 147–154. https://doi.org/10.1016/j.aquabot.2006.03.002.
Matthews, P.G.D., Seymour, R.S., 2014. Stomata actively regulate internal aeration of the sacred lotus *Nelumbo nucifera*. Plant, Cell Environ. 37, 402–413. https://doi.org/10.1111/pce.12163.
Megonigal, J.P., Brewer, P.E., Knee, K.L., 2020. Radon as a natural tracer of gas transport through trees. N. Phytol. 225, 1470–1475. https://doi.org/10.1111/nph.16292.
Megonigal, J.P., Schlesinger, W.H., 1997. Enhanced CH_4 emissions from a wetland soil exposed to elevated CO_2. Biogeochemistry 37, 77–88. https://doi.org/10.1023/A:1005738102545.
Melack, J.M., Hess, L.L., Gastil, M., Forsberg, B.R., Hamilton, S.K., Lima, I.B.T., Novo, E. M.L.M., 2004. Regionalization of methane emissions in the Amazon Basin with microwave remote sensing. Glob. Chang. Biol. 10, 530–544. https://doi.org/10.1111/j.1365-2486.2004.00763.x.
Milberg, P., Törnqvist, L., Westerberg, L.M., Bastviken, D., 2017. Temporal variations in methane emissions from emergent aquatic macrophytes in two boreonemoral lakes. AoB Plants 9, plx029. https://doi.org/10.1093/aobpla/plx029.
Møller, C.L., Sand-Jensen, K., 2008. Iron plaques improve the oxygen supply to root meristems of the freshwater plant, *Lobelia dortmanna*. N. Phytol. 179, 848–856. https://doi.org/10.1111/j.1469-8137.2008.02506.x.
Moorhead, K.K., Reddy, K.R., 1988. Oxygen transport through selected aquatic macrophytes. J. Environ. Qual. 17, 138–142. https://doi.org/10.2134/JEQ1988.00472425001700010022X.
Morin, T.H., Bohrer, G., Naor-Azrieli, L., Mesi, S., Kenny, W.T., Mitsch, W.J., Schäfer, K. V.R., 2014. The seasonal and diurnal dynamics of methane flux at a created urban wetland. Ecol. Eng. 72, 74–83. https://doi.org/10.1016/j.ecoleng.2014.02.002.
Mueller, P., Jensen, K., Megonigal, J.P., 2016. Plants mediate soil organic matter decomposition in response to sea level rise. Glob. Change Biol. 22, 404–414. https://doi.org/10.1111/gcb.13082.
Neubauer, S.C., Givler, K., Velentine, S.K., Megonigal, J.P., 2005. Seasonal patterns and plant-mediated controls of subsurface wetland biogeochemistry. Ecology 86, 3334–3344. https://doi.org/10.1890/04-1951.
Nielsen, C.S., Michelsen, A., Strobel, B.W., Wulff, K., Banyasz, I., Elberling, B., 2017. Correlations between substrate availability, dissolved CH_4, and CH_4 emissions in an arctic wetland subject to warming and plant removal. J. Geophys. Res. Biogeosci. 122, 645–660. https://doi.org/10.1002/2016JG003511.
Oliveira-Junior, E.S., Tang, Y., van den Berg, S.J.P., Cardoso, S.J., Lamers, L.P.M., Kosten, S., 2018. The impact of water hyacinth (*Eichhornia crassipes*) on greenhouse gas emission and nutrient mobilization depends on rooting and plant coverage. Aquat. Bot. 145, 1–9. https://doi.org/10.1016/j.aquabot.2017.11.005.
Oliveira-Junior, E.S., van Bergen, T.J.H.M., Nauta, J., Budiša, A., Aben, R.C.H., Weideveld, S.T.J., de Souza, C.A., Muniz, C.C., Roelofs, J., Lamers, L.P.M., Kosten, S., 2020. Water hyacinth's effect on greenhouse gas fluxes: a field study in a wide variety of tropical water bodies. Ecosystems 24, 988–1004. https://doi.org/10.1007/s10021-020-00564-x.
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. https://doi.org/10.1038/nature24639.
Pangala, S.R., Gowing, D.J., Hornibrook, E.R.C., Gauci, V., 2014. Controls on methane emissions from *Alnus glutinosa* saplings. N. Phytol. 201, 887–896. https://doi.org/10.1111/nph.12561.
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. https://doi.org/10.1111/gcb.12891.
Pangala, S.R., Moore, S., Hornibrook, E.R.C., Gauci, V., 2013. Trees are major conduits for methane egress from tropical forested wetlands. N. Phytol. 197, 524–531. https://doi.org/10.1111/nph.12031.
Parolin, P., Wittmann, F., 2010. Struggle in the flood: tree responses to flooding stress in four tropical floodplain systems. AoB Plants 2010, plq003. https://doi.org/10.1093/aobpla/plq003.
Pitz, S.L., Megonigal, J.P., 2017. Temperate forest methane sink diminished by tree emissions. N. Phytol. 214, 1432–1439. https://doi.org/10.1111/nph.14559.

Pitz, S.L., Megonigal, J.P., Chang, C.H., Szlavecz, K., 2018. Methane fluxes from tree stems and soils along a habitat gradient. Biogeochemistry 137, 307–320. https://doi.org/10.1007/s10533-017-0400-3.

Poindexter, C.M., Baldocchi, D.D., Matthes, J.H., Knox, S.H., Variano, E.A., 2016. The contribution of an overlooked transport process to a wetland's methane emissions. Geophys. Res. Lett. 43, 6276–6284. https://doi.org/10.1002/2016GL068782.

Rice, A.L., Butenhoff, C.L., Shearer, M.J., Teama, D., Rosenstiel, T.N., Khalil, M.A.K., 2010. Emissions of anaerobically produced methane by trees. Geophys. Res. Lett. 37. https://doi.org/10.1029/2009GL041565.

Richards, J.H., Troxler, T.G., Lee, D.W., Zimmerman, M.S., 2011. Experimental determination of effects of water depth on *Nymphaea odorata* growth, morphology and biomass allocation. Aquat. Bot. 95, 9–16. https://doi.org/10.1016/j.aquabot.2011.03.002.

Rietl, A.J., Nyman, J.A., Lindau, C.W., Jackson, C.R., 2017. Wetland methane emissions altered by vegetation disturbance: an interaction between stem clipping and nutrient enrichment. Aquat. Bot. 136, 205–211. https://doi.org/10.1016/j.aquabot.2016.10.008.

Riley, W.J., Subin, Z.M., Lawrence, D.M., Swenson, S.C., Torn, M.S., Meng, L., Mahowald, N.M., 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. https://doi.org/10.5194/bg-8-1925-2011.

Rosentreter, J.A., Borges, A.V., Deemer, B.R., Holgerson, M.A., Liu, S., Song, C., Melack, J., Raymond, P.A., Duarte, C.M., Allen, G.H., Olefeldt, D., Poulter, B., Battin, T.I., Eyre, B.D., 2021. Half of global methane emissions come from highly variable aquatic ecosystem sources. Nat. Geosci. 14, 225–230. https://doi.org/10.1038/s41561-021-00715-2.

Rusch, H., Rennenberg, H., 1998. Black alder (*Alnus glutinosa* (L.) Gaertn.) trees mediate methane and nitrous oxide emission from the soil to the atmosphere. Plant Soil 201, 1–7. https://doi.org/10.1023/A:1004331521059.

Sanders, I.A., Heppell, C.M., Cotton, J.A., Wharton, G., Hildrew, A.G., Flowers, E.J., Trimmer, M., 2007. Emission of methane from chalk streams has potential implications for agricultural practices. Freshw. Biol. 52, 1176–1186. https://doi.org/10.1111/j.1365-2427.2007.01745.x.

Saunois, M.R., Stavert, A., Poulter, B., Bousquet, P.G., Canadell, J.B., Jackson, R.A., Raymond, P.J., Dlugokencky, E., Houweling, S.K., Patra, P., Ciais, P.K., Arora, V., Bastviken, D., Bergamaschi, P.R., Blake, D., Brailsford, G., Bruhwiler, L.M., Carlson, K., Carrol, M., Castaldi, S., Chandra, N., Crevoisier, C.M., Crill, P., Covey, K. L., Curry, C., Etiope, G., Frankenberg, C., Gedney, N.I., Hegglin, M., Höglund-Isaksson, L., Hugelius, G., Ishizawa, M., Ito, A., Janssens-Maenhout, G.M., Jensen, K., Joos, F., Kleinen, T.B., Krummel, P.L., Langenfelds, R.G., Laruelle, G., Liu, L., MacHida, T., Maksyutov, S.C., McDonald, K., McNorton, J.A., Miller, P.R., Melton, J., Morino, I., Müller, J., Murguia-Flores, F., Naik, V., Niwa, Y., Noce, S., O'Doherty, S.J., Parker, R., Peng, C., Peng, S.P., Peters, G., Prigent, C., Prinn, R., Ramonet, M., Regnier, P.J., Riley, W.A., Rosentreter, J., Segers, A.J., Simpson, I., Shi, H.J., Smith, S., Paul Steele, L.F., Thornton, B., Tian, H., Tohjima, Y.N., Tubiello, F., Tsuruta, A., Viovy, N., Voulgarakis, A.S., Weber, T., Van Weele, M.R., Van Der Werf, G.F., Weiss, R., Worthy, D., Wunch, D., Yin, Y., Yoshida, Y., Zhang, W., Zhang, Z., Zhao, Y., Zheng, B., Zhu, Qing, Zhu, Qiuan, Zhuang, Q., 2020. The global methane budget 2000-2017. Earth Syst. Sci. Data 12, 1561–1623. https://doi.org/10.5194/essd-12-1561-2020.

Schindler, T., Machacova, K., Mander, Ü., Escuer-Gatius, J., Soosaar, K., 2021. Diurnal tree stem CH_4 and N_2O flux dynamics from a riparian alder forest. Forests 12, 1–9. https://doi.org/10.3390/f12070863.

Scholz, V., Müller, H., Koren, K., Nielsen, L., Meckenstock, R., 2019. The rhizosphere of aquatic plants is a habitat for cable bacteria. FEMS Microbiol. Ecol. 62, fiz062. https://doi.org/10.1093/femsec/fiz062.

Schröder, P., Grosse, W., Woermann, D., 1986. Localization of thermo-osmotically active partitions in young leaves of *Nuphar lutea*. J. Exp. Bot. 37, 1450–1461. https://doi.org/10.1093/jxb/37.10.1450.

Schuette, J.L., Klug, M.J., 1995. Evidence for mass flow in flowering individuals of the submersed vascular plant *Myriophyllum heterophyllum*. Plant Physiol. 108, 1251–1258. https://doi.org/10.1104/pp.108.3.1251.

Schultz, R.E., Pett, L., 2018. Plant community effects on CH_4 fluxes, root surface area, and carbon storage in experimental wetlands. Ecol. Eng. 114, 96–103. https://doi.org/10.1016/j.ecoleng.2017.06.027.

Seago, J.L., Marsh, L.C., Stevens, K.J., Soukup, A., Votrubová, O., Enstone, D.E., 2005. A Re-examination of the root cortex in wetland flowering plants with respect to aerenchyma. Ann. Bot. 96, 565–579. https://doi.org/10.1093/aob/mci211.

Sebacher, D.I., Harriss, R.C., Bartlett, K.B., 1985. Methane emissions to the atmosphere through aquatic plants. J. Environ. Qual. 14, 40–46. https://doi.org/10.2134/jeq1985.00472425001400010008x.

Sifton, H.B., 1945. Air-space tissue in plants. Bot. Rev. 11, 108–143. https://doi.org/10.1007/BF02861138.

Sifton, H.B., 1957. Air-space tissue in plants. II. Bot. Rev. 23, 303. https://doi.org/10.1007/BF02872447.

Silvey, C., Jarecke, K.M., Hopfensperger, K., Loecke, T.D., Burgin, A.J., 2019. Plant species and hydrology as controls on constructed wetland methane fluxes. Soil Sci. Soc. Am. J. 83, 848–855. https://doi.org/10.2136/sssaj2018.11.0421.

Singh, S.N., Kulshreshtha, K., Agnihotri, S., 2000. Seasonal dynamics of methane emission from wetlands. Chemosph. Glob. Chang. Sci. 2, 39–46. https://doi.org/10.1016/S1465-9972(99)00046-X.

Sjögersten, S., Siegenthaler, A., Lopez, O.R., Aplin, P., Turner, B., Gauci, V., 2020. Methane emissions from tree stems in neotropical peatlands. New Phytol. 225, 769–781. https://doi.org/10.1111/nph.16178.

Smith, L.K., Lewis, W.M., 1992. Seasonality of methane emissions from five lakes and associated wetlands of the Colorado Rockies. Glob. Biogeochem. Cycles 6, 323–338. https://doi.org/10.1029/92GB02016.

Sorrell, B.K., Dromgoole, F.I., 1988. Oxygen transport in the submerged freshwater macrophyte *Egeria densa* planch. II. Role of lacunar gas pressures. Aquat. Bot. 31, 93–106. https://doi.org/10.1016/0304-3770(88)90041-1.

Sorrell, B.K., Boon, P.I., 1994. Convective gas flow in *Eleocharis sphacelata* R. Br.: methane transport and release from wetlands. Aquat. Bot. 47, 197–212. https://doi.org/10.1016/0304-3770(94)90053-1.

Sorrell, B.K., Downes, M.T., 2004. Water velocity and irradiance effects on internal transport and metabolism of methane in submerged *Isoetes alpinus* and *Potamogeton crispus*. Aquat. Bot. 79, 189–202. https://doi.org/10.1016/j.aquabot.2004.02.004.

Sorrell, B.K., Hawes, I., 2010. Convective gas flow development and the maximum depths achieved by helophyte vegetation in lakes. Ann. Bot. 105, 165–174. https://doi.org/10.1093/aob/mcp138.

Sorrell, B.K., Brix, H., 2015. Gas transport and exchange through wetland plant aerenchyma. Methods Biogeochem. Wetl. 10, 177–196. https://doi.org/10.2136/sssabookser10.c11.

Sorrell, B.K., Brix, H., Orr, P.T., 1997. *Eleocharis sphacelata*: Internal gas transport pathways and modelling of aeration by pressurized flow and diffusion. N. Phytol. 136, 433–442. https://doi.org/10.1046/j.1469-8137.1997.00769.x.

Sorrell, B.K., Downes, M.T., Stanger, C.L., 2002. Methanotrophic bacteria and their activity on submerged aquatic macrophytes. Aquat. Bot. 72, 107–119. https://doi.org/10.1016/S0304-3770(01)00215-7.

Sorrell, B.K., Mendelssohn, I.A., McKee, K.L., Woods, R.A., 2000. Ecophysiology of wetland plant roots: a modelling comparison of aeration in relation to species distribution. Ann. Bot. 86, 675–685. https://doi.org/10.1006/anbo.2000.1173.

Soukup, A., Votrubová, O., Čížková, H., 2000. Internal segmentation of rhizomes of *Phragmites australis*: Protection of the internal aeration system against being flooded. N. Phytol. 145, 71–75. https://doi.org/10.1046/j.1469-8137.2000.00555.x.

Soukup, A., Armstrong, W., Schreiber, L., Franke, R., Votrubová, O., 2007. Apoplastic barriers to radial oxygen loss and solute penetration: a chemical and functional comparison of the exodermis of two wetland species, *Phragmites australis* and *Glyceria maxima*. N. Phytol. 173, 264–278. https://doi.org/10.1111/j.1469-8137.2006.01907.x.

Steppe, K., Sterck, F., Deslauriers, A., 2015. Diel growth dynamics in tree stems: Linking anatomy and ecophysiology. Trends Plant Sci. 20, 335–343. https://doi.org/10.1016/j.tplants.2015.03.015.

Sturtevant, C., Ruddell, B.L., Knox, S.H., Verfaillie, J., Matthes, J.H., Oikawa, P.Y., Baldocchi, D., 2016. Identifying scale-emergent, nonlinear, asynchronous processes of wetland methane exchange. J. Geophys. Res. Biogeosci. 121, 188–204. https://doi.org/10.1002/2015JG003054.

Sundqvist, E., Crill, P., Mlder, M., Vestin, P., Lindroth, A., 2012. Atmospheric methane removal by boreal plants. Geophys. Res. Lett. 39, L21806 https://doi.org/10.1029/2012GL053592.

Sutton-Grier, A.E., Megonigal, J.P., 2011. Plant species traits regulate methane production in freshwater wetland soils. Soil Biol. Biochem. 43, 413–420. https://doi.org/10.1016/j.soilbio.2010.11.009.

Terazawa, K., Yamada, K., Ohno, Y., Sakata, T., Ishizuka, S., 2015. Spatial and temporal variability in methane emissions from tree stems of *Fraxinus mandshurica* in a cool-temperate floodplain forest. Biogeochemistry 123, 349–362. https://doi.org/10.1007/s10533-015-0070-y.

Tornberg, T., Bendix, M., Brix, H., 1994. Internal gas transport in *Typha latifolia* L. and *Typha angustifolia* L. 2. Convective throughflow pathways and ecological significance. Aquat. Bot. 49, 91–105. https://doi.org/10.1016/0304-3770(94)90031-0.

Turetsky, M.R., Kotowska, A., Bubier, J., Dise, N.B., Crill, P., Hornibrook, E.R.C., Minkkinen, K., Moore, T.R., Myers-Smith, I.H., Nykänen, H., Olefeldt, D., Rinne, J., Saarnio, S., Shurpali, N., Tuittila, E.S., Waddington, J.M., White, J.R., Wickland, K. P., Wilmking, M., 2014. A synthesis of methane emissions from 71 northern, temperate, and subtropical wetlands. Glob. Chang. Biol. 20, 2183–2197. https://doi.org/10.1111/gcb.12580.

Turner, J.C., Moorberg, C.J., Wong, A., Shea, K., Waldrop, M.P., Turetsky, M.R., Neumann, R.B., 2020. Getting to the root of plant-mediated methane emissions and oxidation in a thermokarst bog. J. Geophys. Res. Biogeosci. 125. https://doi.org/10.1029/2020JG005825.

Verhoeven, J.T.A., 1979. The ecology of *Ruppia*-dominated communities in western Europe. I. Distribution of *Ruppia* representatives in relation to their autecology. Aquat. Bot. 6, 197–267. https://doi.org/10.1016/0304-3770(79)90064-0.

Visser, E., Voesenek, L., 2004. Acclimation to soil flooding-sensing and signal-transduction. Plant Soil 254, 197–214. https://doi.org/10.1007/s11104-004-1650-0.

Visser, E., Colmer, T., Blom, C., Voesenek, L., 2000. Changes in growth, porosity, and radial oxygen loss from adventitious roots of selected mono- and dicotyledonous wetland species with contrasting types of aerenchyma. Plant, Cell Environ. 23, 1237–1245. https://doi.org/10.1046/j.1365-3040.2000.00628.x.

Voesenek, L.A.C.J., Bailey-Serres, J., 2015. Flood adaptive traits and processes: an overview. N. Phytol. 206, 57–73. https://doi.org/10.1111/nph.13209.

Vretare Strand, V., 2002. The influence of ventilation systems on water depth penetration of emergent macrophytes. Freshw. Biol. 47, 1097–1105. https://doi.org/10.1046/j.1365-2427.2002.00834.x.

Waldhoff, D., Parolin, P., 2010. Morphology and anatomy of leaves. In: Junk, W., Piedade, M., Wittmann, F., Schöngart, J., Parolin, P. (Eds.), Amazonian Floodplain Forests. Ecological Studies, vol 210. Springer, Dordrecht. https://doi.org/10.1007/978-90-481-8725-6_9.

Wang, H., Lu, J., Wang, W., Yang, L., Yin, C., 2006. Methane fluxes from the littoral zone of hypereutrophic Taihu Lake, China. J. Geophys. Res. 111, D17109 https://doi.org/10.1029/2005JD006864.

Wang, N., Huang, D., Li, C., Deng, Y., Li, W., Yao, Y., Liao, W., 2020. Regulatory roles of methane in plants. Sci. Hortic. 272, 109492 https://doi.org/10.1016/j.scienta.2020.109492.

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., Feng, J.C., Han, X.G., 2016. Methane emissions from the trunks of living trees on upland soils. N. Phytol. 211, 429–439. https://doi.org/10.1111/nph.13909.

Ward, N.D., Indivero, J., Gunn, C., Wang, W., Bailey, V., McDowell, N.G., 2019. Longitudinal gradients in tree stem greenhouse gas concentrations across six Pacific northwest coastal forests. J. Geophys. Res. Biogeosci. 124, 1401–1412. https://doi.org/10.1029/2019JG005064.

Watson, A., Stephen, K.D., Nedwell, D.B., Arah, J.R.M., 1997. Oxidation of methane in peat: Kinetics of CH_4 and O_2 removal and the role of plant roots. Soil Biol. Biochem. 29, 1257–1267. https://doi.org/10.1016/S0038-0717(97)00016-3.

Welch, B., Gauci, V., Sayer, E.J., 2019. Tree stem bases are sources of CH_4 and N_2O in a tropical forest on upland soil during the dry to wet season transition. Glob. Chang. Biol. 25, 361–372. https://doi.org/10.1111/gcb.14498.

White, S.D., Ganf, G.G., 2000. Flow characteristics and internal pressure profiles in leaves of the Typha domingensis. Aquat. Bot. 67, 263–273. https://doi.org/10.1016/S0304-3770(00)00100-5.

Whiting, G.J., Chanton, J.P., 1992. Plant-dependent CH_4 emission in a subarctic Canadian fen. Glob. Biogeochem. Cycles 6, 225–231. https://doi.org/10.1029/92GB00710.

Whiting, G.J., Chanton, J.P., 1993. Primary production control of methane emission from wetlands. Nature 364, 794–795. https://doi.org/10.1038/364794a0.

Whiting, G.J., Chanton, J.P., 1996. Control of the diurnal pattern of methane emission from emergent aquatic macrophytes by gas transport mechanisms. Aquat. Bot. 54, 237–253. https://doi.org/10.1016/0304-3770(96)01048-0.

Wilcock, R.J., Sorrell, B.K., 2008. Emissions of greenhouse gases CH_4 and N_2O from low-gradient streams in agriculturally developed catchments. Water Air Soil Pollut. 188, 155–170. https://doi.org/10.1007/s11270-007-9532-8.

Winton, R.S., Richardson, C.J., 2017. Top-down control of methane emission and nitrogen cycling by waterfowl. Ecology 98, 265–277. https://doi.org/10.1002/ecy.1640.

Xing, Y., Xie, P., Yang, H., Wu, A., Ni, L., 2006. The change of gaseous carbon fluxes following the switch of dominant producers from macrophytes to algae in a shallow subtropical lake of China. Atmos. Environ. 40, 8034–8043. https://doi.org/10.1016/j.atmosenv.2006.05.033.

Yavitt, J.B., Knapp, A.K., 1998. Aspects of methane flow from sediment through emergent cattail (*Typha latifolia*) plants. N. Phytol. 139, 495–503. https://doi.org/10.1046/j.1469-8137.1998.00210.x.

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*). N. Phytol. 222, 115–121. https://doi.org/10.1111/nph.15346.

Yuan, Fenghui, Wang, Y., Ricciuto, D.M., Shi, X., Yuan, Fengming, Hanson, P.J., Bridgham, S., Keller, J., Thornton, P.E., Xu, X., 2021. An integrative model for soil biogeochemistry and methane processes. II: warming and elevated CO_2 effects on peatland CH4 emissions. J. Geophys. Res. Biogeosci. 126 https://doi.org/10.1029/2020JG005963.

Zeikus, J.G., Ward, J.C., 1974. Methane formation in living trees: a microbial origin. Science 184, 1181–1183. https://doi.org/10.1126/science.184.4142.1181.

Zhang, M., Xiao, Q., Zhang, Z., Gao, Y., Zhao, J., Pu, Y., Wang, W., Xiao, W., Liu, S., Lee, X., 2019. Methane flux dynamics in a submerged aquatic vegetation zone in a subtropical lake. Sci. Total Environ. 672, 400–409. https://doi.org/10.1016/j.scitotenv.2019.03.466.

Zhu, J., Park, J.H., Lee, S., Lee, J.H., Hwang, D., Kwak, J.M., Kim, Y.J., 2020. Regulation of stomatal development by stomatal lineage miRNAs. Proc. Natl. Acad. Sci. U.S.A. 117, 6237–6245. https://doi.org/10.1073/pnas.1919722117.