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Methane emissions from tree stems: a new frontier in the global carbon cycle

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Summary

Tree stems from wetland, floodplain and upland forests can produce and emit methane (CH$_4$). Tree CH$_4$ stem emissions have high spatial and temporal variability, but there is no consensus on the biophysical mechanisms that drive stem CH$_4$ production and emissions. Here, we summarize up to 30 opportunities and challenges for stem CH$_4$ emissions research, which when addressed will improve estimates of magnitudes, patterns, drivers and trace the potential origin of CH$_4$ emissions. We identified the need (i) for both long-term high frequency measurements of stem CH$_4$ emissions to understand the fine scale processes, alongside rapid large-scale measurements designed to understand variability across individuals, species and ecosystems; (ii) to identify microorganisms and biogeochemical pathways associated with CH$_4$ production; and (iii) to develop a mechanistic model including passive and active transport of CH$_4$ from the soil-tree-atmosphere continuum. Addressing these challenges would help to constrain magnitudes and patterns of CH$_4$ emissions, and would allow for the integration of pathways and mechanisms of CH$_4$ production and emissions into process-based models. These advances will facilitate upscaling of stem CH$_4$ emissions to the ecosystem level and quantify the role of stem CH$_4$ emissions for the local-to-global CH$_4$ budget.

Key words: methane emissions, CH$_4$ transport, tree stems, upland forests, wetland forests, methanogenesis, spatial variability, temporal variability

Introduction

Trees can emit methane (CH$_4$) through their stems, but the magnitude of these emissions in the context of the global CH$_4$ budget is uncertain and a matter of debate (Keppler et al., 2006; Nisbet et al., 2009; Lenhart et al., 2012; Saunois et al., 2016; Angle et al., 2017).
Furthermore, the biogeochemical pathways of production, oxidation, and transport leading to tree-stem CH$_4$ emissions are poorly understood and likely vary across species and ecosystem types. There is mounting evidence that tree stems from tropical to boreal forests emit CH$_4$ (Covey & Megonigal, 2018) and, in some circumstances, these emissions are regionally relevant (Wang et al., 2017; Pangala et al., 2017). Yet, biogeochemical models tend to consider soils as the only active surfaces exchanging CH$_4$ with the atmosphere in forests (Kirschke et al., 2013; Saunois et al., 2016). Even in the absence of data to estimate the contribution of tree-stem emissions to the global CH$_4$ budget (Carmichael et al., 2014; Saunois et al., 2016), it is feasible that even low stem emissions for individual trees might upscale to a large global flux considering that the total number of trees in the world is estimated to be about 3 trillion (Crowther et al., 2015).

To date, only a few studies have reported stem CH$_4$ emissions in upland forests under natural conditions (Machacova et al., 2016; Wang et al., 2016, 2017; Warner et al., 2017; Pitz & Megonigal, 2017; Maier et al., 2018). Likewise, there are only a few studies that report stem CH$_4$ emissions in forested wetlands under natural conditions (Terazawa et al., 2007, 2015; Gauci et al., 2010; Pangala et al., 2013, 2015, 2017; Pitz et al., 2018). Collectively, these studies demonstrate that tree stems can emit CH$_4$ regardless of whether trees are growing on upland soils (usually a CH$_4$ sink (Saunois et al., 2016)) or wetland soils (usually a CH$_4$ source (Matthews & Fung, 1987; Le Mer & Roger, 2001)). Ultimately, the net stem flux is the balance between co-occurring methanogenesis (production) and methanotrophy (oxidation) controlling if the trees act as CH$_4$ sinks or sources. However, the origin, temporal and spatial patterns and magnitudes of these emissions are still unclear. Methane could be produced in deep soil layers (even in upland forest where soils are usually net sinks of CH$_4$), and then transported through the plant continuum (root-stem-bark) to the atmosphere (Megonigal & Guenther, 2008; Machacova et al., 2016; Pitz & Megonigal, 2017; Pitz et al., 2018; Maier et al. 2018).
On the other hand, CH$_4$ could be produced in the heartwood of a tree and laterally diffused to the free atmosphere (Zeikus & Ward, 1974; Covey et al., 2012; Wang et al., 2016, 2017; Pitz & Megonigal, 2017; Yip et al., 2018). These processes have usually been studied independently, limiting our capacity to determine if one dominates over the other, or if they act in conjunction depending on tree species and ecosystem types (Warner et al., 2017).

The primary objective of this manuscript is to highlight innovative directions for research on tree stem CH$_4$ emissions. Here, we highlight four key areas that represent a science frontier: (i) spatial variability of stem CH$_4$ emissions; (ii) variability and magnitudes of these emissions at multiple temporal scales; (iii) origin, sources and biochemical pathways associated with stem CH$_4$ emissions; and (iv) improve data-knowledge-model fusion to represent and forecast CH$_4$ production, transport and emissions.

1. Accounting for spatial variability

Accounting for spatial variability of stem CH$_4$ emissions is crucial for describing and quantifying the role of stem emissions in the local-to-global CH$_4$ cycle. This includes variability of emissions within and among tree stems, species, functional types, and ecosystems.

*Stem height (Fig1.1).* Studies measuring tree stem emissions report high variability with a general trend of decreasing CH$_4$ emissions with stem height; particularly, where soil is proposed as the likely source of CH$_4$ for stem emissions (Terazawa et al., 2007; Pangala et al., 2013, 2014, 2017; Wang et al., 2016; Pitz & Megonigal, 2017; Pitz et al., 2018). As such, a larger number of replicates at different heights at multiple trees are required to better quantify patterns and potential relations with sources.
Radial pattern (Fig 1.2). Radial heterogeneity of stem CH$_4$ emissions is likely to be relevant because of the high variability of sapwood and heartwood thickness (Lin et al., 2012), and injuries or wood density in stems. Irregular patterns of internal wood rot also suggest that radial heterogeneity should be expected (Covey et al., 2012), although low internal wood diffusion rates could reduce this effect. Tree wounds further complicate radial emissions pattern by providing preferential diffusion pathways where gases bypass low diffusion rates in intact wood (Teskey et al., 2008). Radial emissions patterns can be measured using multiple chambers covering different sides of a trunk. Chambers covering the full stem circumference better integrate the radial variability (Machacova et al., 2016; Wang et al., 2016; Siegenthaler et al., 2016; Maier et al., 2018), but they do not account for describing specific radial patterns.

Tree diameter (Fig 1.3), species (Fig 1.4) and age. Some studies have suggested that stem emissions could differ among trees of different size (Wang et al., 2017; Pitz et al., 2018), age or species (Wang et al., 2016; Warner et al., 2017; Pitz et al., 2018). Species identification is imperative because certain species have aerenchyma, are more vulnerable to wood rot, or vary in wood density and consequently in wood gas diffusivity. For example, anatomical development of lenticels or lenticels density might be crucial for gas exchange between the interior of the stem and the atmosphere (Kozlowski & Pallardy, 2002; Pangala et al., 2014). Additionally, anatomical differences between gymnosperms and angiosperms species (e.g., tracheid vs vessels) would influence diffusion or microbial colonization, with consequences on CH$_4$ emissions. Species biogeography and ecosystem functional types become topics of interest in order to describe the relative contribution of different habitats on CH$_4$. For instance, there is a limited knowledge of tropical species (compared with temperate species) despite some of them could be very abundant (227 species represent 50% of all tree stems in
the Amazon basin (ter Steege et al., 2016)), which could be very important from an overall greenhouse gases balance.

Stem diameter might have direct physical effects on emissions (e.g., diffusion) (Oberle et al., 2018), but it might also be important to consider the role of age as an independent factor. That is, diameter is not simply a function of age within a species and with increasing stem age there is greater time for methanogenic populations to establish in the heartwood. However, there is evidence that other environmental factors that covary with heartwood age, such as decreasing pH, may limit methanogenic communities in older trees (Yip et al., 2018). Efforts measuring more trees with different diameters, including different species and ages, with stratified designs are needed to describe spatial variability of stem emissions from plot-to ecosystem-scales.

*Environmental conditions.* Despite potential tree-specific emissions, environmental conditions play an important role in controlling spatial and temporal variability of overall stem emissions. Studies reporting different soil moisture conditions, soil temperature, ground water level, or soil pore water CH$_4$ concentration showed contrasting stem emissions within species (Pangala et al., 2014; Terazawa et al., 2015; Machacova et al., 2016; Pitz et al., 2018; Maier et al., 2018). However, there are not enough studies to establish generalities, and research across species and ecosystems with contrasting environmental conditions is needed.

*Additional tree surfaces (Fig 1.5).* Other tree surfaces (e.g., leaves, twigs, shoots, roots) should be considered to properly estimate whole tree emissions. For example, studies have reported that shoot emissions were 10-fold higher than stem emissions in a boreal forest (Machacova et al., 2016), that there were no substantial emissions from leaves and twigs of three species in a temperate forest (Wang et al., 2016), or that some branches of plants act as CH$_4$ sinks in boreal ecosystems (Sundqvist et al., 2012). These studies suggest that different
plant surfaces could have a species- or ecosystem-specific roles on CH$_4$ emissions.

Environmental factors are probably interacting with these results, as it has been shown that solar radiation stimulates CH$_4$ production from leaves (Bruhn et al., 2012). Consequently, studies that simultaneously measure CH$_4$ exchange across different tree surfaces are required to account for an integrated tree-level CH$_4$ balance and possible environmental interactions.

2. Accounting for temporal variability

To better understand the mechanisms controlling stem CH$_4$ emissions, their patterns and to improve our forecasting capabilities, we require more studies assessing sub-diurnal, diurnal, seasonal and interannual variability of stem CH$_4$ emissions.

Long-term experiments (Box 1) spanning multiple years are necessary to assess interannual variability of stem emissions and to identify key environmental drivers. Additionally, measuring both growing and non-growing season is important because methanogenesis responds strongly to flooding level, temperature, moisture and their interactions. Furthermore, long-term experiments become essential to study how dynamic processes such as increasing tree age affect stem emissions. Longer-term studies could also be used to assess how stress (e.g., drought, flooding, herbivore outbreak, pests) or forest dieback influence CH$_4$ fluxes. Drought and other disturbances have a strong control on non-structural carbohydrates (NSCs) (Vargas et al., 2009; Dietze et al., 2014), which may be important substrates for CH$_4$ production in stem wood. Then, if those NSCs are depleted, it is possible that CH$_4$ emissions might decline as well. Long-term experiments could also be a powerful approach for studying forest-dieback direct effects (e.g., changes in phenology, NSCs, decomposition rates, hydraulic conductivity (Galiano et al., 2011; Anderegg et al., 2012; Poyatos et al., 2013)) or indirect effects (e.g., changes in environmental conditions (Giardina, 2000; Bonan, 2008)) on...
stem CH$_4$ emissions. Even when a tree dies both stem-mediated fluxes and stem-produced CH$_4$ processes could continue (Carmichael et al., 2014; Covey et al., 2016; Warner et al., 2017). We recognize that long-term experiments are expensive and could involve complex organizational challenges (Redman et al., 2004), but we highlight the opportunity of continental-scale ecological observatories such as the National Ecological Observatory Network in the United States (NEON) (Schimel & Keller, 2015).

Measuring stem CH$_4$ emissions at high-temporal frequency (Box 1) is one of the main priorities in as they will allow to identify temporal patterns and provide more accurate information on magnitudes and mechanisms. Manual measurements of CH$_4$ stem emissions are an important approach for addressing spatial variability but they fail to capture the temporal variability in emissions. Measurements taken once every 2-4 weeks (Wang et al., 2016; Warner et al., 2017; Pitz et al., 2018) could represent seasonal patterns but high-temporal frequency measurements (e.g., hourly resolution) resolve for hot-moments and patterns at multiple temporal scales (Barba et al., 2017; Pitz & Megonigal, 2017). Multi-temporal information using automated measurements will provide better estimates of stem emissions (Box 1), as has been demonstrated for soil CO$_2$ efflux (Vargas et al., 2011).

3. Sources for CH$_4$ emissions

There is a pressing need to understand the origin of stem CH$_4$ emissions to forecast their response across different climate change scenarios. Studies have suggested that CH$_4$ emitted through stems could be produced in soils (Machacova et al., 2016; Pitz & Megonigal, 2017; Pitz et al., 2018; Maier et al., 2018) or in the heartwood (Zeikus & Ward, 1974; Covey et al., 2012; Wang et al., 2016, 2017; Pitz & Megonigal, 2017; Yip et al., 2018). Yet the relative importance of these origins among species and ecosystems is still poorly understood.
3.1 Looking deeper into the trees

Understanding the processes and biochemical pathways of CH$_4$ production inside the stem will complement our understanding of the patterns and magnitudes of CH$_4$ stem emissions.

**Heartwood CH$_4$ concentrations (Fig1.6).** Tree stems can contain high quantities of CH$_4$ in the heartwood with concentrations as high as 250,000-times atmospheric (K. R. Covey et al., unpublished). These internal concentrations vary by more than 5-orders of magnitude with tree size, age, individual, species or taxonomic groups (particularly between the angiosperms and gymnosperms) (K. R. Covey et al., unpublished), and might result in high stem emissions through diffusion across the wood (Wang et al., 2017). Consequently, there is a need to improve our understanding of the biogeochemical processes involved in CH$_4$ production and transport within stems. Regardless of the origin of CH$_4$ (see sections below), it is critical to develop a mechanistic diffusion model (Fig1.7) for estimating fluxes, especially when there are large CH$_4$ concentrations within tree stems (see section 4). We clarify that high CH$_4$ concentrations within a tree stem does not necessarily relate to high stem CH$_4$ rates as multiple physical factors regulate CH$_4$ oxidation, diffusion and transport (see section 4).

**Identifying microorganisms and biochemical pathways associated with CH$_4$ production** (Fig1.10) are among the most relevant next steps for understanding and modelling stem CH$_4$ emissions. Extraction of microbial DNA or RNA from plant material is challenging when assessing the role of microbes in the CH$_4$ exchange of plants (Ikeda et al., 2009). Both amplicon based and metagenomics approaches could provide a useful tool to characterize the general microbiome within the plant, including Bacteria, Archaea and Fungi, as well as previously unknown microbes that are not necessarily detectable by primers based on identified taxa (Yip et al., 2018). Metagenomics analyses especially could provide more insight into mechanisms, as well as previously unknown microbes that are not necessarily
detectable by primers based on identified taxa. However, to be successfully employed, measures will have to be developed to separate plant and microbial materials from tissue (Utturkar et al., 2016) or DNA (Broberg et al., 2018). Heartwood rot as well as natural wetwood conditions within stems may provide a habitat conducive for microbial CH₄ production (Zeikus & Ward, 1974; Schink et al., 1981). Fungal infection might potentially cause a tree to fill its stem with CO₂, displace O₂ and thus, make the environment more favorable for methanogenic microbes (anoxic or low-redox conditions). Accordingly, species-specific resistance to infections and rot may help in differentiating stem CH₄ emissions among species. An additional field-scale approach would be studying wood functional capacity for CH₄ production and oxidation (Fig1.11), performing wood incubations under CH₄-free air conditions (production) and under CH₄ conditions (oxidation) (Pangala et al., 2017).

Epiphytic organisms (Fig1.12) at the bark surface, which comprise photoautotrophic communities consisting of algae, bryophytes, fungi, lichens, and/or cyanobacteria, should be considered when studying stem emissions. Such surface communities can play an active role exchanging CH₄ with the atmosphere (Lenhart et al., 2015), and could be a confounding factor when studying tree emissions, biogeochemical pathways, or the origin of CH₄ emissions.

Measuring tree transpiration (Fig1.13) (i.e., sap flow) and leaf-to-atmosphere vapor pressure deficit coupled with stem emissions could provide valuable information on the relationship between stem emissions and soil processes. Temporal correlation between stem emissions and transpiration would suggest that CH₄ could be produced in soil, dissolved into the water, absorbed by the roots, transported with sap flow and emitted through the stem by effervescence. This physical process has been described for stem CO₂ emissions (Teskey et al., 2008). It is possible that CH₄ produced in the heartwood could be partially dissolved into
the sap and emitted through the stem, but under these conditions, the xylem would act as a barrier rather than a transport channel. We postulate that emissions resulting from heartwood production might be more likely related to changes in diffusivity across the stems (see Fig2) rather than diurnal variations in transpiration. Consequently, it is possible that temporal correlations between diurnal patterns of transpiration and stem CH₄ emissions indicate transport from soil rather than internal production. Combining transpiration measurements with C isotopic measurements from the emitted CH₄ (see the end of section 3.1) will provide information on the origin of the emissions. A simplified alternative of continuous measurements of transpiration or vapor-pressure-deficit would be comparing stem emissions measured pre-dawn and midday or for deciduous species (such as Fraxinus sp. Terazawa et al., 2015) at growing and non-growing season (Fig1.14). That is, when leaves are present vs. absent, where in the latter case there is no transpiration.

Stem CO₂ emissions (Fig1.15), their biogeochemical pathways, and their origin (both soil and stem production) have been widely studied for decades (Teskey et al., 2008). We encourage researchers to continue measuring stem CO₂ emissions coupled with CH₄ measurements because it could provide valuable information on the underlying physical processes, such as the transport from soil or diffusion through the wood. Additionally, although the mechanistic relationship between CO₂ and CH₄ emissions is not well understood, correlations between CO₂ and CH₄ stem emissions have been observed in individual stems (Barba et al., 2017), but were absent when comparing across multiple stems (Pitz et al., 2018). The pattern for individual trees suggests, at least, that stem CH₄ emissions at tree level could be potentially estimated from CO₂ emissions and presents a promising opportunity for measurements and modeling approaches that could develop functional relationships to estimate CH₄ emissions from stems based on mechanisms and measurements describing stem respiration (which are arguably easier and cheaper than CH₄ measurements with the current available technology).
Heartwood water content (HWC) (Fig1.16). One study found a correlation between HWC and stem emissions of CH$_4$ in a temperate forest in China (Wang et al., 2017). Because of the limited information on this topic, further research is needed to generalize between individuals, species or ecosystems.

3.2 Looking deeper into the soil

Soils are the alternative potential origin for stem CH$_4$ emissions. Plant-mediated transport from soil production of CH$_4$ is possibly the largest transport contributor for CH$_4$ fluxes to the atmosphere in wetland ecosystems (Whiting & Chanton, 1992; Shannon et al., 1996; Pangala et al., 2015; Andresen et al., 2017), but plant-transported CH$_4$ studies have historically not considered trees but just herbs (Whiting & Chanton, 1992; Andresen et al., 2017). A greenhouse experiment under controlled conditions demonstrated that soil production can be the source of stem CH$_4$ emissions (Rice et al., 2010), but this should be tested under natural conditions. Nonetheless, better understanding of net soil CH$_4$ exchange (i.e., the balance between methanogenesis and methanotrophy) at different soil depths, transport mechanisms from soils to stems and potential contributors to this production and transport (e.g., fine or coarse roots) is crucial to describe stem CH$_4$ emissions.

Soil CH$_4$ fluxes (Fig1.17) simultaneously measured with stem emissions are required to compare soil and stem processes and biogeochemical pathways (Pangala et al., 2013, 2015, 2017; Warner et al., 2017; Pitz & Megonigal, 2017) and to improve upscaling approaches to the ecosystem (Warner et al., 2017; Pitz & Megonigal, 2017) or regional scale (Pangala et al., 2017). Coupled variation in CH$_4$ exchange at the soil and the stem surface may be indicative of CH$_4$ processes in deep soil layers. In contrast, uncoupled variations in CH$_4$ fluxes might be due to substantial CH$_4$ oxidation in the soil surface but not on the surface of trees. Measuring
soil water content (SWC), soil temperature (Fig 1.18) and groundwater level (Fig 1.19) would also improve our capacity to understand stem and soil relations.

**CH₄ and O₂ concentrations at different soil depths (Fig 1.20).** Measuring CH₄ concentrations at different soil depths and in groundwater could provide insights into whether CH₄ emitted by stems could be produced in soils or groundwater. Soils could produce CH₄ at depth and still act as net sinks at the surface level (Pitz & Megonigal, 2017; Maier et al., 2018). It has been suggested that CH₄ produced in deep layers could bypass the soil methanotrophic layer via root transport (Megonigal & Guenther, 2008), highlighting the potential relevance of active transport by sap flow for stem emissions. Alternatively, trees may take up CH₄ from upland methanogenic microsites (von Fischer & Hedin, 2007; Yang & Silver, 2016; Brewer et al., 2018) at relatively shallow depths or directly from rhizosphere anoxic microsites (Baggs, 2011). On the other hand, since CH₄ and O₂ biogeochemical pathways are interrelated, measuring O₂ concentrations at different soil depths could provide valuable information on CH₄ production and oxidation.

There is a general agreement that roots (Fig 1.21) might play a pivotal role in stem CH₄ emissions. However, most of our understanding of their role comes from conjectures (Megonigal & Guenther, 2008) rather than direct root-functioning measurements. It is unclear if fine roots, deep tap roots, or structural coarse roots could be the main CH₄-exchange surface with soils. In wetland soils, fine roots (usually located in the uppermost soil layers; Jackson et al., 1996) might be the principal conduits for CH₄ transport, whereas deep tap roots taking water from deeper and more-anoxic layers might be the principal conduit in upland ecosystems (usually with aerobic top soil layers). Differences in root architecture, the degree to which roots are suberized, and/or differences in aerenchyma physiology or conduit density (if present), may help to understand plant-to-soil functioning of stem CH₄ emissions. Two open questions regarding the role of roots deserve further research: (i) since mycorrhizas...
expand the belowground plant surface area and they can more effectively access anaerobic microsites, could they also be a conduit for CH$_4$?; (ii) could coarse roots by themselves be a source of CH$_4$? Due to lower oxygen content, the belowground part of the tree could host methanotrophic bacteria or be more vulnerable to core rot and be a potential source of CH$_4$.

Finally, the study of the origin of CH$_4$ (heartwood vs. soil) could use stable isotopes approaches, which could aid in the separation of the dominant biogeochemical processes and for regional scaling efforts (Conrad, 2005; Ganesan et al., 2018). The isotopic composition of CH$_4$ emitted from tree stems in upland or wetland forests would depend on: (i) the isotopic composition of the source (CO$_2$ reduction vs. acetate fermentation); (ii) CH$_4$ transport in the stem (i.e., effusion, diffusion or pressure driven (Chanton, 2005)), and; (iii) potential oxidation of CH$_4$ by methanotrophs (high vs. low affinity) along the soil-stem-atmosphere continuum (Reeburgh, 2014). To the best of our knowledge, isotope measurements of CH$_4$ stem fluxes have never been made in upland forests, but in tropical floodplain forests initial measurements suggest little and inconsistent difference between pore-water and emitted δ$^{13}$C of CH$_4$ (Pangala et al., 2017). Simultaneous methanogenesis and methanotrophy in stem wood could be disentangled using a stable isotope pool dilution approach under laboratory conditions, a technique that has detected and quantified these simultaneous gross fluxes in upland soils (von Fischer & Hedin, 2007; Brewer et al., 2018). Finally, isotopic labelling experiments would also be a useful approach for unravelling where methane emitted from trees comes from as has been done for CH$_4$ emissions from soils (Chowdhury & Dick, 2013) and lakes (Conrad et al., 2010).
4. Modeling stem $CH_4$ emissions

Current modeling, upscaling and forecasting capabilities are hampered by limited information on spatial and temporal patterns of stem $CH_4$ emissions (sections 1 and 2), and our lack of understanding of the underlying mechanisms for stem $CH_4$ production, transport and efflux (section 3). As discussed previously, $CH_4$ production can happen in the soil, in the plant, or a combination of soil and plant origin. Furthermore, production (regardless of origin) could be represented by models as a steady state or a non-steady state, which in combination with transport mechanisms will influence the spatial and temporal variability of $CH_4$ stem emissions. The combination of the origin of $CH_4$ production along with transport mechanisms could explain axial (i.e., vertical) and radial (i.e., horizontal) $CH_4$ emissions (Fig2).

There are two possible transport mechanisms of $CH_4$ from stems to the atmosphere that can be described as passive or active. Passive $CH_4$ transport could be divided as passive axial transport (i.e., vertical movement) or passive radial transport (i.e., horizontal movement). The most studied passive axial transport mechanism is the transfer of $CH_4$ from plants to the atmosphere via plant aerenchyma in wetland plants (Cronk & Fennessy, 2001), which is possibly the largest transport contributor for $CH_4$ fluxes to the atmosphere (Whiting & Chanton, 1992; Shannon et al., 1996; Pangala et al., 2015; Andresen et al., 2017). However, another potential passive axial transport could be simple vertical diffusion within the stem heartwood, arguably more relevant in upland forests since those trees do not have aerenchyma. Passive radial transport could be present in plants with aerenchyma as they have hypertrophied lenticels that would facilitate horizontal $CH_4$ diffusion (Megonigal & Day, 1992; Kozlowski, 1997), or in plants without aerenchyma through direct horizontal diffusion. In woody plants, changes in radial $CH_4$ diffusivity along the stem will influence the radial transport and ultimately $CH_4$ efflux rates (Fig2). Ecosystem models usually just focus on the
passive diffusion of CH$_4$ through aerenchyma considering the concentration gradient and the conductivity of a particular medium (equation 1).

$$J = D_{CH_4}(z,t) \frac{\delta[CH_4](z,t)}{\delta z}$$

where $J$ is the diffusion flux, $D_{CH_4}$ is methane diffusivity at depth $z$ and time $t$, and $[CH_4]$ is methane concentration gradient. We highlight that there is evidence of a correlation between CH$_4$ emissions and wood density (Fig1.8; Wang et al., 2017); consequently, this wood property and its vertical and radial variability should be considered in modeling approaches.

Active transport in plants with aerenchyma could be influenced by pressurized ventilation or convective throughflow, which is driven by temperature and water vapor pressure differences between the leaf tissues and the surrounding air (Cronk & Fennessy, 2001). Active CH$_4$ transport in trees without aerenchyma is likely driven by sap flow rates (where CH$_4$ can be dissolved in the sap) and is localized within the xylem of the woody plant. Arguably, current modeling efforts have focused on passive transport but there are new opportunities for model development with new recently measurements that incorporate sap flow with stem CH$_4$ emissions (Barba et al., 2017).

Since plant-mediated transport has been mainly modeled for herbaceous plants (e.g., grasses, ferns, and sedges), the potential emissions along the transport route - the stems - have been largely ignored (Wania et al., 2009). There is a challenge to explore and integrate into models (i) morphological adaptations of woody components, such as parameterizing for root distribution by depth, tree height, stem diameter, leaf type, or wood density; (ii) different radial diffusivity rates depending on different variability in plant tissues (e.g., heartwood, sapwood, and bark); (iii) differences in fluxes from stem and leaves since they have different diffusion mechanisms; (iv) CH$_4$ profiles within stems, as well as O$_2$ profile and potential CH$_4$
production in living trees to make flux estimations comparable with in-situ measurements; and (v) changes in atmospheric pressure, since pressure drops could likely influence active and passive CH$_4$ transport. We recognize that simultaneous or competing mechanisms may be present within a tree, and better communication and collaboration is needed between modelers and experimental scientists in this emerging field. Overall, we see the need to employ emerging temporal and spatial observations to address parameter uncertainties in models, as well as to integrate and evaluate new process-level knowledge into models to address structural uncertainties. By focusing on these two uncertainties together, CH$_4$ flux forecasts can appropriately represent the error and confidence we have in the available data and knowledge about the stem CH$_4$ emission pathway.

Conclusions

The role of tree stems for carbon cycle science is an emerging research frontier, and addressing the aforementioned opportunities and challenges will have large implications for our understanding of the global carbon cycle under changing environmental conditions. We hope that the ideas presented here will promote research to better quantify magnitudes, describe patterns, identify biophysical mechanisms and result in data-knowledge-model fusion. Particularly, we recommend that future studies should simultaneously explore diverse methods and challenges to unravel mechanisms of stem CH$_4$ production and fluxes, including high-frequency measurements or landscape scale survey campaigns, to allow for regional and global scaling. Finally, as the community provides insights into this emerging research field, we must incorporate these findings into predictive models to forecast ecological responses under different management and climate scenarios.
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Author contributions

JB and RV conceived the study. JB wrote the first draft of the manuscript with feedback from RV. JB, MAB, PEB, DB, KC, JvH, JPM, TNM, SRP, MP, BP, ARU, CWS, KT, DLW, ZZ and RV reviewed and edited the manuscript.

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**Figure 1.** Conceptual framework for research frontiers on stem methane (CH₄) emissions. A combined effort on measuring stem and soil processes, concentrations, drivers and emissions at different spatial and temporal scales can provide relevant information on flux magnitudes, biogeochemical pathways and origin of the emissions. Different numbers are described in the main text. Red areas within the stem and soil represent potential locations of CH₄ production. Red arrows represent CH₄ emissions. Acronyms: SWC for soil water content; HWC for heartwood water content; SF for sap flow; DₛV, DₛB, DₛH and DₛS for vertical diffusivity of CH₄ in the stem and radial diffusivity in bark, heartwood and sapwood, respectively.

**Figure 2.** Potential different axial (I-IV) and radial patterns (V) of stem methane (CH₄) emissions depending on the CH₄ production site (i.e., soil, coarse roots, base of the stem or heartwood), type of CH₄ production (steady vs non-steady state), and CH₄ transport mechanisms within a tree (e.g., aerenchyma, direct diffusion, sap flow). Dₛ for diffusivity.
Box 1. Suitability of high-frequency measurements for studying magnitudes and temporal dynamics of stem methane (\(CH_4\)) emissions. To illustrate the suitability of high-frequency measurements and the main differences between these and discrete measurements, we used data (panels II, III and IV) from 100 days of hourly measurements of \(CH_4\) stem emissions at 75-cm stem height for one bitternut hickory tree (\(Carya cordiformis\)) (in blue) (Barba et al., 2017; J. Barba et al. unpublished). Additionally, we sampled a subset from the same dataset including only midday measurement every 2 weeks (in red), which are analogous measurements to manual discrete measurements, with the same commonly performed frequency and time of day of measurements as several previous studies (Wang et al., 2016; Warner et al., 2017; Pitz et al., 2018). Short-term variability of stem \(CH_4\) emissions is so high that measuring \(CH_4\) stem emissions only once every two weeks (red dots, panel II) is inadequate for resolving seasonal patterns (red line). However, high-frequency measurements (blue dots) can integrate short-term variability and unravel the seasonal pattern (blue line). This example demonstrates the usefulness of high-frequency data for studying temporal patterns at seasonal scales, which suggests that high-frequency data could allow quantification of interannual variability in stem \(CH_4\) emissions (panel I). High-frequency measurements also provide improved estimates of mean fluxes, as well as data-deviation estimates over time (panel III). In this specific example, the selected discrete measurements significantly underestimate stem \(CH_4\) emissions by about 50% compared with high-frequency measurements. This is due to the fact that averages of discrete measurements could be strongly influenced by short-term variability of emissions if they happen to capture a few rare, extreme values. Furthermore, because manual measurements are usually performed at midday, they may potentially introduce a systematic bias when averaging stem \(CH_4\) emissions over long periods by ignoring diurnal patterns when present. Thus, having several measurements per day is critical for studying the diurnal patterns (panel IV) and potential...
drivers of stem CH$_4$ emissions, especially if estimating total fluxes over extended time periods.
Progressive decrease of CH₄ emissions with stem height might result from soil CH₄ production in trees with aerenchyma; or either soil, stem base or coarse root production in trees with high D₂ radial rates.

Homogeneous CH₄ emissions along stem height might result from steady-state stem CH₄ production with constant radial D₂; or from soil, stem base or coarse root production in trees with low radial D₂.

Irregular patterns of CH₄ emissions with stem height might result from non-steady-state stem CH₄ production with constant radial D₂; from soil, stem base, roots or steady-state stem CH₄ production with variable radial D₂; or from different density of lenticels and pores in trees with aerenchyma.

Different combinations of soil, stem, steady-state and non-steady-state CH₄ production with heterogeneous radial D₂ patterns in trees with or without aerenchyma might result in a combination of patterns showed in panels I, II and III.

Constant radial D₂, or homogeneous lenticels distribution might result in homogeneous radial CH₄ emissions (A), whereas radial variability of D₂ or lenticels distribution might produce heterogeneous radial CH₄ emissions pattern (B).