**Methane Production and Emissions in Trees and Forests**

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## Abstract

Forest ecosystem $CH_4$ research has focused on soils, but trees are also important sources and sinks in forest $CH_4$ budgets. Living and dead trees transport and emit $CH_4$ produced in soils; living trees and deadwood emit $CH_4$ produced inside trees by microorganisms; and trees produce $CH_4$ through an abiotic photochemical process. We review the state of the science on the production, consumption, transport, and emission of $CH_4$ by living and dead trees, and the spatial and temporal dynamics of these processes across hydrologic gradients inclusive of wetland and upland ecosystems. Emerging research demonstrates that tree $CH_4$ emissions can significantly increase the source strength of wetland forests, and modestly decrease the sink strength of upland forests. Scaling from stem or leaf measurements to trees or forests is limited by knowledge of the mechanisms by which trees transport soil-produced $CH_4$, microbial processes produce and oxidize $CH_4$ inside trees, a lack of mechanistic models, the diffuse nature of forest $CH_4$ fluxes, complex overlap between sources and sinks, and extreme variation across individuals. Understanding the complex processes that regulate $CH_4$ source-sink dynamics in trees and forests requires cross-disciplinary research and new conceptual models that transcend the traditional binary classification of wetland versus upland forest.

## Keywords

tree, forest, methane, tree microorganism, anaerobic metabolism, methane oxidation, climate, greenhouse gases

## I. Introduction

Forests are a dominant feature of the global carbon cycle and play an important role in regulating climate and climate change (Bonan, 2008; Pan *et al.*, 2011). Research on forests in the context of the global carbon cycle is focused primarily on carbon dioxide ($CO_2$) dynamics because the fluxes are large, and carbon sequestration in wood and soil organic matter influence century-scale projections of radiative forcing (Canadell & Raupach, 2008). Less attention is directed to forests as sources and sinks of other carbon trace gases such as methane ($CH_4$). Soils are fairly well characterized in forest $CH_4$ budgets, but trees were only recently recognized as sources or sinks of this important greenhouse gas (Carmichael *et al.*, 2014; Saunois *et al.*, 2016). We review evidence that $CH_4$ dynamics in forests are far more complex than previously believed due to a combination of plant, microbial, and abiotic processes mediated by living and dead trees.

Methane causes 32-45 times more radiative forcing in a century than $CO_2$ on a mass basis (Neubauer & Megonigal, 2015) and contributes ~20% of radiative forcing (Denman, 2007; Myhre *et al.*, 2013; Neubauer & Megonigal, 2015). Because $CH_4$ is more responsive than $CO_2$ to changes in sources or sinks (Hansen *et al.*, 2000), forest $CH_4$ budgets are a meaningful aspect of management directed at slowing the pace of global climate change (UNFCCC, 2016). A more nuanced understanding of forests is needed across fundamental forest-climate interactions to improve Earth system models and manage forests for climate mitigation (Canadell & Raupach, 2008). It is increasingly clear that forest $CH_4$ cycling is one such interaction.

Despite efforts to constrain and refine the strength of the many sources and few sinks of atmospheric $CH_4$, the global $CH_4$ budget remains highly uncertain (Saunois *et al.*, 2016). The total size of the global $CH_4$ pool is well-constrained in the range of 539-609 Tg $CH_4$ $yr^{-1}$, but mismatches between bottom-up models and top-down estimates leave considerable uncertainty about individual components (Dlugokencky *et al.*, 2011; Allen, 2016; Saunois *et al.*, 2017).

Wetland ecosystems are the largest natural source of $CH_4$ globally and forested wetlands are ~60% of total global wetland area (Matthews & Fung, 1987; Prigent *et al.*, 2007), suggesting that forested wetlands are a significant global source of $CH_4$. Reports of a discrepancy between emissions-based estimates and satellite-based estimates of $CH_4$ sources in tropical forests (Frankenberg et al., 2008) sparked new interest in tree surfaces as an overlooked source (Terazawa *et al.*, 2007; Gauci *et al.*, 2010). Most of the research effort on wetland $CH_4$ cycling has been in herbaceous wetland systems, but emerging literature on soil- and plant-mediated $CH_4$ emissions in wetland forests indicates that this source alone may account for 5-10% of global $CH_4$ emissions (Pangala *et al.*, 2017).

Upland ecosystems on freely drained soils are recognized as $CH_4$ sinks in global budgets, and have been the focus of studies on $CH_4$ consumption by soils (Le Mer & Roger, 2001; Saunois *et al.*, 2016). Transient periods of $CH_4$ emission have been reported in nominally upland forests, but such emissions are cryptic and easily overlooked (Megonigal & Guenther, 2008). It is now clear that all biological surfaces in upland and wetland forests have the potential to emit or consume $CH_4$ (Carmichael *et al.*, 2014).

The emphasis on wetland forests as *net* atmospheric $CH_4$ sources and upland forests as *net* sinks masks the complex interplay of aerobic and anaerobic processes that occur to varying degrees in all forest ecosystems (Fig. 1). The outcome of this dynamic

can change the radiative balance of forests over temporal scales of minutes to decades and spatial scales of microsites to biomes. It is perhaps because of the focus on forests as either net sources or net sinks that research on the interrelated processes of $CH_4$ production and oxidation has centered exclusively on just one process or the other. This perspective fundamentally limits our ability to fully represent the dynamic nature of forests in budgets and Earth system models. The goal of this review is to emphasize the common processes that exist across all forested ecosystems in order to advance a holistic understanding of carbon cycling and the radiative balance of forest ecosystems.

## II. Tree $CH_4$ Fluxes

Global budgets, Earth system models, and carbon accounting policies generally assume that the contribution of $CH_4$ in upland forests can be measured as the rate of exchange at the soil surface (Saunois *et al.*, 2016). The focus on soil fluxes reflects the difficulty of enclosing whole trees in gas flux chambers, the most common method for quantifying trace gas fluxes. Improved instrumentation and growing interest in the role of forests in global $CH_4$ dynamics is providing new insights on variation in tree $CH_4$ fluxes across tree species, tissue types within living trees, and stages of dead tree decay. This review draws from 84 studies on $CH_4$ dynamics in living trees and deadwood (Table S1).

### 1. Fluxes modeled from stem $CH_4$ concentration in upland forests

Gas concentrations inside tree stems are useful for judging the potential of trees to act as net sources or sinks of a gas, and to efficiently assess sources of variation before investing in flux measurements. Such measurements are common in upland forests on freely drained soils where $CH_4$ fluxes are low and variation in time, space, species and environmental gradients is large. There are no published reports of *in situ* wood $CH_4$ concentrations from wetland forests to our knowledge. $CH_4$ can accumulate to very high concentrations in upland trees (Mukhin & Voronin, 2007; Covey *et al.*, 2012; Hietala *et al.*, 2015), in some cases reaching >65% of total stem gas (Bushong, 1907). These high concentrations explain dramatic images of flaming trees (Fig. 2), and suggest that $CH_4$ emission rates from tree surfaces are restricted by slow diffusion through trunk wood (Sorz & Hietz, 2006; Wang *et al.*, 2017). Super-ambient $CH_4$ concentrations in trees were first reported 120 years ago in cottonwood (Bushong, 1907). Subsequent studies confirmed this observation (Zeikus & Ward, 1974; Wang *et al.*, 2016), and extended it to many other tree species (Covey *et al.*, 2012; Wang *et al.*, 2017).

Methane emissions from upland trees have been modeled from concentration data using a modified version of Fick's Law (Covey *et al.*, 2012), but concentration data alone cannot be interpreted as conclusive evidence that $CH_4$ is emitted from trees at meaningful rates. The only study to compare measured and modelled stem $CH_4$ fluxes reported that they were poorly correlated at diurnal scales, but better correlated at seasonal scales when sample sizes are large (Wang *et al.*, 2017). The processes that regulate gas dynamics in tree stems are poorly understood compared to soils, but were reviewed in detail for $CO_2$ by Teskey *et al.* (2008). Stem $CO_2$ efflux rates differ from modeled rates due to factors such as the temperature dependence of stem respiration, translocation of dissolved $CO_2$ by the transpiration stream, and $CO_2$ consumption by corticular photosynthesis (Teskey & McGuire, 2007). $CH_4$ shares each of these characteristics with $CO_2$, including the

existence of both sources and sinks, and transport in the transpiration stream.

Advances in modeling tree $CH_4$ fluxes from concentration data, and in scaling flux data to whole, mature trees requires detailed process studies that link sites of production and oxidation to pathways of transport in lateral and longitudinal dimensions. Direct measurement of $CH_4$ fluxes are required to develop and validate models, and high frequency measurements may be a particularly insightful analytical tool in such efforts. For example, flux measurements on a *Liriodendron tulipifera* stem at 45 minute intervals over three days showed a diurnal cycle that peaked in late afternoon, at about the time of minimum tree diameter and 4 hours after peak sap flux (Fig. 3; Pitz and Megonigal 2017). The timing of the $CH_4$ emissions peak suggests it is related to physical factors such as stem water content that control gas diffusion rates (Wang *et al.*, 2017). A second species (*Fagus grandifolia*) behaved differently, and it is certain that more extensive data sets of this type will show even more complex patterns. High frequency records over seasons and weather events, combined with knowledge of gas and heat transfer kinetics in trees will enable inferences about the processes controlling $CH_4$ production, transport, and emissions. A strategy that combines near-continuous measurements to elucidate fine-scale processes, easily deployed manual stem chambers (Siegenthaler *et al.*, 2016) for high replication, and improved stem flux models is likely to be the best scaling approach for forests.

## 2. Methane fluxes from direct measurement

Direct measurements show that all trees – living or dead – have the potential to be $CH_4$ sources, $CH_4$ sinks or both. Most *in situ* tree flux measurements are made on trunks, and show either net positive or null emissions, with net consumption a less common result (Table 1). Variation in $CH_4$ fluxes from tree surfaces arises from species, ages, tissue types, site characteristics, and environmental conditions. When averaged over many individuals or time points at a given site, variability ranges from emissions of nearly 17,000 μmol $m^{-2}$ $h^{-1}$ to consumption of 0.7 μmol $m^{-2}$ $h^{-1}$ (Table 1). Methane emissions are generally higher from wetland than upland trees, presumably reflecting a far larger contribution from soil-derived $CH_4$ in wetter forests. Within upland or wetland forests, emissions from living trees tend to be higher than dead trees, and emissions from fresh deadwood are higher than from decayed debris (Table 1). This pattern suggests that the endogenic $CH_4$ emitted by trees is produced from a non-structural photosynthate source that declines after tree death.

The lowest rates of site-wide tree emissions are from a three-month study of the conifer *P. sylvestris* in an upland forest, with median trunk $CH_4$ emission of 0.01 to 0.001 μmol $m^{-2}$ stem $h^{-1}$ (Machacova *et al.*, 2016). Emissions were lower in a relatively dry plot than a wet plot. Low emission rates are consistent with reports of low $CH_4$ concentrations inside the stems of gymnosperms, but this is the only published study of a gymnosperm and the only boreal site studied. Average rates are 1-2 orders of magnitude higher in other upland forests, all of which are dominated by angiosperm species (Table 1). The highest upland rates reported were made in a *Populus davidiana* forest, and were comparable to rates for upland forests modeled from internal $CH_4$ concentrations. Trees in wetland and floodplain forests tend to emit $CH_4$ at rates that are higher than upland forests, but of the same order of magnitude. A dramatic exception to this generalization is in the Amazon

basin where average stem emissions are 1-2 order of magnitude higher than any other system studied to date (Pangala *et al.*, 2017).

Tree diameter is a measure of size that is often interpreted as a surrogate for age. Emissions from small trees are often different than from large trees, but the direction of the difference varies by ecosystem type. In wetland forests small trees often have higher $CH_4$ emissions than mature trees (Pangala *et al.*, 2015, 2017), while the opposite is often the case in upland forests (Wang *et al.*, 2017; Pitz et 2018).

Patterns of $CH_4$ flux vary by tissue type and positon in the tree. Emissions tend to decrease in order main stem > shoots (branches) > leaves (Table 1), a pattern that may be caused by a number of factors such as tissue volume, tissue type (sapwood or hardwood, Wang et al., 2016), or distance from the source. Direct measurements on leaves showed no net flux in mature tropical forest trees *in situ* (Pangala et al., 2017), while the leaves of wetland saplings and seedings ranged from no net flux to net emissions in mesocosm and microcosm studies (Pangala et al., 2017; Garnet *et al.*, 2004). Tree pneumatophores emit $CH_4$ in wetland forests (Pulliam 1992; Pangala *et al.*, 2013; Purvaja *et al.*, 2004).

Net $CH_4$ consumption by leaves or stems occurs in upland and wetland forests. Most measurements on upland trees show stems to be a net source, but there have been reports of net consumption (Machacova *et al.*, 2016; Pitz & Megonigal, 2017; Warner *et al.*, 2017). Wetland tree stem studies report fewer observations of net $CH_4$ consumption than upland studies, but instances of consumption were observed in a temperate wetland forest (Pitz *et al.*, 2018) and a wet boreal forest (Machacova *et al.*, 2016). Direct measurements on the leaves and stems of several species in an upland forest canopy demonstrated $CH_4$ consumption *in situ* (Sundqvist *et al.*, 2012), with rates postively related to gross primary production in some cases (Fig. 4). Subsequent laboratory studies found that rates of leaf $CH_4$ uptake increased with photosynthetically active radiation and stomatal conductance, suggesting that the site of $CH_4$ consumption was inside the leaf.

## III. Tree Emissions of Soil-Produced $CH_4$

A major challenge to explaining spatial and temporal variation in tree $CH_4$ fluxes is to distinguish between soils versus trees as sites of methanogenesis. The distinction is fundamental for scaling $CH_4$ emission rates to site-, regional-, and global-scale budgets and models, and it applies equally to upland and wetland forests. It is well established that saturated soils support microbial $CH_4$ production in wetlands, and that herbaceous plants transport and emit soil-produced $CH_4$ (Laanbroek, 2010). High $CH_4$ emission rates from wetland trees is evidence that mature trees also transport soil-produced $CH_4$ (Table 1). Less well established is the observation that $CH_4$ is produced in freely drained upland soils in anaerobic microsites (Von Fischer & Hedin, 2002; Brewer *et al.*, 2018). Mature upland trees may transport $CH_4$ produced in soil microsites or groundwater (Megonigal & Guenther, 2008), but this has not been demonstrated conclusively *in situ* . In principle all trees are capable of transporting and emitting soil-produced $CH_4$ by diffusion or xylem transport. Aside from transporting soil-produced $CH_4$, trees also regulate soil $CH_4$ fluxes through plant-soil-microbe interactions that control rates of soil $CH_4$ production and oxidation.

### 1. Tree support of soil methanogenesis and methanotrophy

Plants regulate the production, oxidation and export of soil-produced $CH_4$ by acting as electron donors and acceptors that support microbial respiration (Megonigal *et al.*, 2004). Evidence of such regulation by trees is limited, but tree root exudates regulate decomposition in upland soils (Phillips *et al.*, 2011) and are expected to be an important organic carbon source to anaerobic microbial communities in forest soils. Tight coupling between tree carbon metabolism and anaerobic microbial metabolism was demonstrated in a study of *Taxodium distichum* seedlings in which net $CH_4$ emissions were strongly ($r^2 \geq 0.87$) related to whole-plant photosynthesis (Vann & Megonigal, 2003). Elevated $CO_2$ increased $CH_4$ emissions by >60% in the study, suggesting that understanding tree sources of labile carbon to forested wetland microbial communities is an important step in modeling wetland tree $CH_4$ emissions.

Aerobic methanotrophic bacteria consume $CH_4$ in the presence of $O_2$ (Fritz *et al.*, 2011). $CH_4$ oxidation in wetland soils occurs at the soil surface above the water table, and around roots where plant-transported $O_2$ diffuses into anaerobic soil (Denier van der Gon & Neue, 1996). In one forested wetland, methanotrophy reduced $CH_4$ emissions by up to 80% (Megonigal & Schlesinger, 2002). The study did not distinguish between oxidation at the aerobic soil surface versus the rhizosphere, but it is likely that plant-mediated $CH_4$ oxidation was important because the soils were consistently anaerobic below 6 cm depth. Root $O_2$ release by wetland trees into anaerobic soils can also indirectly inhibit $CH_4$ emissions by generating Fe(III) oxides, which then act as competing terminal electron acceptors that suppress methanogenesis (Weiss et al., 2005). Anaerobic $CH_4$ oxidation occurs in tropical and boreal forest soils (Blazewicz *et al.*, 2012), but nothing is known about the role of plants, if any, in regulating the process. Upland soils tend to support higher rates of atmospheric $CH_4$ consumption than other terrestrial ecosystems, a pattern that has been linked to the influence of trees on methanotrophy and soil gas diffusivity (Dalal *et al.*, 2007).

## 2. Gas transport through trees

Tree stems can be the dominant pathway for $CH_4$ egress from forested wetlands, emitting soil-produced $CH_4$ at higher rates than other ecosystem surfaces (Pangala *et al.*, 2017). A large portion of the volume of a tree stem is gas, estimated at about 25% of the heartwood in angiosperms and 50% in gymnosperms (MacDougal, 1927; Gartner *et al.*, 2004). Connections among gas-filled spaces is one mechanism by which gases such as $O_2$, $CO_2$ and $CH_4$ pass through trees (MacDougal, 1932). The most well studied tree-mediated pathway for transport of soil-produced $CH_4$ is aerenchyma, a specialized tissue characterized by enlarged gas spaces that forms in roots and stems following exposure to hypoxic soil conditions (Topa & McLeod, 1986; Drew *et al.*, 2000; Evans, 2004). Aerenchyma tissue allows rapid gas transport between soils and the atmosphere, and it is a ubiquitous adaptation in wetland plants for supplying $O_2$ to aerobically respiring roots (Jackson & Armstrong, 1999). Wetland trees develop aerenchyma tissue in response to anoxic soil conditions (Topa & McLeod, 1986; Megonigal & Day, 1992), and they show evidence of $O_2$ transport in the form of oxidized rhizospheres (Huikari, 1954; Armstrong, 1967; Hook *et al.*, 1972; Schröder, 1989). Although trees do not develop aerenchyma tissue under freely drained, upland conditions, they nonetheless transport gases through

connected gas-filled porespaces (Armstrong, 1980).

Gas flux through trees can proceed by passive or active mechanisms, a potential source of variation in gas flux rates across species and time. Molecular diffusion occurs in all trees to some extent, and is a slow, passive process that accounts for ongoing plant-mediated gas exchange between the soil and atmosphere even when transpiration is near-zero (Nietch *et al.*, 1999). Rusch & Rennenberg (1998) demonstrated that $CH_4$ moves by diffusion alone through stems of the wetland-adapted species *Alnus glutinosa*. Gas can also be transported in trees by pressurized ventilation, a rapid process that creates mass flow of $O_2$ between the atmosphere and soils. Pressurized ventilation of $O_2$ is driven by temperature gradients that develop between sunlit tree stems and ambient air (Große & Schröder, 1984), and has also been shown to occur in *A. glutinosa* (Schröder, 1989). It is not clear whether pathways of $O_2$ and $CH_4$ transport are coupled orndependent, but the absence of diurnal variation in $CH_4$ emissions in *A. glutinosa* saplings grown under full sunlight suggests that the dominant pathway for $CH_4$ *in situ* is diffusive transport despite the potential for pressurized transport in this species (Pangala *et al.*, 2014). Flux studies have also detected significant diurnal variation in both upland (Pitz & Megonigal, 2017) and wetland (Pangala *et al.*, 2015) tree species, suggesting the possibility that hotspots of tree gas emissions via pressurized ventilation or transpiration-driven mass flow can be predicted in part from the tree species composition of a forest.

Transpiration can also support mass flow of gases between soils or roots and the atmosphere, and has been shown to be a mechanism for transporting $CH_4$ dissolved in soil solutions to the atmosphere through the seedlings of the wetland tree species *Alnus glutinosa* (Rusch & Rennenberg, 1998), *Fraxinus latifolia*, *Populus trichocarpa*, *Salix fluviatilis* (Rice *et al.*, 2010), and *Taxodium distichum* (Garnet *et al.*, 2005). Similar observations have been made for xylem transport of soil-produced $CO_2$ (Bloemen *et al.*, 2014). Garnet *et al.* (2005) demonstrated that transpiration-driven $CH_4$ emissions varies with $CO_2$ concentration, humidity, and other variables that affect stomatal conductance. Diffusive transport of soil-produced CH4 can continue after tree death, though net $CH_4$ consumption on standing dead trees has also been observed (Carmichael *et al.*, 2018).

Radial diffusion transports gases from the inside the tree to the atmosphere ($CH_4$) or vice versa ($O_2$) and determines both the rate and location of gas exchange at the tree surface (Teskey *et al.*, 2008). High internal $CH_4$ concentrations in trees reflect barriers to transport and diffusion of gases related to wood anatomy or water-filled wood porespace. Lenticels are specialized tissues that facilitate radial gas exchange across plant surfaces, and are a particularly important adaptation to flooded environments in trees. Pangala et al. (2014) found that lenticel density and porewater $CH_4$ concentration explained 84% of the variation in stem $CH_4$ emissions in flooded *Alnus glutinosa* saplings (Fig. 5).

High frequency diurnal measurements of $CH_4$ emissions from mature trees can be used to assess the relative contributions of diffusion and mass flow to transporting and emitting tree gases *in situ*. However, it is likely that the pathways interact such that gases produced in soils or inside trees move by multiple pathways before being emitted from a tree surface. Macropores in the form of cracks, holes, or wood rot can be preferential transport pathways, complicating direct gas flux measurements (Teskey *et al.*, 2008). Unraveling the complex processes that govern $CH_4$ production, transport, consumption, and emissions requires detailed mechanistic studies coupled with modeling aimed at

scaling processes to whole-tree scales.

## IV. Tree-Produced $CH_4$

### 1. Abiotic aerobic methanogenesis in trees

The discovery of a novel aerobic, abiotic pathway of $CH_4$ production from plant tissue by (Keppler *et al.*, 2006) sparked a new wave of research on $CH_4$ emissions from plants, and inspired the first sustained investigations of $CH_4$ emissions from upland trees and forests. Keppler *et al.* (2006) estimated aerobic emissions of 236 Tg $CH_4$ $yr^{-1}$ globally, a flux large enough to explain higher-than-expected atmospheric $CH_4$ pools over tropical forests (Frankenberg *et al.*, 2005). The study received significant criticism based on three points: (i) a mechanism was not provided, (ii) purported experimental design flaws, and (iii) scaling metrics that significantly overestimated the global source, with significant implications for managing forests for climate protection (Lowe, 2006; Schiermeier, 2006; Evans, 2007). It is now clear that abiotic $CH_4$ production from plant tissue is real, with several independent groups reporting rates similar to those of Keppler *et al*. (2006) (Bruhn *et al.*, 2012; Liu *et al.*, 2015) (Table S1). However, rigorous scaling exercises have also confirmed that the global impact of aerobic plant $CH_4$ emissions is far less than initially estimated (Bloom *et al.*, 2010; Fraser *et al.*, 2015).

The precise chemical reaction underlying abiotic aerobic methanogenesis is not clear, but evidence suggests that reactive oxygen species (ROS) commonly produced in response to plant stress are a proximal driver of abiotic emissions. Agents that incite ROS production are associated with abiotic $CH_4$ production, and those that remove ROS from plant tissues limit production (Messenger *et al.*, 2009). Furthermore, the presence of enzymes that inhibit ROS removal are directly involved in stimulating production (Bruhn *et al.*, 2012; Liu *et al.*, 2015). Reactive oxygen species may initiate non-enzymatic photo-chemical reactions that foster the breakdown of pectin (Keppler *et al.*, 2006; Bruhn *et al.*, 2009; Messenger *et al.*, 2009), but other structural and non-structural plant compounds such as waxes, lignin, cellulose, MET protein, and ascorbic acid are also potential precursors (Vigano *et al.*, 2008; Keppler *et al.*, 2009; Vigano *et al.*, 2009; Althoff *et al.*, 2010).

Abiotic $CH_4$ emissions are triggered by a number of physical stressors, with UVB radiation as the most commonly documented inciting agent. UVB triggers abiotic $CH_4$ production from detached plant parts (Fig. 6) (McLeod *et al.*, 2008; Vigano *et al.*, 2008; Bruhn *et al.*, 2009), from structural components such as pectin (Keppler *et al.*, 2008; Megonigal & Guenther, 2008; Messenger *et al.*, 2009), and whole plants (Qaderi & Reid, 2009). By contrast, exposure to visible light alone does not incite abiotic methanogenesis in plants (Bruhn *et al.*, 2009). In one case abiotic $CH_4$ emissions were triggered by the lack of light (Martel & Qaderi, 2017). Wang *et al.* (2009) noted that emissions increased with physical wounding of both cuttings and connected stems. High temperature (Keppler *et al.*, 2008; McLeod *et al.*, 2008), drought stress (Qaderi & Reid, 2011), and bacterial infection (Messenger *et al.*, 2009) can also incite abiotic methanogenesis in the presence of $O_2$. The highest rates of aerobic $CH_4$ emissions in lab experiments occur when multiple stress factors interact, suggesting that multi-factor experiments may best reproduce *in situ* rates of abiotic $CH_4$ emissions (Liu *et al.*, 2015; Abdulmajeed *et al.*, 2017).

Evidence of $CH_4$ production through an abiotic pathway is increasingly robust in laboratory studies (see reviews by (Keppler *et al.*, 2009; Bruhn *et al.*, 2012; Liu *et al.*, 2015). However, *in situ* evidence of abiotic $CH_4$ production is weak because the process cannot be effectively isolated from the many potential microbial $CH_4$ sources (Sanhueza & Donoso, 2006; Cao *et al.*, 2008; Wang, S *et al.*, 2009; Bruhn *et al.*, 2012). One cannot assume that $CH_4$ emitted *in situ* from plants on freely drained soils has an abiotic source because plants can transport $CH_4$ from anaerobic microsites in both soils and plant stems. Also, evidence that methanogenic microorganisms can tolerate atmospheric levels of $O_2$ (Megonigal *et al.*, 2004) suggest that not all aerobic $CH_4$ production is abiotic. Microbial $CH_4$ sources may explain why $CH_4$ emission rates from *in situ* intact foliage are nearly twice those from detached leaves (Qaderi & Reid, 2009). Based on laboratory rates of UVB-irradiated plants and typical Earth surface UVB irradiances, abiotic $CH_4$ production produces 7 to 50 ng $CH_4$ g $dw^{-1}$ $hr^{-1}$ across a temperature range from 25 to 40°C (Vigano *et al.*, 2008).

## 2. Microbial methanogenesis and methanotrophy inside trees

Methanogenesis in living trees has been recognized for nearly five decades, but remains little studied despite the availability of molecular tools for probing anaerobic microbial communities. Zeikus and Ward (1974) observed flammable concentrations of $CH_4$ inside hardwood trees, and determined that it was produced *in situ* by methanogens. Subsequent authors confirmed an Archaeal $CH_4$ source (Van Der Kamp *et al.*, 1979; Schink & Ward, 1984; Xu & Leininger, 2001); Archaea have been isolated from trees (Zeikus & Henning, 1975); Archaeal OTUs such as *Methanobacterium* can be dominate (>40% of sequence abundance) in wood microbial communities (Yip *et al.*, 2018); and anaerobic incubations of tree wood cores demonstrate active methanogenesis (Covey *et al.*, 2012; Wang *et al.*, 2016). Archaea in tree stems are accompanied by a variety of decay fungi, non-decay fungi, and bacteria, in competitive, mutualistic, and synergistic relationships (Fig. 7.; Shortle *et al.*, 1978; Schink *et al.*, 1981). Tree methanogenesis is expected to be sensitive to the totality of these interactions that collectively regulate the concentrations of methanogenic substrates.

Degradation of complex biopolymers such as cellulose and pectin to produce $CH_4$ generally requires the collective activities of fungi, bacteria, and archaeal methanogens operating syntrophically (Wolin & Miller, 1987; Cicerone & Oremland, 1988; Beckmann *et al.*, 2011). The process begins with enzymatic hydrolysis of complex compounds, then fermentation to yield $H_2$ and low molecular-weight organic acids such as acetate, formate and citrate, all of which occur to varying degrees in tree heartwood (Warshaw *et al.*, 1985; Schmidt, 2006; Worm *et al.*, 2011). Methanogenesis is the terminal step in which the products of fermentation (low molecular weight organic acids and $H_2$) are consumed, yielding inorganic gases ($CO_2$, $CH_4$). Methanogens tend to specialize in one of two respiration pathways, acetate fermentation ($CH_3COOH \rightarrow CO_2 + CH_4$) or $CO_2$ reduction ($4H_2 + CO_2 \rightarrow CH_4$), both of which occur in the wood of living trees (Schink *et al.*, 1981; Schink & Ward, 1984). The two pathways yield distinct $\delta^{13}C$ signatures that can be used to infer mechanisms.Wang *et al.* (2016) reported a $\delta^{13}C$-$CH_4$ of <-70‰ in living *Populus* trees, a highly depleted ratio suggesting that $CH_4$ production through $CO_2$ reduction. The $\delta^{13}C$ of emitted from stems in the Amazon basin ranged from -76.3 to -59.1‰ (Pangala et

al., 2017), indicating possible species- or site-related differences in $CH_4$ production pathways, though $CH_4$ oxidation may have also affected the ratios. It is likely that dominance of one pathway over the other varies by internal carbon source. Based on soil studies, we expect that $CO_2$ reduction dominates when the carbon source is highly aromatic or complex, while acetate fermentation dominates when supported by less complex compounds such as carbohydrates (Conrad & Klose, 1999).

The carbon sources supporting methanogenesis in living trees have important implications for forest $CH_4$ emission potential. Methanogenesis driven by wood decay must end once the structural wood is consumed, but wood decay (e.g. heart rot) is not a pre-requisite for methanogenesis. Indeed, elevated $CH_4$ levels are commonly present in trees with no evidence of wood decay (Mukhin & Voronin, 2008; Mukhin & Voronin, 2011; Covey *et al.*, 2012), and such trees have been shown to emit $CH_4$ through the trunk at high rates (Wang *et al.*, 2016). This pattern along with evidence that $CH_4$ production from dead wood declines rapidly with decay, is circumstantial evidence that non-structural carbohydrates (NSC) – free sugars and starches stored in wood (Dietze *et al.*, 2014) – are a carbon source to methanogens active in living tree stems (Covey *et al.*, 2016). The few studies of NSC in trees show interspecific patterns that mirror those of $CH_4$ concentrations in living and dead trees (Covey *et al.*, 2012; Covey *et al.*, 2016; Oberle *et al.*, 2017), such as far higher NSC stem sapwood concentrations in angiosperms than gymnosperms (Hoch *et al.*, 2003), and increasing stem NSC storage in angiosperms with age (Würth *et al.*, 2005). NSCs are a large portion of the total carbon stored in living trees (Würth *et al.*, 2005), rapidly metabolized (Cowling & Merrill, 1966), and continually replenished from newly fixed photosynthates (Richardson *et al.*, 2013; Dietze *et al.*, 2014). Collectively, this suggests an untested mechanism by which living trees could continually produce $CH_4$ at high rates over their lifetime.

Methanotrophy is a ubiquitous $CH_4$-consuming process that is certain to influence the direction and magnitude of $CH_4$ fluxes across tree surfaces, yet there is little evidence for the process in living trees despite the fact they contain both $CH_4$ and $O_2$ (Table 2). Potential methanotrophic species (OTUs) were rare in the heartwood and sapwood of *Populus deltoids* (Yip *et al.*, 2018), and $CH_4$ oxidation was not detected in incubations of wood from two other temperate forest tree species (Wang *et al.*, 2016). No clear evidence of the *pmoA* gene of methanotrophic bacteria was found in the roots and shoots of boreal forest shrubs (Halmeenmäki et al., 2018). However, the *pmoA* gene is abundant in dead wood where methanotrophs appear to contribute to $N_2$-fixation (Mäkipääa *et al.*, 2018). Because $CH_4$ concentrations in living wetland and upland trees vary from ambient to super-ambient, it is expected that trees harbor both high- and low-affinity methanotrophic bacteria. Indeed, net $CH_4$ uptake from the atmosphere has been observed across living tree surfaces (Table 1 and references therein).

## 3. Regulation of microbial methanogenesis in trees

Archaeal methanogenesis in living trees is likely to be regulated by the same factors that operate in analogous environments such as soils. Molecular oxygen ($O_2$) availability is generally the single most important regulator of $CH_4$ production rates because aerobic microbes outcompete archaeal methanogens for organic compounds, and $O_2$ is toxic to many, though not all, methanogens (Megonigal *et al.*, 2004). Tree stems

can be hypoxic or anoxic, with stem concentrations of 0.5-19% $O_2$ that decline from the bark to the heartwood (Table 2). Low $O_2$ concentrations develop because aerobic plant and microbial respiration consume $O_2$ faster than it is supplied by physical transport (Sorz & Hietz, 2006; Teskey *et al.*, 2008). Fermentative and methanogenic microbial communities develop under such conditions in systems ranging from wetlands to insects, but have not been a subject of detailed studies in trees.

Stem water content will prove to be a powerful explanatory variable for variation in $CH_4$ emissions from wetland and upland trees at diurnal, seasonal, and annual scales. Water regulates the $O_2$ supply by acting as a barrier to gas transport, reducing the $O_2$ diffusion rate by a factor of $10^4$ compared to diffusion in air. Wang *et al.* (2017) observed that stem $CH_4$ emissions increase dramatically above about 50% stem water content, and continue to increase with water content above this threshold value. High water content also favors high wood $CH_4$ concentrations as a barrier to $CH_4$ diffusion out of the tree (Wang *et al.*, 2017), which sets the $CH_4$ diffusion gradient. If a larger sample of trees validates such relationships, models coupling soil and tree hydraulics should be able to capture temporal and spatial variation in tree $CH_4$ emissions.

Stem water content may help explain why high $CH_4$ concentrations and emissions in living upland trees are associated with wetwood, an anatomically distinct and sometimes saturated area of heartwood (Boyce, 1961; Xu & Leininger, 2001; Wang *et al.*, 2016; Wang *et al.*, 2017). Wetwood is also associated with bacterial and fungal infection (Jennings, 1996), and it is known that the wood immediately surrounding fungal colony centers can become highly depleted in $O_2$ (Schmidt, 2006).

## V. Trees in Forest $CH_4$ Budgets

### 1. Scaling Challenges

It is no longer sufficient to equate soil fluxes to ecosystem fluxes in forested ecosystems, but quantifying $CH_4$ budgets is challenging because forests are a complex composite of environments and surfaces that produce, consume, transport, and emit $CH_4$ (Fig. 1). Eddy covariance flux techniques are promising in wetland forests, but in upland forests the near balance between diffuse sources and sinks is a challenge given the current detection limits of the technology (Saunois *et al.*, 2016).

Phylogeny is an important source of variation in stem $CH_4$ dynamics in living and dead trees, an observation that applies equally to wetland forests (Pangala et al. 2013) and upland forests (Pitz & Megonigal, 2017; Warner *et al.*, 2017). Wang *et al.* (2017) classified 22 upland forest species into three groups based on internal stem $CH_4$ concentration—consistently high, consistently low, and variable—suggesting an approach to simplify phylogenetic-based scaling through identification of functional groups.

The physiological and anatomical causes of phylogenetic-based variation in $CH_4$ emissions are not clear, but should differ depending on whether $CH_4$ sourced from the soil or the stem. For example, $CH_4$ production rates inside trees should scale positively with factors that regulate the stem's anaerobic volume, such as stem moisture content (Wang *et al.*, 2017). In upland forests, wetwood species are among the most consistent emitters because they maintain high moisture content under a wide range of soil moisture conditions (Wang *et al.*, 2017). Indeed, super-ambient $CH_4$ concentrations in trees were

first discovered in the wetwood genus *Populus* (Bushong, 1907). Anaerobic sites at the center of stems coincide with the distribution of heartwood, which may explain positive correlations between stem $CH_4$ emissions and the ratio of heartwood diameter or total diameter in upland forests (Wang *et al.*, 2017).

Negative relationships between $CH_4$ emissions and wood density are observed in both upland (Wang et al., 2017) and wetland trees (Pangala *et al.*, 2013). Relationships with density and stem moisture content may be useful for scaling, but they are difficult to interpret mechanistically because of opposing effects on rates of $CH_4$ production and diffusion. High wood density and moisture content should enhance $CH_4$ production by slowing $O_2$ diffusion and increasing stem anoxia, but any such effects are masked in the flux data by the fact that these factors also slow $CH_4$ diffusion to the stem surface.

Methanogenesis in wetland forests occurs primarily in soils rather than inside tree stems (Pangala *et al.*, 2017), and should produce different scaling relationships compared to upland forests. $CH_4$ transport from the soil to the atmosphere through trees is governed by factors embedded in Fick's law, including the $CH_4$ concentration gradient, distance from the source to the atmosphere, and resistance to flux through the stem. Indeed, stem emissions in wetland forests are related positively to porewater $CH_4$ concentration (Pangala *et al.*, 2013, 2014, 2015; Terazawa *et al.*, 2015) and negatively to specific wood density (Pangala *et al.*, 2013), and emissions decrease rapidly with stem height above the water table (Pangala *et al.*, 2017). Stem emissions also relate to factors that control the rate of $CH_4$ production in soils such as temperature and water table depth (Pangala *et al.*, 2015; Pitz *et al.*, 2018). Similar relationships in upland forests are either weak or absent (Warner *et al.*, 2017; Pitz *et al.*, 2018).

Stem diameter is expected to be a useful scaler for tree $CH_4$ emissions because it is a proxy for several factors that should influence $CH_4$ production or transport. However, relationships between stem diameter and stem emission vary among studies, with upland forests showing positive (Wang *et al.*, 2017) or null relationships (Warner *et al.*, 2017; Pitz *et al.*, 2018), and wetland forests showing negative (Pangala *et al.*, 2015) or null relationships (Pitz *et al.*, 2018). These contrasting results may reflect sampling limitations such as a small range of diameters, small sample sizes, or conflation with factors such as stem age, species, life history, or habitat type. Indeed, the most highly replicated tree $CH_4$ emissions study to date found consistently higher emissions from young trees than mature trees in wetland forests (Pangala *et al.*, 2017).

Spatial and temporal variation in stem $CH_4$ emissions are a significant challenge to bottom-up scaling. This is especially the case in upland forests where most tree species are capable of emitting $CH_4$ at least intermittently, but the distribution of emissions is highly skewed across individuals and time such that a few individuals or time points dominate annual emissions ((Maier *et al.*, 2017; Pitz & Megonigal, 2017; Wang *et al.*, 2017; Warner *et al.*, 2017). The sampling challenge in upland forests is even greater to the extent that small stems (branches), leaves, and deadwood can each emit $CH_4$ (Covey *et al.*, 2016; Machacova *et al.*, 2016; Oberle *et al.*, 2017), consume $CH_4$ (Sundqvist *et al.*, 2012), or have no net flux (Wang *et al.*, 2016; Warner *et al.*, 2017), all of which are observed. Collectively, these positive and negative fluxes determine the degree to which upland trees offset or enhance soil $CH_4$ fluxes, and whether the system is a net source or sink of atmospheric $CH_4$. The same challenges of scaling across large stems, small stems

and leaves apply equally to wetland forests. Wetland forest tree emissions are sensitive to variation water table depth (Pangala *et al.*, 2015; Terazawa *et al.*, 2015; Pitz *et al.*, 2018) and presumably soil factors that regulate the production and oxidation of $CH_4$ such as Fe(III) and $SO_4$ content (Megonigal *et al.*, 2014).

## 2. Wetland and Upland Forest $CH_4$ Budgets

Regional and global estimates of tree contributions to $CH_4$ budgets to date have been highly speculative (Carmichael *et al.*, 2014; Saunois *et al.*, 2016) and are not a goal of this review. One exception is a comprehensive regional analysis of the contribution of trees to ecosystem $CH_4$ budgets in the 6.7 $x10^6$ $km^2$ Amazon basin. (Pangala *et al.*, 2017) sampled 13 sites stratified by soil type and geomorphology, 2,357 individual tree stems across a wide range of species and size classes, and hundreds of flux observations using chambers placed on soil-, water-, and floating macrophyte surfaces. Stem surfaces emitted up to 17,000 μmol $CH_4$ $m^{-2}$ $h^{-1}$, with mean rates an order of magnitude higher than any other system measured to date (Table 1). Stem emissions generally decreased with stem height, and emissions from leaves occurred only on younger trees and at far lower rates. Although stem surface rates from small stems were higher than those from large stems, when expressed on a soil area basis, large trees were a far larger $CH_4$ source at the ecosystem scale (Table 3). In total, 15-21 Tg $CH_4$ $yr^{-1}$ is transported through trees in the Amazon floodplain, which increases the previous bottom-up estimate by 50% and amounts to 3% of the global $CH_4$ budget (Pangala *et al.* (2017). Their bottom-up estimate for all surfaces (30 to 48 Tg $CH_4$ $yr^{-1}$) compared well with their top-down estimate derived from a high-resolution air column budget (43±6 Tg $CH_4$ $yr^{-1}$). Methane production potentials based on incubation of tree cores showed *in situ* production in relatively few stems, establishing soil transport as the primary $CH_4$ source to the atmosphere. This impressive campaign highlights the exigent need to account for multiple flux pathways in forests across large scales.

Trees are important $CH_4$ sources in forested wetlands outside the Amazon basin as well (Table 3), such as peatland forests of the Sebangau River catchment in Borneo where trees contribute up to 87% of $CH_4$ efflux (Pangala *et al.*, 2013). In a temperate forested wetland, emissions from *Alnus glutinosa* and *Betula pubescens* stems accounted for a maximum of 27% of ecosystem $CH_4$ emissions (Pangala *et al.*, 2015). Because both soils and trees are $CH_4$ sources, previous studies in forested wetlands appear to have underestimated the $CH_4$ budget of these ubiquitous ecosystems (Gauci et al. 2010, Pitz et al. 2018).

Trees and soils in upland forests on freely drained soils typically have opposing effects on forest $CH_4$ budgets, with soils acting primarily as net sinks and tree stems primarily as net sources than sinks. The consequences of upland trees as $CH_4$ sources are potentially important because upland soils are the single largest terrestrial $CH_4$ sink, with net consumption estimated to be 36 Tg $CH_4$ $yr^{-1}$ (Saunois *et al.*, 2016). Ecosystem scaling based on measurements from trunks, branches and shoots in a *Populus*-dominated upland temperate deciduous forest in China suggests that tree emissions may offset up to 63% of the soil $CH_4$ sink (Wang *et al.*, 2016) (Table 3). This estimate may be an upper boundary to the contribution of trees on freely drained soils with consistently deep (>1 m) water tables because wetwood is common in *Populus*, and stem $CH_4$ flux estimates from other

599 species are lower (Table 1). Large offsets of the upland soil $CH_4$ sink are also suggested
600 in sites where the water table depth fluctuates into the upper meter of the soil profile, a
601 condition that can simultaneously increase soil-derived $CH_4$ emissions and decrease the
602 soil $CH_4$ uptake (Pitz & Megonigal, 2017). In a *Fraxinus*-dominated seasonal floodplain
603 in Japan, stem surface fluxes reduced the estimated forest $CH_4$ sink by more than two
604 thirds (Terazawa *et al.*, 2007), while the stems and shoots of *Pinus sylvestris* offset 35%
605 of the soil sink on a wet upland site in Finland (Machacova *et al.*, 2016). In other studies
606 tree $CH_4$ emissions have little impact on upland forest $CH_4$ budgets. Two independent
607 estimates of the soil sink offset in North American temperate forests ranged from 1-6%
608 (Pitz & Megonigal, 2017; Warner *et al.*, 2017), and the soil sink offset in a relatively dry
609 upland *Pinus sylvestris* site was 0.8% (Machacova *et al.*, 2016). Finally, the net effect of
610 trees can also be to increase the soil $CH_4$ sink. In the only field experiment involving tree
611 stem fluxes published to date, a stand replanted in *Quercus petraea* saplings had two-fold
612 higher $CH_4$ uptake than an unplanted site (Plain *et al.*, 2018). This result was a caused by
613 a combination of very low $CH_4$ emission rates by the nine year-old trees, and an increase
614 in soil $CH_4$ uptake caused by unknown factors such as a transpiration-driven decrease in
615 soil water potential or the presence of understory herbaceous plants.
616 A holistic understanding of the contribution of forests to the global $CH_4$ budget
617 requires identifying common processes that exist across all forested ecosystems. Water
618 table depth is a master variable that controls rates of $CH_4$ consumption by upland soils
619 (Topp & Pattey, 1997), $CH_4$ emission by wetland soils (Turetsky *et al.*, 2014), and $CH_4$
620 emissions by both wetland and upland tree stems (Pangala *et al.*, 2015; Terazawa *et al.*,
621 2015; Pitz *et al.*, 2018). Water table depth was a likely source of spatial variation in an
622 upland boreal forest that appeared to be a net $CH_4$ sink when tree and soil fluxes were
623 measured by small-scale chambers, but a net source when measured by large-scale
624 micrometeorological methods (Sundqvist *et al.*, 2015). In this case, small areas of wet
625 soils in the tower footprint may have been strong $CH_4$ sources. In a floodplain forest,
626 stem $CH_4$ emissions increased sharply during periods when the water table rose into the
627 rooting zone (Terazawa *et al.*, 2015).
628 Small rates of tree $CH_4$ emissions may have a role in forests switching between
629 net $CH_4$ sources and sinks (Shoemaker *et al.*, 2014). For example, a temperate upland
630 forest changed briefly from a net $CH_4$ sink to a source during a warm, wet period when
631 soil uptake decreased and tree emissions increased simultaneously (Pitz and Megonigal,
632 2017). This suggests that the global importance of tree emissions is related to the
633 importance of nominally upland systems that periodically emit $CH_4$. A rigorous effort to
634 quantify $CH_4$ emissions from these ecosystems was provided by Spahni *et al.* (2011) who
635 modeled "wet-mineral soil" moisture thresholds ranging from 0.28 to 0.55 fractional
636 water-filled pore space, varying with edaphic factors such as texture. Modeled upland
637 fluxes were about a factor of 10 smaller than wetland fluxes on an aerial basis, but the
638 global area of soils with sufficient soil moisture to periodically emit $CH_4$ were extensive,
639 yielding a large global emission of ~60 Tg $CH_4$ $yr^{-1}$. This figure is double the global soil
640 $CH_4$ sink, 23-36% of global emissions from wetlands, and 10% of all global $CH_4$ sources
641 (Denman, 2007). Upland ecosystems are analogous to oceans in that a low rate of some
642 biogeochemical process (e.g. NPP) can dramatically influence global cycles because of
643 their large global footprint.

## VI. Conclusions

The growing body of literature on $CH_4$ dynamics in forest ecosystems shows that they are far more complex biogeochemical environments than previously believed, and that our previous focus on soil processes alone is insufficient for a rigorous understanding of forests greenhouse gas balance and radiative climate forcing. Progress toward this goal will be most effective if we recognize that all $CH_4$-generating and consuming processes occur in all forest ecosystems regardless of their classification as upland or wetland. Advances in forest ecosystem $CH_4$ dynamics require a new focus on the complex interplay between productive and consumptive processes occurring from the top of the canopy to the subsurface ground water, and their implications for generalized scaling. The subject is ripe for collaborations between people with expertise in plant physiology, soil physics, hydrology, geomorphology, and microbial ecology, all of which interact to determine the distribution and activity of microbial communities and abiotic reactions that produce and consume $CH_4$ as a single coupled process (Megonigal *et al.*, 2004; Liu *et al.*, 2015). Of particular importance is collaborations between experts in biogeochemistry, wood anatomy, and tree physiology because they regulate $CH_4$ production and exchange across arboreal surfaces. Indeed, a growing research community with diverse interests in tree $CH_4$ dynamics has developed an agenda for advancing the field (Barba *et al.*, in press).

Further study is needed to refine ecosystem-scale estimates, determine the most appropriate scaling metrics, and resolve the distinctions between the arboreal $CH_4$ flux pathways. Whole-ecosystem studies currently provide the most robust information for global budgeting efforts, but many studies do not distinguish between the three pathways identified here in order to inform mechanistic numerical models. Laboratory studies can isolate specific pathways of $CH_4$ production or consumption, but they often fail to capture the substantial temporal and spatial scales of variation that drive *in situ* fluxes. In addition to flux measurements, there is a need for thoughtful integration of existing techniques across sub-disciplinary boundaries. Until additional integrative empirical studies are conducted, and process-based models are developed and tested, the contribution of forests to global $CH_4$ dynamics will remain poorly resolved.

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## Author Contributions

KRC and JPM contributed equally in all aspects of the manuscript.

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## Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

**Table S1** Compilation of primary publications on methane as it relates to trees or forests.

**Table 1.** Methane emission rates from tree stems. All fluxes were directly measured using static chambers and are expressed as per area of stem or knee. Measures of central tendency and errors are in the original forms reported in the citation. When no statistical information is reported the data are means with standard errors in parentheses; exceptions are reported in the "emission surface" column as median for central tendency, or standard deviations (SD) or 95% confidence intervals (CI) for errors. Not all studies reported errors.

| Tree Condition | Ecosystem Type | Forest Type | Plant Community | Site | Emission Surface | Rate ($\mu$mol $CH_4$ $m^{-2}$ stem $h^{-1}$) | Citation |
|---|---|---|---|---|---|---|---|
| Living Trees | Wetland | Temperate Floodplain | *Taxodium distichum* | | Taxodium knees | 2.34 (0.78)† | Pulliam 1992 |
| | | Temperate Floodplain | *Fraxinus mandshurica* | | Stem at 15 cm | 11 | Terazawa *et al.* 2007 |
| | | Temperate Floodplain | *Alnus glutinosa* | | Stem at 30 cm | 0.26 to 6.31 | Gauci *et al.* 2010 |
| | | Tropical Peatland | Diverse angiosperms | | Stem at 20-50 cm | 1.06 (0.9) to 11.56 (0.44) | Pangala *et al.* 2013 |
| | | Temperate Floodplain | *Fraxinus mandshurica* | | Stem at 15 cm | 5.1 to 81.6 | Terazawa *et al.* 2015 |
| | | Temperate Peatland | *Alnus glutinosa* | | Young stem at 20-50 cm | 140.42 (18.43) | Pangala *et al.* 2015 |
| | | | | | Mature stem at 20-50 cm | 9.79 (1.29) | |
| | | | *Betula pubescens* | | Young stem at 20-50 cm | 51.47 (8.18) | |
| | | | | | Mature stem at 20-50 cm | 6.71 (0.83) | |
| | | Tropical Floodplain | Diverse angiosperms | Negro River | Large stems | 1,887.50 (1,293.75) | Pangala *et al.* 2017 |
| | | | | | Small stems | 3,687.5 (1,762.5) | |
| | | | | | Small leaves | 1 (2.5) | |
| | | Tropical Floodplain | Diverse angiosperms | Madeira River | Large stems | 2,075 (1625) | |
| | | | | | Small stems | 3,137.5 (2,056.25) | |
| | | | | | Small leaves | 1.19 (2.5) | |
| | | Tropical Floodplain | Diverse angiosperms | Amazon River | Large stems | 2,900 (2,106.25) | |
| | | | | | Small stems | 6,437.5 (2,806.25) | |
| | | | | | Small leaves | 2.38 (4.38) | |
| | | Tropical Floodplain | Diverse angiosperms | Solimoes River | Large stems | 5,200 (2,675) | |
| | | | | | Small stems | 9,375 (4,212.5) | |
| | | | | | Small leaves | 3.19 (5.63) | |
| | | Tropical Floodplain | Diverse angiosperms | Tapajos River | Large stems | 8,812.5 (4,462.5) | |
| | | | | | Small stems | 16,937.5 (6,812.5) | |
| | | | | | Small leaves | 5.63 (6.88) | |
| | | Temperate Floodplain | Diverse angiosperms | Wetland | Stem at 30-60 cm | 35.49 (10.91) | Pitz *et al.* 2018 |

**Table 1.** Continued.

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Living Trees | Upland | Boreal Evergreen | *Pinus sylvestris* | Dry Plot | Stem chamber‡ (median) | 0.0008 | Machacova *et al.* 2016 |
| | | | | Wet Plot | | 0.0063 | |
| | | | | Dry Plot | Shoot (median) | 0.0031 | |
| | | | | Dry Plot | Stems (median) | 0.00031 | |
| | | Temperate Deciduous | *Populus* | Upper Plot | Stem at 30 cm | 5.33 | Wang *et al.* 2016 |
| | | | | Lower Plot | | 6.44 | |
| | | Temperate Deciduous | *Fagus sylvatica* | Stina Site | Stem at 40-200 cm (SD) | 1.87 (3.31) | Maier *et al.* 2017 |
| | | | | Conventwald Site | | 0 | |
| | | Temperate Deciduous | Diverse angiosperms | | Stem at 130 cm (CI) | 0.396 (0.180) | Warner *et al.* 2017 |
| | | Temperate Deciduous | Diverse angiosperms | | Stem at 30-60 cm (CI) | 1.59 (0.88) | Pitz and Megonigal 2017 |
| | | Temperate Deciduous | *Populus* | Upper Site | Stem at 30 cm | 12.63 | Wang *et al.* 2017 |
| | | | | Middle Site | | 20.72 | |
| | | | | Lower Site | | 17.05 | |
| | | Temperate Deciduous | Diverse angiosperms | Highest Elevation | Stem at 30-60 cm | 4.3 (0.81) | Pitz *et al.* 2018 |
| | | | | Wetland Adjacent | Stem at 30-60 cm | 11.29 (3.45) | |
| | | Temperate Deciduous | *Quercus petrea* | Vegetated Plots | Stem at 25-45 cm (CI) | 0.032 (0.022) | Plain *et al.* 2018 |
| Dead Trees | Wetland | Temperate Deciduous | | | Standing dead trees | 25 (6.25) | Carmichael *et al.* 2017 |
| | | | | | Standing dead trees | -37.5 (18.75) | |
| Dead Trees | Upland | Temperate Deciduous | Diverse angiosperms | | Coarse wood debris (CI) | -1.15 (0.94) | Warner *et al.* 2007 |
| | | | | | Fresh woody debris | 1.15 (2.05) | |
| | | | | | Decayed debris | -1.44 (0.72) | |

†Flux units are μmol knee$^{-1}$ h$^{-1}$

‡Chamber height not reported

**Table 2. Oxygen concentrations in living tree stems. All studies are from upland ecosystems.**

| Forest Type | Plant Genera or Species | $[O_2]$ | Study |
|---|---|---|---|
| Not specified | *Unspecified Populous sp.* | 1.2% | Bushong 1907 |
| Temperate Forest | *Quercus rubra, Quercus macrocarpa, Ulmus* | 0.02- | Chase 1937 |
| Temperate Hardwood Forest | *Quercus rubra* | 5.5-7.5% | Jensen 1967 |
| Temperate Hardwood Forest | *Populus delectans* | 0.02-2.9 | Van Der Kamp *et al.* 1979 |
| Conifer Forest | *Picea abies* | 5.6-15.1% | Eklund 1990 |
| Hardwood Forest | *Quercus robar, Acer platanoides* | 5-19% | Eklund 1993 |
| Upland Conifer Forest | *Picea abies* | 0.5-21% | Eklund 2000 |
| Hardwood Forest | *Betula pendula* | 1-5% | Gansert *et al.* 2001 |
| Greenhouse Study | *Olea europaea* | 1-5% | Mancuso and Marras 2003 |
| Temperate Arboretum | *Fagus orientalis, Carya ovata, Larix sibirica,* | 13-20% | del Hierro *et al.* 2002 |
| Conifer Forest | *Pseudotsuga menziesii* | 0.5-20% | Pruyn *et al.* 2002 |
| Hardwood Forest | *Acer rubrum, Fraxinus americana, Tsuga* | 3-20% | Spicer and Holbrook 2004 |

**Table 3.** Tree methane emissions scaled to forest area.

| Ecosystem Type | Forest Type | Plant Community | Site | Emission Surface | Description | Portion of Ecosystem flux† | Tree Flux ($g\ CH_4\ ha^{-1}\ d^{-1}$)‡ | Other Surfaces | Other Surface Flux ($g\ CH_4\ ha^{-1}\ d^{-1}$) | Study |
|---|---|---|---|---|---|---|---|---|---|---|
| Wetland | Tropical Peatland | Diverse Angiosperm | | Tree stems | Scaled to 15 m | 87.0% | 28.5 (3.4) | Soil hollows | 3.9 (1.0) | Pangala *et al.* 2013 |
| | | | | Tree stems | Scaled to 3 m | 62.0% | 6.7 (0.7) | | | |
| | Temperate Peatland | | | Tree stems | Summer | 13.5% | 13.2 (1.34) | Soil hollows | 37.3 (10.2) | Pangala *et al.* 2015 |
| | | | | | | | | Soil hummocks | 2.51 (2.03) | |
| | | | | Tree stems | Winter | 24.6% | 5.65 (0.9) | Soil hollows | 11.3 (3.57) | |
| | | | | | | | | Soil hummocks | 0.09 (0.1) | |
| | Tropical Floodplain | Diverse Angiosperms | Negro River | Large stems | | 58.3% | 47.4 (11) | Soil | 67.7 (56) | Pangala *et al.* 2017 |
| | | | | Small stems | | 5.8% | 67.7 (56) | Aquatic surface | 219 (544) | |
| | | | | Small leaves | | 0.5% | 3.86 (4.6) | | | |
| | | | Madeira River | Large stems | | 58.3% | 47.4 (11) | Soil | 251 (289) | |
| | | | | Small stems | | 5.2% | 251 (289) | Aquatic surface | 423 (148) | |
| | | | | Small leaves | | 0.3% | 5.07 (4.8) | | | |
| | | | Amazon River | Large stems | | 43.6% | 50.3 (13.3) | Soil | 49 (179) | |
| | | | | Small stems | | 2.7% | 49 (179) | Aquatic surface | 768 (1,792) | |
| | | | | Small leaves | | 0.3% | 5.93 (7.3) | Floating macrophytes | 190 (745) | |
| | | | Solimoes River | Large stems | | 53.0% | 157 (40.5) | Soil | 88.6 (108) | |
| | | | | Small stems | | 4.4% | 88.6 (108) | Aquatic surface | 1,269 (1,111) | |
| | | | | Small leaves | | 5.8% | 67.7 (56) | Floating macrophytes | 134 (261) | |
| | | | Tapajos River | Large stems | | 41.5% | 181 (56.1) | Soil | 456 (564) | |
| | | | | Small stems | | 2.6% | 456 (564) | Aquatic surface | 2,426 (2,898) | |
| | | | | Small leaves | | 0.2% | 17.3 (15.7) | Floating macrophytes | 966 (2105) | |
| Upland | Temperate Floodplain | *Fraxinus mandshurica* | | Tree Stems | Scaled 5-80 cm | 69% | 0.17 | Soil | -0.24 | Terazawa *et al.* 2007 |
| | | *Pinus sylvestris* | Dry plot | Stems | | 0.02% | 0.00072 | Soil | -3.43 | Machacova *et al.* 2016 |
| | | | | Shoots | | 0.8% | 0.0264 | | | |
| | | | Wet plot | Stems | | 0.6% | 0.01 | Soil | -1.7 | |
| | | | | Shoots | | 33.5% | 0.57 | | | |
| | | Diverse angiosperms | | Stems (SD) | | 3.5% | 0.75 (2.21) | Soil (SD) | -3.92 (0.25) | Warner *et al.* 2017 |
| | | | | | | | | Deadwood (SD) | -0.37 (0.25) | |
| | | Diverse angiosperms | | Tree Stems (95% CI) | Scaled to 3 m | 4.5% | 0.79 (0.44) | Soil (95% CI) | -17.4 (2.5) | Pitz and Megonigal 2017 |
| | | *Quercus petrea* | Vegetated Plots | Tree Stems (95% CI) | Scaled to full height | 0.3% | 0.07 (0.02) | Soil (95% CI) | -220 (45.5) | Plain *et al.* 2018 |

†Represents the contribution of trees to total ecosystem efflux in wetlands studies. In upland studies it is the fraction of soil oxidation that is offset by tree emissions.

‡Values and errors are in the original units reported in the citation. When no statistical information is reported the data are means with standard errors in parentheses; exceptions are reported in the "emission surface" column as either standard deviations (SD) or 95% confidence intervals (CI). Not all studies reported errors.

Figure Legends

Figure 1. The complex variety of $CH_4$ sources and sinks in upland and wetland forests. Red arrows are $CH_4$ sources and blue arrows are sinks. See Carmichael *et al.* (2014) for a treatment of the role of vegetation in $CH_4$ dynamics across a variety of terrestrial ecosystems.

Figure 2. Flammable concentrations of $CH_4$ in the heartwood of living trees are common even on upland sites, such as this *Quercus cerris* tree in Hungary that was cored and the pressurized stem gas ignited. Photo by Balazas Nyitrai.

Figure 3. Methane emissions from a *Liriodendron tulipifera* (closed circles) and a *Fagus grandifolia* (open circles) at 75 cm above the soil surface. Note that the y-axes for the two gases are scaled differently. From Pitz & Megonigal, 2017.

Figure 4. Correlation between $CH_4$ exchange and GPP for a Spruce tree. The best-fit line to the points has a correlation coefficient is 0.57. Notice that a negative GPP means uptake from the atmosphere. From Sundqvist *et al.*, 2012.

Figure 5. Stem $CH_4$ emissions and stem lenticel density at a height of 2–12 cm above the soil surface are strongly related in *Alnus glutinosa* saplings. From Pangela *et al.* (2014).

Figure 6. Snapshot of raw $CH_4$ concentration data over 24 hours. Peak values (~2.01 ppm) are a response to UV irradiation, while troughs (~1.95 ppm) are the result of UV lamps that shut down every 105 minutes to monitor instrument function. From Vigano et al., 2008.

Figure 7. Mean relative abundance of dominant phyla (bacteria and archaea) and subphyla (Proteobacteria) across wood tissue types in *Populus deltoids*. From Yip *et al.*, 2018.