Methane Production and Emissions in Trees and Forests

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Abstract

Forest ecosystem CH\textsubscript{4} research has focused on soils, but trees are also important sources and sinks in forest CH\textsubscript{4} budgets. Living and dead trees transport and emit CH\textsubscript{4} produced in soils; living trees and deadwood emit CH\textsubscript{4} produced inside trees by microorganisms; and trees produce CH\textsubscript{4} through an abiotic photochemical process. We review the state of the science on the production, consumption, transport, and emission of CH\textsubscript{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\textsubscript{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\textsubscript{4}, microbial processes produce and oxidize CH\textsubscript{4} inside trees, a lack of mechanistic models, the diffuse nature of forest CH\textsubscript{4} fluxes, complex overlap between sources and sinks, and extreme variation across individuals. Understanding the complex processes that regulate CH\textsubscript{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 (CO₂) 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 (CH₄). Soils are fairly well characterized in forest CH₄ 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 CH₄ 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 CO₂ on a mass basis (Neubauer & Megonigal, 2015) and contributes ~20% of radiative forcing (Denman, 2007; Myhre et al., 2013; Neubauer & Megonigal, 2015). Because CH₄ is more responsive than CO₂ to changes in sources or sinks (Hansen et al., 2000), forest CH₄ 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 CH₄ cycling is one such interaction.

Despite efforts to constrain and refine the strength of the many sources and few sinks of atmospheric CH₄, the global CH₄ budget remains highly uncertain (Saunois et al., 2016). The total size of the global CH₄ pool is well-constrained in the range of 539–609 Tg CH₄ 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 CH₄ 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 CH₄. Reports of a discrepancy between emissions-based estimates and satellite-based estimates of CH₄ 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 CH₄ cycling has been in herbaceous wetland systems, but emerging literature on soil- and plant-mediated CH₄ emissions in wetland forests indicates that this source alone may account for 5–10% of global CH₄ emissions (Pangala et al., 2017).

Upland ecosystems on freely drained soils are recognized as CH₄ sinks in global budgets, and have been the focus of studies on CH₄ consumption by soils (Le Mer & Roger, 2001; Saunois et al., 2016). Transient periods of CH₄ 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 CH₄ (Carmichael et al., 2014).

The emphasis on wetland forests as net atmospheric CH₄ 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 CH₄ 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 CH₄ Fluxes

Global budgets, Earth system models, and carbon accounting policies generally assume that the contribution of CH₄ 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 CH₄ dynamics is providing new insights on variation in tree CH₄ fluxes across tree species, tissue types within living trees, and stages of dead tree decay. This review draws from 84 studies on CH₄ dynamics in living trees and deadwood (Table S1).

1. Fluxes modeled from stem CH₄ 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 CH₄ fluxes are low and variation in time, space, species and environmental gradients is large. There are no published reports of in situ wood CH₄ concentrations from wetland forests to our knowledge. CH₄ 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 CH₄ emission rates from tree surfaces are restricted by slow diffusion through trunk wood (Sorz & Hietz, 2006; Wang et al., 2017). Super-ambient CH₄ 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 CH₄ is emitted from trees at meaningful rates. The only study to compare measured and modelled stem CH₄ 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 CO₂ by Teskey et al. (2008). Stem CO₂ efflux rates differ from modeled rates due to factors such as the temperature dependence of stem respiration, translocation of dissolved CO₂ by the transpiration stream, and CO₂ consumption by corticular photosynthesis (Teskey & McGuire, 2007). CH₄ shares each of these characteristics with CO₂, including the
existence of both sources and sinks, and transport in the transpiration stream.

Advances in modeling tree CH₄ 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 CH₄ 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 CH₄ 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 CH₄ 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 CH₄ sources, CH₄ 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 CH₄ 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 CH₄ 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 CH₄ 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 CH₄ 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 CH₄ 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 CH₄ concentrations. Trees in wetland and floodplain forests tend to emit CH₄ 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

5
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 al. 2018).

Patterns of CH_4 flux vary by tissue type and position 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 seedlings 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 positively 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 ($r^2$ ≥ 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
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 CH₄ 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 O₂ between the atmosphere and soils. Pressurized ventilation of O₂ 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 O₂ and CH₄ transport are coupled or independent, but the absence of diurnal variation in CH₄ emissions in A. glutinosa saplings grown under full sunlight suggests that the dominant pathway for CH₄ 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 & Megenigal, 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 CH₄ 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 CO₂ (Bloemen et al., 2014). Garnet et al. (2005) demonstrated that transpiration-driven CH₄ emissions vary with CO₂ concentration, humidity, and other variables that affect stomatal conductance. Diffusive transport of soil-produced CH₄ can continue after tree death, though net CH₄ 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 (CH₄) or vice versa (O₂) and determines both the rate and location of gas exchange at the tree surface (Teskey et al., 2008). High internal CH₄ 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 CH₄ concentration explained 84% of the variation in stem CH₄ emissions in flooded Alnus glutinosa saplings (Fig. 5).

High frequency diurnal measurements of CH₄ 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 CH₄ production, transport, consumption, and emissions requires detailed mechanistic studies coupled with modeling aimed at...
IV. Tree-Produced CH₄

1. Abiotic aerobic methanogenesis in trees

The discovery of a novel aerobic, abiotic pathway of CH₄ production from plant tissue by (Keppler et al., 2006) sparked a new wave of research on CH₄ emissions from plants, and inspired the first sustained investigations of CH₄ emissions from upland trees and forests. Keppler et al. (2006) estimated aerobic emissions of 236 Tg CH₄ yr⁻¹ globally, a flux large enough to explain higher-than-expected atmospheric CH₄ 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 CH₄ 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 CH₄ 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 CH₄ 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 CH₄ emissions are triggered by a number of physical stressors, with UVB radiation as the most commonly documented inciting agent. UVB triggers abiotic CH₄ 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 CH₄ 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 O₂. The highest rates of aerobic CH₄ emissions in lab experiments occur when multiple stress factors interact, suggesting that multi-factor experiments may best reproduce in situ rates of abiotic CH₄ emissions (Liu et al., 2015; Abdulmajeed et al., 2017).
Evidence of CH₄ 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 CH₄ production is weak because the process cannot be effectively isolated from the many potential microbial CH₄ sources (Sanhueza & Donoso, 2006; Cañ et al., 2008; Wang, S et al., 2009; Bruhn et al., 2012). One cannot assume that CH₄ emitted in situ from plants on freely drained soils has an abiotic source because plants can transport CH₄ from anaerobic microsites in both soils and plant stems. Also, evidence that methanogenic microorganisms can tolerate atmospheric levels of O₂ (Megonigal et al., 2004) suggest that not all aerobic CH₄ production is abiotic. Microbial CH₄ sources may explain why CH₄ 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 CH₄ production produces 7 to 50 ng CH₄ 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 CH₄ inside hardwood trees, and determined that it was produced in situ by methanogens. Subsequent authors confirmed an Archaeal CH₄ 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 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 CH₄ 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 H₂ 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 H₂) are consumed, yielding inorganic gases (CO₂, CH₄). Methanogens tend to specialize in one of two respiration pathways, acetate fermentation (CH₃COOH → CO₂ + CH₄) or CO₂ reduction (4H₂ + CO₂ → CH₄), both of which occur in the wood of living trees (Schink et al., 1981; Schink & Ward, 1984). The two pathways yield distinct δ¹³C signatures that can be used to infer mechanisms. Wang et al. (2016) reported a δ¹³C-CH₄ of -70% to -59.1% in living Populus trees, a highly depleted ratio suggesting that CH₄ production through CO₂ reduction. The δ¹³C of emitted from stems in the Amazon basin ranged from -76.3 to -59.1% (Pangala et al., 2011).
al., 2017), indicating possible species- or site-related differences in CH₄ production pathways, though CH₄ 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 CO₂ 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 CH₄ 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 CH₄ 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 CH₄ through the trunk at high rates (Wang et al., 2016). This pattern along with evidence that CH₄ 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 CH₄ 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 CH₄ at high rates over their lifetime.

Methanotrophy is a ubiquitous CH₄-consuming process that is certain to influence the direction and magnitude of CH₄ fluxes across tree surfaces, yet there is little evidence for the process in living trees despite the fact they contain both CH₄ and O₂ (Table 2). Potential methanotrophic species (OTUs) were rare in the heartwood and sapwood of *Populus deltoids* (Yip et al., 2018), and CH₄ 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 (Halmeeenmäki et al., 2018). However, the *pmoA* gene is abundant in dead wood where methanotrophs appear to contribute to N₂-fixation (Mäkipää et al., 2018). Because CH₄ 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 CH₄ 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 (O₂) availability is generally the single most important regulator of CH₄ production rates because aerobic microbes outcompete archaeal methanogens for organic compounds, and O₂ 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<sub>2</sub> that decline from the bark to the heartwood (Table 2). Low O<sub>2</sub> concentrations develop because aerobic plant and microbial respiration consume O<sub>2</sub> 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<sub>4</sub> emissions from wetland and upland trees at diurnal, seasonal, and annual scales. Water regulates the O<sub>2</sub> supply by acting as a barrier to gas transport, reducing the O<sub>2</sub> diffusion rate by a factor of 10<sup>4</sup> compared to diffusion in air. Wang et al. (2017) observed that stem CH<sub>4</sub> 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<sub>4</sub> concentrations as a barrier to CH<sub>4</sub> diffusion out of the tree (Wang et al., 2017), which sets the CH<sub>4</sub> 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<sub>4</sub> emissions.

Stem water content may help explain why high CH<sub>4</sub> 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<sub>2</sub> (Schmidt, 2006).

V. Trees in Forest CH<sub>4</sub> Budgets

1. Scaling Challenges

It is no longer sufficient to equate soil fluxes to ecosystem fluxes in forested ecosystems, but quantifying CH<sub>4</sub> budgets is challenging because forests are a complex composite of environments and surfaces that produce, consume, transport, and emit CH<sub>4</sub> (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<sub>4</sub> dynamics in living and dead trees, an observation that applies equally to wetland forests (Pangala et al. 2013) and upland forests (Pitz & Megenigal, 2017; Warner et al., 2017). Wang et al. (2017) classified 22 upland forest species into three groups based on internal stem CH<sub>4</sub> 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<sub>4</sub> emissions are not clear, but should differ depending on whether CH<sub>4</sub> sourced from the soil or the stem. For example, CH<sub>4</sub> 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<sub>4</sub> 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 conflations 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 CH₄ such as Fe(III) and SO₄ content (Megonigal et al., 2014).

2. Wetland and Upland Forest CH₄ Budgets

Regional and global estimates of tree contributions to CH₄ 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 CH₄ budgets in the 6.7 x10⁶ km² 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 CH₄ 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 CH₄ source at the ecosystem scale (Table 3). In total, 15-21 Tg CH₄ 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 CH₄ budget (Pangala et al. (2017). Their bottom-up estimate for all surfaces (30 to 48 Tg CH₄ yr⁻¹) compared well with their top-down estimate derived from a high-resolution air column budget (43±6 Tg CH₄ 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 CH₄ 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 CH₄ 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 CH₄ 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 CH₄ emissions (Pangala et al., 2015). Because both soils and trees are CH₄ sources, previous studies in forested wetlands appear to have underestimated the CH₄ 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 CH₄ budgets, with soils acting primarily as net sinks and tree stems primarily as net sources than sinks. The consequences of upland trees as CH₄ sources are potentially important because upland soils are the single largest terrestrial CH₄ sink, with net consumption estimated to be 36 Tg CH₄ 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 CH₄ 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 CH₄ flux estimates from other
species are lower (Table 1). Large offsets of the upland soil CH₄ sink are also suggested in sites where the water table depth fluctuates into the upper meter of the soil profile, a condition that can simultaneously increase soil-derived CH₄ emissions and decrease the soil CH₄ uptake (Pitz & Megonigal, 2017). In a Fraxinus-dominated seasonal floodplain in Japan, stem surface fluxes reduced the estimated forest CH₄ sink by more than two thirds (Terazawa et al., 2007), while the stems and shoots of Pinus sylvestris offset 35% of the soil sink on a wet upland site in Finland (Machacova et al., 2016). In other studies, tree CH₄ emissions have little impact on upland forest CH₄ budgets. Two independent estimates of the soil sink offset in North American temperate forests ranged from 1-6% (Pitz & Megonigal, 2017; Warner et al., 2017), and the soil sink offset in a relatively dry upland Pinus sylvestris site was 0.8% (Machacova et al., 2016). Finally, the net effect of trees can also be to increase the soil CH₄ sink. In the only field experiment involving tree stem fluxes published to date, a stand replanted in Quercus petraea saplings had two-fold higher CH₄ uptake than an unplanted site (Plain et al., 2018). This result was a caused by a combination of very low CH₄ emission rates by the nine year-old trees, and an increase in soil CH₄ uptake caused by unknown factors such as a transpiration-driven decrease in soil water potential or the presence of understory herbaceous plants.

A holistic understanding of the contribution of forests to the global CH₄ budget requires identifying common processes that exist across all forested ecosystems. Water table depth is a master variable that controls rates of CH₄ consumption by upland soils (Topp & Pattey, 1997), CH₄ emission by wetland soils (Turetsky et al., 2014), and CH₄ emissions by both wetland and upland tree stems (Pangala et al., 2015; Terazawa et al., 2018). Water table depth was a likely source of spatial variation in an upland boreal forest that appeared to be a net CH₄ sink when tree and soil fluxes were measured by small-scale chambers, but a net source when measured by large-scale micrometeorological methods (Sundqvist et al., 2015). In this case, small areas of wet soils in the tower footprint may have been strong CH₄ sources. In a floodplain forest, stem CH₄ emissions increased sharply during periods when the water table rose into the rooting zone (Terazawa et al., 2015).

Small rates of tree CH₄ emissions may have a role in forests switching between net CH₄ sources and sinks (Shoemaker et al., 2014). For example, a temperate upland forest changed briefly from a net CH₄ sink to a source during a warm, wet period when soil uptake decreased and tree emissions increased simultaneously (Pitz and Megonigal, 2017). This suggests that the global importance of tree emissions is related to the importance of nominally upland systems that periodically emit CH₄. A rigorous effort to quantify CH₄ emissions from these ecosystems was provided by Spahni et al. (2011) who modeled “wet-mineral soil” moisture thresholds ranging from 0.28 to 0.55 fractional water-filled pore space, varying with edaphic factors such as texture. Modeled upland fluxes were about a factor of 10 smaller than wetland fluxes on an aerial basis, but the global area of soils with sufficient soil moisture to periodically emit CH₄ were extensive, yielding a large global emission of ~60 Tg CH₄ yr⁻¹. This figure is double the global soil CH₄ sink, 23-36% of global emissions from wetlands, and 10% of all global CH₄ sources (Denman, 2007). Upland ecosystems are analogous to oceans in that a low rate of some biogeochemical process (e.g. NPP) can dramatically influence global cycles because of 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 (Mégignon 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.

Acknowledgements

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Author Contributions

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


Shoemaker JK, Keenan TF, Hollinger DY, Richardson AD. **2014.** Forest ecosystem changes from annual methane source to sink depending on late summer water balance. *Geophysical research letters* **41**: 673-679.


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>
<thead>
<tr>
<th>Tree Condition</th>
<th>Ecosystem Type</th>
<th>Forest Type</th>
<th>Plant Community</th>
<th>Site</th>
<th>Emission Surface</th>
<th>Rate (μmol CH(_4) m(^{-2}) stem h(^{-1}))</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Living Trees</td>
<td>Wetland</td>
<td>Temperate Floodplain</td>
<td><em>Taxodium distichum</em></td>
<td>Stem at 15 cm</td>
<td>Taxodium knees</td>
<td>2.34 (0.78)(^t)</td>
<td>Pulliam 1992</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Temperate Floodplain</td>
<td><em>Fraxinus mandshurica</em></td>
<td>Stem at 30 cm</td>
<td>Stem at 15 cm</td>
<td>11</td>
<td>Terazawa <em>et al.</em> 2007</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Temperate Floodplain</td>
<td><em>Alnus glutinosa</em></td>
<td>Stem at 20-50 cm</td>
<td>Stem at 15 cm</td>
<td>0.26 to 6.31</td>
<td>Gaucci <em>et al.</em> 2010</td>
</tr>
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<td></td>
<td>Tropical Peatland</td>
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<td><em>Fraxinus mandshurica</em></td>
<td>Stem at 15 cm</td>
<td>Stem at 20-50 cm</td>
<td>1.06 (0.9) to 11.56 (0.44)</td>
<td>Pangala <em>et al.</em> 2013</td>
</tr>
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<td></td>
<td></td>
<td>Temperate Floodplain</td>
<td><em>Alnus glutinosa</em></td>
<td>Young stem at 20-50 cm</td>
<td>Mature stem at 20-50 cm</td>
<td>5.1 to 81.6</td>
<td>Terazawa <em>et al.</em> 2015</td>
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<td>9.79 (1.29)</td>
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<td></td>
<td>6.71 (0.83)</td>
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<td><em>Betula pubescens</em></td>
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<td>Young stem at 20-50 cm</td>
<td>140.42 (18.43)</td>
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<td></td>
<td>Small stems</td>
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<td>51.47 (8.18)</td>
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<td>Pangala <em>et al.</em> 2017</td>
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<td>6.71 (0.83)</td>
<td>Pangala <em>et al.</em> 2017</td>
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<td>Large stems</td>
<td>1,887.50 (1,293.75)</td>
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<td>3,687.5 (1,762.5)</td>
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<td>Small leaves</td>
<td>1 (2.5)</td>
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<td>Large stems</td>
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<td>Small leaves</td>
<td>1.19 (2.5)</td>
<td>Pangala <em>et al.</em> 2017</td>
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<td><em>Amazon River</em></td>
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<td>Large stems</td>
<td>2,900 (2,106.25)</td>
<td>Pangala <em>et al.</em> 2017</td>
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<td>Small leaves</td>
<td>2.38 (4.38)</td>
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<td>5,200 (2,675)</td>
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<td></td>
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<td>Small stems</td>
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<td>Small leaves</td>
<td>3.19 (5.63)</td>
<td>Pangala <em>et al.</em> 2017</td>
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<td>8,812.5 (4,462.5)</td>
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<td>5.63 (6.88)</td>
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<td>Stem at 30-60 cm</td>
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<td>Boreal Evergreen</td>
<td>Pinus sylvestris</td>
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<td>Stem chamber‡ (median)</td>
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<td>Machacova et al. 2016</td>
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<td>Populus</td>
<td>Upper Plot</td>
<td></td>
<td>Stem at 30 cm</td>
<td>5.33</td>
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<tr>
<td></td>
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<td>Lower Plot</td>
<td></td>
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<td>Fagus sylvatica</td>
<td>Stina Site</td>
<td></td>
<td>Stem at 40-200 cm (SD)</td>
<td>1.87 (3.31)</td>
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<td>Conventwald Site</td>
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<td>Upper Site</td>
<td>Stem at 130 cm (CI)</td>
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<td>Warner et al. 2017</td>
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<td>Middle Site</td>
<td>Stem at 30-60 cm (CI)</td>
<td>1.59 (0.88)</td>
<td></td>
<td>Pitz and Megonigal 2017</td>
<td></td>
</tr>
<tr>
<td>Temperate Deciduous</td>
<td>Populus</td>
<td>Lower Site</td>
<td>Stem at 30 cm</td>
<td>12.63</td>
<td>20.72</td>
<td>17.05</td>
<td>Wang et al. 2017</td>
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<tr>
<td>Temperate Deciduous</td>
<td>Diverse angiosperms</td>
<td>Upper Site</td>
<td>Stem at 30-60 cm</td>
<td>4.3 (0.81)</td>
<td></td>
<td>Pitz et al. 2018</td>
<td></td>
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<tr>
<td>Temperate Deciduous</td>
<td>Diverse angiosperms</td>
<td>Middle Site</td>
<td>Stem at 30-60 cm</td>
<td>11.29 (3.45)</td>
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<tr>
<td>Temperate Deciduous</td>
<td>Wetland Adjacent</td>
<td>Lower Site</td>
<td>Stem at 25-45 cm (CI)</td>
<td>0.032 (0.022)</td>
<td></td>
<td>Plain et al. 2018</td>
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<tr>
<td>Temperate Deciduous</td>
<td>Quercus petrea</td>
<td>Vegetated Plots</td>
<td>Standing dead trees</td>
<td>25 (6.25)</td>
<td></td>
<td>Carmichael et al. 2017</td>
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</tr>
<tr>
<td>Dead Trees</td>
<td>Wetland</td>
<td>Temperate Deciduous</td>
<td>Standing dead trees</td>
<td>-37.5 (18.75)</td>
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<td>Dead Trees</td>
<td>Upland</td>
<td>Temperate Deciduous</td>
<td>Coarse wood debris (CI)</td>
<td>-1.15 (0.94)</td>
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<td>Warner et al. 2007</td>
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</table>

Table 1. Continued.

†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.

<table>
<thead>
<tr>
<th>Forest Type</th>
<th>Plant Genera or Species</th>
<th>$[O_2]$</th>
<th>Study</th>
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<td>Not specified</td>
<td><em>Unspecified Populous sp.</em></td>
<td>1.2%</td>
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<td>Temperate Forest</td>
<td><em>Quercus rubra, Quercus macrocarpa, Ulmus</em></td>
<td>0.02-</td>
<td>Chase 1937</td>
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<td>Temperate Hardwood Forest</td>
<td><em>Quercus rubra</em></td>
<td>5.5-7.5%</td>
<td>Jensen 1967</td>
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<td><em>Populus delectans</em></td>
<td>0.02-2.9</td>
<td>Van Der Kamp et al. 1979</td>
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<td><em>Picea abies</em></td>
<td>5.6-15.1%</td>
<td>Eklund 1990</td>
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<tr>
<td>Hardwood Forest</td>
<td><em>Quercus robur, Acer platanoides</em></td>
<td>5-19%</td>
<td>Eklund 1993</td>
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<td>Upland Conifer Forest</td>
<td><em>Picea abies</em></td>
<td>0.5-21%</td>
<td>Eklund 2000</td>
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<tr>
<td>Hardwood Forest</td>
<td><em>Betula pendula</em></td>
<td>1-5%</td>
<td>Gansert et al. 2001</td>
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<td>Greenhouse Study</td>
<td><em>Olea europaea</em></td>
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<td>Mancuso and Marras 2003</td>
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<td><em>Fagus orientalis, Carya ovata, Larix sibirica,</em></td>
<td>13-20%</td>
<td>del Hierro et al. 2002</td>
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<td>Conifer Forest</td>
<td><em>Pseudotsuga menziesii</em></td>
<td>0.5-20%</td>
<td>Pruyn et al. 2002</td>
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<td>Hardwood Forest</td>
<td><em>Acer rubrum, Fraxinus americana, Tsuga</em></td>
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<td>Spicer and Holbrook 2004</td>
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<td>Forest Type</td>
<td>Plant Community</td>
<td>Site</td>
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<tr>
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<td>Tree stems</td>
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<tr>
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<td></td>
<td></td>
<td>Tree stems</td>
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<td>Diverse Angiosperms</td>
<td>Negro River</td>
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<td>Small leaves</td>
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<td>Tapajos River</td>
<td>Diverse Angiosperms</td>
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<td>Small stems</td>
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<td></td>
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<td>Small leaves</td>
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<td>Upland</td>
<td>Temperate Floodplain</td>
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<td>Tree Stems</td>
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<td>Pinus sylvestris</td>
<td>Dry plot</td>
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<td>Shoots</td>
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<td>Wet plot</td>
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<td>Shoots</td>
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<td>Diverse angiosperms</td>
<td>Tree Stems (SD)</td>
<td>3.5%</td>
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<td>Quercus petra</td>
<td>Vegetated Plots</td>
<td>Tree Stems (95% CI) Scaled to full height</td>
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</tbody>
</table>

†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 \( \text{CH}_4 \) sources and sinks in upland and wetland forests. Red arrows are \( \text{CH}_4 \) sources and blue arrows are sinks. See Carmichael et al. (2014) for a treatment of the role of vegetation in \( \text{CH}_4 \) dynamics across a variety of terrestrial ecosystems.

Figure 2. Flammable concentrations of \( \text{CH}_4 \) 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 \( \text{CH}_4 \) 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 \( \text{CH}_4 \) 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 \( \text{CH}_4 \) 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.