



# The Role Of Vegetation In Methane Flux To The Atmosphere: Should Vegetation Be Included As A Distinct Category In The Global Methane Budget?

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## Abstract

Currently, the global annual flux of methane (CH<sub>4</sub>) to the atmosphere is fairly well constrained at ca. 645 Tg CH<sub>4</sub> year<sup>-1</sup>. However, the relative magnitudes of the fluxes generated from different natural (e.g. wetlands, deep seepage, hydrates, ocean sediments) and anthropogenic sources remain poorly resolved. Of the identified natural sources, the contribution of vegetation to the global methane budget is arguably the least well understood. Historically, reviews of the contribution of vegetation to the global methane flux have focused on the role of plants as conduits for soil-borne methane emissions from wetlands, or the aerobic production of methane within plant tissues. Many recent global budgets only include the latter pathway (aerobic methane production) in estimating the importance of terrestrial vegetation to atmospheric CH<sub>4</sub> flux. However, recent experimental evidence suggests several novel pathways through which vegetation can contribute to the flux of this globally important, trace greenhouse gas (GHG), such as plant cisterns that act as cryptic wetlands, heartwood rot in trees, the degradation of coarse woody debris and litter, or methane transport through herbaceous and woody plants. Herein, we synthesize the existing literature to provide a comprehensive estimate of the role of modern vegetation in the global methane budget. This first, albeit uncertain, estimate indicates that vegetation may represent up to 22 % of the annual flux of methane to the atmosphere, contributing ca. 32–143 Tg CH<sub>4</sub> year<sup>-1</sup> to the global flux of this important trace GHG. Overall, our findings emphasize the need to better resolve the role of vegetation in the biogeochemical cycling of methane as an important component of closing the gap in the global methane budget.

## **Introduction:**

Over a period of 100 years, methane has a global warming potential ca. 28-349 that of CO<sub>2</sub> (Myhre et al. 2013); it is arguably the most well-studied trace greenhouse gas (GHG), as well as the second most abundant non-CO<sub>2</sub> GHG in the atmosphere today (Montzka et al. 2011; Wuebbles and Hayhoe 2002), contributing ca. 25% of the total climate forcing

over the past 250+ years (Shindell et al. 2009). The increase of atmospheric methane has been attributed to human activity (Montzka et al. 2011; Dlugokencky et al. 2011; Diffenbaugh and Field 2013), although there appears to be considerable interannual variability in methane emissions that cannot be clearly linked to corresponding variations in fossil fuel or agricultural emissions (Dlugokencky et al. 1998; Bousquet et al. 2006; Schlesinger and Bernhardt 2013; Wuebbles and Hayhoe 2002; Kirschke et al. 2013). Fluctuation in the strength of natural sources of methane emissions (e.g. wetlands, fire) due to interannual variations in temperature, precipitation, and large-scale climate events (e.g. El Niño, volcanic eruptions) have been suggested as the cause of this variation (Bousquet et al. 2006; Dlugokencky et al. 2011; Kirschke et al. 2013). However, due to a lack of field-based evidence to support long-term decreases in wetland emissions, changes in anthropogenic-related (e.g. agriculture) emissions have also been implicated (Wuebbles and Hayhoe 2002; Khalil and Rasmussen 1994). The source of this interannual variation is currently unresolved and knowledge regarding interannual variation in the source-sink dynamics of the various components of the global methane budget remains highly uncertain (Kirschke et al. 2013).

Methane is formed by methanogenesis, the terminal step in the anaerobic degradation of carbon, which occurs in nutrient-depleted, anoxic microsites within the environment. There are a variety of substrates that are known to fuel methanogenesis, which can be broadly classified as CO<sub>2</sub>-type substrates (e.g. carbon dioxide, formate, carbon monoxide), methylated substrates (e.g. methanol, methylamine, dimethylamine, trimethylamine, methylmercaptan, and dimethylsulfide), and acetotrophic substrates (e.g. acetate or pyruvate), giving rise to the three main classifications of this group as hydrogenotrophic, methylotrophic, or acetotrophic. At present, all known methanogens are archaea (Paul et al. 2012; Garcia 1990).

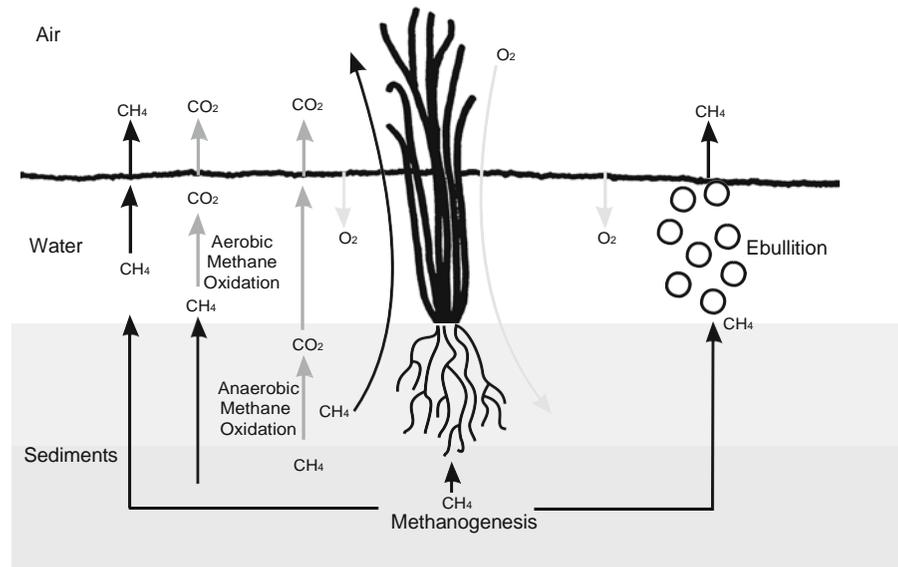
Once methane is produced, this potent trace GHG has a variety of fates that include consumption by methanotrophic guilds in aerobic zones within the soil/water column (Hanson and Hanson 1996), consumption by methane-oxidizing guilds in anaerobic zones coupling to denitrification (Haroon et al. 2013) or in syntrophic relationships with sulfate-reducers (Valentine and Reeburgh 2000), or flux to the atmosphere from the soil/water/plant interface. A classic view of the biogeochemical cycling of methane at the soil/

water/plant-atmosphere interface is shown schematically in Fig. 1. The major global sink of methane occurs via the photochemical oxidation of methane to carbon monoxide by the OH radical in the troposphere (Prinn 2003).

The global annual flux of methane to the atmosphere has been fairly well constrained, estimated with some accuracy at ca. 500–600 Tg CH<sub>4</sub> year<sup>-1</sup> (Schlesinger and Bernhardt 2013; Conrad 2009; Dlugokencky et al. 1998; IPCC 2007; Kirschke et al. 2013). For the purpose of the present review, all calculations were made using the annual flux estimate of 645 Tg CH<sub>4</sub> year<sup>-1</sup> proposed by Schlesinger and Bernhardt (2013), a value that represents the most recent comprehensive estimate reported in the literature to date that includes vegetation as a distinct, natural source of methane flux to the atmosphere. Overall, the major sources of methane emissions can be divided into natural and anthropogenic emissions. Natural sources of methane include wetlands, oceans, geological seepage, termites, and vegetation. When combined, these sources are estimated to contribute 215 Tg CH<sub>4</sub> to the atmosphere each year, or ca. 33 % of the annual global methane flux (Schlesinger and Bernhardt 2013). The largest source of natural methane emissions is wetlands, which exhibit considerable inter-annual variability (Bousquet et al. 2006; Conrad 2009) due primarily to a variety of meteorological factors. Anthropogenic sources include those associated with fossil fuel extraction and combustion, waste and waste management, ruminants, rice cultivation, biomass burning, and reservoirs. Overall, these sources contribute an estimated 430 Tg CH<sub>4</sub> to the atmosphere each year (Schlesinger and Bernhardt 2013), representing ca. 67 % of the annual global methane flux.

Because of the substantial role that methane plays as a contributor to global warming, it is essential to gain a better understanding of the sources and sinks in the global methane budget to reduce uncertainties in modeling future climate scenarios (Arnth et al. 2010; Bousquet et al. 2006; Kirschke et al. 2013). Among the aforementioned natural sources of methane, the contribution of vegetation to the global flux of methane is arguably the least well understood, despite being recognized as influencing both the production and consumption of methane via several pathways. For example, plants can influence soil carbon dynamics indirectly through the quality and quantity of litter, as well as directly by the exudation of carbon compounds

Fig. 1 A classic view of methane production, consumption, and transport in saturated soils. Methane flux across the soil-atmosphere interface occurs via diffusion, ebullition, and plant-mediated transport. Modified from Schütz et al. (1991)



into the rhizosphere that fuel methanogenesis (Schimel 1995; Joabsson et al. 1999; Vann and Megonigal 2003; Chanton et al. 2008; King and Reeburgh 2002; Megonigal and Guenther 2008). Plants can also influence methane-oxidation by rhizosphere oxygenation (Colmer 2003); in extreme cases this process has led to the complete attenuation of methane emissions from wetlands (Fritz et al. 2011). Additionally, vascular plants can play a role in the transport of methane, acting as a conduit from the soil (Dacey and Klug 1979; Rusch and Rennenberg 1998) that bypasses the attenuating role of soil and/or aquatic microbiota. More recently, Keppler et al. (2006) identified a novel aerobic mechanism of methane production stemming from pectin-degradation in plants (Keppler et al. 2008), implicating plant material as an important direct source of methane emissions. Thus, the role of vegetation in both the direct and indirect modulation of methane flux to the atmosphere has been established through both field and laboratory analyses.

Several field-based and modeling studies have included vegetation as a relevant agent in the biogeochemical control of trace GHG emissions and/or fluxes [for a good example see Matthews and Fung 1987]. However, there can be difficulty in accounting for the relative importance of vegetation when individual components (e.g. soil-atmosphere, water-atmosphere, or plant-atmosphere) of plot-level or ecosystem-level methane flux are not measured. In addition, when

vegetation flux is measured, it would be helpful for researchers to identify the hierarchical level at which their analysis occurred (e.g. species, plant functional type, community), as differences may exist in flux rates based on the scale of analysis. When included in global budgets, the contribution of vegetation to the flux of methane is often limited to aerobic methane production (Conrad 2009; Schlesinger and Bernhardt 2013; IPCC 2007; USEPA 2010). However, the most recent global methane budget produced by the IPCC (Ciais et al. 2013) eliminated vegetation entirely as a distinct category of methane flux to the atmosphere due to concern regarding the significance of the aerobic production of methane by vegetation on a global scale. Historically, these global budgets have neglected additional ways that vegetation could contribute to the global methane budget indirectly, as conduits for soil-borne emissions and by facilitating the colonization of anaerobic microenvironments by methanogenic microorganisms. Therefore, the specific goal of the present literature review was twofold: (1) to synthesize the existing information regarding the role of vegetation in the biogeochemical cycling of methane in natural environments, thus vegetation-related sources such as rice cultivation and ruminants were not included within the scope of this review, and (2) to attempt to quantify the relative importance of direct and indirect plant-based emissions of CH<sub>4</sub> on a global scale. As a result, the literature selection strategy for this review targeted newer studies that provide

methane flux estimates and did not focus on the development of a process-based understanding of the mechanisms supporting methane flux to the atmosphere by vegetation. Although the focus of this synthesis is on extant vegetation in natural ecosystems, it is important to note that, over geological time scales, plant derived carbon supports the modern methane budget through the anaerobic degradation of organic matter and carbon compounds that can ultimately be traced to the autotrophic activity of either plants or microorganisms.

### **Direct emission of methane by vegetation: aerobic methane production**

Until recently, the scientific consensus existed that the major methane sources had been identified. However, Keppler et al.'s (2006) finding of aerobic methane production from plant biomass (recently reviewed by Bruhn et al. 2012 and Keppler et al. 2009) caused scientists to re-evaluate the global methane budget. Field emissions from Keppler et al.'s 2006 study were upscaled using annual net primary production, indicating a source strength in the range of 62–236 Tg CH<sub>4</sub> year<sup>-1</sup>, ca. 10–37 % of the annual global methane budget (Table 1). Uncertainties in the global methane budget can easily accommodate an additional methane source in the range of 50–100 Tg year<sup>-1</sup> (Keppler et al. 2009; Frankenberg et al. 2005). Thus, the identification of this novel pathway of aerobic methane production in plants had the potential to reduce uncertainty regarding methane flux to the atmosphere. However, Keppler et al.'s findings were controversial (Dueck et al. 2007; Houweling et al. 2006; Kirschbaum et al. 2006; Parsons et al. 2006), due to the choice of annual net primary production as a method of upscaling in situ methane emissions, along with errors in calculations. Therefore, several researchers attempted to revise Keppler et al.'s estimation of source strength by using more appropriate methods of upscaling such as modeling, mass balance, and/or estimates of above-ground net primary productivity (Table 1). The large range in these upscaled values (0–236 Tg CH<sub>4</sub> year<sup>-1</sup>; Table 1) indicates a high degree of uncertainty, which was reinforced by the varying degree of success in other's attempts to replicate Keppler et al.'s initial findings using a variety

of methods employed at various structural hierarchical levels in plants (Table 2).

An additional degree of uncertainty regarding aerobic methane production in plants exists due to a fundamental lack of understanding of the mechanistic pathways involved in aerobic methane production. As a result, recent research has focused on the biochemical level to better elucidate the mechanism(s) of aerobic methane production in plant tissue (Table 3). Many of these studies point to stress-induced degradation of the methoxyl groups contained in either pectin (Vigano et al. 2008; Messenger et al. 2009; McLeod et al. 2008; Keppler et al. 2008) or lignin (Vigano et al. 2008) as possible sources for methane production. It is important to note that these structural tissues can comprise a large percentage of plant biomass. Pectin can represent 7–35 % of the cell wall material in leaves, and lignin can represent up to 31 % of total woody tissue content (Keppler et al. 2004). In addition, a few common pathways exist among the recognized mechanisms for aerobic methane production. All seem to involve environmental stressors (e.g. UV irradiance, temperature, H<sub>2</sub>O, microbial attack, herbivory) and appear to operate via the generation of reactive oxygen species (ROS), leading to methoxyl group degradation and the production of methane.

It is worthwhile to note that a few of the environmental stressors mentioned, such as UV irradiance, temperature, and herbivory by insect pathogens, are predicted to increase (McKenzie et al. 1999; Kurz et al. 2008; IPCC 2007) as a result of stratospheric ozone depletion, increases in GHGs, and drought and temperature induced stress in vegetation respectively, making it tempting to speculate that aerobic methane production by vegetation may exert an increasingly strong impact on the annual flux of methane to the atmosphere in the future. However, future experiments on the role of environmental stressors in inducing aerobic methane production in plants should be carefully designed to include a range of UV exposure and/or temperatures that are likely to occur according to future predictions of climate change models. In addition, new lines of research should be established to investigate the impact of herbivory on aerobic methane production, addressed by only a single experiment conducted to date that simulated herbivory by excising leaf material (Wang et al. 2008).

Table 1 Global yearly CH<sub>4</sub> emissions as a result of plant-based aerobic methane emissions

Study	Method of scaling	Upscaled CH <sub>4</sub> emissions (Tg CH <sub>4</sub> year <sup>-1</sup> )	Percent of global CH <sub>4</sub> budget <sup>a</sup>
Houweling et al. (2006)	Atmospheric transport model and mass balance	85–125	13.2–19.4
Kepler et al. (2006)	Measured rates scaled using net primary productivity (NPP)	62–236	9.6–36.6
Kirschbaum et al. (2006)	Kepler et al. (2006) emission rates scaled using leaf biomass and photosynthetic rates	Leaf biomass: 15.1–60.3 Photosynthetic rates: 9.6	Leaf biomass: 2.3–9.3 Photosynthetic rates: 1.5
Parsons et al. (2006)	Kepler et al. (2006) emission rates scaled using biome leaf biomass	42	6.5
Butenhoff and Khalil (2007)	Kepler et al. (2006) emission rates scaled using a model which included cloud cover, canopy shade, and either leaf area index or foliage biomass (as an estimate of above ground NPP)	Leaf Area Index: 14–60 Foliage Biomass: 8–34	Leaf Area Index: 2.2–9.3 Foliage Biomass: 1.2–5.3
Ferretti et al. (2007)	Mass balance approach using ice cores and estimates of fossil fuel and biomass combustion	Pre-industrial: 0–46 Modern: 0–176	Pre-industrial: 0–7.1 Modern: 0–27.3
Bloom et al. (2010)	Weighted methane production from pectin, global UV radiation models, leaf area index, and air temperature data	0.2–1.0	ca. 0–0.1

<sup>a</sup> Calculated using the estimated annual flux of methane to the atmosphere (645 Tg CH<sub>4</sub> year<sup>-1</sup>) as reported in Schlesinger and Bernhardt (2013)

According to biochemical studies of plant structural tissues, it is clear that plants can be a source of methane. However, fundamental questions remain, namely: (1) the importance of this process on a global scale (Table 1) and (2) the prevalence of this process in natural environments (Tables 2 and 3). The impact of environmental stressors on aerobic methane production has largely been studied in highly artificial lab settings, while field-based studies are lacking. Future work should address these issues, in addition to investigating the potential role of leaf litter and coarse and fine woody debris as possible additional sources of aerobic methane emissions (Dueck and van der Werf 2008). Currently, the most accurate estimates regarding the role of aerobic methane production in plants in the global methane budget are likely those that include measures of above-ground, net primary productivity as a way of upscaling to the landscape level (Kirschbaum et al. 2006; Parsons et al. 2006; Butenhoff and Khalil 2007). So far, these studies indicate a source strength in the range of 8–60 Tg CH<sub>4</sub> year<sup>-1</sup>, ca. 1.2–9 % of the mean annual global methane budget (Table 1; Fig. 2). However, the significance of aerobic methane emissions by vegetation on a global scale has recently been questioned, as evidenced by the elimination of vegetation as a distinct source in the most recent global methane budget produced by the IPCC (Ciais et al. 2013).

## Indirect emissions of methane by vegetation

### Cryptic wetlands

Globally, wetlands represent 8,219–10,119 km<sup>2</sup>, or 6.2–7.6 % of the total land surface area (Lehner and Döll 2004). These water-saturated terrestrial environments typically generate anoxic conditions conducive to methanogenesis (Conrad 2009) and are the dominant natural source of methane globally (Wuebbles and Hayhoe 2002; Dlugokencky et al. 1998; Conrad 2009; Schlesinger and Bernhardt 2013). In addition to the large-scale, permanently flooded wetlands that are easily observed across a landscape, there are several other types of wetland communities, termed cryptic wetlands (Table 4) that are either smaller, only seasonally inundated, or are simply difficult to delineate visually by an observer or via remote sensing.

These cryptic wetlands (Table 4) form as a result of changes in landscape topography and geomorphology

**Table 2** Studies investigating the potential for aerobic methane production in plants on various structural/architectural hierarchies

Ecosystem or canopy level		Whole plant		Plant part		Plant structural component
+	-	+	-	+	-	+
Mikkelsen et al. (2010)	Bowling et al. (2009)	Brüggemann et al. (2009)	Kirschbaum and Walcroft (2008)	Keppler et al. (2006)	Dueck et al. (2007)	Keppler et al. (2008)
	Smeets et al. (2009)		Nisbet et al. (2009)	McLeod et al. (2008)	Beerling et al. (2008)	McLeod et al. (2008)
				Vigano et al. (2008)	Kirschbaum and Walcroft (2008)	Vigano et al. (2008)
				Wang et al. (2008)	Wang et al. (2008)	Messenger et al. (2009)

Inspired by Bruhn et al. (2012)

+, plants emitted CH<sub>4</sub>; -, plants did not emit CH<sub>4</sub>

**Table 3** Environmental stressors that induce aerobic methane emission in plants

UV irradiance		Temperature	H <sub>2</sub> O stress	Microbial attack	Herbivory
+	-	+	+	+	+
Keppler et al. (2008)	Bowling et al. (2009)	Keppler et al. (2008)	Quaderi and Reid (2009)	McLeod et al. (2008)	Wang et al. (2008)
McLeod et al. (2008)		Vigano et al. (2008)			
Vigano et al. (2008)					
Messenger et al. (2009)					

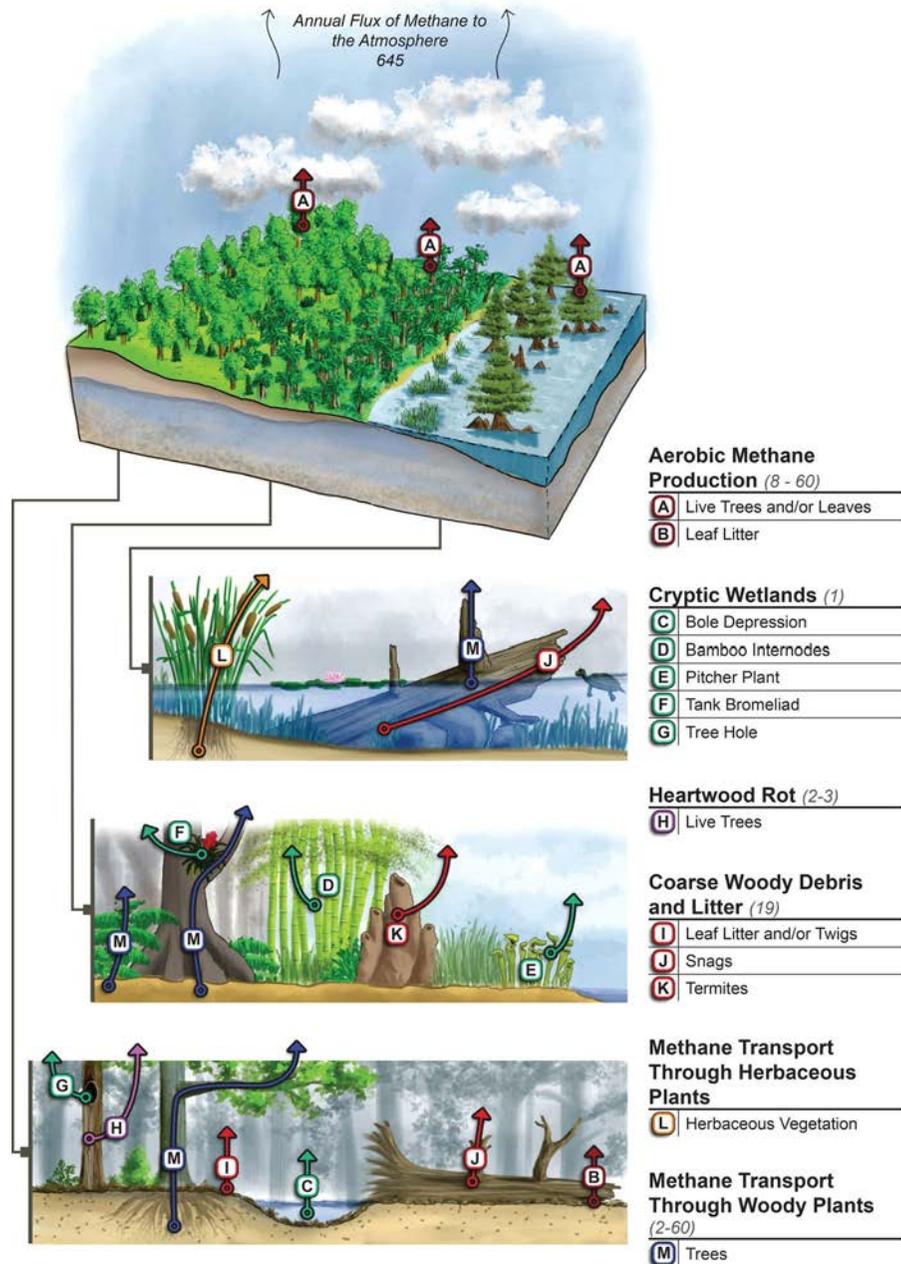
+, plants emitted CH<sub>4</sub>; -, plants did not emit CH<sub>4</sub>

(e.g. bole depressions) or by water being trapped in plant cisterns (e.g. phytotelmata such as hollow bamboo internodes, non-bromeliad leaf axils, pitcher plants, tank bromeliads, tree holes). As with their larger/more easily recognized counterparts, the development of anoxic conditions in these types of cryptic wetlands can lead to colonization by methanogenic archaea (Krieger and Kourtev 2012) and/or production of methane (Goffredi et al. 2011; Martinson et al. 2010). Though individually small, the vast numbers of plant cisterns could lead to a high cumulative atmospheric methane flux, emphasizing the importance of including these ecosystems in the global methane budget (Yavitt 2010).

The quantification of methane flux generated by cryptic wetlands is difficult due to uncertainty regarding the global extent of these environments. Two separate studies (Goffredi et al. 2011; Martinson et al.

2010) have attempted to upscale emissions from one category of cryptic wetland, tropical tank bromeliads to the global level. Goffredi et al. (2011) utilized in vitro tank water cultures to estimate tank bromeliad methane emissions, and then upscaled measured values to the global level using bromeliad density estimates from previously published studies. Martinson et al. (2010) measured field emission rates and then utilized density estimates for bromeliads at the site, plus previously reported values for the total area of neotropical forests found worldwide, to upscale emissions estimates to the global level. These studies indicated a maximum contribution to the global methane budget of 1 Tg year<sup>-1</sup> for tank bromeliads, or 0.2 % of the annual global methane budget, calculated for the present review using the mean global methane budget of 645 Tg CH<sub>4</sub> year<sup>-1</sup> (Schlesinger and Bernhardt 2013). Overall, this value represents a

Fig. 2 A contemporary view of the role of modern vegetation in the biogeochemical cycling of methane in natural ecosystems. *Arrows* represent possible sources of methane flux to the atmosphere and are *color-coded* by the emission categories listed in the text. *Values* in the legend represent the estimated quantity of methane flux to the atmosphere (when known) in Tg CH<sub>4</sub> year<sup>-1</sup> from vegetation sources as reported in this manuscript. Please reference Fig. 1 for the processes of methane production, consumption, and transport in soils. (Color figure online)



relatively small but highly uncertain contribution to the global methane budget. When contributions of this level include future estimates for other classes of cryptic wetlands (Table 4), most of which are poorly researched, the overall contribution by cryptic wetlands may become significant on a global scale. However, it is pertinent to note that the magnitude of the importance of these smaller classes of cryptic

wetlands to the global methane budget is highly dependent on accurate estimates of their global coverage and corresponding rate of methane production.

#### Heartwood rot

In 1907 Bushong first documented the release of a flammable gas from tree trunks that was accompanied

**Table 4** Classification of cryptic wetlands

Broad classification	Type	Methane production potential
Landscape geomorphology	Bole depressions	Defined as the depression left after a tree falls. When water-filled, these could act as microscale wetlands. The development of anoxic conditions could lead to methane production
Phytotelmata	Hollow bamboo internodes <sup>a</sup>	Water trapped in bamboo internodes could lead to the development of anoxic microsites and possibly methanogenesis
	Non-bromeliad leaf axils <sup>a</sup>	Water trapped in leaf axils could lead to the development of anoxic conditions and methanogenic colonization
	Pitcher plants <sup>a</sup>	Water trapped in pitcher plants can develop anoxic conditions, which leads to colonization by methanogens (Krieger and Kourtev 2012)
	Tank bromeliads <sup>a</sup>	Water trapped in tank bromeliads can lead to the development of anoxic conditions and methanogenic colonization (Martinson et al. 2010; Goffredi et al. 2011)
	Tree holes <sup>a</sup>	Water trapped in tree holes could lead to the development of anoxic conditions and methanogenic colonization.

<sup>a</sup> As suggested by Martinson et al. (2010)

by what was later described as a “fetid, rumen-like odor” (Schink et al. 1981; Zeikus and Ward 1974). This observation led researchers to investigate the origin of these high-pressure gas emissions from tree trunks, leading to the first identification of microbial colonization of wetwood and/or hardwood (Zeikus and Henning 1975; Zeikus and Ward 1974) as the source of this flammable gas, methane. These methanogens likely exist in a syntrophic relationship with facultative, anaerobic bacterial populations that are

responsible for the decomposition of wood (Zeikus and Henning 1975; Zeikus and Ward 1974; Schink and Ward 1984; Schink et al. 1981; Beckmann et al. 2011a, b). Trees are generally resistant to decay and microbial infection as long as structural integrity is maintained (Wagener and Davidson 1954), but may become infected as a result of an exposed wound on the axis of a stem or xylem (Shigo and Hillis 1973). Microbial migration leads to colonization within wetwood and heartwood and leads to decay and decomposition of plant structural components (Wilcox 1970).

A variety of tree species are vulnerable to heartwood rot, and an individual tree’s susceptibility to microbial colonization and decay varies by species, site, age-class, and management history, as well as among individuals (Wagener and Davidson 1954). Yet, methane release from plants as a result of heartwood or wetwood rot is largely ignored on a global scale (Bonan 2008; Conrad 2009); and, until recently, estimations of emission rates from rotting trees were non-existent. Covey et al. (2012) recently quantified methane production from heartwood rot in a temperate upland forest, documenting methane concentrations in trunks greater than 15,000  $\mu\text{L/L}$ , ca. 80,000  $\mu\text{atm}$  atmospheric methane concentration. Trees located in well-drained upland soils had trunk methane concentrations 2.39 greater than trees in more poorly drained lowland areas, providing evidence that trees were the source of in situ methane production, rather than simple conduits for soil-borne emissions. Anaerobic cultures of wood core material produced methane at a flux of  $7.1 \pm 1.3 \text{ } \mu\text{g CH}_4 \text{ m}^{-3} \text{ s}^{-1}$ , a value that was upscaled to a local field flux of  $52 \pm 9.5 \text{ ng CH}_4 \text{ m}^{-2} \text{ s}^{-1}$ . Assuming that this flux is typical of temperate tree species worldwide, Covey et al.’s field estimates can be further upscaled using values reported in Schlesinger and Bernhardt (2013), adjusted for the average standing timber loss from heartwood rot for the United States as reported in Wagener and Davidson (1954) (Table 5), to generate a global estimate of methane emissions due to heartwood rot in temperate forests worldwide of ca. 2–3 Tg  $\text{CH}_4 \text{ year}^{-1}$ , or 0.3–0.4 % of the annual global methane budget (Fig. 2). This figure represents a conservative estimate for this source of methane due to the lack of data regarding timber loss worldwide.

Although Covey et al. (2012) reported that decay processes in living vegetation may be a source of

**Table 5** Methane emissions from heartwood rot in temperate forests worldwide

Field emission rates (ng CH <sub>4</sub> m <sup>-2</sup> s <sup>-1</sup> )	Converted field emission rates (Tg CH <sub>4</sub> km <sup>-2</sup> year <sup>-1</sup> )	Upscaled CH <sub>4</sub> emissions (Tg CH <sub>4</sub> year <sup>-1</sup> )	Percent of global CH <sub>4</sub> budget <sup>b</sup>
61.5 (High) <sup>a</sup>	6.15 × 10 <sup>-14</sup>	2.6	0.4
52 (Average) <sup>a</sup>	5.2 × 10 <sup>-14</sup>	2.2	0.3
42.5 (Low) <sup>a</sup>	4.25 × 10 <sup>-14</sup>	1.8	0.3

<sup>a</sup> Field emission rates are taken from Covey et al. (2012) and upscaled using the global area for temperate forests as reported in Schlesinger and Bernhardt (2013), adjusted for the average standing timber loss from heartwood rot for the United States as reported in Wagener and Davidson (1954)

<sup>b</sup> Calculated using the estimated annual flux of methane to the atmosphere (645 Tg CH<sub>4</sub> year<sup>-1</sup>) as reported in Schlesinger and Bernhardt (2013)

methane flux to the atmosphere, experimental results did not clarify whether or not the methane produced might be released from the tree, plant canopy, or both. Thus, it remains unclear whether heartwood rot contributes to atmospheric methane flux. Future research should seek to address this question, in addition to (1) determining whether methane production due to heartwood rot is important globally, (2) validating the importance of this process in both upland and lowland forests, and (3) investigating the potential for the occurrence of methanotrophic bacterial guilds within infected trees that may act to attenuate methane emissions and/or provide a non-atmospheric source of CO<sub>2</sub> to the plant host (Raghoebaring et al. 2005). If the latter is demonstrated, our view of this interaction between plant host and microbe may shift from that of parasitism to mutualism, as sapwood is rarely impacted by heartwood infection (Wagener and Davidson 1954) and trees can survive for many years after infection.

#### *Coarse woody debris and litter; methane flux from dead vegetation*

Dead vegetation in the form of standing or fallen woody debris could contribute to the flux of methane in three possible ways: (1) aerobic methane production in dead plant material (Dueck and van der Werf 2008; Keppler et al. 2008), (2) dead culms and/or trees acting as conduits for soil-born methane emissions (Brix 1990; Dingemans et al. 2011), and (3) as woody debris or standing dead vegetation facilitating anaerobic

microenvironments that could be colonized by methanogenic archaea. This section of the synthesis will focus on the latter topic, as the first two are addressed in the sections on *Direct Emissions of Methane by Vegetation: Aerobic Methane Production* and *Methane Transport through Herbaceous and Woody Plants* respectively.

Dead vegetation is an important component of forest carbon budgets (Litton et al. 2007) and represents a substantial, dynamic carbon stock (Cornelissen et al. 2012). There are four major classes of dead vegetation: standing biomass (e.g. dead trees), coarse woody debris (e.g. fallen trees and large logs), fine woody debris (with a diameter between 0.5 and 10 cm), and leaf litter. Decomposition of woody debris by weathering and microbial activity can be influenced by a variety of factors (Chambers et al. 2000; Cornelissen et al. 2012; Cornwell et al. 2009; van Geffen et al. 2010; Freschet et al. 2012; Harmon 2001; Janisch and Harmon 2002; McCarthy and Bailey 1994), some of which (e.g. anatomical traits such as high bark thickness, high wood density and low wood porosity, and chemical traits such as wood composition) are conducive to the formation of methanogenic microenvironments that are characterized by slow decay rates, poor oxygen diffusion, and rapid consumption of oxygen when available. However, a lack of detailed knowledge regarding how these traits interact quantitatively confounds the ability to predict carbon, and thus methane, fluxes as a result of decomposition processes (Cornwell et al.

2009). Regardless, decomposition, depending on microsite environmental factors, ultimately leads to the evolution of CO<sub>2</sub> or CH<sub>4</sub>.

In aerobic environments, CO<sub>2</sub> evolution, as a result of microbial degradation of coarse woody debris, has been reported to contribute to a substantial portion of the total carbon loss in tropical forests (Saleska et al. 2003; Chambers et al. 2001). Methane evolution as a result of methanogenic degradation of woody debris in anaerobic microsites could also contribute to the carbon flux; however, it has yet to be quantified at the landscape-level. Methanogenic colonization has been documented in decaying logs in abandoned gold mines (Abraham et al. 1989; Beckmann et al. 2011a, b; Krüger et al. 2008) and in the guts of xylophagous (e.g. wood-eating) arthropods (Brune and Friedrich 2000; Rasmussen and Khalil 1983; Hackstein and Stumm 1994), both of which are sources of methane emission. Termites in particular have been recognized for several years as a potentially important source of atmospheric methane (Zimmerman et al. 1982). Globally, methane emissions from termites were estimated to contribute ca. 19 Tg CH<sub>4</sub> year<sup>-1</sup> to the total annual flux of methane (Sanderson 1996). Moreover, this total would likely increase considerably if methane emissions from other classes of xylophagous insects were included.

Globally, forests cover up to 30 % (42.9 × 10<sup>6</sup> km<sup>2</sup>) of the land surface area (Anderegg et al. 2012, 2013) and represent one of the largest carbon stocks on the Earth. Climate change is predicted to impact the biogeochemistry of forest ecosystems both directly and indirectly through a variety of mechanisms (Dale et al. 2001), many of which (e.g. higher temperatures and increased drought worldwide) may act synergistically to compound ecosystem stress and result in an increase in the stock of dead vegetation due to mortality events. In addition to exerting direct physiological effects that can lead to mortality, stress can also indirectly impact healthy vegetation by increasing the susceptibility of vegetation to colonization by insects and/or pathogens (Dale et al. 2001), which can ultimately lead to mortality events capable of converting forests from net carbon sinks to sources (Kurz et al. 2008).

The measurement of dead carbon stocks in forests can be an overwhelming task (Brown 2002). As a result, there is massive uncertainty regarding the contribution of dead wood decomposition to the global carbon budget (Delaney et al. 1998; van Geffen et al.

2010), which has the potential to become increasingly important in future climate change scenarios due to predicted increases in forest loss (Bonan 2008; Anderegg et al. 2012, 2013). Understanding the contribution of all classes of dead vegetation in the global methane budget is a glaring omission in the existing knowledge regarding the global carbon cycle. At present, the only estimated flux we can include in this category is the CH<sub>4</sub> produced by termites feeding on dead wood, representing an almost certain underestimate of dead wood fluxes of 19 Tg CH<sub>4</sub> year<sup>-1</sup>, ca. 3 % of the annual global methane budget (Fig. 2).

#### *Methane transport through herbaceous plants*

Herbaceous plants are defined by a lack of woody tissue in stems, and along with aquatic macrophytes, are often dominant members of wetland plant communities. Wetland plants often exhibit a suite of traits (e.g. development of aerenchyma, elongated shoot formation, pressurized ventilation, and underwater photosynthesis) to combat the exceedingly slow diffusivity of nutrient gases (e.g. O<sub>2</sub> and CO<sub>2</sub>) in water (Colmer 2003; Voesenek et al. 2006). These structural adaptations, along with the transpiration stream of the plant, act to move O<sub>2</sub> into the plant tissue and rhizosphere, and also provide a pathway for the efflux of CO<sub>2</sub> and other soil-borne gasses. It is widely recognized that both live and dead wetland vegetation can act as a conduit for methane efflux from the soil (Brix 1990; Dingemans et al. 2011; Joabsson et al. 1999; Laanbroek 2010; Singh and Singh 1995; Sebacher et al. 1985). This flux represents a direct pathway from the soil to the atmosphere, thus bypassing the attenuating role of soil (van der Nat and Middelburg 1998) and aquatic (Heilman and Carlton 2001) guilds of methanotrophic microorganisms. However, Raghoebarsing et al. (2005) recently identified a novel symbiosis between *Sphagnum* spp. and methanotrophic symbionts, whereby the microflora associated with *Sphagnum* stems oxidized methane, providing a non-atmospheric source of CO<sub>2</sub> to the plant. These findings suggest that the methane trapped in vascular plant conduits may be partially attenuated by plant-associated microbiota and assimilated subsequently by the plant host.

As previously mentioned, there is an extensive existing body of literature on the role of herbaceous plant species in methane flux from wetlands, the dominant source of methane worldwide. These studies

**Table 6** Herbaceous plant species in boreal and arctic ecosystems as conduits for methane emissions

Study	Species	Structure	Factors that impact plant CH <sub>4</sub> flux	CH <sub>4</sub> emissions (Tg CH <sub>4</sub> km <sup>-2</sup> year <sup>-1</sup> )	Estimated contribution to ecosystem flux (if known)
Smith and Lewis (1992)	<i>Nuphar lutea</i>	Leaf-level	Porewater methane concentration, soil organic C, soil temperature	$6.7 \times 10^{-5}$	51–99 %
Whiting and Chanton (1992)	<i>Carex</i> sp. dominated fen	Stand	Above-ground plant biomass	$2.8 \times 10^{-5}$	94 %
Morrissey et al. (1993)	<i>Carex</i> sp. dominated wetland	Stand	Cuticular and stomatal conductance	$2.5 \times 10^{-5}$ – $5.9 \times 10^{-5}$	–
Whiting and Chanton (1993)	–	Ecosystem	Net ecosystem production	–	–
Schimel (1995)	–	Whole Plant	Plant architecture, soil C dynamics, spatial and temporal factors, species composition, transport kinetics	–	37–100 %, average of 75 %
Brix et al. (1996)	<i>Phragmites australis</i>	Culm	Diurnal and seasonal variation, measurement technique, sediment characteristics	$4.6 \times 10^{-5}$ – $5.0 \times 10^{-5}$	–
Kelker and Chanton (1997)	–	Whole plant	Herbivory	–	–
King et al. (1998)	–	Vegetation removal	Plant species composition	–	–
Verville et al. (1998)	–	Vegetation removal	Soil temperature, thaw depth, vegetative composition, water table depth	–	–
Öquist and Svensson (2002)	Site A: minerotrophic peatland dominated by <i>Eriophorum angustifolium</i> Site B: ombrotrophic peatland dominated by <i>Eriophorum vaginatum</i> and <i>Carex rotundata</i>	Stand	Number of shoots, photosynthetic rate, soil temperature, water table position	Site A: $1.1 \times 10^{-5}$ – $1.6 \times 10^{-4}$ Site B: $1.5 \times 10^{-6}$ – $1.6 \times 10^{-4}$	–
Kankaala et al. (2003)	<i>Phragmites australis</i> <i>Schoenoplectus lacustris</i> <i>Equisetum fluviatile</i> <i>Nuphar lutea</i> <i>Sparganium gramineum</i> <i>Potamogeton natans</i>	Stand	Leaf biomass, solar radiation	$1.1 \times 10^{-4}$ – $2.1 \times 10^{-3}$ $9.8 \times 10^{-6}$ – $1.5 \times 10^{-5}$ $8.4 \times 10^{-6}$ – $1.1 \times 10^{-5}$ $7.0 \times 10^{-6}$ – $4.1 \times 10^{-6}$ $7.0 \times 10^{-6}$ – $4.2 \times 10^{-6}$ $4.2 \times 10^{-6}$ – $1.4 \times 10^{-6}$	–
Bodelier et al. (2006)	–	Cultures	Herbivory	–	–

**Table 6** continued

Study	Species	Structure	Factors that impact plant CH <sub>4</sub> flux	CH <sub>4</sub> emissions (Tg CH <sub>4</sub> km <sup>-2</sup> year <sup>-1</sup> )	Estimated contribution to ecosystem flux (if known)
Bergström et al. (2007)	<i>Phragmites australis</i> and <i>Equisetum fluviatile</i> dominated littoral zone	Data compilation	Coverage of dominant species, species-specific factors, temperature	–	Vegetated areas had 2.4–3.99 increased in methane emissions compared to non-
Cao et al.	<i>Kobresia humilis</i> meadow	Vegetation removal	Species	$2.57 \times 10^{-7}$ – $2.2 \times 10^{-7}$ $7.8 \times 10^{-8}$ – $5.9 \times 10^{-8}$	
Dingemans et al. (2011)	<i>Potentilla fruticosa</i> meadow	Stand and whole plant	Herbivory	–	–

have come from boreal and arctic ecosystems (Table 6) and temperate latitudes (Table 7). After an extensive literature search, we were unable to find any evidence of studies on herbaceous plants as sources of methane emissions in natural environments within the tropics. However, it is important to note that tropical latitudes represent a significant source of methane (Frankenberg et al. 2005), and vegetation-mediated pathways are probably important, given the extensive range of permanently and seasonally inundated tropical soils. It is also worth noting that, like seasonally inundated wetlands, cryptic wetland environments such as roadside ditches, are typically colonized by a variety of herbaceous plant species and may be a significant source of methane flux to the atmosphere. The importance of these environments to the annual flux of methane to the atmosphere is currently unknown, but could be determined using resources such as the Global Roads Open Access Data Set (Center for International Earth Science Information Network-CIESIN-Columbia University 2013) when combined with published methane flux estimates from species such as *Typha* spp. (Yavitt and Knapp 1995, 1998) that typically colonize these environments. Collectively, existing studies indicate that herbaceous plants represent ca. 28 to 90 % of the total ecosystem-level methane flux from wetlands, and that there are a variety of factors from soil characteristics to plant structural traits, ecosystem-level controls, and species interactions, that modulate methane flux in wetland ecosystems (Tables 6, 7, additionally reviewed by Whalen 2005). Though not included within the scope of this review, there is an extensive body of literature that addresses gas transport mechanisms in plants, which is an important component for the understanding the environmental and structural controls on plant-associated methane flux. Further reading on this topic can be found in (Arkebauer et al. 2001; Chanton et al. 2002, 1993; Grosse et al. 1996, 1991, 1992; Morrissey et al. 1993; Whiting and Chanton 1996; Yavitt and Knapp 1998).

At present, upscaling methane flux from herbaceous plants to the landscape and globe is difficult. Any ability to estimate the global contribution of this source depends on the existence of (1) a standardized method for methane flux measurements, in terms of the structural hierarchy of possible measurements (e.g. leaf, whole plant, stand, or canopy level) and the protocol chosen for quantifying of methane flux, (2) flux measurements taken across the complete

**Table 7** Herbaceous plant species in temperate latitudes as conduits for methane emissions

Study	Species	Structure	Factors that impact plant CH <sub>4</sub> flux	CH <sub>4</sub> emissions (Tg CH <sub>4</sub> km <sup>-2</sup> year <sup>-1</sup> )	Estimated contribution to ecosystem flux (if known)
Dacey and Klug (1979)	<i>Nuphar luteum</i>	Leaf	Diurnal variation	$5.9 \times 10^{-5}$	75 %
Sebacher et al. (1985)	26 Species <i>Cladium jamaicense</i> <i>Sagittaria lancifolia</i>	Emergent parts of aquatic plants	Species	– <sup>a</sup>	–
Holzappel-Pschorn et al. (1986)	<i>Oryza sativa</i>	Whole plant and stand	Species composition, soil redox potential	$2.2 \times 10^{-4}$	60–94 %
Whiting et al. (1991)	<i>Cladium</i> sp.	Stand	Biomass, factors that enhance primary production	$9.4 \times 10^{-6}$	91 %
Whiting and Chanton (1993)	–	Ecosystem	Net ecosystem production	–	–
Shannon et al. (1996)	<i>Scheuchzeria palustris</i>	Stand	Presence of flooding adaptations, rhizosphere interactions	$7.8 \times 10^{-5}$ – $1.0 \times 10^{-4}$	64–90 %
Sugimoto and Fujita (1997)	Marsh trefoil Reeds <i>Sphagnum</i> sp.	Whole plant	Soil decomposition rates, soil redox potential, soil temperature water table depth	$1.6 \times 10^{-4}$ $1.1 \times 10^{-4}$ $2.6 \times 10^{-5}$	–
Greenup et al. (2000)	<i>Eriophorum vaginatum</i> L.	–	Above- and belowground biomass, rhizosphere interactions, species composition	$1.3 \times 10^{-5}$	–
Ding et al. (2005)	<i>Carex lasiocarpa</i> <i>Carex meyeriana</i> <i>Deyeuxia angustifolia</i>	Whole plant	Plant transport capacity, porewater methane concentration, species	– <sup>b</sup>	73–82 % 75–86 % 28–31 %

<sup>a</sup> Study included 26 species; emissions were calculated by volume. Emissions ranged from  $5.48 \times 10^{-14}$  Tg CH<sub>4</sub> year<sup>-1</sup> in *Cladium jamaicense* to  $1.13 \times 10^{-12}$  Tg CH<sub>4</sub> year<sup>-1</sup> in *Sagittaria lancifolia*

<sup>b</sup> Methane emissions in this study were measured by stem. Emissions from *Carex lasiocarpa*, *Carex meyeriana*, and *Deyeuxia angustifolia* were  $1.6 \times 10^{-17}$ ,  $2.08 \times 10^{-17}$ , and  $8.0 \times 10^{-18}$  Tg CH<sub>4</sub> stem<sup>-1</sup> h<sup>-1</sup> respectively

**Table 8** Woody plants as conduits for methane emissions in temperate wetlands

Study	Species	Structure	Factors that impact plant CH <sub>4</sub> flux	CH <sub>4</sub> emissions (Tg CH <sub>4</sub> km <sup>-2</sup> year <sup>-1</sup> )	Estimated contribution to ecosystem flux (if known)	Upscaled CH <sub>4</sub> emissions (Tg CH <sub>4</sub> year <sup>-1</sup> )
Sebacher et al. (1985)	<i>Avicennia nitida</i>	Pneumatophore	– <sup>a</sup>	N/A <sup>b</sup>	N/A	N/A
Pulliam (1992)	<i>Taxodium distichum</i>	Knee	Knee density	2.0 × 10 <sup>-7</sup> <sup>c</sup>	0.14 %	0.1
Terazawa et al. (2007)	<i>Fraxinus mandshurica</i> var. <i>japonica</i>	Stem	Stem height from ground level	9.6 × 10 <sup>-7</sup>	N/A	0.2
Gauci et al. (2010)	<i>Alnus glutinosa</i>	Stem	Season	3.6 × 10 <sup>-8</sup> – 8.8 × 10 <sup>-7</sup>	16 %	0–0.2

Field emission rates are taken from each study and upscaled (when possible) using the global area for temperate forested wetlands as reported in Matthews and Fung (1987)

<sup>a</sup> No observations by authors

<sup>b</sup> Emissions were calculated by volume (4.7 × 10<sup>-14</sup> Tg CH<sub>4</sub> year<sup>-1</sup>) and therefore cannot be extrapolated to area

<sup>c</sup> Calculation represents emissions for the highest knee density in the study

geographic extent of a species or community type, and (3) an accurate quantification of the total release of methane based upon the distribution range of each species and their corresponding flux values. At the site level, much of the work that would be required to more accurately measure plant-atmosphere flux in wetlands would be labor intensive. Therefore, the application of micrometeorological techniques for measuring ecosystem-level flux could be a more feasible way to address some of these issues across a larger footprint. However, the use of large-scale techniques does not provide the finer scale resolution required to determine (1) the relative contribution of soil-atmosphere, water-atmosphere, and plant-atmosphere methane flux in a wetland system or (2) controls on plant-atmosphere methane flux. Therefore, the use of micrometeorological techniques should be coupled with bottom-up measurements of the individual components (e.g. soil/water/plant-atmosphere methane flux) to further resolve the uncertainties mentioned above.

With the variety of factors that appear to impact plant flux, methodological differences in both the scale of measurements and the method of flux quantification (a source of bias), and the difficulty of estimating global species distributions, it is difficult to provide an accurate estimate of the relative contribution of herbaceous plants to the global methane budget.

However, it is clear that this source is a potentially important pathway for global methane flux from wetlands, and that studies of wetland methane flux solely at the soil-level may be missing an important pathway (ca. 28 to [90 %) of the total methane flux from wetland ecosystems. This omission introduces a major degree of uncertainty in the global estimation of methane emissions from wetlands, the dominant source of methane flux to the atmosphere worldwide and the dominant source of uncertainty from any emission category within the global methane budget (Kirschke et al. 2013). We suggest that a significant portion of this uncertainty is tied to the historic omission of the role of the herbaceous and woody plant pathways in methane flux from wetlands.

#### *Methane transport through woody plants*

Schütz et al. (1991) first proposed tree stems as a possible source of methane flux to the atmosphere in wetlands. This proposal was later confirmed in 1998 when Rusch and Rennenberg first identified woody plants as potential conduits for methane and nitrous oxide flux from soils. In this study, researchers raised commercially-purchased black alder [*Alnus glutinosa* (L.) Gaertn.] trees in pots in the field using soil that was transplanted from an alder swamp. After 1 year of

growth in the field, the trees were moved to the greenhouse where roots were fumigated with CH<sub>4</sub> and N<sub>2</sub>O. Trunk/stem emissions of CH<sub>4</sub> were measured using a static flux chamber and quantified by gas chromatography. Results showed that (1) stem methane efflux increased with methane concentrations in the roots and (2) that flooded soil conditions led to methane flux rates up to 3,750 μmol CH<sub>4</sub> m<sup>-2</sup>h<sup>-1</sup>. In addition, these flux rates were dependent on stem porosity and tree size. These results are especially important when considering the large number of tree species found in wetland habitats, suggesting that woody plants may be an important and overlooked source of methane emissions in wetlands.

Since the initial study above, there have been only a handful of subsequent studies to evaluate the role of woody plants in ecosystem methane flux. Two additional greenhouse studies (Garnet et al. 2005; Vann and Megonigal 2003) have investigated this pathway in another common forest species of wetlands/swamps, the bald cypress (*Taxodium* sp.). This species is well known for the growth of pneumatophores as an adaptation to anoxic conditions in flooded soils. Vann and Megonigal (2003) study found (1) an increase in whole-plant methane emissions in response to flooded soil conditions and (2) a correlation between methane efflux and photosynthesis. Garnet et al.'s (2005) study revealed a possible link between plant leaf-level physiological controls and methane emissions in commercially grown plants raised in a greenhouse. However, researchers did not address the importance of plant structural traits, especially those that can have a strong influence on internal gas diffusion, which ultimately control gas fluxes. Regardless, these greenhouse studies demonstrated the potential role of woody plants in methane efflux from soils, but it remains unclear how well the experimental design in these studies simulated field conditions as data represent two species that were obtained from a limited set of commercial lineages.

In order to bridge the gap between greenhouse and field measurements, recent studies have utilized mesocosm experiments in an attempt to more closely approximate field conditions. Rice et al. (2010) investigated methane flux in three common wetland species, *Fragaria latifolia*, *Populus trichocarpa*, and *Salix fluviatilis*, using a combination of whole-plant, flux chambers fitted with tedlar bags around branches to

confirm methane emission from plant biomass. Results from this experiment confirmed that woody plants are a source of methane flux to the atmosphere; however, the dominant pathway for methane emission (e.g. leaf vs. stem) was not clearly elucidated by these experimental results. Rice et al. (2010) used their atmospheric flux estimates to provide the first global estimate for methane flux from woody vegetation ( $60 \pm 20$  Tg CH<sub>4</sub> year<sup>-1</sup>), indicating that the woody plant pathway is important globally. However, emission rates were normalized using leaf area, which assumes stomatal control as the dominant pathway for methane flux to the atmosphere in woody plant species. Recent studies, such as those by Pangala et al. (2013, 2012), indicate that trunk and stem emissions may play a more important role than leaf emissions in some woody species, adding a source of uncertainty for the initial estimates (Rice et al. 2010). A second mesocosm study by Pangala et al. (2013) took a mechanistic approach to the woody plant pathway, seeking to determine controls on methane emission from *Alnus glutinosa* saplings. This study demonstrated that stem surfaces are a dominant pathway of methane emissions from *A. glutinosa* and that water table depth and stem lenticel density exert strong controls on methane flux values.

Several recent studies have addressed the role of woody plants in methane flux under field conditions in both temperate (Table 8) and tropical (Table 9) wetlands. Collectively, these studies demonstrate (1) that there are a broad range of woody plant species that are capable of conducting methane from wetland sediments to the atmosphere and (2) there are a variety of factors, from rhizosphere interactions, to plant structural traits, to abiotic controls, that impact the magnitude of methane flux from soils via this pathway. In temperate wetlands, existing data indicates that woody plants may be responsible for ca. 0–16 % of the total ecosystem methane flux (Table 8), while in tropical wetlands this contribution may be much higher, representing 62–81 % of total ecosystem level flux (Table 9, Pangala et al. 2012). In addition to tropical areas with permanently flooded soils, seasonal/ephemeral wetlands may also represent a source of methane flux via woody plants. These transient ecosystems are dominant seasonal landscape features in the tropics (Hess et al. 1995, 2003) and are known sources of methane emissions (Boon et al. 1997; Melack et al. 2004).

**Table 9** Woody plants as conduits for methane emissions in tropical wetlands

Study	Species	Structure	Factors that impact plant CH <sub>4</sub> flux	CH <sub>4</sub> emissions (Tg CH <sub>4</sub> km <sup>-2</sup> year <sup>-1</sup> )	Estimated contribution to ecosystem flux (If Known)	Upscaled CH <sub>4</sub> emissions (Tg CH <sub>4</sub> year <sup>-1</sup> )
Kreuzwieser et al. (2003)	<i>Avicennia marina</i> <sup>a</sup>	Prop root	Soil nutrient status, substrate availability	$2.3 \times 10^{-8}$ <sup>b</sup>	N/A	N/A
Purvaja et al. (2004)	<i>Avicennia marina</i> <sup>a</sup>	Pneumatophore	Number of pneumatophores, water level, season	– <sup>c</sup>	N/A	$1 \times 10^{-11}$
Pangala et al. (2012)	<i>Diospyros bantamensis</i> <i>Elaeocarpus mastersii</i> <i>Litsea elliptica</i> <i>Mesua</i> sp.1 <i>Shorea balangeran</i> <i>Tristaniaopsis</i> sp. 2 <i>Xylocarpus fusca</i>	Stem	Stem diameter, wood density, porewater methane concentration	$1.4 \times 10^{-7}$ – $1.7 \times 10^{-6}$	62–81 %	0.2–1.8

Field emission rates are taken from each study and upscaled (when possible) using the global area for tropical forested wetlands as reported in Matthews and Fung (1987)

<sup>a</sup> Globally, mangrove forests represent 0.7 % of the global tropical forest area (Giri et al. 2011) and have been estimated to contribute 1.95 Tg CH<sub>4</sub> year<sup>-1</sup> to the atmosphere (Chauhan et al. 2008)

<sup>b</sup> CH<sub>4</sub> emissions were measured as a function of pneumatophore surface area, therefore this value cannot be upscaled to a global emission

<sup>c</sup> Actual flux values are not reported precisely enough to calculate these emissions (see Fig. 2 in reference); however, the authors report a yearly CH<sub>4</sub> flux of  $1 \times 10^{-11}$  Tg CH<sub>4</sub> year<sup>-1</sup> from monthly average values from sites with intermediate salinity

Acknowledging the limitations of current data, we made a first attempt at estimating the contribution of woody plants to global methane emissions (Fig. 2) using data obtained from field measurements. To estimate the contribution of woody plants in temperate (Table 8) and tropical (Table 9) wetlands, we up-scaled field emission rates from each study (when possible) using the global area for temperate and tropical forested wetlands respectively as reported in Matthews and Fung (1987). These calculations indicate a maximum contribution to the global annual flux of methane of 0.2 Tg CH<sub>4</sub> year<sup>-1</sup> from temperate forested wetlands and 1.8 Tg CH<sub>4</sub> year<sup>-1</sup> from tropical forested wetlands, or ca. 0.2 % of the global annual methane flux. Our preliminary estimates are based on two core assumptions that are unlikely to be met: that the flux from woody plants is constant both

inter- and intra-specifically and spatially and temporally. For the purpose of this review, a range in estimating the contribution of the woody plant pathway to methane flux to the atmosphere, will be presented, one that is our conservative estimate calculated from published field values compared to a more liberal estimate from mesocosm experiments (Rice et al. 2010). Even though there is a large degree of uncertainty in these estimated values, it is clear that woody plants likely play a significant role in methane flux from wetlands globally. Thus, studies that ignore the role of woody species in methane flux from wetland ecosystems probably underestimate source-strength at the site level, especially in the tropics where woody plants pathway may represent up to 81 % of the total ecosystem level methane flux (Pangala et al. 2012).

**Table 10** The impact of clipping vegetation, an artificial manipulation resembling the effect of herbivory, on methane flux from soil–plant systems

Vegetation clipped above water level		Vegetation clipped below water level
+	-	-
Schimel (1995)	Schimel (1995)	Ding et al. (2005)
Arctic Tundra	Arctic Tundra	Temperate Mire
Kelker and Chanton (1997)	Sanhueza and Donoso (2006)	Cheng et al. (2007)
Boreal Fen	Tropical Savannah	Experimental Mesocosms
	Cheng et al. (2007)	
	Experimental Mesocosms	

+, indicates that clipping resulted in an increase in methane flux from the soil–plant system; -, Indicates that clipping resulted in a decrease in methane flux from the soil–plant system

### Herbivory and methane transport through herbaceous and woody plants

An emerging viewpoint regarding the role of the plants in wetland methane emissions is the influence of herbivory on methane fluxes. Several studies have evaluated the potential impact of herbivory on methane emissions from herbaceous plant species using artificial manipulation of vegetation (e.g. clipping) in a variety of environments (Table 10). These clipping experiments suggested a dependence on multiple variables, including where the vegetation is severed (e.g. above or below the water level), the plant species studied (Cheng et al. 2007; Ding et al. 2005), and a host of abiotic environmental factors. At present, there are only two studies that have addressed the impact of herbivory on herbaceous plant methane fluxes under natural field conditions (Bodelier et al. 2006; Dingemans et al. 2011). Bodelier et al.'s study reported that soil bioturbation, as a result of foraging activity by swans feeding on *Potamogeton pectinatus* L. (fennel pondweed) tubers, had both direct and indirect impacts on methane flux, resulting likely in an attenuation of methane emissions from the soil. In a more recent study, Dingemans et al. (2011) indicate that shoot clipping by grazing geese increased plot-level methane flux approximately fivefold when compared to control plots without grazing. This increase in flux

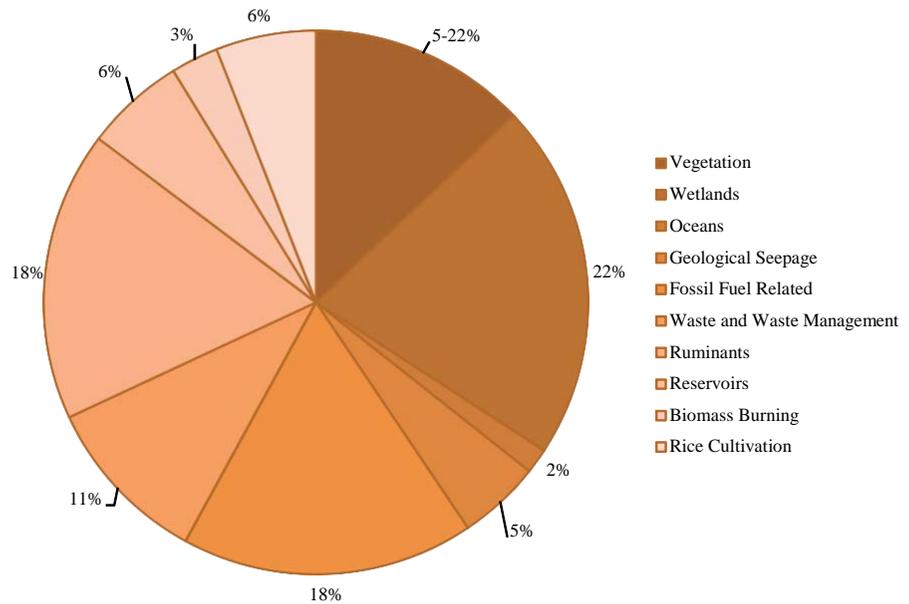
could result from a decreased resistance to methane diffusion (as a result of shoot clipping), or possibly as a result of Venturi-induced pressure flows in the clipped stems (Armstrong et al. 1992, 1996). In addition, it is unknown how browsing activities by herbivores may impact methane emissions from woody plant tissue (discussed below).

Browsing represents a specialized subset of herbivory in which animals obtain nutrition from grasses, as well as leaves, stems, and bark. To our knowledge, the impact of browsing on vegetation has not been studied with respect to the global methane budget. Nevertheless, there are several possible links between this form of herbivory and methane flux from vegetation. First, as with herbivory, browsing activity could result in an increase in methane flux from

vegetation as plant tissue is severed. This release of methane could occur as a result of a decrease in gas diffusion resistance, a release of the build-up of the partial pressure of methane in plant adaptations to waterlogged conditions (as suggested by Kelker and Chanton 1997), or as a result of Venturi-induced pressure flow (Armstrong et al. 1992, 1996) in clipped vegetation. Currently, the impact of severed vegetation due to browsing has not been evaluated, although browsing simulation experiments, similar to those described in McLaren (1996), would be useful to provide preliminary evidence to support or refute this proposed pathway of methane flux to the atmosphere.

The activity of wood-boring insects represents an additional dynamic interaction that could influence the atmospheric flux of methane from vegetation in both positive and negative ways. Wood-boring insects can colonize healthy trees, but are often attracted to weakened, stressed, or dead vegetation (Drees et al. 1994). As the larvae of these insects tunnel their way through the protective outer layers of a tree to reach the sapwood, they leave an intricate network of passages that can (1) increase the porosity of wood and (2) provide channels for gas exchange that may also promote pathogenic infection of both living (e.g. sapwood) and non-living (e.g. heartwood) tissue by bypassing structural defenses. As a result, an increase in the incidence of heartwood rot may occur. If a tree is already infected by the causative agents of heartwood rot, holes produced by wood-boring insects could lead to the efflux of methane from anaerobic microsites within the tree. After this pressure-induced blow out, the increase in wood porosity would also allow oxygen

Fig. 3 Global methane sources as a percent of the total methane budget of 645 Tg CH<sub>4</sub> year<sup>-1</sup> (Schlesinger and Bernhardt 2013). Vegetation emissions are taken from this study; all other categories are as presented by Schlesinger and Bernhardt (2013)



to penetrate deeper into the core, decreasing the potential for further methane production. Wood-boring insects are also known to colonize dead vegetation (Zhong and Schowalter 1989), in which case an increase in the porosity of wood would potentially result to similar effects as those described above. Although the scenarios described here are speculative in nature, it is worthwhile to point out these potential interactions between vegetation and woody plant herbivores that could impact the annual flux of methane to the atmosphere.

## Conclusions

As estimated in this literature synthesis, plant-based methane emissions, represent a source of 32–143 Tg CH<sub>4</sub> year<sup>-1</sup>, roughly 5–22 % of the total global methane budget (Figs. 2, 3). Direct emissions of methane via the aerobic methane production pathway account for ca. 25–42 % of plant-based emissions, with indirect pathways representing ca. 58–75 % of the total contribution of vegetative fluxes. There is a large degree of uncertainty in these estimates, primarily because historically recognized plant-based pathways have received little attention. In addition, several of the pathways discussed herein (e.g. aerobic methane production, heartwood rot, and the role of woody plants in methane flux) have only recently been recognized by researchers. However, if the

greatest values of these estimates are accurate, vegetation would match wetlands as the dominant source of methane flux to the atmosphere from natural systems (Fig. 3) and provide a compelling argument for the re-introduction of vegetation as a distinct category of natural methane emissions in the global methane budget.

The most recent global methane budget published was constructed in a review by Kirschke et al. (2013) that estimated the global methane budget over the past three decades by comparing top-down and bottom-up approaches and providing estimates for uncertainty in each emission category. Vegetation was not included as distinct categories in this review, but sources associated with vegetation (e.g. natural wetlands and other natural sources) were included. For these sources, the agreement between top-down and bottom-up estimates was medium to low, partially due to the limited number of studies available to make comparisons and draw conclusions. However, the values associated with methane flux from natural wetlands and other natural sources exhibited a high degree of uncertainty, 50 and 100 % for natural wetlands and other natural sources, respectively. Anthropogenic sources were estimated with much higher confidence and a lower degree of uncertainty. In the 2000<sup>s</sup>, Kirschke et al. estimated a global methane source strength of 548 (range 526–569) Tg CH<sub>4</sub> year<sup>-1</sup> via a top-down approach. The low and high end of this estimate create a range of 43 Tg CH<sub>4</sub>

year<sup>-1</sup>, which nicely matches other studies which indicate that the global methane budget can accommodate an additional source(s) in the range of 50–100 Tg CH<sub>4</sub> year<sup>-1</sup> (Frankenberg et al. 2005; Keppler et al. 2009). The values for plant-based emissions estimated in the present review fall within the same order of magnitude as this range. Therefore, research in this area appears to be an important component for closing the global methane budget and will clarify whether the contribution of vegetation-based emissions of methane is closer to 50 or 100 Tg CH<sub>4</sub> year<sup>-1</sup>.

Over the past 30 years, the annual flux of methane to the atmosphere has varied considerably, demonstrating significant interannual variations (Dlugokencky et al. 2011; Kirschke et al. 2013). Fluctuation in the methane growth rate could be linked to changes in the strength of known and/or well quantified sources or sinks, or to changes in the strength of yet to be identified, or poorly quantified, sources or sinks such as vegetation. Although the estimates in this review have considerable uncertainty, they provide a first step towards the development of a more integrated view of the contribution of various natural sources to the annual atmospheric flux of this globally important GHG. Clearly, better elucidating the contribution of plant-based pathways to the global methane budget represents a critical area for future research, where primary emphasis should be placed on providing better resolution regarding the role of plant-based methane sources such as aerobic methane production, coarse woody debris and litter (e.g. dead vegetation), and methane transport through herbaceous and woody plants that are both highly uncertain and likely to exercise a significant contribution to the annual flux of methane to the atmosphere.

This literature synthesis provides a first attempt, albeit uncertain, to more comprehensively estimate the role of vegetation in the global methane budget (Figs. 2, 3). Future studies should focus on resolving the magnitude of emissions pathways discussed herein to further increase the accuracy of these preliminary estimates. In addition, the role of the vegetative pathway in the flux of other globally important trace GHGs is a critical line of future study (Pihlatie et al. 2005). For example, nitrous oxide emissions can be facilitated by grasses (Mosier et al. 1990) and woody plants (Kreuzwieser et al. 2003; Pihlatie et al. 2005; Rusch and Rennenberg 1998). Overall, further elucidating the role of vegetation-based pathways of trace GHG fluxes of all types will add a degree resolution to existing climate

models that often include biogeochemical processes (Bonan 2008) at a rudimentary level, but largely ignore the role of vegetation (Pangala et al. 2012). In turn, future models will more accurately represent biogeochemical cycling (Kirschke et al. 2013), theoretically increasing our ability to predict future climate scenarios.

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