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Emissions of anaerobically produced methane by trees

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[1] Recent studies indicate that plants may be a previously overlooked but significant source of atmospheric CH₄, though there is considerable disagreement on the mechanism of production. Our work sought to verify that woody deciduous trees grown under inundated conditions had the capacity for transporting CH₄ from an anaerobic subsurface to the atmosphere and to consider if such a source could be important globally. Here, we report results from a greenhouse mesocosm study that indicate significant emissions of anaerobically produced CH₄ transmitted to the atmosphere through broadleaf riparian tree species grown under flooded conditions. Using a leaf area normalized mean emission rate ($0.7 \pm 0.3 \mu\text{g cm}^{-2} \text{hr}^{-1}$), results were scaled globally for flooded forest regions and estimated to be $60 \pm 20 \text{ Tg year}^{-1}$, $\sim 10\%$ of the global CH₄ source. The carbon isotopic composition of CH₄ emitted was found to be significantly enriched compared with expectations ($\delta^{13}\text{C} \sim -54\%$) and provided an important isotopic constraint on the global source which coincides with the mean of the globally scaled greenhouse-based estimate. **Citation:** Rice, A. L., C. L. Butenhoff, M. J. Shearer, D. Teama, T. N. Rosenstiel, and M. A. K. Khalil (2010), Emissions of anaerobically produced methane by trees, *Geophys. Res. Lett.*, 37, L03807, doi:10.1029/2009GL041565.

1. Introduction

[2] Methane (CH₄) is an important radiative and chemically reactive trace gas that has more than doubled in concentration in the Earth's atmosphere over the past 200 years as a result of mankind's activities, primarily rice cultivation, ruminant animal husbandry, biomass burning, and fossil fuel usage [Rasmussen and Khalil, 1984]. Despite more than two decades of research, there are considerable uncertainties in the magnitudes and trends of natural and anthropogenic sources of methane to the atmosphere. Renewed interest in atmospheric CH₄ has recently resulted from observations of larger than expected emissions in tropical forests and studies that upset the conventional wisdom by proposing that plants could produce CH₄ in oxic environments [do Carmo *et al.*, 2006; Frankenberg *et al.*, 2008; Keppler *et al.*, 2006; Miller *et al.*, 2007; Nisbet *et al.*, 2009; Vigano *et al.*, 2008; Wang *et al.*, 2008]. Both the mechanism and the magnitude of source estimations have been disputed in the literature [Butenhoff and Khalil, 2007; Dueck *et al.*, 2007; Kirschbaum and Walcroft, 2008; Nisbet *et al.*, 2009].

[3] Though there has been significant research on emissions of CH₄ from natural wetlands, early work concluded that the majority of emissions in natural wetland systems are mediated by aquatic macrophytes and through ebullition [Cicerone and Oremland, 1988]. Several more recent studies have indicated that woody tree systems could present a mechanism for transporting CH₄ to the atmosphere from an anaerobic root zone under inundated conditions or, potentially, bypassing an aerobic oxidation layer that lies between deep roots and the atmosphere [Garnet *et al.*, 2005; Megonigal and Guenther, 2008; Rusch and Rennenberg, 1998; Terazawa *et al.*, 2007]. These tree emissions could particularly enhance CH₄ flux in tropical regions that experience regular seasonal inundation.

[4] In this paper, we present a study of emissions of anaerobically produced CH₄ from three deciduous riparian tree species and a global upscaling of results to determine the potential of tree emissions to impact the global CH₄ budget.

2. Experimental Methods

[5] Three woody riparian tree species were grown in small mesocosms and studied in a research greenhouse: ash (*Fraxinus latifolia*), cottonwood (*Populus trichocarpa*), and willow (*Salix fluviatillis*). These experiments were conducted adjacent to ongoing mesocosm experiments with a rice cultivar reference (*Oryza sativa* L. 'M-103') and unplanted control plots. Plants were grown in triplicate in a sandy loam (71.8% sand, 25.6% silt, 2.6% clay and 3.23% organic matter, 1.6% C, 0.12% N, 0.01% S, 126 ppm P, 101 ppm K) contained in fiberglass tubs (61 × 48 × 36 cm). Soil organic content was enhanced through the addition of rice straw equivalent to 3 tons per hectare to stimulate below ground anaerobic methane production. All plants and controls were grown under fully inundated conditions except during one mid-season drainage.

[6] Static flux samples were drawn from translucent chambers enclosing each plant and its air-water interface approximately two times weekly between July and October primarily during morning hours (9–11 AM local time). Chambers were reinforced translucent polyethylene sheeting on a frame of PVC pipe (66 × 51 × 90 cm), with a gas sampling port and a 12 Volt battery powered fan that stirred the air inside the chamber during sampling. Tedlar bag branch enclosures were also used to confirm CH₄ emissions through the tree biomass. Leaf area and above ground biomass were determined destructively at the end of the experiment.

[7] Over the course of the study, approximately 60 fluxes were measured from each species. Samples from inside the chambers were removed at 10 minute intervals for 30 minutes and CH₄ concentrations were measured on a Agilent model

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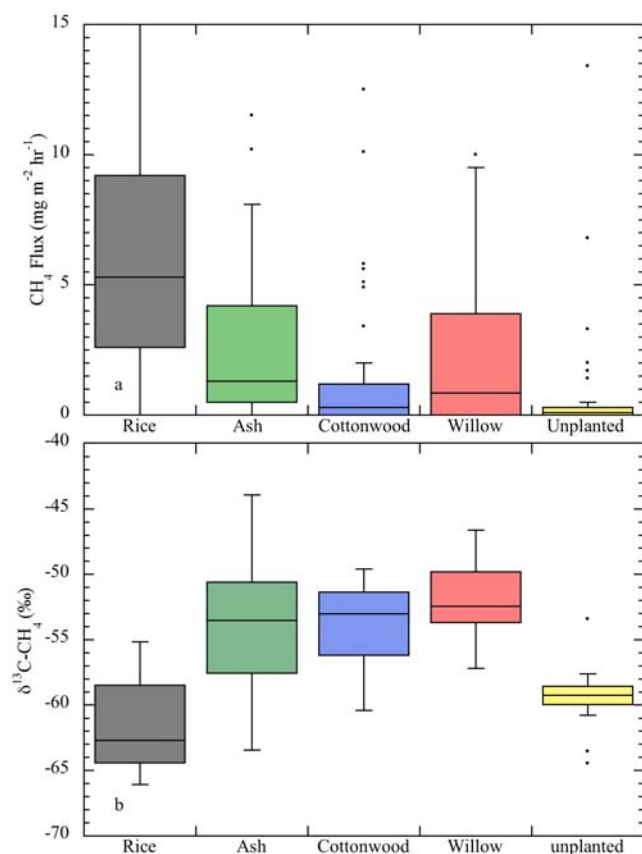


Figure 1. Box and whisker plots showing the distribution of (a) methane fluxes and (b) the carbon isotopic composition of emitted CH₄ measured for rice (black), ash (green), cottonwood (blue), willow (red), and control plots (yellow).

6890 gas chromatograph with a flame ionization detector (GC-FID) [Khalil *et al.*, 1998]. Net CH₄ flux is determined by linear regression of the change in concentration with time ($\Delta\text{CH}_4/\Delta t$) and expressed m^{-2} of water-atmosphere interface [Khalil *et al.*, 1998]. Analyses were filtered for strong ebullition events and operator error, identified by their non-linearity ($r^2 < 0.9$, $\sim 10\%$ of data). Belowground porewater samples at 5, 10, 15, and 20 cm depths were collected bi-weekly and CH₄ concentrations were measured by extracting samples in ultra-high purity N₂, and analyzing them *via* GC-FID.

[8] During a sampling intensive period, flux ($t = 30$ min) and porewater samples were drawn once per week and measured for the carbon isotopic composition ($\delta^{13}\text{C}$) of CH₄. The $\delta^{13}\text{C}$ of CH₄ was determined by continuous-flow gas chromatography-isotope ratio mass spectrometry on a Thermo Scientific Delta V Advantage IRMS using a method previously described [Rice *et al.*, 2001]. Values of $\delta^{13}\text{C}$ of CH₄ were measured relative to a calibrated CO₂ reference gas and are reported relative to the VPDB scale using the delta (δ) notation such that $\delta^{13}\text{C} = [({}^{13}\text{C}/{}^{12}\text{C}_{\text{sample}}/{}^{13}\text{C}/\text{C}_{\text{VPDB}}) - 1] \times 1000$ as established by the International Atomic Energy Agency (IAEA) in Vienna, Austria [Coplen, 1995]. All samples were corrected for the ambient atmosphere in the greenhouse (~ 2 ppm CH₄), collected at initial chamber placement ($t = 0$ min).

[9] For purposes of global upscaling of results, inundated forests were identified using the Global Land Cover 2000 product with a spatial resolution of ~ 1 km [Bartholomé *et al.*, 2002]. Land cover classification included regularly and permanently flooded forests. We assumed that tropical riparian forests were flooded annually for five months which is consistent with the duration of the wet season and measurements of tropical inundation using satellite techniques [Eva *et al.*, 2002]. We assumed that mangroves and coastal forests were flooded permanently as inundation here is primarily determined by sea level [Eva *et al.*, 2002]. Tundra shrubland was considered waterlogged over the northern hemisphere summer. The canopy leaf area was derived from the Collection 5 MODIS Leaf Area Index (LAI) product at 1 km resolution [Yang *et al.*, 2006]. The monthly averages from 2000 to 2001 were used. Emissions were calculated for each grid cell i and month m by:

$$E_{i,m} = F \times \text{LA}_{i,m} \times D_{i,m} \times I_i$$

where F is the mean methane flux, LA is the leaf area, D is the number of daylight hours, and I is either 0 or 1, depending on whether the pixel is inundated during the current month. Monthly emissions were summed to annual.

3. Results and Discussion

[10] All three riparian tree species showed average flux of CH₄ greater than control, with mean emission rates of 2.6, 1.5, and 3.2 $\text{mg m}^{-2} \text{hr}^{-1}$ for ash, cottonwood, willow and 0.9 $\text{mg m}^{-2} \text{hr}^{-1}$ for control plots (Figure 1a). All tree plots produced lower fluxes than rice which averaged 6.6 $\text{mg m}^{-2} \text{hr}^{-1}$. The effect of daily temperature variations was determined to have only a small impact on CH₄ flux (temperature range 19–36°C, $r^2 = 0.14$) and no clear seasonal behavior in CH₄ flux was observed in tree fluxes [Khalil *et al.*, 1998].

[11] The flux distributions were fit using gamma distributions and the method of moments was applied to assess the variability of each species [Rice, 2007]. Emissions from ash, cottonwood, and willow were higher than control plots at high levels of significance (p -value < 0.01 , two-sided t -test). For purposes of calculating CH₄ flux through the trees, the control plot distribution was subtracted from the aggregate tree distribution. Resulting data were then normalized to tree leaf area and the average tree CH₄ emission rate was calculated to be $0.7 \pm 0.3 \mu\text{g cm}^{-2} \text{hr}^{-1}$. This estimate is higher, but within collective error, than recent estimates of $\sim 0.5 \mu\text{g cm}^{-2} \text{hr}^{-1}$ from Bald Cypress (*Taxodium distichum*) [Garnet *et al.*, 2005].

[12] Tedlar bag branch enclosures revealed significant emission in all species, but concentrations in the bags were non-linear on short time scales and resulting quantitative flux estimates using this approach were problematic. The origin of this response is unknown, but its rapidity is suggestive of stomatal control of CH₄ conductance [Farquhar and Sharkey, 1982].

[13] The $\delta^{13}\text{C}$ of emitted CH₄ from chamber enclosure and bag samples are shown in Figure 1b. Rice and control plots had $\delta^{13}\text{C}$ values of $-62 \pm 3\text{‰}$ and $-59 \pm 2\text{‰}$ respectively for emitted CH₄ which is characteristic of rice agriculture and anaerobic wetland environments [Tyler *et al.*, 1997]. All three tree species emitted CH₄ enriched in ^{13}C relative to rice and control plots with $\delta^{13}\text{C}$ values of $-54 \pm$

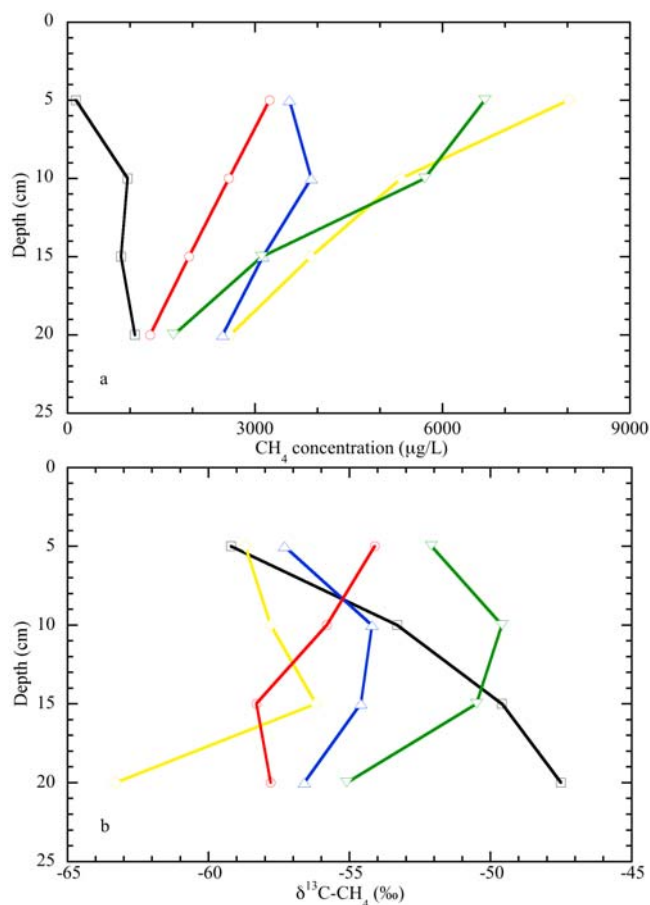


Figure 2. (a) Belowground concentrations and (b) carbon isotopic composition of CH₄ measured for rice (black squares), ash (green inverted triangles), cottonwood (blue triangles), willow (red circles), and control plots (yellow diamonds).

5‰ from ash, -54 ± 3 ‰ from cottonwood, and -52 ± 3 ‰ from willow. Though differences between tree species were not found, the difference between δ¹³C from aggregate tree data (-54 ± 4 ‰) and rice plots (and controls) is significant at high levels of confidence (p-value < 0.01).

[14] The ~8‰ δ¹³C difference between rice and tree emitted CH₄ can result from differences in CH₄ production, gas transport, or oxidation. Though recent photosynthates can be an important source of carbon for methanogenesis, all plant species used in this work were C3 in photosynthetic pathway and likely have similar isotopic signatures in their organic matter (δ¹³C ~ -25‰) [King and Reeburgh, 2002]. Active rhizodeposition of organic acids fixed via the enzyme PEP-carboxylase have been observed in some systems, including anaerobic root zones [Johnson et al., 1996; Jones, 1998]. The enriched δ¹³C signature observed could indicate this form of root exudates driving methanogenesis in the rhizosphere. Differences in carbon isotope fractionation factors with different methanogenic community structure could also potentially explain the observed 8‰ difference between rice and tree emitted CH₄ [Chidthaisong et al., 2002].

[15] Alternatively, isotopic fractionation occurs in plants due to diffusive and effusive transport processes which are mass dependent, the magnitude of which depends largely on

pore size [Chanton, 2005]. If responsible, the observed 8‰ shift in δ¹³C would suggest that CH₄ transport in tree tissue is more convective in nature, which is at odds with measured fluxes which indicate a slower turnover time. CH₄ oxidation in the rhizosphere, upper layers of soil, and potentially on the surfaces of the plant stems and leaves will enrich the isotopic composition of emitted CH₄ due to a significant kinetic isotope effect ($k_{12C}/k_{13C} \sim 1.025$) in aerobic bacterial CH₄ oxidation [Raghoebarsing et al., 2005; Tyler et al., 1994]. Under this mechanism, measurements of δ¹³C above and below ground indicate that ~20% of CH₄ was oxidized in rice plots whereas 50–70% was oxidized in tree plots [Tyler et al., 1997]. Finally, it is noteworthy that the average δ¹³C of -54‰ emitted by trees is close to the δ¹³C of CH₄ produced in aerobic environments of recent chamber studies involving whole C3 plants (-52‰) [Keppler et al., 2006]. Thus, in future field studies it may not be possible to distinguish between aerobic and anaerobic mechanisms of CH₄ production based on the δ¹³C of emitted CH₄ alone.

[16] Porewater CH₄ concentrations were found to be significantly lower in rice plots (mean 760 μg/L) than in either tree (mean 1570 μg/L) or control (mean 4960 μg/L) plots (Figure 2a) because of enhanced CH₄ transport from the rhizosphere to the atmosphere. In fact, average belowground CH₄ concentration was found to be inversely related to aboveground flux ($r^2 = 0.94$), supporting the assertion that transport was a controlling mechanism of belowground CH₄ concentrations. The isotopic composition of belowground CH₄ was found to be highly variable (δ¹³C -63 to -48‰, Figure 2b) with no clear differences between species. The absence of a large δ¹³C difference between rice and tree species belowground tends to favor the oxidative hypothesis for explaining the 8‰ difference in δ¹³C of emitted CH₄. However, given the variability in belowground δ¹³C and CH₄ concentration, more measurements will be necessary to verify this result.

[17] To determine if tree emissions have the potential to impact the global CH₄ budget, emissions were scaled using mean leaf area emission rate ($0.7 \pm 0.3 \mu\text{g cm}^{-2} \text{hr}^{-1}$) across all broadleaf tree species in flooded environments from the Global Land Cover 2000 data set. The leaf area of the vegetation canopy from MODIS LAI in these regions during times of inundation was then used to scale the measured emissions. With this technique, global CH₄ emissions were estimated at $60 \pm 20 \text{ Tg year}^{-1}$. Delineated spatially (Figure 3), the majority of CH₄ emissions (40 Tg) were in the tropical Amazon region of South America, the African Congo, and Indonesia. Significant emissions were also found in the northern mid to high-latitude regions of Eurasia (20 Tg). We note that these estimates assume belowground CH₄ concentrations similar to those in the greenhouse experiments, concentrations that may be higher than in natural settings by the amendment of organic matter [Khalil et al., 2008].

[18] If this source of CH₄ is significant on the global scale as our bottom up approach suggests, it will have important implications for the pre-anthropogenic CH₄ budget. Recently, preindustrial atmospheric CH₄ was observed to be unexpectedly ¹³C enriched based on an ice core record during the period 0–1300 AD (δ¹³C ~ -47.5‰), which may have resulted from enhanced biomass burning and a higher than previously considered geological CH₄ source [Etioppe et

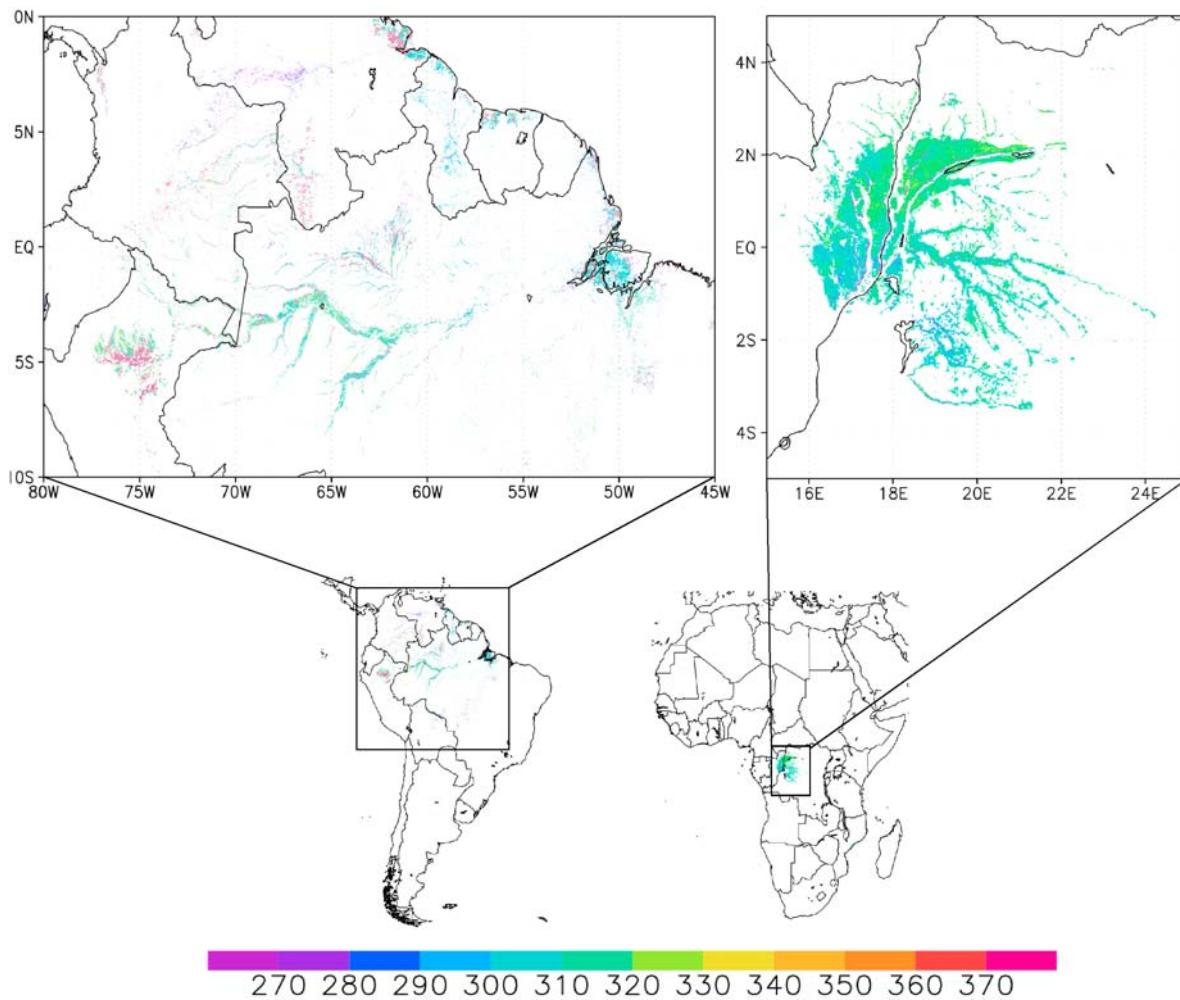


Figure 3. Emissions of CH_4 from trees scaled globally using the Collection 5 MODIS Leaf Area Index and the Global Land Cover 2000 product. Shown are CH_4 emissions from the tropical Amazon region of South America and the Congo Basin in Africa. Units are tons of CH_4 per year.

al., 2008; Ferretti *et al.*, 2005]. This compares with observations from ~ 1700 AD that are depleted in ^{13}C relative to modern CH_4 ($\delta^{13}\text{C} \sim -49\%$). Because trees appear to emit CH_4 enriched in $\delta^{13}\text{C}$ by $\sim 8\%$ compared with conventional wetland sources, this biogenic source can provide an alternative mechanism to shift the $\delta^{13}\text{C}$ of biogenic CH_4 . To better constrain the tree source we employed a box model of the atmosphere that includes categories for biogenic, biomass burning, and geological sources for the preindustrial period 0–1700 AD (Table 1). The atmospheric kinetic isotope effect was estimated at $-6 \pm 1\%$ [$(k_{13\text{C}}/k_{12\text{C}} - 1) \times 1000$] and assumed to be constant [Lassey *et al.*, 2007]. With CH_4 sources kept to lower estimates and source $\delta^{13}\text{C}$ values from the literature, we estimate the maximum global tree source strength to be 60 Tg (Table 1) [Houweling *et al.*, 2000; Quay *et al.*, 1999]. This global constraint coincides with the mean of bottom-up estimates of 60 ± 20 Tg year $^{-1}$.

4. Conclusions

[19] These results suggest that woody trees could present a sizeable global source of CH_4 to the budget, plausibly as

large as 60 Tg yr $^{-1}$, and may help explain observed tropical enhancements in atmospheric CH_4 without a large aerobic plant source. Though we have confirmed the potential of such a source in our greenhouse mesocosm study and identified key regions that may represent significant sources of tree CH_4 emissions, field studies will be needed to confirm the magnitude and spatial distribution of this CH_4

Table 1. Global Emissions Strengths and Isotopic Compositions Used in the Box Model

	0–1000 AD	
	Strength (Tg yr $^{-1}$) ^a	$\delta^{13}\text{C}\text{-CH}_4$ (‰) ^a
Wetland (conventional)	83	-60
Trees	60	-54
Termites	10	-60
Ocean	5	-40
Geological	5	-40
Biomass Burning	23	-20
Rice agriculture	5	-60
Ruminant Animals	20	-60
Total	211	-53

^aBase budget for 0–1000 AD and isotopic signatures from previous work [Houweling *et al.*, 2000; Quay *et al.*, 1999].

source. Laboratory, greenhouse, and field studies across a wide variety of tree species (particularly tropical species) and grown in differing soil and water conditions would also be particularly useful to better characterize the variability in CH₄ emission rates. There are also several unanswered mechanistic issues including the pathway of conductance through the plant tissue to the atmosphere and the reason for the difference in $\delta^{13}\text{C}$ of emitted CH₄ between woody trees and herbaceous aquatic macrophytes.

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References

- Bartholomé, E., A. S. Belward, F. Achard, S. Bartalev, C. Carmona-Moreno, H. Eva, S. Fritz, J. M. Gregoire, P. Mayaux, and H.-J. Stibig (2002), GLC 2000: Global Land Cover mapping for the year 2000, *Rep. EUR 20524 EN*, Eur. Comm., Luxembourg.
- Butenhoff, C. L., and M. A. K. Khalil (2007), Global methane emissions from terrestrial plants, *Environ. Sci. Technol.*, *41*(11), 4032–4037, doi:10.1021/es062404i.
- Chanton, J. P. (2005), The effect of gas transport on the isotope signature of methane in wetlands, *Org. Geochem.*, *36*(5), 753–768, doi:10.1016/j.orggeochem.2004.10.007.
- Chidthaisong, A., et al. (2002), A comparison of isotope fractionation of carbon and hydrogen from paddy field rice roots and soil bacterial enrichments during CO₂/H₂ methanogenesis, *Geochim. Cosmochim. Acta*, *66*(6), 983–995, doi:10.1016/S0016-7037(01)00812-2.
- Cicerone, R. J., and R. S. Oremland (1988), Biogeochemical aspects of atmospheric methane, *Global Biogeochem. Cycles*, *2*(4), 299–327, doi:10.1029/GB002i004p00299.
- Coplen, T. B. (1995), Reporting of stable carbon, hydrogen, and oxygen isotopic abundances, in *Reference and Inter-comparison Materials for Light Elements*, *Rep. TECDOC-825*, pp. 31–34, Int. At. Energy Agency, Vienna.
- do Carmo, J. B., M. Keller, J. D. Dias, P. B. de Camargo, and P. Crill (2006), A source of methane from upland forests in the Brazilian Amazon, *Geophys. Res. Lett.*, *33*, L04809, doi:10.1029/2005GL025436.
- Dueck, T. A., et al. (2007), No evidence for substantial aerobic methane emission by terrestrial plants: A C-13-labelling approach, *New Phytol.*, *175*(1), 29–35, doi:10.1111/j.1469-8137.2007.02103.x.
- Etiopie, G., K. R. Lassey, R. W. Klusman, and E. Boschi (2008), Reappraisal of the fossil methane budget and related emission from geologic sources, *Geophys. Res. Lett.*, *35*, L09307, doi:10.1029/2008GL033623.
- Eva, H. D., et al. (2002), A vegetation map of South America, *Map EUR 20159*, Eur. Comm., Luxembourg.
- Farquhar, G. D., and T. D. Sharkey (1982), Stomatal conductance and photosynthesis, *Annu. Rev. Plant Physiol.*, *33*, 317–345, doi:10.1146/annurev.pp.33.060182.001533.
- Ferretti, D. F., et al. (2005), Unexpected changes to the global methane budget over the past 2000 years, *Science*, *309*(5741), 1714–1717, doi:10.1126/science.1115193.
- Frankenberg, C., P. Bergamaschi, A. Butz, S. Houweling, J. F. Meirink, J. Notholt, A. K. Petersen, H. Schrijver, T. Warneke, and I. Aben (2008), Tropical methane emissions: A revised view from SCIAMACHY onboard ENVISAT, *Geophys. Res. Lett.*, *35*, L15811, doi:10.1029/2008GL034300.
- Garnet, K. N., et al. (2005), Physiological control of leaf methane emission from wetland plants, *Aquat. Bot.*, *81*(2), 141–155, doi:10.1016/j.aquabot.2004.10.003.
- Houweling, S., F. Dentener, and J. Lelieveld (2000), Simulation of pre-industrial atmospheric methane to constrain the global source strength of natural wetlands, *J. Geophys. Res.*, *105*, 17,243–17,255, doi:10.1029/2000JD900193.
- Johnson, J. F., et al. (1996), Phosphorus deficiency in *Lupinus albus* (altered lateral root development and enhanced expression of phosphoenolpyruvate carboxylase), *Plant Physiol.*, *112*, 31–41, doi:10.1104/pp.112.1.31.
- Jones, D. L. (1998), Organic acids in the rhizosphere—A critical review, *Plant Soil*, *205*, 25–44, doi:10.1023/A:1004356007312.
- Keppler, F., et al. (2006), Methane emissions from terrestrial plants under aerobic conditions, *Nature*, *439*, 187–191, doi:10.1038/nature04420.
- Khalil, M. A. K., R. A. Rasmussen, and M. J. Shearer (1998), Flux measurements and sampling strategies: Applications to methane emissions from rice fields, *J. Geophys. Res.*, *103*(D19), 25,211–25,218, doi:10.1029/98JD00690.
- Khalil, M. A. K., M. J. Shearer, R. A. Rasmussen, C. Duan, and L. Ren (2008), Production, oxidation, and emissions of methane from rice fields in China, *J. Geophys. Res.*, *113*, G00A04, doi:10.1029/2007JG000461.
- King, J. Y., and W. S. Reeburgh (2002), A pulse-labeling experiment to determine the contribution of recent plant photosynthates to net methane emission in arctic wet sedge tundra, *Soil Biol. Biochem.*, *34*(2), 173–180, doi:10.1016/S0038-0717(01)00164-X.
- Kirschbaum, M. U. F., and A. Walcroft (2008), No detectable aerobic methane efflux from plant material, nor from adsorption/desorption processes, *Biogeosciences*, *5*(6), 1551–1558.
- Lassey, K. R., et al. (2007), Centennial evolution of the atmospheric methane budget: What do the carbon isotopes tell us?, *Atmos. Chem. Phys.*, *7*(8), 2119–2139.
- Megonigal, J. P., and A. B. Guenther (2008), Methane emissions from upland forest soils and vegetation, *Tree Physiol.*, *28*(4), 491–498.
- Miller, J. B., L. V. Gatti, M. T. S. d'Amelio, A. M. Crowell, E. J. Dlugokencky, P. Bakwin, P. Artaxo, and P. P. Tans (2007), Airborne measurements indicate large methane emissions from the eastern Amazon basin, *Geophys. Res. Lett.*, *34*, L10809, doi:10.1029/2006GL029213.
- Nisbet, R. E. R., et al. (2009), Emission of methane from plants, *Proc. R. Soc. B*, *276*(1660), 1347–1354, doi:10.1098/rspb.2008.1731.
- Quay, P., J. Stutsman, D. Wilbur, A. Snover, E. Dlugokencky, and T. Brown (1999), The isotopic composition of atmospheric methane, *Global Biogeochem. Cycles*, *13*(2), 445–461.
- Raghoebarsing, A. A., et al. (2005), Methanotrophic symbionts provide carbon for photosynthesis in peat bogs, *Nature*, *436*, 1153–1156, doi:10.1038/nature03802.
- Rasmussen, R. A., and M. A. K. Khalil (1984), Atmospheric methane in the recent and ancient atmospheres: Concentrations, trends, and interhemispheric gradient, *J. Geophys. Res.*, *89*, 11,599–11,605, doi:10.1029/JD089iD07p11599.
- Rice, J. (2007), *Mathematical Statistics and Data Analysis*, 3rd ed., Thomson, Brooks, and Cole, Belmont, Calif.
- Rice, A. L., et al. (2001), High-precision continuous-flow measurement of $\delta^{13}\text{C}$ and δD of atmospheric CH₄, *Anal. Chem.*, *73*(17), 4104–4110, doi:10.1021/ac0155106.
- Rusch, H., and H. Rennenberg (1998), Black alder (*Alnus glutinosa* (L.) Gaertn.) trees mediate methane and nitrous oxide emission from the soil to the atmosphere, *Plant Soil*, *201*(1), 1–7, doi:10.1023/A:1004331521059.
- Terazawa, K., et al. (2007), Methane emissions from stems of *Fraxinus mandshurica* var. *japonica* trees in a floodplain forest, *Soil Biol. Biochem.*, *39*(10), 2689–2692, doi:10.1016/j.soilbio.2007.05.013.
- Tyler, S. C., et al. (1994), $^{13}\text{C}/^{12}\text{C}$ fractionation of methane during oxidation in a temperate forested soil, *Geochim. Cosmochim. Acta*, *58*(6), 1625–1633, doi:10.1016/0016-7037(94)90564-9.
- Tyler, S. C., R. S. Bilek, R. L. Sass, and F. M. Fisher (1997), Methane oxidation and pathways of production in a Texas paddy field deduced from measurements of flux, $\delta^{13}\text{C}$, and δD of CH₄, *Global Biogeochem. Cycles*, *11*(3), 323–348.
- Vigano, L., et al. (2008), Effect of UV radiation and temperature on the emission of methane from plant biomass and structural components, *Biogeosci. Discuss.*, *5*, 243–270.
- Wang, Z. P., et al. (2008), Aerobic methane emission from plants in the Inner Mongolia steppe, *Environ. Sci. Technol.*, *42*(1), 62–68, doi:10.1021/es071224i.
- Yang, W., et al. (2006), Analysis of leaf area index products from combination of MODIS Terra and Aqua data, *Remote Sens. Environ.*, *104*, 297–312, doi:10.1016/j.rse.2006.04.016.

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