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Methane emissions from upland forest soils and vegetation

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Summary Most work on methane (CH_4) emissions from natural ecosystems has focused on wetlands because they are hotspots of CH_4 production. Less attention has been directed toward upland ecosystems that cover far larger areas, but are assumed to be too dry to emit CH_4. Here we review CH_4 production and emissions in upland ecosystems, with attention to the influence of plant physiology on these processes in forests. Upland ecosystems are normally net sinks for atmospheric CH_4 because rates of CH_4 consumption exceed CH_4 production. Production of CH_4 in upland soils occurs in microsites and may be common in upland forest soils. Some forests switch from being CH_4 sinks to CH_4 sources depending on soil water content. Plant physiology influences CH_4 cycling by modifying the availability of electron donors and acceptors in forest soils. Plants are the ultimate source of organic carbon (electron donor) that microbes process into CH_4. The availability of O_2 (electron acceptor) is sensitive to changes in soil water content, and therefore, to transpiration rates. Recently, abiotic production of CH_4 from aerobic plant tissue was proposed, but has not yet been verified with independent data. If confirmed, this new source is likely to be a minor term in the global CH_4 budget, but important to quantify for purposes of greenhouse gas accounting. A variety of observations suggest that our understanding of CH_4 sources in upland systems is incomplete, particularly in tropical forests which are stronger sources then expected.

Keywords: aerobic methane emission, forest methane production.

Introduction

The exchange of CO_2 between forested ecosystems and the atmosphere has received significant attention in recent years in the context of global carbon cycling. In contrast, the role of forests as sources or sinks of less abundant carbon trace gases such as methane (CH_4), methanol, and other volatile organic carbon compounds is relatively poorly understood. It is challenging to measure the atmospheric exchange of such gases because of low fluxes and high spatial variability, yet scaled over large areas the mass flux of these compounds is sufficient to influence atmospheric chemistry and climate. Methane is particularly noteworthy because it is an important greenhouse gas, contributing about 20% of current radiative forcing, and a key compound governing hydroxyl radical concentrations that regulate much atmospheric chemistry. This paper provides a brief review of recent evidence suggesting that our knowledge of CH_4 production in upland forests is insufficient to meet the demand for accurate accounting of radiatively active gas sources. It was motivated by the groundswell of interest that followed the first report of CH_4 production by aerobic plant tissue (Keppler et al. 2006). We begin with an overview of CH_4 cycling because the topic is unfamiliar to many tree physiologists.

Methane as a greenhouse gas

The balance between sources and sinks of CH_4 changed in the past century, resulting in an increase in atmospheric CH_4 of about 1.1 μl l^{-1} (ppmv), or 160%, since the 1850s. Atmospheric CH_4 concentrations are currently double the highest concentration recorded in a 420,000-year ice core (Petit et al. 1999). Global anthropogenic sources of CH_4 amount to 375 Tg $year^{-1}$ (Schlesinger et al. 1997). These include fossil-fuel-related industries (100 Tg $year^{-1}$), waste management (90 Tg $year^{-1}$), enteric fermentation (85 Tg $year^{-1}$), rice agriculture (60 Tg $year^{-1}$) and biomass burning (40 Tg $year^{-1}$). Of the natural sources, wetlands are 70% (160 Tg $year^{-1}$) of the total. Upland ecosystems are generally considered to be net sinks for CH_4, consumption by soils amounting to 30 Tg $year^{-1}$ or about 6% of the global sink (Schlesinger et al. 1997). Global CH_4 budgets generally estimate a missing source of about 10 Tg $year^{-1}$, which might be explained by unexpected emissions from upland ecosystems or adjustments to any of the known CH_4 sources and sinks. Keppler et al. (2006) estimated an aerobic plant source of 149 Tg $year^{-1}$ (mean estimate), which rivals all natural CH_4 sources and would force a reevaluation of the global CH_4 budget. Revised estimates of the proposed aerobic plant source are low enough to be accommodated within the uncertainty in the global CH_4 budget (e.g., Butenhoff and Khalil 2007).

Interest in CH_4 emissions as a cause of radiative climate forcing arises because, on a molar basis, CH_4 is 3–22 times stronger as a greenhouse gas than CO_2, depending on the timeframe considered. Methane concentrations are more re-

sponsive than CO_2 to changes in sources or sinks because of a far shorter atmospheric residence time (12 years versus > 100 years), inspiring recommendations that efforts to slow the pace of global warming should focus initially on abating CH_4 emissions (Hansen et al. 2000). For this reason, the Keppler et al. (2006) report of aerobic CH_4 emissions generated much public interest (Lowe 2006).

Overview of methane cycling

Our current understanding is that CH_4 is an end product of organic carbon degradation performed by a consortium of microbes in an O_2-free environment (Megonigal et al. 2004). After a series of hydrolytic and fermentation reactions that simplify complex organic matter, microorganisms within the domain Archaea—the methanogens—produce CH_4 as a respiratory end product of either H_2 oxidation coupled to CO_2 reduction, or acetate fermentation. Because methanogens are poor competitors for H_2 and acetate, their activity is suppressed by other microbes that couple oxidation of the same electron donors to the reduction of nitrate, ferric iron and sulfate (i.e., denitrification, iron reduction and sulfate reduction). Exposure to O_2 inhibits methanogens indirectly by regenerating oxidized forms of N, Fe and S that support competing microorganisms, and directly through O_2 toxicity.

Methane can be produced in soils without being emitted to the atmosphere because it is also consumed by aerobic microorganisms that oxidize CH_4 to CO_2. Methanotrophic bacteria grow by coupling the oxidation of CH_4 to the reduction of O_2. They are ubiquitous in soils (LeMer and Roger 2001) and explain why upland soils are generally net CH_4 sinks (Smith et al. 2000). Despite much research on methanotrophs in upland soils, there are no isolates of these organisms to date and little is known about their ecology. To our knowledge, no one has investigated the possibility that methanotrophs exist on the surfaces of upland plants. However, they occur symbiotically on (and within) *Sphagnum* tissue where they provide CO_2 to support photosynthesis (Raghoebarsing et al. 2005).

Methane is produced abiotically from combustion of organic carbon during biomass burning (Crutzen and Andreae 1990) and by thermal alteration of sedimentary organic carbon. It has been proposed that CH_4 is produced abiotically in aerobic plant tissue (Keppler et al. 2006).

Methane production in upland ecosystems

Despite generally inhospitable conditions, there is abundant evidence of methanogenic activity in upland soils. Andersen et al. (1998) used a $^{14}CH_4$-labeling technique to infer that two forest soils produced CH_4 even though the soils as a whole were net CH_4 sinks. von Fischer and Hedin (2002) used a stable isotope technique to make direct measurements of gross CH_4 production in 130 soil cores from 17 sites and found that even dry, oxic soils produced CH_4. Aerobic forest and agricultural soils have been reported to switch from net CH_4 uptake to CH_4 emission in the presence of a compound that blocks CH_4 oxidation (Yavitt et al. 1995, Chan and Parkin 2001). Finally, upland soils incubated anaerobically begin producing CH_4 within days or weeks (Megraw and Knowles 1987, Mayer and Conrad 1990, Wang and Bettany 1997). Collectively, these studies suggest that upland soils harbor populations of methanogens and are capable of becoming net sources of CH_4 when sufficiently wet.

The possibility of CH_4 production in upland soil microsites is consistent with the occurrence of denitrification (Tiedje et al. 1982) and Fe(III) reduction (Küsel et al. 2002) in upland soils, and observations that acetate, a CH_4 precursor, is found in upland soils (Küsel and Drake 1994, 1995). Although studies of methanogen isolates suggest they are extremely O_2 sensitive, other evidence suggests that they can tolerate a certain amount of O_2 (Kiener and Leisinger 1983, Fetzer and Conrad 1993). Methanogens have been reported to survive long periods in dry and oxic soils (Mayer and Conrad 1990, Ueki et al. 1997), perhaps protected from O_2 by reactive soil minerals (Fetzer et al. 1993).

The evidence that upland soils can support low rates of methanogenesis suggests that CH_4 oxidizing bacteria consume CH_4 from two sources, the atmosphere and the soil itself (Conrad 1994, Chan and Parkin 2001). The juxtaposition of these sources may explain a puzzling observation about the response of CH_4 fluxes to changes in soil water content. Andersen et al. (1998) reported that an intact upland forest soil core left uncovered at room temperature changed from a net sink for atmospheric CH_4 to a net source. Isotopic data showed that CH_4 oxidation fell to almost zero over this period, suggesting that CH_4 oxidizing bacteria attached to soil surfaces were more sensitive to soil drying than methanogens buried in the anaerobic center of soil aggregates. The cessation of CH_4 oxidation could have been caused by a physiological drought response among methanotrophic bacteria, more rapid CH_4 diffusion from the soil to the atmosphere due to low tortuosity (i.e., a shorter soil residence time for CH_4), or both. In other circumstances, decreases in soil water content can enhance CH_4 oxidation in upland soils by increasing CH_4 diffusion from the atmosphere into soil pore spaces (Castro et al. 1995).

In addition to microsites, anaerobic conditions occur in saturated zones that coincide with the water table surface. Soils with a deep source of CH_4 have a soil CH_4 concentration profile characterized by two maxima—one at the soil surface and the other near the water table—separated by a minimum. Such profiles have been observed in a variety of upland ecosystems, including desert (Striegl et al. 1992), temperate hardwood forest (Yavitt et al. 1990) and temperate coniferous forest (P. Megonigal, personal observation). It is possible that plants transport CH_4 from a deep groundwater source through the transpiration stream, effectively bypassing the zone of CH_4 oxidation (see next section).

The most direct evidence of methanogenesis in upland soils is that they occasionally emit CH_4 to the atmosphere. There are numerous reports of upland forests and savannas that switched for periods of time to CH_4 sources (Scharffe et al. 1990, Whalen et al. 1991, Yavitt et al. 1995, Silver et al. 1999, Sjögersten and Wookey 2002, Davidson et al. 2004), and wet-

land forests that switched to CH_4 sinks (Harriss et al. 1982, Megonigal and Schlesinger 2002). In most cases the proximate cause for the shift was a change in soil water content, but the ultimate cause varied from seasonal shifts in precipitation and evapotranspiration (Yavitt et al. 1995, Silver et al. 1999, Davidson et al. 2004), to plant community successional stage (Whalen et al. 1991), to experimentally imposed warming (Sjögersten and Wookey 2002). Because transpiration helps regulate soil water content, these studies suggest that tree physiology influences CH_4 fluxes between upland forests and the atmosphere.

Influence of tree physiology on methane emissions

Tree physiology influences both the production and oxidation of CH_4, and can play an important role in determining whether a particular forest is a net source or sink of CH_4. In the near absence of studies on plant regulation of CH_4 cycling in upland forests, it is instructive to consider studies in wetland systems. Plants are the ultimate source of organic carbon—in the form of root exudates or detritus—that microorganisms metabolize to CH_4, and several isotope tracer studies have demonstrated a tight coupling between plant photosynthesis and methanogenesis (Megonigal et al. 1999, King and Reeburgh 2002, Megonigal et al. 2004). A full cycle of CO_2 assimilation by plants, release of photosynthate into soils and emission as CH_4 requires as little as 2 hours, and up to 6% of the assimilated CO_2 is emitted as CH_4 in wetland ecosystems. Elevated CO_2 concentration ($[CO_2]$) stimulates CH_4 emissions from wetland soils (Megonigal and Schlesinger 1997), an effect that is directly proportional to the stimulation of photosynthesis by elevated $[CO_2]$ (Vann and Megonigal 2003). Although most studies relating the effects of elevated $[CO_2]$ to CH_4 emissions from wetland soils have been with herbaceous plants, a single study confirmed a linear relationship between CH_4 emissions and photosynthesis in the wetland tree *Taxodium distichum* (L.) Rich. (Vann and Megonigal 2003). It is reasonable to hypothesize that similar relationships between plant productivity and methane production occur in upland forests. For example, increasing inputs of labile carbon to upland soils may promote CH_4 production both by enhancing the electron donor supply to methanogens, and expanding anaerobic microsites via increased microbial O_2 demand.

Trees exert indirect regulation of CH_4 production and oxidation through their influence on soil water content, which determines the proportion of the soil profile that is anaerobic and producing CH_4 versus aerobic and oxidizing CH_4. An example of tree physiology influencing CH_4 cycling in upland forests is provided by the Duke FACE experiment. McLain et al. (2002) found that elevated $[CO_2]$ increased soil water content, which simultaneously increased CH_4 production and decreased CH_4 oxidation. The increase in soil water content was caused by reduced transpiration in the elevated $[CO_2]$ treatment, and the net effect was a positive feedback on radiative forcing by CH_4.

A possible mechanism for CH_4 emissions from upland vegetation is transport from the saturated zone below the water table through the transpiration stream. In most ecosystems, the deepest 5% of roots occur at depths greater than 1 m (Schenk and Jackson 2002) and maximum rooting depths can exceed 4 m (Schenk and Jackson 2005). The deepest root systems are found in tropical areas where high concentrations of atmospheric methane have been observed (see next section). Specifically, they occur in tropical semiarid to humid savanna, and tropical seasonally dry semideciduous to evergreen forests (Schenk and Jackson 2005). Deep roots that access the water table may contribute disproportionately to transpiration fluxes (Stone and Kalisz 1991, Nepstad et al. 1994, Jackson et al. 1999). In such cases, CH_4 dissolved in groundwater would presumably be entrained in the transpiration stream in a manner similar to CO_2 from root respiration (Teskey and McGuire 2002). We are unaware of any published measurements of CH_4 concentrations in xylem sap.

Unexplained methane sources in tropical forests

There are several recent reports suggesting that tropical forests may be larger sources of CH_4 than previously believed. The most comprehensive analysis used a satellite-mounted instrument to show that atmospheric CH_4 concentrations are far greater than expected from ground-based emissions inventories of tropical rain forests (Frankenberg et al. 2005). The deviation between modeled and observed column-averaged atmospheric CH_4 concentrations was especially large over the Amazon Basin and was correlated with the distribution of broadleaf evergreen forest.

Frankenberg et al. (2005) noted that the discrepancies in measured and modeled CH_4 concentrations could be explained by underestimates of known emissions sources such as wetlands, biomass burning, termites and cattle. The measurements were taken during the dry season (August through November) when wetland emissions should be lowest and biomass burning emissions should be highest, suggesting the biomass burning was the more important source. However, localized measurements of atmospheric CH_4 concentrations show that there can be significant biogenic CH_4 sources in tropical upland forests. Methane concentration profiles in three upland forests of the Brazilian Amazon showed a CH_4 source within the lower 10 m of the forest canopy (Carmo et al. 2006, Table 2), and nighttime pooling of CH_4 at 2 m above the soil surface was observed in a mixture of forest and savanna in Venezuela (Scharffe et al. 1990, Crutzen et al. 2006; Table 2). In both cases, when extrapolated to large areas, the estimated CH_4 emission rates were potentially significant on a global scale (4–38 Tg $year^{-1}$ for the Amazon region and 30–60 Tg $year^{-1}$ for global savanna). Scharffe et al. (1990) concluded that soil emissions were a relatively small contribution to CH_4 sources at the Venezuelan site and suggested that termite mounds and waterlogged pools were unmeasured CH_4 emission hotspots. Crutzen et al. (2006) reinterpreted these data as evidence of an aerobic plant CH_4 source. Regardless of whether the source of the CH_4 in these systems was vegetation or a combination of several known sources, none of which can

be distinguished by these studies, it is clear that CH_4 exchange between tropical upland ecosystems and the atmosphere has not been adequately characterized.

Aerobic methane emissions

Frankenberg et al. (2005) recognized that the discrepancies in measured and modeled CH_4 concentrations could be explained by a "… hitherto unknown methane source that might be directly related to the broadleaf evergreen forest." Just 7 months later, Keppler et al. (2006) published the first observations supporting one possible unknown CH_4 source—direct emissions from aerobic vegetation. They reported that CH_4 was emitted from every plant tissue tested, including detached leaves from 30 species, leaf litter and intact plants. The data of Keppler et al. (2006) suggested that sunlight, temperature and physiological activity were key variables regulating aerobic CH_4 emissions. The sunlit rates for intact plants (mean 374 ng g^{-1} h^{-1}) were significantly higher than those for detached leaves (mean 9 ng g^{-1} h^{-1}), dark emission rates for intact plants and detached leaves were significantly lower than sunlit leaves (mean 119 and 2 ng g^{-1} h^{-1}, respectively), and the temperature coefficient (Q_{10}) was about 2 over the range 30–70 °C. The process appeared to be non-enzymatic because emissions increased monotonically up to 70 °C and CH_4 was emitted from commercially available apple pectin.

More recently, Dueck et al. (2007) used an isotope-labeling technique in an attempt to verify emissions of CH_4 from aerobic plant tissue. This approach indicated rates (–10 to 42 ng g^{-1} h^{-1}, mean 21 ng g^{-1} h^{-1}) that were not significantly different from zero, and at best, an order of magnitude lower than those of Keppler et al. (2006). Increasing the amount of plant biomass in the experimental chambers improved the detection limit of their technique and suggested that little or no CH_4 is emitted by plant tissue. These data suggest that the fluxes reported by Keppler et al. (2006) were an artifact of their methods. The experiments performed by Dueck et al. (2007) were more controlled and physiologically relevant than those by Keppler et al. (2006), but it is unclear whether the hydroponic system they used effectively excluded CH_4 oxidizing bacteria, which are aerobic and capable of consuming CH_4 produced by plant tissue. The negative rates of CH_4 production reported by Dueck et al. (2007) were reasonably interpreted as experimental error, but they could also be interpreted as net consumption of CH_4 and it is unclear whether the leak tests they performed were long enough to allow for this possibility.

Given the absence of in situ measurements of aerobic plant CH_4 emissions, it is instructive to compare the Keppler et al. (2006) rates to other volatile organic carbon compounds (VOCs) such as methanol, which are relatively well understood. There are many different VOCs, but the total flux from foliage is dominated by a few compounds such as isoprene and methanol. The initial studies of methanol emissions from plants reported rates from mature leaves that typically ranged from about 0.8 to 44 μg g^{-1} h^{-1} (Nemecek-Marshall et al. 1995), which is at least an order of magnitude higher than the CH_4 emission rates (0.08 to 0.87 μg g^{-1} h^{-1}) observed by Keppler et al. (2006) under similar conditions of light and of temperature. Methanol emission rates from young leaves are even higher than rates observed for mature leaves (Nemecek-Marshall et al. 1995). Lower methanol emission rates have since been reported for most plants, but average methanol emission rates for mature sunlit leaves are at least 1.5 μg g^{-1} h^{-1}, which is four times the CH_4 emission rate reported by Keppler et al. (2006). These figures suggest that the global contribution of CH_4 from aerobic plant biomass, if it occurs at all, are considerably less than global emissions of methanol, which are estimated to be between 100 and 260 Tg $year^{-1}$ (Jacob et al. 2005).

Global extrapolations of aerobic plant CH_4 emissions

Keppler et al. (2006) offered a provocative global extrapolation of their intact plant CH_4 emission rates that suggested up to 243 Tg $year^{-1}$ of CH_4 was emitted from this new source. This figure was derived by scaling leaf-mass-based emission rates to the globe with day length, growing season length and total net primary productivity (leaves, woody stems and roots) as driving variables, all stratified by the major biomes. Alternative extrapolations of the same data were subsequently published that accounted for differences in foliage turnover rates between biomes, significantly lowering the global strength of a putative aerobic plant source (Kirschbaum et al. 2006, Parsons et al. 2006, Butenhoff and Khalil 2007; Table 1).

To further constrain the potential magnitude of global CH_4 emissions from upland plants, we used a foliar VOC emissions model—MEGAN or Model of Emissions of Gases and Aerosols from Nature—to incorporate certain canopy and physical processes that were not considered by Kirschbaum et al. (2006) and Parsons et al. (2006). In particular, we used the temperature responses reported by Keppler et al. (2006) and accounted for the effects of self-shading within the plant canopy. We used MEGAN with the assumption that the mechanism of CH_4 production, if it exists at all, shares some features of the biochemical pathways that produce other VOCs such as methanol. MEGAN includes a detailed canopy environment model that calculates solar radiation and leaf temperature of sun and shade leaves for each of five canopy depths. Driving variables include wind speed, humidity, soil water content, above-canopy direct and diffuse solar radiation, and ambient temperature. MEGAN includes emission factors for light-dependent and light-independent components of emissions, and irradiances that vary because of self-shading in the plant canopy. Light-dependent and light-independent emissions of CH_4 were estimated based on the emission factors recommended by Keppler et al. (2006) (374 and 119 ng g^{-1} h^{-1} for sunlit and dark emission, respectively). Although Keppler et al. (2006) did not report light response curves, we assumed that emissions increase nearly linearly with irradiance to a saturation point. This is the behavior we observe for other biogenic VOC and is thus a reasonable starting point for the CH_4 extrapolation. The emission algorithm for dark emissions was based on

Table 1. Estimates of global aerobic methane emissions.

Scaling approach or system	Mean or range	Notes	Ref[1]
Global extrapolations (Tg year^{-1})			
Net primary production	150	Global mean; low and high estimates ranged from 62–236 Tg year^{-1}	6
Foliage biomass	36	Global mean; based on mean rate for intact plants in Reference 6	7
Photosynthesis	10	Global mean; based on mean rate for intact plants in Reference 6	7
Global model, foliage biomass	20	Global mean; based on mean rate for intact plants in Reference 6	1
Global model, leaf area index	36	Global mean; based on mean rate for intact plants in Reference 6	1
Global model, leaf area index	36	Global mean; based on mean rate for intact plants in Reference 6	1
Global VOC emissions model	34–56	Range due to different land cover and weather scenarios	8
Mass balance, $\delta^{13}CH_4$	0–176	"Best" estimate of 2000 AD source; range due to different isotope fraction factors and C_3:C_4 ratios	4
Mass balance, $\delta^{13}CH_4$	0–213	Maximum estimate of 2000 AD source	4
Mass balance, $\delta^{13}CH_4$	0–46	"Best" estimate of 1700 AD source	4
Mass balance, $\delta^{13}CH_4$	9–103	Maximum estimate of 1700 AD source	4
Mass balance, $\delta^{13}CH_4$, model	25	"Most stringent" constraints based on $\delta^{13}CH_4$	1
Mass balance, isotopes, model	85–125	Global range; range is "plausible" to "highest" maximum rates	6
Localized estimates (mg CH_4 m^{-2} day^{-1})			
Tropical forest	2–21	Range due to different sites and seasons	2
Tropical savanna	7–14	Reason for the range in estimates was not reported	9, 3

[1] References: 1, Butenhoff and Khalil 2007; 2, Carmo et al. 2006; 3, Crutzen et al. 2006; 4, Ferretti et al. 2007; 5, Houweling et al. 2006; 6, Keppler et al. 2006; 7, Kirschbaum et al. 2006; 8, Megonigal and Guenther, this study; and 9, Scharffe et al. 1990.

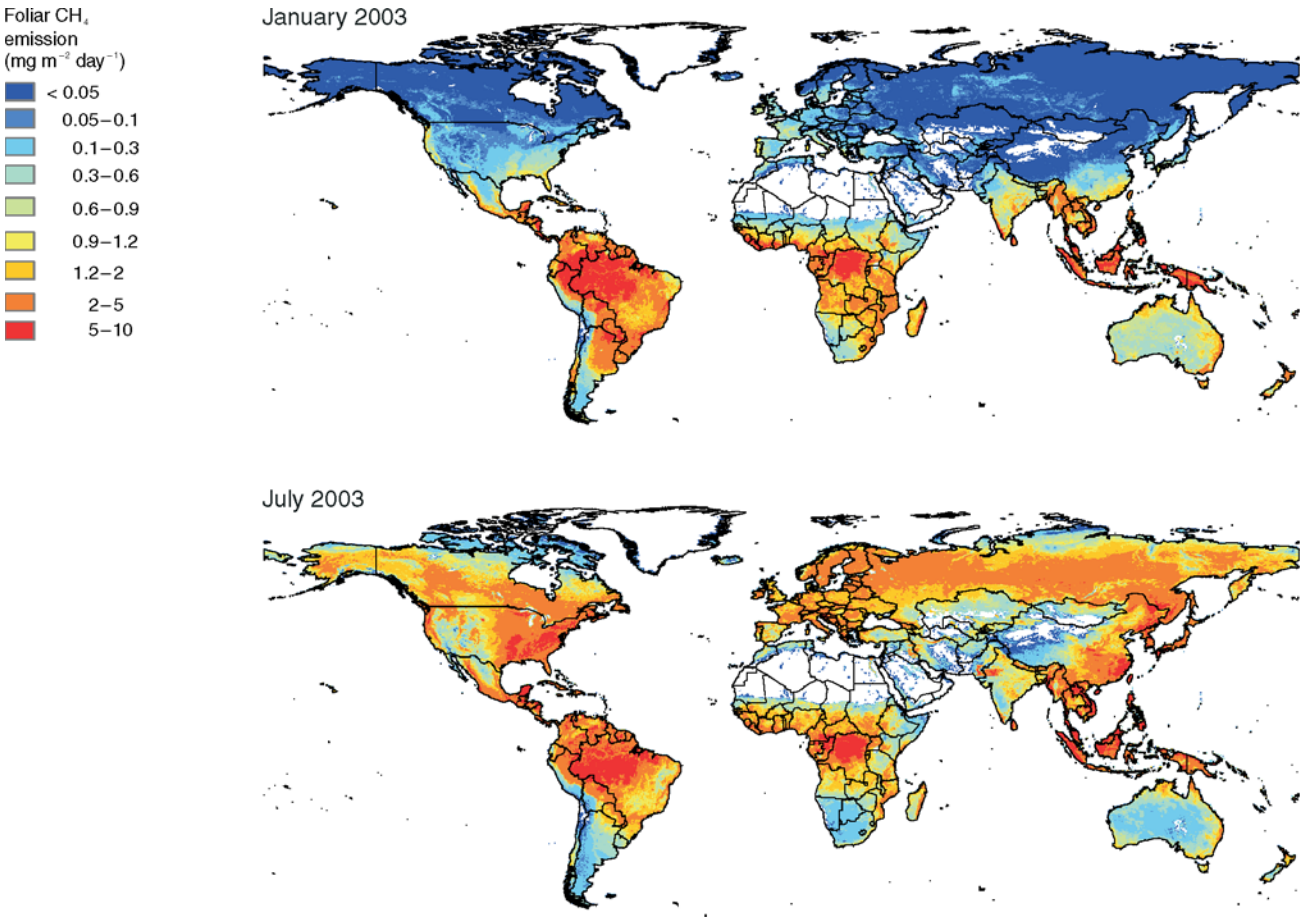

Figure 1. The global distribution of CH_4 emissions from living foliage simulated by MEGAN (Model of Emissions of Gases and Aerosols from Nature) parameterized with the emission rates reported by Keppler et al. (2006).

the temperature response shown in Figure 1 of Keppler et al. (2006). A range of global annual CH_4 emission estimates was generated using different combinations of the alternative landcover (e.g., MODIS and AVHRR satellite data, vegetation models) and weather (e.g., NCEP, MM5, IIASA) databases described by Guenther et al. (2006). Our parameterization of light and temperature in the MEGAN model is similar to the global model of aerobic CH_4 emissions developed by Butenhoff and Khalil (2007).

The global distribution of CH_4 emissions from foliage simulated with MEGAN is shown in Figure 1. Tropical forests are a major source region, which agrees with the predictions of Keppler et al. (2006) and the observations of Frankenberg et al. (2005). The annual global CH_4 emission from living vegetation estimated with MEGAN ranged from 34–56 Tg $year^{-1}$, depending on the land cover and weather data used to drive the model. This figure is nearly one order of magnitude lower than the highest estimates provided by Keppler et al. (2006) and is consistent with the magnitude of alternative extrapolations provided by Kirschbaum et al. (2006) and Parsons et al. (2006), and the global model developed by Butenhoff and Khalil (2007). Our estimates would be about an order of magnitude lower if we had used the mean rate reported by Dueck et al. (2007) of 21 ng g^{-1} h^{-1}.

Isotope-based estimates of aerobic plant CH_4 emissions

Keppler et al. (2006) reported that aerobic plant CH_4 emissions were ^{13}C-enriched compared with wetland CH_4 emissions (–50‰ versus –60‰, respectively), raising the possibility that plant emission rates can be estimated through a stable isotope mass balance approach. Ferretti et al. (2007) used ice core records of CH_4 concentration and $\delta^{13}CH_4$ over the past 2000 years to calculate that current plant emissions are not likely to exceed 213 Tg $year^{-1}$ (Table 1), and the figure may be as little as 0 Tg $year^{-1}$. Houweling et al. (2006) used stable isotope mass balance, atmospheric transport modeling and spatially explicit comparisons of $\delta^{13}CH_4$ and CH_4 to arrive at a "most plausible" maximum for plant emissions of 85 Tg CH_4 $year^{-1}$ (Table 1). These estimates are 36–90% of the maximum estimate reported by Keppler et al. (2006).

As with the CH_4 flux data, some caution is necessary in using the $\delta^{13}CH_4$ data of Keppler et al. (2006) to discriminate plant CH_4 fluxes from wetland fluxes. First, the isotope ratios used in these calculations are based on a single set of published observations that has not been independently verified. Second, the assumption that plant $\delta^{13}CH_4$ is about –50‰ was based on CH_4 collected from intact plants (Table S2 of Keppler et al. 2006); however, there was just a 2‰ difference in the $\delta^{13}CH_4$ of C_3 and C_4 species in this dataset. By comparison, $\delta^{13}CH_4$ emitted from detached leaves of C_3 and C_4 plant differed by about 8‰ (–58.2‰ versus –49.5‰), which is close to the 10‰ difference expected for C_3 and C_4 plant biomass. Using the data for detached leaves yields a $\delta^{13}CH_4$ for plant CH_4 of –55‰, which is closer to the commonly accepted value for $\delta^{13}CH_4$ from wetlands of –60‰. Finally, it is worth noting that it may be incorrect to assume all wetlands emit highly depleted CH_4. Tropical wetland sources can have $\delta^{13}CH_4$ values of –53 to –55‰ (Quay et al. 1991). Using these more enriched values, Schaefer et al. (2006) concluded that ^{13}C-enriched CH_4 during the Younger Dryas–Preboreal transition could have been due either to an aerobic plant CH_4 source or enhanced emissions from tropical wetlands.

Resolving unexplained sources of CH_4 in forests

Observations of unexpectedly high atmospheric CH_4 concentrations in forested landscapes (Frankenberg et al. 2005, Carmo et al. 2006, Crutzen et al. 2006) have revealed a gap in our understanding of trace gas emissions. The wide variety of plausible explanations offered for these observations encompass specialties ranging from soil microbiology to plant physiology to atmospheric chemistry. These disparate research communities should continue to study the problem in order to inform modeling and public policy related to climate change.

It is doubtful that these observations can be explained by the aerobic plant CH_4 source proposed by Keppler et al. (2006) because independent extrapolations and rate measurements suggest emission rates from plant tissue are far lower than initially believed (Dueck et al. 2007; Table 1). The possibility that plants transport microbially produced CH_4 from deep sources via transpiration remains to be investigated, but it may be more fruitful to concentrate on emissions from known sources such as biomass burning or soils. Increased attention should be directed to hotspots and hot moments of CH_4 emissions (McClain et al. 2003), which are concentrated in space or time and generally difficult to measure. For example, bubble emissions of CH_4 from Siberian peatlands are spatially heterogenous and episodic, yet they account for 95% of annual CH_4 emissions (Walter et al. 2006). Similarly, there is ample evidence in the literature to suggest that upland soils have the potential to be net sources of CH_4, but this is likely to occur during relatively brief episodes of wetting or drying. High spatial and temporal resolution monitoring of CH_4 emissions from a variety of known sources may be needed to explain unexpectedly large CH_4 concentrations in tropical forest canopies.

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