Elevated methane concentrations in trees of an upland forest

Kristofer R. Covey,[1] Stephen A. Wood,[2,3] Robert J. Warren II,[1,4] Xuhui Lee,[1] and Mark A. Bradford[1]

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[1] There is intense debate about whether terrestrial vegetation contributes substantially to global methane emissions. Although trees may act as a conduit for methane release from soils to atmosphere, the debate centers on whether vegetation directly produces methane by an uncharacterized, abiotic mechanism. A second mechanism of direct methane production in plants occurs when methanogens – microorganisms in the domain Archaea – colonize the wood of living trees. In the debate this biotic mechanism has largely been ignored, yet conditions that promote anaerobic activity in living wood, and hence potentially methane production, are prevalent across forests. We find average, growing season, trunk-gas methane concentrations >15,000 $\mu L \cdot L^{-1}$ in common, temperate-forest species. In upland habitat (where soils are not a significant methane source), concentrations are 2.3-times greater than in lowland areas, and wood cores produce methane in anaerobic, lab-assays. Emission rate estimates from our upland site are 52 ± 9.5 ng CH_4 m^{-2} s^{-1}; rates that are of a similar magnitude to the soil methane sink in temperate forest, and equivalent in global warming potential to ~18% of the carbon likely sequestered by this forest. Microbial infection of one of the largest, biogenic sinks for carbon dioxide, living trees, might result in substantial, biogenic production of methane. **Citation:** Covey, K. R., S. A. Wood, R. J. Warren II, X. Lee, and M. A. Bradford (2012), Elevated methane concentrations in trees of an upland forest, *Geophys. Res. Lett.*, *39*, L15705, doi:10.1029/2012GL052361.

1. Introduction

[2] Containing more than 75% of terrestrial carbon, forests are globally-important sinks and stores for carbon [*Houghton*, 2007]. Because in upland soils the activities of methane-consuming bacteria (i.e. methanotrophs) generally dominate those of methane-producing archaea (methanogens), forests are also considered sinks for atmospheric methane (CH_4) [*Conrad*, 2009]. However, recent work indicates that forests may be producing and emitting huge quantities of CH_4. Using remotely-sensed data *Frankenberg et al.* [2005] showed unexpectedly high concentrations of CH_4 over the tropics. On-the-ground measurements of CH_4 flux suggested the emissions might come from a novel, aerobic mechanism through which live vegetation and litter in forests act as a methane source [*Keppler et al.*, 2006]. More than 30 studies have attempted to explain, measure, and verify observations of CH_4 production via this pathway and two recent reviews conclude that the phenomenon does occur [*Bruhn et al.*, 2012; *Keppler et al.*, 2009]. Yet there is still no definitive confirmation or rejection that forests on well-drained soils are a significant CH_4 source [*Anderson*, 2010].

[3] If vegetation does produce CH_4, the magnitude of emissions may contribute significantly to global fluxes. At the low end, the U.S. Environmental Protection Agency estimates emissions from vegetation of 20 $Tg \cdot yr^{-1}$; roughly equivalent to the global warming potential (GWP) of CO_2 released through U.S. residential use of fossil fuels. At the high end, emissions from vegetation may be 60 $Tg \cdot yr^{-1}$; approximately equal to the GWP of fossil-fuel CO_2 emissions from combined U.S. industrial, residential and commercial sources [*Anderson et al.*, 2010; *Environmental Protection Agency*, 2011]. To quantify CH_4 emissions from vegetation, two general methods have been used: bottom-up approaches where flux measurements for individual plants or field plots are extrapolated to regional or global scales [*Keppler et al.*, 2006; *Kirschbaum et al.*, 2006; *Parsons et al.*, 2006]; and top-down approaches that identify "missing" CH_4 from global models and reconcile it with proposed emissions from land [*Aydin et al.*, 2011; *Bousquet et al.*, 2006; *Frankenberg et al.*, 2005; *Houweling*, 1999; *Kai et al.*, 2011]. The validity of global CH_4 emission estimates from both approaches hinges on whether vegetation directly produces CH_4 [*Nisbet et al.*, 2009]. Certainly, in water-inundated soils, trees can act as a conduit for CH_4 release from soils to the atmosphere [*Rice et al.*, 2010; *Rusch and Rennenberg*, 1998; *Terazawa et al.*, 2007]. And although UV light does seem responsible for direct CH_4 production from vegetation, this aerobic mechanism remains uncharacterized [*Bruhn et al.*, 2012; *Keppler et al.*, 2009]. This has led to omission of CH_4 production from living plants as a source in recent, global CH_4 budgets [*Dlugokencky et al.*, 2011]. However, a second mechanism of direct CH_4 production from living plants exists: the archael methanogens colonizing the wood of trees [*Schink and Ward*, 1984; *Van Der Kamp et al.*, 1979; *Xu and Leininger*, 2001; *Zeikus and Ward*, 1974; *Zeikus and Henning*, 1975].

[4] In the natural world, disease and decay commonly occur together. Decay of organic matter produces gases such as CO_2 and CH_4, and hence is a fundamental determinant of global biogeochemical cycling rates and atmospheric chemistry. Concentrations of CH_4 as high as 60% have been found in tree boles [*Bushong*, 1907]. At least one

[1]School of Forestry and Environmental Studies, Yale University, New Haven, Connecticut, USA.
[2]Department of Ecology, Evolution, and Environmental Biology, Columbia University, New York, New York, USA.
[3]Tropical Agriculture and Rural Environment Program, Earth Institute at Columbia University, New York, New York, USA.
[4]Department of Biology, Buffalo State College, State University of New York, Buffalo, New York, USA.

Corresponding author: K. R. Covey, School of Forestry and Environmental Studies, Yale University, New Haven, CT 06511, USA. (kristofer.covey@yale.edu)

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Table 1. Species-Level Differences in CH_4 Production, Timber Volume and Susceptibility to Fungal Decay

Species	Mean Production Potential (μg CH_4 m^{-3} s^{-1})	Percent of Cores Showing CH_4 Production	Range of Production[a] (μg CH4 m^{-3} s^{-1})	Standing Bole Volume (m^3 ha^{-1})	Percentage of Volume Lost to Heart Rot[b]
Pinus strobus L. (eastern white pine)	0.067	40	.161–.175	8.6	5%
Tsuga canadensis L. (eastern hemlock)	0.115	40	.190–.383	11.5	12%
Quercus rubra L. (red oak)	0.107	60	.165–.192	28.2	19%
Betula lenta L. (black birch)	1.555	80	.191–6.884	8.6	21%
Acer rubrum L. (red maple)	1.239	60	.236–3.522	8.6	21%

[a]Range of production includes only those samples demonstrating measureable production of CH_4. Reported means are for all samples.
[b]*Wagener and Davidson* [1954].

source of high trunk-gas CH_4 concentrations has been known for more than forty years: bacterial infection of heartwood (i.e. non-living tissue that primarily accumulates in trunks as trees age). This infection promotes wetwood and, with it, production of CH_4 through classical methanogenesis [*Zeikus and Ward*, 1974]. Wetwood CH_4 production has not been quantified for its contribution to global CH_4 emissions [*Conrad*, 2009]. Similarly, neither have contributions from heart rot – the decay of heartwood instead caused by fungal infection [*Boyce*, 1961] – which also promotes anaerobic decay and colonization by methanogens, but is much more prevalent in living trees. Indeed, in temperate forests ~20% of the commercial timber harvest, for genera such as oaks and maples, is lost to fungal decay [*Wagener and Davidson*, 1954]. Notably, symptoms of heart rot are often not outwardly visible for standing trees [*Zillgitt and Gevorkiantz*, 1948] and anaerobes can be active before decay is measurable [*Shortle et al.*, 1978; *Wilcox*, 1970].

[5] In low O_2 and high CO_2 environments, such as those in tree trunks [*Teskey et al.*, 2008], aerobic heart-rot fungi are incapable of completing their metabolic processes [*Jensen*, 1967; *Schmidt*, 2006]. This incomplete fermentation provides substrates suitable for use by bacteria and archaea. In turn, these bacteria and archaea accelerate fungal growth by removing the waste products of fungal metabolism and by enriching the wood substrate through N-fixation [*Beckmann et al.*, 2011]. These syntrophic (i.e. "feeding together") consortia are capable of breaking down complex biopolymers that individual organisms cannot digest [*Bryant et al.*, 1967]. Such consortia are known to degrade wood and produce CH_4 in ruminant animals [*Bauchop*, 1981; *Joblin and Naylor*, 1989], in digesters [*Zinder*, 1993] and in timbers stored under conditions similar to those found inside living trees [*Beckmann et al.*, 2011; *Krüger et al.*, 2008]. Even in predominately aerobic environments, fungal metabolism can lead to anaerobic microsites and the formation of large quantities of CH_4 by archaea [*Reith et al.*, 2002].

[6] Given the expectation of widespread and abundant fungal infection of living wood, we selected individuals in lowland and upland habitat of six trees species that vary in their vulnerability to heart rot [*Scheffer*, 1966] and that commonly occur in temperate forest. We reasoned that if trees primarily serve as conduits of CH_4 release from soils to the atmosphere, then we should only observe elevated CH_4 concentrations in tree trunks where the soil might be a significant CH_4 source (i.e. lowland habitat). A second source in these lowland habitats would be wetwood, which would also yield elevated CH_4 concentrations in trees. In contrast, in upland habitat the soil is a CH_4 sink and wetwood is rare. We therefore reasoned that elevated CH_4 concentrations in tree trunks of species known to be susceptible to fungal-mediated heart rot would suggest an abundant and widespread CH_4 production source in living trees. Using trunk-gas CH_4 concentrations, and lab-based CH_4 production potentials from wood samples, we provide estimates of emissions from living trees of CH_4 produced by the microbial consortia that occur with heart rot.

2. Methods

2.1. Field and Laboratory Measurements

[7] Because decay is more likely to be found in larger and older trees [*Berry and Beaton*, 1972; *Browne*, 1956; *Zillgitt and Gevorkiantz*, 1948], we selected 58 trees with diameters at breast height (dbh; 1.3 m) >25 cm (indicative in our region of mature, canopy trees in middle-aged stands). Trees were selected by order-of-encounter, stratified across six species (Table 1), in lowland and well-drained upland habitat at Yale-Myers Forest, Connecticut, USA (Lat. 41°56′15″ Long. −72°10′45″). Stands were of similar age-class (~80–100 years), and representative of the oak-dominated hardwood forest type common to the eastern U.S. [*Meyer and Plusnin*, 1945].

[8] To determine *in situ* trunk-gas CH_4 concentrations, prior to (April) and post (July) leaf-out in 2011, trees were drilled horizontally at breast height to center with a 5/16″ drill bit (Speedbor, Irwin, Huntersville, NC, USA) and immediately plugged with an 8-mm stopper (SubaSeal, Sigma-Aldrich, St. Louis, MO, USA). A 50-mL gas-syringe (SGE, Ringwood, AU) was inserted through the SubaSeal and into the cavity to remove 50 mL of trunk-gas from each tree, 15 mL of which was injected into a vacuum-sealed 12-mL pre-evacuated sample vial (Exetainer, Labco, High Wycombe, UK) and 0.2 mL analyzed by gas chromatography on an FID Gas Chromatograph (310C, SRI, Menlo Park, CA, USA) equipped with a 1-m silica-gel column, with helium as a carrier gas and an oven temperature of 40°C.

[9] We evaluated trunk-gas CH_4 concentrations using General Linear Mixed Models to assess effect of habitat and time of year, with tree species as a random factor, therefore accounting for spatial and temporal associations in our sampling design. To discern species-level differences, we used ANOVA to assess time-of-year by species effects. All models were run in the statistical freeware R [*R Development Core Team*, 2010].

[10] To confirm that trunk-wood had the potential to produce CH_4, in October 2011 we removed bark-to-pith increment cores from the same trees, sectioned them to fit in 37-mL anaerobic bottles, flushed them with 50 mL of 100%-N_2 and returned them to the laboratory within 12 h of collection. Headspaces were flushed again with N_2 for 3 min

at 1 L·min^{-1} and incubated for 12 h at 20°C, after which a 15 mL sample was withdrawn and measured in the same manner as the trunk-gas samples. These lab assays only provide evidence for CH_4 production from trunk wood and rate comparisons are probably not reliable. For example, CH_4 production can drop rapidly following disturbance of methanogenic communities and similar assays with wetwood-infected materials show that N_2 assays underestimate production potentials by a factor of ~3 [*Mukhin and Voronin*, 2011; *Zeikus and Ward*, 1974].

2.2. Scaling to Field Rates for Upland Forest

[11] Past work investigating tree-mediated CH_4 transport from anoxic soils has demonstrated that CH_4 diffuses through bark [*Gauci et al.*, 2010; *Pulliam*, 1992; *Rusch and Rennenberg*, 1998; *Terazawa et al.*, 2007], and studies of other trunk gases have shown bark flux rates are positively and linearly related to trunk gas concentrations [*Steppe et al.*, 2007]. Given these relationships, we estimated *in situ* bark effluxes for our upland site from trunk-gas CH_4 concentrations and radial diffusivity in wood. Ignoring longitudinal diffusion, we obtain the diffusion equation in the cylinder coordinate as:

$$F = -f\rho\rho_a D\frac{r_1}{r_2}\left(\frac{\partial\omega}{\partial r}\right)_{r_2}$$

where F is the radial diffusion flux, f is a radial diffusivity scale factor (= 0.017) [*Zohoun et al.*, 2003] similar to the tortuosity factor used to describe gas diffusion in soils, ρ is air filled-porosity estimated to be 0.07 according to the water content reported for wet wood [*Nord-Larsen et al.*, 2011], ρ_a is air density, D is CH_4 diffusivity in ambient air (= 0.21 cm^2 s^{-1}, [*Massman*, 1998], ω is CH_4 molar mixing ratio, and r_1 and r_2 are the radius of the heartwood and tree trunk, respectively. We used the mean tree radius (r_2 = 23.5 cm) and assumed the central half of this radius was heartwood (r_1 = 11.7 cm), giving 11.7 cm of trunk wood for CH_4 diffusion. The mixing ratio gradient at r_1 was estimated from the observed difference in the mixing ratio between the trunk air and ambient air. The flux computed from the above equation has the dimensions of μg CH_4 m^{-2} s^{-1} (unit surface area of the tree trunk) and was converted to μg CH_4 m^{-3} s^{-1} (unit wood volume) for the purpose of upscaling. Mean calculated flux rates were scaled to per hectare field rates using standing live bole volume (Table 1) estimated from region and species-specific volume equations [*Meyer and Kienholz*, 1944]. Volumes estimates were based on randomized variable-radius plot sampling (n = 5 plots) in our upland site using a factor 10 basal area prism (Cruise Master, Forestry Suppliers, Jackson, MS, USA). Emissions from those species not sampled (11% of total volume), where scaled using the mean concentration of all sampled species.

3. Results and Discussion

[12] Our data suggest that trees – by supporting environments suitable for classical methanogenesis – could make upland forests significant contributors to global CH_4 emissions. At our upland site, trunk-gas CH_4 concentrations were as high as ~80,000 times atmospheric, and mean growing-season concentrations in the three species (red maple, red oak, black birch; Table 1) known to be most susceptible to heart rot were above 15,000 μL L^{-1} (Figure 1), leading to species-level differences in CH_4 trunk-gas concentrations ($P < 0.01$). A similar trend across species was present in lab assays with black birch and red maple producing more consistently and at higher rates than the two conifer species studied (eastern white pine, eastern hemlock). These assays confirm the production of significant quantities of methane in outwardly healthy tree wood under anaerobic headspace. The large variation present may be due to high spatial variability of production within individuals or could stem from the sensitivity of microbial communities to disturbance. We assessed increment cores and found visible decay was not correlated with trunk-gas CH_4 concentrations and/or production potentials. This lack of correlation is not surprising, and we would not expect a direct correlation with rot for several reasons. For example, trees may respond to injury and microbial infection by generating anoxia in trunk wood, favoring methanogens but generating little visible decay [*Shortle*, 1979]. It is at these decay frontiers where microsites favoring methanogenesis are most likely to occur and advanced decay would likely reduce or shut-down methanogenesis because it increases permeability facilitating O_2 diffusion [*Schwarze*, 2007; *Sorz and Hietz*, 2006]. Notably, in the upland site, we had a red maple individual in which the center was hollow and trunk CH_4 concentrations approximated those in ambient air.

[13] Trunk CH_4 concentrations were 2.3-times greater (P = 0.06) in trees of upland habitat, where heart rot is expected to be more prevalent than at lowland sites [*Basham*, 1973]. More importantly, upland soils typically consume rather than produce CH_4 [*Bradford et al.*, 2001], suggesting that the bulk of the trunk CH_4 was produced internally and did not accumulate via soil-tree diffusion pathways [*Rice et al.*, 2010]. Further support for this interpretation was provided when we returned to the upland site in February 2012 and, in 10 red oak individuals, found CH_4 concentrations lower at the trunk base (5 cm above the soil) than at 1.3 m (i.e. dbh; mean difference = 9,551 μL L^{-1}, P = 0.08). This pattern is opposite to that observed when trees are functioning as conduits for release of CH_4 produced in soils [*Rusch and Rennenberg*, 1998]. Lastly, relative CH_4 accumulation in individual trees appeared consistent across seasons, being temporally correlated ($\log_{10}$ [pre-leaf out CH_4] = 0.7556*$\log_{10}$ [post-leaf out CH_4] + 0.8574, r^2 = 0.43, $P < 0.05$) and on average 3.1-times greater (P = 0.083) in summer than spring, following the expected temperature sensitivity of methanogenesis [*Conrad*, 2009].

[14] Mean *in situ* diffusion fluxes across all species, estimated from the trunk-gas CH_4 concentrations and lateral gas diffusivity in wood, were 7.1 ± 1.3 μg CH_4 m^{-3} s^{-1} (mean ± SE, per unit wood volume). Scaling field-diffusion flux estimates to local field rates, emission rates are 52 ± 9.5 ng CH_4 m^{-2} s^{-1}, respectively. These emissions have a GWP equal to ~18% of the carbon these stands likely sequester per annum [*Law et al.*, 2002], and are of a similar magnitude to annual mean CH_4 consumption rates by bacteria (i.e. methanotrophs) in temperate forest upland soils [*Bradford et al.*, 2001]. The resulting net fluxes are therefore below the minimum detection limit for eddy covariance [*Kroon et al.*, 2010], providing a parsimonious explanation as to why such measurement approaches have not previously identified this potential source.

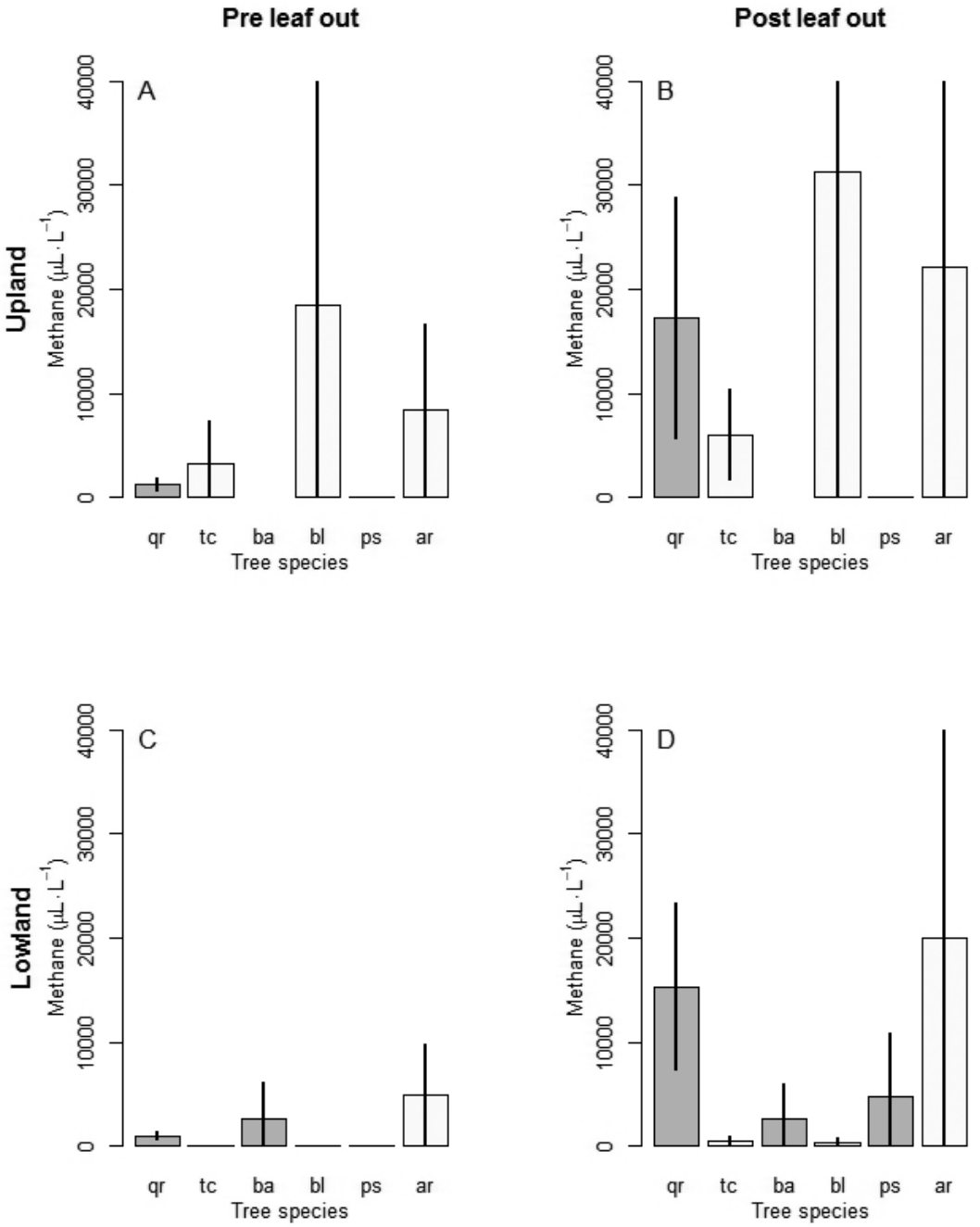

Figure 1. Trunk-gas methane concentrations in *Quercus rubra* (qr: red oak), *Tsuga canadensis* (tc: eastern hemlock), *Betula alleghaniensis* (ba: yellow birch), *Betula lenta* (bl: black birch), *Pinus strobus* (ps: eastern white pine) and *Acer rubrum* (ar: red maple), in lowland and well-drained upland habitat. Ambient air concentrations at 1.3-m height were consistently below 2 μL L^{-1}. Values are means $\pm$ 95% CIs; n = 5 in upland and 5 or 6 in lowland.

[15] The production of CH_4 by the heart rot pathway questions whether upland forests can be considered a net sink for atmospheric CH_4 (through soil consumption). To answer this question, further work is required to refine our CH_4 emission estimates and determine their contribution to the global CH_4 budget. Specifically, our work was conducted in intermediate-aged stands in temperate woodland on ~60 trees, and applying these rates to large areas would assume similarity across disparate forest types. Instead, susceptibility to fungal decay varies by species, site, age-class, past management regimes, and between and within individuals [*Wagener and Davidson*, 1954]. For example, within individuals, heart rot often starts at the base or "butt" of the tree [*Krause and Gagnon*, 2005; *Wagener and Davidson*, 1954] but we observed higher CH_4 concentrations at 1.3 m height, as opposed to 5 cm above the soil. This

is probably because trunk-gas O_2 concentrations are highest at the base and lowest mid-way up the stem [*Eklund*, 2000], potentially decoupling extent of heart rot from CH_4 production rates. At the stand level, tree age and successional status will likely impact CH_4 emissions. For example, age is closely related to the likelihood of heart rot, and older stands generally have higher standing-wood volumes [*Hennon*, 1995], meaning older stands will presumably have higher CH_4 emissions. Although stand-level emissions may increase with age (as long as trunk decay remains enclosed within the tree), heart rot is also known to affect younger trees, particularly when subjected to managements such as coppice. Lastly, positive relationships between temperature, moisture and decay rates could result in a latitudinal gradient in forest CH_4 production, with tropical biomes – where heart rot can cause as much as 30% loss in merchantable timber volume [*Grogan and Schulze*, 2008] – having greater emissions than temperate and boreal forests. Such a latitudinal pattern would be consistent with observed atmospheric CH_4 concentrations, which are highest above the moist tropics [*Frankenberg et al.*, 2005].

[16] Our data, uncertainties in global CH_4-emission sources [*Heimann*, 2011], the ubiquity of heart rot [*Wagener and Davidson*, 1954], and the fact CH_4 production from heartwood occurs through a known, biological mechanism [*Beckmann et al.*, 2011; *Zeikus and Ward*, 1974], makes plausible globally-significant production of CH_4 from living trees via the heart rot pathway. To gain precise global-scale estimates of CH_4 production by living trees through this pathway will require on-the-ground assessments of individual trees across all major forest types, managements and age classes. Until such work is conducted, uncertainties in the size of CH_4 emission sources, and in explanations of temporal and spatial dynamics in global, atmospheric CH_4 concentrations, are unlikely to be reduced.

4. Conclusion

[17] The potential for disease to regulate biogeochemical cycling is recognized [*Hudson*, 2006], but disease of one of the largest, biogenic sinks for carbon – the wood of living trees – has received little to no consideration in how it might affect atmospheric chemistry and associated climate change. Our data reveal trunk-gas CH_4 concentrations many times atmospheric on both lowland and upland sites. The highest concentrations were found for the upland site, and in species known to be susceptible to heart rot, suggesting this disease as the pathway of CH_4 production. The common infection of trees by heart rot fungus, and associated bacteria and archaea, has long been a concern of commercial forestry. These findings suggest decay in living trees is also important to biogeochemists and atmospheric scientists seeking to understand the role of forests in the global CH_4 budget.

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