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Gauci, Vincent; Gowing, David J. G.; Hornibrook, Edward R. C.; Davis, Joanna M. and Dise, Nancy B. (2010). Woody stem methane emission in mature wetland alder trees. *Atmospheric Environment*, 44(17) pp. 2157–2160.

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Version: Accepted Manuscript

Link(s) to article on publisher's website:

<http://dx.doi.org/doi:10.1016/j.atmosenv.2010.02.034>

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Accepted Manuscript

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PII: S1352-2310(10)00161-5

DOI: [10.1016/j.atmosenv.2010.02.034](https://doi.org/10.1016/j.atmosenv.2010.02.034)

Reference: AEA 9542

To appear in: *Atmospheric Environment*

Received Date: 2 September 2009

Revised Date: 19 February 2010

Accepted Date: 24 February 2010

Please cite this article as: Gauci, V., Gowing, D.J., Hornibrook, E.R., Davis, J.M., Dise, N.B. Woody stem methane emission in mature wetland alder trees, *Atmospheric Environment* (2010), doi: 10.1016/j.atmosenv.2010.02.034

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Short Communication – FINAL REVISION

Woody stem methane emission in mature wetland alder trees

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Key words: fluxes; emission pathway; wetlands; forest; anaerobic

Abstract

Methane (CH₄) is an important greenhouse gas that is predominantly emitted to the atmosphere from anoxic wetland ecosystems. Understanding the sources and emissions of CH₄ is crucially important for climate change predictions; however, there are significant discrepancies between CH₄ source estimates derived via so-called bottom-up and top-down methods. Here we report CH₄ emission from the stems of mature wetland alder (*Alnus glutinosa*) trees in the UK, a common tree of northern hemisphere floodplains and wetlands. The alder stems most likely behave as conduits for soil-produced CH₄ either in the gaseous or aqueous phase, and may, therefore, help to reconcile methodological differences in the way the wetland CH₄ source is estimated.

Alder tree stems emitted average peak CH₄ fluxes of 101 µg CH₄ m⁻² hr⁻¹ (on a stem area basis) in early October, a rate that is similar to that obtained from mature Japanese ash (*Fraxinus mandshurica* var. *japonica*) in Japan and amounting to approximately 20% of the measured CH₄ flux from the soil surface. The finding suggests that trees, which occupy 60% of Earth's wetlands and are normally excluded from the measurement programmes that form the basis for bottom-up estimates of the global wetland source, could be important contributors to overall terrestrial ecosystem CH₄ flux.

Introduction

Wetlands form the largest source of methane (CH_4) to the atmosphere, a powerful greenhouse gas that is thought to have contributed approximately 50% of the enhanced greenhouse effect of CO_2 since 1850 (Hansen *et al.*, 2000). Great importance is therefore placed on characterizing the various CH_4 sources and emission pathways to enable changes observed in atmospheric growth rate to be better understood. Methane has received considerable recent attention as satellite and airborne measurements have yielded an unexpected spatial distribution of sources with strong emission plumes identified over tropical forests, many of which are seasonally flooded (Frankenberg *et al.*, 2005; Miller *et al.*, 2007). In many such regions, there continues to be a discrepancy between bottom-up emissions-based estimates and top-down inverse or satellite-based estimates of the CH_4 source (Frankenberg *et al.*, 2008).

The recent reporting of novel aerobic CH_4 production pathways in plants (Keppler *et al.*, 2006) has been invoked as a potential explanation for discrepancies between low, bottom-up and high, top-down satellite-based or inverse method derived estimates of CH_4 sources. However, the large size estimates initially made for this hypothesized source (up to $\sim 240 \text{ Tg CH}_4 \text{ yr}^{-1}$ (Keppler *et al.*, 2006)) have since been revised down to between zero and 85 Tg CH_4 (e.g. Howelling *et al.*, 2006; Dueck *et al.*, 2007). Here we provide evidence for a more straightforward and almost completely overlooked pathway for CH_4 emissions from anaerobic soils and sediments that may account for at least part of the discrepancy in the way CH_4 sources and balances are estimated.

Emission of CH_4 produced in anaerobic soils to the atmosphere is the largest individual source of CH_4 . Fluxes are thought to be controlled by three transport mechanisms: diffusion, ebullition and vascular transport in herbaceous plants, all of which are measurable using established small-scale enclosure methods. In peatlands, aerenchyma in sedges and

certain other vascular plants allows CH₄ to bypass an oxic 'acrotelm' layer at the top of the peat column (Joabsson *et al.* 1999). Without this escape route, methanotrophic bacteria in the acrotelm would consume a large proportion of produced CH₄. Aerenchyma tissue provides a diffusion pathway for oxygen, enabling sedges and other herbaceous wetland plants to maintain active roots in anoxic environments (Armstrong and Boatman, 1967). Similarly, flood-tolerant trees growing in soil with a high water table or exposed to periodically flooded conditions develop important adaptations that collectively facilitate oxygen supply to roots, thus preventing hypoxia (Kozlowski 1997). Such features are classically evident in trees such as mangrove and swamp cypress where morphological adaptations, principally aerial roots and pneumatophores, facilitate gaseous exchange, and from which CH₄ emission has been measured (Vann and Megonigal 2003; Purvaja *et al.*, 2004). However, many other tree species also grow under flooded conditions without overtly exhibiting such morphological adaptations. The trees prevent hypoxia via the formation of aerenchyma in root tissue and hypertrophied lenticels on tree stems and submerged roots (Kozlowski 1997).

A relatively unexplored pathway of CH₄ flux from such wetland trees is the transfer of anaerobically-produced CH₄ from soils into roots via the aqueous phase, and emission to the atmosphere via transpiration. This mechanism is similar to that described for N₂O transport in *Fagus sylvatica*, (e.g. Pihlatie *et al.* 2005) and, like N₂O, there are no physical or chemical barriers to the entry of apolar dissolved CH₄ into roots during uptake of soil water. The CH₄-bearing water can be transported through xylem tissue, ultimately releasing CH₄ to the troposphere via leaf stomata or lenticels. This emission pathway may be an important mechanism for mediating CH₄ flux from wetland- or fine-textured soils where moisture levels allow for the existence of anaerobic microsites (Teh *et al.*, 2005).

The only previous report of CH₄ flux from mature, non-pneumatophore-forming trees was made for Japanese ash (*Fraxinus mandshurica* var. *japonica* (Terazawa *et al.*, 2007)).

Other species have not been investigated in mature trees, despite the morphological features thought to be responsible for CH₄ emission being reported for a wide range of tree species (e.g. Kozłowski 1997).

Here we report findings from a study to examine the potential for a new family of mature freshwater wetland trees to serve as a conduit for trace gas transport to the atmosphere. Common or Black Alder (*Alnus glutinosa*) are the most common tree species in riparian forests and are found throughout Europe, Russia and Siberia and are also commonly found in the Northeast USA and Eastern Canada. Taken together with the work of Terazawa *et al.* (2007), our study is designed to examine the potential for a wide variety of wetland trees to collectively serve as a significant source of CH₄ to the atmosphere.

Methods

We examined CH₄ emission from *Alnus glutinosa* trees at Flitwick Moor nature reserve in Bedfordshire, United Kingdom (52°00' N, 00°28' W). Three mature trees having diameters of 10 to 30 cm at a height of 30 cm above the forest floor were selected for the study. The site consists of a peat soil which is spring fed which allows the water-table to remain consistently at or just above the soil surface. Three site visits were made from May to October 2006 to monitor changes in headspace CH₄ concentration with time in temporary gas-exchange chambers that enclosed the entire stem section 30 cm above the forest floor for 3 hours. The chambers were constructed from four clear acrylic walls, each having dimensions of 500 x 350 x 6 mm (Figure 1). The headspace was defined by enclosing the volume with transparent sheets of gas-impermeable FEP film (Adtech Ltd.) to form the top and bottom of the enclosure. Strips of closed cell foam (3-cm wide) were attached to the stem 35 cm apart, providing an effective seal with the tree on which the FEP film could be attached. Measurements were initiated at approximately midday, and headspace samples (3 x 20 ml) were drawn via a septum into 3 gas-tight syringes fitted with 3-way valves at $t = 0$,

60, 120, 180 minutes. The samples were transported to the lab within 48 hours for analysis using a Cambridge AI gas chromatograph (GC) equipped with a flame ionisation detector (FID) with a measured $[\text{CH}_4]$ standard error of 23 ppbv. The minimum measurable flux using our approach was $2.4 \mu\text{g CH}_4 \text{ m}^{-2} \text{ hr}^{-1}$. Soil CH_4 fluxes were measured during the October sampling from 3 chambers positioned on the ground surface using established methods (Gauci *et al.*, 2002). Fluxes were estimated using linear regression analysis of the change in headspace methane concentration with time. The phenological status of the sampled trees was also recorded at each site visit. During the May site visit, alder tree leaves had yet to emerge on sampled trees. In June leaves had fully emerged and in October the trees remained in full leaf.

Results and Discussion

Significant tree stem CH_4 emission was measured during each sampling visit (linear regression analysis, $P < 0.05$). Fluxes (expressed per unit area of stem) ranged from a mean of $4.1 \mu\text{g CH}_4 \text{ m}^{-2} \text{ hr}^{-1}$ in May to $101 \mu\text{g CH}_4 \text{ m}^{-2} \text{ hr}^{-1}$ in early October (Table 1), the peak month measured. Stem fluxes measured in October were about 20% of soil fluxes measured at the same time ($536 \mu\text{g CH}_4 \text{ m}^{-2} \text{ hr}^{-1}$). They were also of the same order of magnitude as CH_4 fluxes measured from mature *Fraxinus mandshurica* sp. in Japan (Terazawa *et al.*, 2007). In contrast to the Japanese study, CH_4 fluxes from Flitwick Moor showed a pronounced seasonal pattern, being an order of magnitude smaller in spring than summer and autumn.

Collectively, our data and those of Terazawa *et al.*, (2007) suggest that many wetland trees that lack outwardly obvious morphological features commonly associated with flood adaptation and gas transport may emit CH_4 that has been produced in anaerobic soils. The data further suggest that estimates of CH_4 flux from forested wetlands, whether seasonally or

151 permanently flooded, are likely to underestimate the emission of anaerobically-produced CH₄
152 if trees are excluded from measurement. For example, the development of hypertrophied
153 lenticels in response to flooding has been reported for 15 angiosperm and 22 gymnosperm
154 species (Kozłowski 1997 and references therein) and root aeration via either pressurised gas
155 transport or stem photosynthesis has been measured in genera of *Alnus* and *Salix* as well as
156 *Betula pubescens*, *Populus tremula* and *Taxodium distichum* (Grosse *et al.* 1996; Armstrong
157 and Armstrong 2005). These morphological adaptive features to flooding, together with our
158 findings of CH₄ emission from the stems of mature *Alnus glutinosa* and fluxes reported by
159 Terazawa *et al.* (2007), suggest that gaseous and/or aqueous phase transport of CH₄ (and
160 possibly other trace gases) may be common among trees adapted to wet soils in both
161 temperate and tropical forested wetland ecosystems.

162 The development of aerenchyma has also been reported in the roots of tree species that
163 normally experience prolonged saturated conditions in central Amazonian várzeas (De
164 Simone *et al.* 2002). This area is particularly interesting because it has been the site of
165 numerous soil chamber-based CH₄ flux measurements (e.g., Bartlett *et al.*, 1988, 1990; Crill
166 *et al.*, 1988; Devol *et al.*, 1988; Wassmann *et al.*, 1992; Engle & Melack, 2000), all of which
167 excluded tree stems. Scaling up these chamber-based estimates of methane emission
168 consistently results in lower regional CH₄ estimates than top-down flight data estimates
169 (Miller *et al.*, 2007).

170 Evidence therefore suggests that this ‘woody plant pathway’ first proposed by Rusch
171 and Rennenberg (1998) may be important in forested wetland ecosystems and could have
172 implications for global CH₄ emission inventories. Given that 60% of Earth's wetlands are
173 forested (Matthews and Fung 1987) and that the majority of CH₄ flux studies have used
174 chamber sampling methods that exclude trees, this mechanism may represent an important
175 uncharacterised component of terrestrial CH₄ flux. Omission of this pathway from process

models may result in an underestimation of total CH₄ emissions from global wetlands.

The ‘fourth pathway’ of stem methane emission (in addition to pore water diffusion, herbaceous aerenchymatous transport, and ebullition) may help to reconcile differences between smaller, emission-based (‘bottom up’) estimates of the global CH₄ source (Matthews and Fung 1987; Aselman and Crutzen 1989; Cao *et al* 1996) and larger atmospheric chemistry-based inverse (‘top down’) estimates (e.g. Houweling *et al* 1999).

Acknowledgements

The work was funded by NERC grant number NER/B/S/2003/00842 to VG, DJG and NBD. The authors would like to thank C. Rooney and G. Howell for field and laboratory assistance. NBD would like to thank Villanova University, USA, for hosting her as a guest scientist during the initiation of this research. The authors would like to thank the contributions of two anonymous reviewers which have improved the manuscript.

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274 **Figure and Table Captions:**

275

276 **Figure 1** Experimental methods for measuring methane fluxes from stems of *Alnus glutinosa*

277

278 **Table 1** Tree stem (T) and forest floor (S) methane emission rates for Flitwick Moor in 2006.

279 R^2 values are derived from linear regression analysis. SD = standard deviation

Table 1 Tree stem (T) and forest floor (S) methane emission rates for Flitwick Moor in 2006. R^2 values are derived from linear regression analysis. SD = standard deviation.

Date	Chamber (T = Tree S = Soil)	Tree Diameter /m	CH ₄ flux ($\mu\text{gCH}_4\text{m}^{-2}\text{hr}^{-1}$)	R^2 of regression (all $P < 0.05$, $n=6$)	Mean CH ₄ flux $\mu\text{gCH}_4\text{m}^{-2}\text{hr}^{-2}$ (SD)
<i>3rd May</i>	T1	0.3	4.37	0.99	4.1 (0.8)
	T2	0.18	4.78	0.97	
	T3	0.16	3.22	0.83	
<i>8th June</i>	T1	0.3	35.7	0.70	65 (59)
	T2	0.18	26.4	0.97	
	T3	0.16	132	0.90	
<i>12th October</i>	T1	0.3	92.6	0.71	101 (22)
	T2	0.18	126.5	0.85	
	T3	0.16	84.2	0.93	
	S1		328	0.87	536 (268)
	S2		441	0.79	
	S3		838	0.86	

Figure 1 Experimental methods for measuring methane fluxes from stems of *Alnus glutinosa*.