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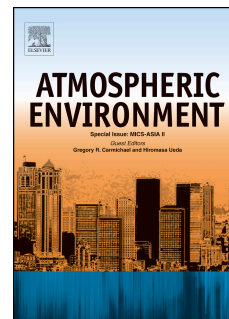
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1 Short Communication – FINAL REVISION

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5 Woody stem methane emission in mature wetland alder trees

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

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32

33 **Abstract**

34

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

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

51 Introduction

52 Wetlands form the largest source of methane (CH₄) to the atmosphere, a powerful greenhouse
53 gas that is thought to have contributed approximately 50% of the enhanced greenhouse effect
54 of CO₂ since 1850 (Hansen *et al.*, 2000). Great importance is therefore placed on
55 characterizing the various CH₄ sources and emission pathways to enable changes observed in
56 atmospheric growth rate to be better understood. Methane has received considerable recent
57 attention as satellite and airborne measurements have yielded an unexpected spatial
58 distribution of sources with strong emission plumes identified over tropical forests, many of
59 which are seasonally flooded (Frankenberg *et al.*, 2005; Miller *et al.*, 2007). In many such
60 regions, there continues to be a discrepancy between bottom-up emissions-based estimates
61 and top-down inverse or satellite-based estimates of the CH₄ source (Frankenberg *et al.*,
62 2008).

63 The recent reporting of novel aerobic CH₄ production pathways in plants (Keppler *et*
64 *al.*, 2006) has been invoked as a potential explanation for discrepancies between low, bottom-
65 up and high, top-down satellite-based or inverse method derived estimates of CH₄ sources.
66 However, the large size estimates initially made for this hypothesized source (up to ~240 Tg
67 CH₄ yr⁻¹ (Keppler *et al.*, 2006)) have since been revised down to between zero and 85 Tg CH₄
68 (e.g. Howelling *et al.*, 2006; Dueck *et al.*, 2007). Here we provide evidence for a more
69 straightforward and almost completely overlooked pathway for CH₄ emissions from anaerobic
70 soils and sediments that may account for at least part of the discrepancy in the way CH₄
71 sources and balances are estimated.

72 Emission of CH₄ produced in anaerobic soils to the atmosphere is the largest
73 individual source of CH₄. Fluxes are thought to be controlled by three transport mechanisms:
74 diffusion, ebullition and vascular transport in herbaceous plants, all of which are measurable
75 using established small-scale enclosure methods. In peatlands, aerenchyma in sedges and

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

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

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

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

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

111 **Methods**

112 We examined CH₄ emission from *Alnus glutinosa* trees at Flitwick Moor nature
113 reserve in Bedfordshire, United Kingdom (52°00' N, 00°28' W). Three mature trees having
114 diameters of 10 to 30 cm at a height of 30 cm above the forest floor were selected for the
115 study. The site consists of a peat soil which is spring fed which allows the water-table to
116 remain consistently at or just above the soil surface. Three site visits were made from May to
117 October 2006 to monitor changes in headspace CH₄ concentration with time in temporary
118 gas-exchange chambers that enclosed the entire stem section 30 cm above the forest floor for
119 3 hours. The chambers were constructed from four clear acrylic walls, each having
120 dimensions of 500 x 350 x 6 mm (Figure 1). The headspace was defined by enclosing the
121 volume with transparent sheets of gas-impermeable FEP film (Adtech Ltd.) to form the top
122 and bottom of the enclosure. Strips of closed cell foam (3-cm wide) were attached to the
123 stem 35 cm apart, providing an effective seal with the tree on which the FEP film could be
124 attached. Measurements were initiated at approximately midday, and headspace samples (3
125 x 20 ml) were drawn via a septum into 3 gas-tight syringes fitted with 3-way valves at t = 0,

126 60, 120, 180 minutes. The samples were transported to the lab within 48 hours for analysis
127 using a Cambridge AI gas chromatograph (GC) equipped with a flame ionisation detector
128 (FID) with a measured [CH₄] standard error of 23 ppbv. The minimum measurable flux
129 using our approach was 2.4 µg CH₄ m⁻² hr⁻¹. Soil CH₄ fluxes were measured during the
130 October sampling from 3 chambers positioned on the ground surface using established
131 methods (Gauci *et al.*, 2002). Fluxes were estimated using linear regression analysis of the
132 change in headspace methane concentration with time. The phenological status of the
133 sampled trees was also recorded at each site visit. During the May site visit, alder tree leaves
134 had yet to emerge on sampled trees. In June leaves had fully emerged and in October the
135 trees remained in full leaf.

136

137 **Results and Discussion**

138 Significant tree stem CH₄ emission was measured during each sampling visit (linear
139 regression analysis, P < 0.05). Fluxes (expressed per unit area of stem) ranged from a mean
140 of 4.1 µg CH₄ m⁻² hr⁻¹ in May to 101 µg CH₄ m⁻² hr⁻¹ in early October (Table 1), the peak
141 month measured. Stem fluxes measured in October were about 20% of soil fluxes measured
142 at the same time (536 µg CH₄ m⁻² hr⁻¹). They were also of the same order of magnitude as
143 CH₄ fluxes measured from mature *Fraxinus mandshurica* sp. in Japan (Terazawa *et al.*,
144 2007). In contrast to the Japanese study, CH₄ fluxes from Flitwick Moor showed a
145 pronounced seasonal pattern, being an order of magnitude smaller in spring than summer and
146 autumn.

147 Collectively, our data and those of Terazawa *et al.*, (2007) suggest that many wetland
148 trees that lack outwardly obvious morphological features commonly associated with flood
149 adaptation and gas transport may emit CH₄ that has been produced in anaerobic soils. The
150 data further suggest that estimates of CH₄ 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

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

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

182

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273 transport. *Global Biogeochemical Cycles* 6, 3–13.

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

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

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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	

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