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The contribution of trees to ecosystem methane emissions in a temperate forested wetland

SUNITHA R. PANGALA¹, EDWARD R.C. HORNIBROOK², DAVID J. GOWING¹ and VINCENT GAUCI⁴

¹Centre for Earth, Planetary, Space and Astronomical Research (CEPSAR), Department of Environment, Earth and Ecosystems, The Open University, Walton Hall, Milton Keynes MK7 6AA, UK, ²School of Earth Sciences, Bristol Biogeochemistry Research Centre & Cabot Institute, University of Bristol, Will Memorial Building, Queen’s Road, Bristol BS8 1RJ, UK

Abstract

Wetland-adapted trees are known to transport soil-produced methane (CH₄), an important greenhouse gas to the atmosphere, yet seasonal variations and controls on the magnitude of tree-mediated CH₄ emissions remain unknown for mature forests. We examined the spatial and temporal variability in stem CH₄ emissions in situ and their controls in two wetland-adapted tree species (Alnus glutinosa and Betula pubescens) located in a temperate forested wetland. Soil and herbaceous plant-mediated CH₄ emissions from hollows and hummocks also were measured, thus enabling an estimate of contributions from each pathway to total ecosystem flux. Stem CH₄ emissions varied significantly between the two tree species, with Alnus glutinosa displaying minimal seasonal variations, while substantial seasonal variations were observed in Betula pubescens. Trees from each species emitted similar quantities of CH₄ from their stems regardless of whether they were situated in hollows or hummocks. Soil temperature and pore-water CH₄ concentrations best explained annual variability in stem emissions, while wood-specific density and pore-water CH₄ concentrations best accounted for between-species variations in stem CH₄ emission. Our study demonstrates that tree-mediated CH₄ emissions contribute up to 27% of seasonal ecosystem CH₄ flux in temperate forested wetland, with the largest relative contributions occurring in spring and winter. Tree-mediated CH₄ emissions currently are not included in trace gas budgets of forested wetland. Further work is required to quantify and integrate this transport pathway into CH₄ inventories and process-based models.

Keywords: Alnus glutinosa, Betula pubescens, methane, seasonal variation, stem CH₄ emissions, tree-mediated CH₄ emissions, wetlands

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Introduction

Wetlands cover only c. 5% of the Earth’s ice-free land surface (Prigent et al., 2007) yet they constitute the largest individual source of methane (CH₄) to the atmosphere. Wetlands comprised of open waters, herbaceous vegetation and wetland-adapted trees release as much as 170 Tg CH₄ a⁻¹ globally (Bergamaschi et al., 2007); however, there is large uncertainty associated with this estimate (Bousquet et al., 2006; Dlugokencky et al., 2011), which has hindered efforts to accurately predict ecosystem feedbacks to climate change. Furthermore, there have been contradictory explanations for recently observed variations in atmospheric CH₄ concentration (Aydin et al., 2011; Kai et al., 2011; Simpson et al., 2012) with recent reports invoking new and previously unaccounted for sources of CH₄ in forested wetlands (Martinson et al., 2010; Bastviken et al., 2011; Pangala et al., 2013), principally in tropical and subtropical regions. An improved understanding of the magnitude and relative contributions of different wetland CH₄ production processes and transport pathways is essential to constrain uncertainties and accurately predict wetland ecosystem response to future changes in climate.

Tree-mediated CH₄ emission, which involves release of CH₄ via stem and/or leaf surfaces from trees adapted to soil anoxia, arguably is one of the least studied CH₄ emission pathways. In contrast, herbaceous plant-mediated CH₄ emissions have been investigated for over two decades across a range of wetland types, including rice paddies (e.g. Holzapfel-Pschorr & Seiler, 1986; van Bodegom et al., 2001), tropical wetlands (e.g. Bartlett et al., 1988) and boreal peatlands (e.g. Whiting & Chanton, 1992; Waddington et al., 1996; Alm et al., 1999). These efforts have led to a basic understanding
of species differences, seasonal variation and controls on CH$_4$ emissions (e.g. Schütz et al., 1991; Chanton et al., 1995; Whiting & Chanton, 1996; Grünfeld & Brix, 1999), and consequently, herbaceous plant-mediated CH$_4$ emissions generally are well represented in ecosystem CH$_4$ flux estimates. Similarly, a substantial body of literature also exists on diffusion and ebullition pathways, resulting in these pathways being adequately represented in flux estimates for a wide range of ecosystems (e.g. Bartlett et al., 1988; Engle & Melack, 2000; Comas et al., 2007; Coulthard et al., 2009).

Early studies by Rusch & Rennenberg (1998) of wetland-adapted seedlings (Alnus glutinosa) revealed significant CH$_4$ emissions via stem surfaces and a relationship between flux strength and the quantity of CH$_4$ present in the root zone. A small number of subsequent studies of other tree species have consistently reported the presence of tree-mediated CH$_4$ emissions and attempted to identify controls on the process (e.g., Vann & Megonigal, 2003; Garnet et al., 2005). Despite these preliminary studies and strong evidence for tree-mediated CH$_4$ emissions, direct evidence of their contribution to wetland CH$_4$ budget has been lacking until recently (Rice et al., 2010; Pangala et al., 2013). Rice et al. (2010) estimated that wetland trees contribute up to 10% of the global CH$_4$ budget based upon data obtained from a mesocosm experiment. More recently, Pangala et al. (2013) demonstrated that trees are the largest source of CH$_4$ in a south-east Asian tropical peat forest, contributing up to 87% of total ecosystem CH$_4$ flux. However, to date, most studies of tree-mediated CH$_4$ flux have been laboratory based and conducted using mesocosms or microcosms (e.g. Rusch & Rennenberg, 1998; Garnet et al., 2005). In situ investigations are few in number and generally conducted over a short-term period (e.g. Terazawa et al., 2007; Gauci et al., 2010; Pangala et al., 2013). Further work is required to characterise the annual contributions of tree-mediated emissions relative to other gas evasion processes in wetlands, in particular, given that c. 60% (Matthews & Fung, 1987; Prigent et al., 2007) of wetlands globally are forested.

Spatial and seasonal variations in CH$_4$ emissions from northern wetlands are driven by variations in temperature, water-table depth and plant species composition (e.g. Whiting & Chanton, 1992; Christensen et al., 2000, 2003; Ström et al., 2003, 2005). Seasonal variations in tree-mediated CH$_4$ emissions and their primary drivers are yet to be characterised in forested wetlands.

In this study, we measured CH$_4$ emissions from trees and peatland surface (ponded hollows and hummocks) in a temperate forested wetland to quantify the relative contribution of different CH$_4$ transport pathways to total annual flux. Measurements of tree-mediated CH$_4$ emissions were focused on two wetland-adapted tree species, Alnus glutinosa and Betula pubescens, which were dominant at the site and occur extensively throughout forested riparian wetlands in the northern hemisphere. We hypothesised that: (i) wetland trees adapted to anoxic soil transport significant quantities of CH$_4$ via stems; (ii) CH$_4$ emission rates from trees vary seasonally due to changes in environmental variables that regulate tree growth and soil production of CH$_4$ and (iii) CH$_4$ emission characteristics vary between tree species because of differences in morphological adaptations.

Materials and methods

Site description

Methane emissions were measured in a temperate spring-fed forested peatland (c. 59 ha) located in Flitwick, Bedfordshire, UK (52$^\circ$0'N, 0$^\circ$28'W), about 45 miles north of London. This site has been previously described by Gauci et al. (2010) but briefly consists of a valley mire system of alkaline fen, acidic spring mosaic fens, meadows and wet woodlands. The average summer and winter temperatures are 15.5 $^\circ$C and 3.9 $^\circ$C, respectively, and the 10-year (2002–2012) precipitation average is 647 mm yr$^{-1}$ with 576 mm yr$^{-1}$ falling during the study period. The observation period from April 2011 to April 2012 was atypical because of a longer than normal growing season, a late autumn and a short and relatively warm winter.

The wetland is dominated by Alnus glutinosa (L.) Gaertner and Betula pubescens (Ehrh), with A. glutinosa more abundant in some parts of the wetland. The forest understorey consists of large stands of Phragmites australis, Typha latifolia, Holcus lanatus, Lythrum salicaria, Scrophularia auriculata, Alisma plantago-aquatica, Potamogeton spp., Carex spp. and Sphagnum spp. The system is spring-fed water, and the water-table level is near the soil surface year round, including within hummocks. River Flit, which is susceptible to occasional flooding, flows through the peatland.

Study plot

A 20 $\times$ 30 m plot was selected on the south-east side of the peatland, which contained 10- to 20-m-tall mature A. glutinosa and B. pubescens. In addition, P. australis and Carex spp. were abundant and present predominantly on hummocks. Locations of trees and the distribution of hollows and hummocks (vegetated and nonvegetated) were mapped within the plot. The relative distribution of hummocks and hollows was approximately 65% and 35%, respectively, and remained unchanged during the observation period. The stem diameter of mature trees ($\geq$ 7 cm) was measured at 1.3 m height (diameter at breast height, DBH), and the basal diameter was estimated by measuring the stem diameter at 10 cm above the soil surface. The distribution, stem and basal diameters of...
young trees ≤ 7 cm also were measured and included in the tree density inventory for the site. Approximately 92% of trees measured had a DBH ≤ 20 cm (Fig. S1).

Phenology within the study plot was regularly documented during the observation period. New understory vegetation started to appear in late April 2011, grew to full height (1.2 m) in May and entered dormancy in November. Fully expanded tree leaves appeared at the beginning of May 2011 on both A. glutinosa and B. pubescens. Autumnal leaf senescence occurred in November 2011 followed by vegetative dormancy between December 2011 and February 2012. Early bud burst and understory vegetation growth began in March 2012, and fully expanded leaves were observed by the end of April 2012.

Measurement of CH₄ flux

Static chambers were used to measure CH₄ emissions from tree stems, and peatland hollows and hummocks (vegetated and nonvegetated) fortnightly from April 2011 to April 2012 with the exception of January and February 2012 when measurements were conducted monthly. Static chambers used to measure CH₄ emissions from nonvegetated hollows and hummocks (six each) were constructed of polyvinyl chloride (PVC) pipe (30 cm diameter × 25 cm height) permanently inserted 5 cm into peat. A transparent lid (30 cm diameter × 1.5 cm thickness) equipped with a pressure regulator and sampling port was used to seal the soil camber prior to collection of gas samples. Measurement of CH₄ emissions from vegetated hollows and hummocks (four each) required taller soil chambers, which were constructed of circular aluminium wire mesh sandwiched between two sheets of gas-impermeable fluorinated ethylene propylene (FEP; Adtech Polymer Engineering Ltd., Stroud, UK) film (36 cm diameter × 140 cm height) permanently inserted 10 cm into the soil surface, enclosing both vegetation and the soil surface. An acrylic lid (36 cm diameter × 0.8 cm thickness) fitted with a pressure regulator and sampling port was used to seal the static chambers. The two herbaceous species (mix of P. australis and Carex spp.) enclosed within all 8 chambers grew to a full length of 1.2 m; therefore, there was no need to bend or cut the vegetation to enclose them within the chamber. The average ratio of P. australis to Carex spp. within each of the chamber was 50:50. The soil chambers were installed two weeks prior to the experiment and were left in place until the end of the experiment. Soil chambers were closed carefully to minimise disturbance. Data that displayed evidence of induced ebullition at t = 0 were rejected (~8% of samples collected).

Static chambers used to measure CH₄ emissions from tree stems have been described previously by Pangala et al. (2013). Briefly, cubical static chambers (30 × 30 × 30 cm) were constructed from gas-impermeable acrylic sheets and fitted with a gas sampling port and pressure regulator. The cubes were cut into half and connected with hinges and spring clips. A round central opening (20 cm diameter) was cut into the chamber to accommodate the tree stem. An airtight seal was formed between the chamber and the tree stem using closed cell neoprene foam strips (5-cm wide) and gas-impermeable FEP plastic sheets.

Methane emissions from stems of A. glutinosa and B. pubescens (eight trees each) that had a DBH in the range of 7 to 19 cm were measured at three stem heights in August 2011 to assess (i) spatial variability of stem CH₄ emissions within the plot, and (ii) controls affecting CH₄ emissions. Secondly, during September 2011, November 2011, January 2012 and April 2012, CH₄ emissions were measured at 10-cm intervals between 5 and 175 cm stem height from young trees (stem diameter of 3–7 cm) of both A. glutinosa and B. pubescens (8 trees each) to compare stem fluxes with mature trees. These data also were used to estimate stem CH₄ emissions from young trees in the study plot during summer, autumn, winter and spring because young trees were not included in the fortnightly measurements.

The concentration of CH₄ in pore water was measured using pore-water equilibrators installed at five locations within the study plot: two in hummocks and three in hollows. Briefly, gas-permeable silicon tubing (6 mm diameter) was wrapped in 5-cm interval slots cut into a PVC column (80 cm long) at 11 depths (5, 10, 15, 20, 25, 30, 40, 50, 60, 70 and 80 cm). The internal volume of silicon tube was ~17 cm³ for each 5-cm interval in contact with pore water. Both ends of the silicon tube were fitted with a barbed nylon reduction fitting to which a length of gas-impermeable polyurethane tubing (3 mm diameter) was attached and extended to the ground surface. One end of the polyurethane tube was fitted with a three-way gas-tight valve that enabled gas to be sampled from specific depths using gas-tight syringes. The second polyurethane tube was sealed with a nylon plug. The thick-walled PVC column tube provided the necessary surface and support for the silicon tubes to be installed at specific depth. The pore-water samplers were installed in May 2011, and the replicates of 4.5 ml gas samples were extracted from 11 soil depths monthly beginning July 2011. The gas samples were transferred and stored in evacuated 4.5 ml Exetainers® (Labco Ltd, Ceredigion, UK).

During August 2011, when stem CH₄ emissions were measured from an additional 30 trees, temporary pore-water samplers were installed within a 1-m radius of the trees that were sampled. The design of the temporary pore-water samplers and method of their use have been reported previously by Gauci et al. (2002). The pore-water samplers were used to
extract soil water from 20 to 30 cm soil depth for analysis of CH₄ concentration.

**CH₄ analysis**

The gas samples extracted from the static chambers (t = 5, 20, 40, 60, 80 min for tree stems and t = 5, 15, 30, 45 min for peat surface) using a plastic syringe (30 ml) were transferred immediately into pre-evacuated 12 ml Exetainers® (Labco Ltd., Ceredigion, UK). The gas samples extracted from the pore-water equilibrators were transferred into pre-evacuated 4.5 ml Exetainers® and all the gas samples were analysed for CH₄ within two weeks after sampling. Methane concentrations from gas samples obtained *in situ* were determined using a cavity ring down laser spectroscopy (Los Gatos Research RMA-200 Fast Methane Analyser; Los Gatos Research, Mountain View, CA, USA) modified to employ the ‘closed-loop’ principle described by Baird et al. (2010). The CH₄ emission rate was calculated using the rate of increase of CH₄ within the chamber, the CH₄ emitting surface area and the volume of the chamber. Fluxes calculated from gas samples that displayed either nonlinearity or step changes in gas concentration (~12% of gas samples analysed) were included but classified as emissions via ebullition. Pore-water CH₄ concentrations were calculated using Henry’s gas law. Methane fluxes per plot for each month were estimated as described by Pangala et al. (2013) using the net CH₄ fluxes measured in this study (monthly average) and the corresponding CH₄ emitting surface area. Therefore, the stem CH₄ emission rates per tree varied monthly.

**Environmental parameters**

Two thermocouples (Type T Thermocouple, RS® components Ltd., Corby, UK) were installed at 30 cm soil depth at two locations within the plot, each with hollows and hummocks, which recorded soil temperature. The soil–water temperature at the surface was also recorded at two locations in hollows (64K HOBO Pendant Temp Logger, Temcon Instrumentation, West Sussex, UK). Additionally, on each measurement occasion, air temperature, relative humidity and atmospheric pressure also were recorded using a hand-held probe (TR-73U thermo recorder, T & D Corporations, Nagano, Japan). Within the study plot, two piezometers (2.5-cm-diameter PVC pipes with 0.5-cm holes drilled at various intervals) were installed each within hollows and hummocks, and water-table levels were measured manually on each measurement occasion. Due to the upwelling hydrology, the water-table always stayed at the surface in the hollows (average of 3.5 cm above soil surface) and fluctuations were small in hummocks, with a maximum water-table drawdown of 14.5 cm measured in the hummocks (May 2011). Incident photosynthetically active radiation (PAR) was recorded three times during each sampling visit using a quantum sensor (Skye Instruments Ltd., Powys, UK) at a location c. 750 m from the study plot and forest canopy.

An increment borer that had an internal diameter of 5.1 mm (Hagløf Sweden AB, Långsele, Sweden) was used to extract wood samples at stem heights of 35, 75, 115 and 130 cm from *B. pubescens* (26 samples) and *A. glutinosa* (20 samples). The wood samples were collected after flux measurements were concluded in June 2012. Specific density of the wood was determined based upon its dry mass and volume as described by Pangala et al. (2013).

**Statistical analysis**

Statistical analyses were performed using SPSS v.19 (SPSS, Chicago, IL, USA) at a significance level of P ≤ 0.05. All values presented are mean ± SE. Data sets were first tested for the following: (i) normal distribution using a Shapiro–Wilk test; (ii) equality (homogeneity) of variances in different subpopulations using Levene’s test; and (iii) outliers using box-plots. Methane emissions from vegetated hollows and the three stem heights for *B. pubescens* were not normally distributed. A variety of data transformations were attempted, but none was able to meet the criteria for normal distribution. Consequently, the nonparametric Kruskal–Wallis test was used to compare averages of CH₄ flux from each pathway for each sampling visit followed by group comparisons using the Mann–Whitney U-test. Relationships between CH₄ emissions from stem and soil surfaces (vegetated and nonvegetated), and independent variables were analysed using univariate regression analysis. Only data collected when both dependant and independent variables were measured were included in this analysis. This resulted in all dependant variables meeting the assumption of regression analysis. Stepwise multiple regression analysis was used to identify best explanatory variables. Soil temperature and air temperature were highly correlated (R = 0.98), and therefore, only soil temperature at 30 cm depth was used in multiple regression analysis. Means of stem CH₄ emissions measured from an additional 30 trees in August were compared using a t-test. Relationships between stem diameter, wood-specific density, pore-water CH₄ concentration and stem CH₄ emissions were examined using regression analysis and a mixed model.

**Results**

**Stem CH₄ emissions**

Both *A. glutinosa* and *B. pubescens* released significant quantities of CH₄ via stems during the observation period. Fluxes varied significantly with time (P < 0.001) and between the two species (Fig. 1). Stem CH₄ emission rates were similar for trees located in hollows and hummocks (P = 0.164 for *A. glutinosa*; P = 0.279 for *B. pubescens*), and flux measurements from an additional 30 trees in August 2011 further support this observation. In August, average CH₄ fluxes from hollows and hummocks, respectively, were 188 ± 21.4 μg m⁻² h⁻¹ and 174 ± 8.64 μg m⁻² h⁻¹ for *B. pubescens* (n = 18) and were 178 ± 6.3 μg m⁻² h⁻¹ and 166 ± 13.8 μg m⁻² h⁻¹ for *A. glutinosa* (n = 12). Stem CH₄ fluxes measured from
the additional 30 trees did not differ significantly ($P = 0.332$ for *A. glutinosa*; $P = 0.418$ for *B. pubescens*) during August from CH$_4$ emission rates for the eight trees investigated throughout the study, supporting the assumption that the latter trees were representative of the study plot as a whole.

Stem CH$_4$ emission rates varied seasonally ($P < 0.0001$) and differed between *A. glutinosa* and *B. pubescens*. Stem CH$_4$ flux from *A. glutinosa* increased from April to June, stayed relatively constant between July and October, increased in November to a peak of 194 ± 21 µg m$^{-2}$ h$^{-1}$, and then decreased from late December to March. Although emissions from *B. pubescens* displayed similar patterns to *A. glutinosa* between April and October, rates of stem emission decreased in November and then remained relatively constant until March (Fig. 1). In general, stem CH$_4$ emission rates from both the tree species were lower in winter. The highest rates of stem CH$_4$ flux from *A. glutinosa* and *B. pubescens* and the timing of their occurrence were 194 ± 21 (November) and 216 ± 22 µg m$^{-2}$ h$^{-1}$ (July), respectively (Fig. 1).

Stem CH$_4$ emissions from *B. pubescens* were significantly higher in the summer (June–August) than from *A. glutinosa*, while the opposite was true in autumn (September–November) and winter (December–February). Furthermore, the seasonality of stem emissions was more pronounced from *B. pubescens* than *A. glutinosa*. Stem CH$_4$ emission rates from *A. glutinosa* were 175 ± 14 µg m$^{-2}$ h$^{-1}$ in summer, which was 1.5 times greater than winter emission rates (118 ± 16 µg m$^{-2}$ h$^{-1}$). However, summer stem fluxes (203 ± 21 µg m$^{-2}$ h$^{-1}$) from *B. pubescens* were 3.8 times greater than winter stem fluxes (53.5 ± 10 µg m$^{-2}$ h$^{-1}$).

Stem CH$_4$ emissions within and between the two tree species were highly variable. In general, the rates of stem CH$_4$ flux decreased with stem height in both the tree species. However, the relationship between stem emission rate and stem height varied for *B. pubescens* throughout the observation period. Between April and October, a power function relationship between stem height and CH$_4$ flux was observed for both the tree species. Between November and March, stem emissions were related linearly to stem sampling height in *B. pubescens*, while *A. glutinosa* continued to display a power function relationship (Table S1). Stem CH$_4$ emissions measured at the fourth stem height (140–170 cm above the peatland surface) were consistent with relationships observed for the three lower sampling heights.

Methane fluxes from young *A. glutinosa* and *B. pubescens* were significantly greater than emission rates from mature trees during all months (Fig. 2) although the magnitude of difference varied for the two species (Fig. 2). In September, young *A. glutinosa* released 2242 ± 347 µg m$^{-2}$ h$^{-1}$ from stem heights 5 to 35 cm stem height c.14 times more than mature *A. glutinosa* (160 ± 14 µg m$^{-2}$ h$^{-1}$ from 20 to 50 cm stem height). Similarly, young *B. pubescens* released c. 6.5 times more CH$_4$ than mature trees, averaging 1248 ± 228 µg m$^{-2}$ h$^{-1}$ and 194 ± 16 µg m$^{-2}$ h$^{-1}$, respectively, for the same stem height intervals. The size of the difference in stem CH$_4$ emission rates between mature and young trees decreased for *B. pubescens* in November and January but stayed relatively constant for *A. glutinosa* during the same period. Notably, the relationship between CH$_4$ emission rate and stem height was linear for young trees of both species (Table S2) in contrast to the power function relationship observed in mature trees.
Nontree CH$_4$ emission pathways

Vegetated soil surfaces (hollows and hummocks) released significantly more CH$_4$ than nonvegetated surfaces during the growing season (Fig. 3). Methane emissions from hollows (vegetated and nonvegetated) showed a similar pattern, flux rates were more variable due to their response to fluctuations in water-table levels. Methane emission rates from vegetated soil surfaces (hollows and hummocks) were greater than tree-stem CH$_4$ fluxes from May to November but were significantly smaller in winter (December–February).

Ecosystem contributions

Hollows (nonvegetated) and hummocks (vegetated) contributed the most to total CH$_4$ flux from the study plot because of their high rates of CH$_4$ emission and larger surface area (Table 1). The contributions of tree-mediated CH$_4$ emissions (based upon lowest 3 m of stem) varied from 5.73 ± 0.59 g ha$^{-1}$ day$^{-1}$ in summer to 2.08 ± 0.31 g ha$^{-1}$ day$^{-1}$ in winter. However, estimating tree CH$_4$ emissions based upon an average tree height of 10 m and the linear and power function relationships in Table 1 increased the flux rates to 10.8 ± 1.1 g ha$^{-1}$ day$^{-1}$ in summer and 4.23 ± 0.58 g ha$^{-1}$ day$^{-1}$ in winter. Inclusion of CH$_4$ emissions from young trees increased rates further to 13.2 ± 1.34 g ha$^{-1}$ day$^{-1}$ in summer and 5.65 ± 0.9 g ha$^{-1}$ day$^{-1}$ in winter (Table 1). The relative contributions of each CH$_4$ emission pathway to total ecosystem flux varied with season. The proportion of herbaceous plant-mediated CH$_4$ flux (vegetated hollows and hummocks) decreased from summer to winter. In contrast, tree-mediated CH$_4$ emissions displayed the opposite trend, increasing from summer (8.8–13.5%) to winter (17–25% winter; young trees included in both estimates) with the largest contribution from trees occurring during spring (11–27%; Table 1). Notably, summer CH$_4$ emissions comprise the bulk of total annual CH$_4$ emissions (~40.7%), whereas winter emissions constitute only 9%.

Environmental controls on CH$_4$ emissions

Pore-water CH$_4$ concentration varied significantly with soil depth and differed between hollows and hummocks (Fig. 4; three months averaged). Pore-water CH$_4$ concentration in hummocks was lower than in hollows, but measurable concentrations were observed at 15 to 70 cm beneath the hummock surface at all times. The concentrations between 5 and 20 cm depth differed with variations in water-table level. In hollows, the highest and lowest concentrations were measured...
between 15 to 30 cm and 60 to 80 cm, respectively. Pore-water CH4 concentrations between 5 and 40 cm depth in hollows fluctuated seasonally and variations in hollows between 20 and 40 cm depth related positively with changes in soil temperature. In contrast, CH4 concentrations between 5 and 15 cm depth in hollows did not change notably with shifts in soil temperature but instead increased in November and remained relatively high until February. The increase in shallow pore-water CH4 concentration in November coincided with an increase in CH4 emissions from A. glutinosa stems and nonvegetated hollows. Pore-water CH4 concentration measured between 20 and 25 cm soil depth in hollows accounted for a significant proportion of seasonal variation in CH4 emissions from A. glutinosa (75%), B. pubescens (69%), vegetated (72%) and nonvegetated hollows (48%) (Table S3). Variations in CH4 emission rate from vegetated hummocks was explained largely by variations in pore-water CH4 concentration at 10–20 cm and 40–50 cm soil depth (Table S3).

Soil and air temperature were important regulators of seasonal variations in CH4 emissions from all pathways (Tables S3, S5, S6). Emission rates from hollows (vegetated and nonvegetated), hummocks (vegetated) and stems of A. glutinosa and B. pubescens varied exponentially in relation to changes in soil and air temperature (Table S3). Water-table fluctuations exerted a strong control on CH4 flux from hummocks (vegetated and nonvegetated) but had a minor influence on CH4 emissions from A. glutinosa and B. pubescens, and hollows (vegetated and nonvegetated) due to a consistently high water-table level. The results of stepwise multiple regression analysis varied for the different CH4 emission pathways (Table S5, S6) but in general showed that soil temperature and pore-water CH4 concentration explained most of the seasonal variation in CH4 flux rate for all pathways, including tree-stem CH4 emissions. Changes in water-table level explained variations in CH4 emission rates only from hummocks (vegetated and nonvegetated).

Wood-specific densities at four stem heights in A. glutinosa and B. pubescens are listed in Table 2. The contribution of stem diameter, wood-specific density and pore-water CH4 concentrations to differences in CH4 emissions from A. glutinosa and B. pubescens stems is reported in Table S4. Wood-specific density generally increased with stem height but varied among tree species, and was statistically different between A. glutinosa and B. pubescens at the three stem heights that were sampled. However, pore-water CH4 concentrations and stem diameters were similar between the two tree species but varied within trees of the same species. Stem diameter and wood-specific density were negatively related to stem CH4 emission rates from both tree species. The relationship was strongest at 20 to 50 cm stem height (Table S4). Pore-water CH4 concentration was positively related to stem CH4 fluxes from A. glutinosa and B. pubescens. While wood-specific density and pore-water CH4 concentration mostly explained between-species differences, all three variables (pore-water CH4 concentration, wood-specific density and stem diameter) contributed to within-species variations in stem CH4 flux (Table S4, S5, S7).

Discussion
Our findings demonstrate that tree-mediated CH4 emissions contribute significantly to ecosystem CH4 flux (6

![Fig. 3 Mean CH4 fluxes (±SE) from hollows (vegetated; n = 4), hummocks (vegetated; n = 4), hollows (nonvegetated; n = 6) and hummocks (nonvegetated; n = 6).](image)
Table 1 Estimated ecosystem contributions (flux per plot and percentage contributions*) of CH₄ emissions from *A. glutinosa*, *B. pubescens*, hollows and hummocks (vegetated and nonvegetated)

<table>
<thead>
<tr>
<th></th>
<th>Ecosystem CH₄ emissions (g ha⁻¹ day⁻¹) (%)*</th>
<th>Alnus glutinosa</th>
<th>Betula pubescens</th>
<th>Tree-mediated emissions</th>
<th>Hollows</th>
<th>Hummocks</th>
<th>Hollows (vegetated)</th>
<th>Hummocks (vegetated)</th>
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<tr>
<td>Mature trees</td>
<td>1.73 ± 0.16 (5.7)</td>
<td>4.11 ± 0.39 (11.9)</td>
<td>1.62 ± 0.17 (6.4)</td>
<td>3.53 ± 0.36 (10.9)</td>
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<td>0.20 ± 0.87 (0.7-1)</td>
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<tr>
<td>Young trees</td>
<td>1.63 ± 0.21 (10.4)</td>
<td>1.63 ± 0.21 (15.7)</td>
<td>0.43 ± 0.11 (6.4)</td>
<td>0.43 ± 0.11 (10.9)</td>
<td>2.06 ± 0.32 (16.8)</td>
<td>2.06 ± 0.32 (26.6)</td>
<td>10.9 ± 3.01 (33.9-30)</td>
<td>0.20 ± 0.87 (0.6-0.6)</td>
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<tr>
<td><strong>Summer</strong></td>
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<tr>
<td>Mature trees</td>
<td>2.29 ± 0.20 (2.5)</td>
<td>5.43 ± 0.48 (5.7)</td>
<td>3.44 ± 0.39 (3.8)</td>
<td>5.35 ± 0.62 (5.6)</td>
<td>5.73 ± 0.59 (6.4)</td>
<td>10.8 ± 1.10 (11.4)</td>
<td>37.3 ± 10.2 (41.5-39)</td>
<td>2.51 ± 2.03 (2.8-3)</td>
</tr>
<tr>
<td>Young trees</td>
<td>1.66 ± 0.14 (4.3)</td>
<td>1.66 ± 0.14 (7.3)</td>
<td>0.68 ± 0.1 (4.5)</td>
<td>0.68 ± 0.1 (6.2)</td>
<td>2.35 ± 0.24 (8.8)</td>
<td>2.35 ± 0.24 (13.5)</td>
<td>37.3 ± 10.2 (40.4-38.3)</td>
<td>2.51 ± 2.03 (2.7-6)</td>
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<tr>
<td><strong>Autumn</strong></td>
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<tr>
<td>Mature trees</td>
<td>2.30 ± 0.21 (2.9)</td>
<td>5.46 ± 0.50 (6.4)</td>
<td>2.52 ± 0.22 (3.1)</td>
<td>5.25 ± 0.33 (6.1)</td>
<td>4.81 ± 0.43 (6.0)</td>
<td>10.7 ± 1.04 (12.5)</td>
<td>39.8 ± 10.0 (49.8-46)</td>
<td>1.56 ± 1.47 (1.9-2)</td>
</tr>
<tr>
<td>Young trees</td>
<td>2.18 ± 0.18 (5.4)</td>
<td>2.18 ± 0.18 (8.6)</td>
<td>0.43 ± 0.09 (3.6)</td>
<td>0.43 ± 0.09 (6.4)</td>
<td>2.62 ± 0.27 (9)</td>
<td>2.62 ± 0.27 (15.1)</td>
<td>39.8 ± 10.0 (48.2-45)</td>
<td>1.56 ± 1.47 (1.9-1.8)</td>
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<tr>
<td><strong>Winter</strong></td>
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<tr>
<td>Mature trees</td>
<td>1.57 ± 0.20 (8.1)</td>
<td>3.73 ± 0.48 (17.6)</td>
<td>0.51 ± 0.11 (2.7)</td>
<td>0.51 ± 0.11 (2.4)</td>
<td>2.08 ± 0.31 (10.9)</td>
<td>4.23 ± 0.58 (20)</td>
<td>11.3 ± 3.57 (59.3-53)</td>
<td>0.09 ± 0.10 (0.5-0)</td>
</tr>
<tr>
<td>Young trees</td>
<td>1.18 ± 0.22 (13.2)</td>
<td>1.18 ± 0.22 (21.3)</td>
<td>0.23 ± 0.12 (3.6)</td>
<td>0.23 ± 0.12 (3.2)</td>
<td>1.42 ± 0.32 (16.8)</td>
<td>1.42 ± 0.32 (24.6)</td>
<td>11.3 ± 3.57 (56-50.7)</td>
<td>0.09 ± 0.10 (0.4-0.4)</td>
</tr>
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*The percentage contribution range for hollows and hummocks (vegetated and nonvegetated) represents the individual contributions when 3 m and 10 m of the stem height is considered. The percentage contributions listed under young trees represent the contributions of young and mature trees combined.
to 22% excluding and 9 to 27% including young trees; Table 1) and that the largest contribution from trees occurs during spring and winter (Table 1). The proportion of ecosystem flux is notable given that trees occupy less than 2% of the ground area in the study plot. A. glutinosa and B. pubescens stems released significant quantities of CH₄ throughout the year, but the magnitude and pattern of the emissions differed between the two species. Wetland vegetation has long been known to impact CH₄ emissions by influencing its production, consumption and transport (Whiting & Chanton, 1992; Christensen et al., 2003; Ström et al., 2003); however, the role of wetland-adapted trees in mediating CH₄ flux has only been recognised during the last decade (Rusch & Rennenberg, 1998; Vann & Megonigal, 2003; Gauci et al., 2010; Rice et al., 2010; Pangala et al., 2013, 2014). This study provides the first assessment of the contributions of trees to ecosystem CH₄ flux over a full annual cycle in relation to other CH₄ emission pathways.

Methane emissions through herbaceous plants situated in hollows and hummocks was the largest contributor to ecosystem CH₄ flux during the growing season (Table 1), consistent with other studies that have noted the importance of CH₄ transport via herbaceous plants (e.g. van der Nat et al., 1998; Grünfeld & Brix, 1999; Ström et al., 2003). Phragmites australis and Carex spp., the two dominant graminoid species at Flitwick Moor (our study site), are well known for their capacity to mediate CH₄ emissions (Morrissey et al., 1993; Ding et al., 2005; Bergström et al., 2007). These plants covered 35% of the soil surface within the study plot in comparison with c. 2% for A. glutinosa and B. pubescens. The large proportion of area covered by P. australis and Carex spp. will have contributed to their dominance of ecosystem CH₄ flux, but the species also are known for their propensity to transport CH₄ via well-developed aerenchyma and to release labile root exudates enhancing rates of soil CH₄ production (Sutton-Grier & Megonigal, 2011). Consequently, late spring and summer CH₄ emissions were dominated by herbaceous plant-mediated transport (> 48%), while a greater quantity of CH₄ flux was derived from nonvegetated hollows during autumn and winter. The shift in ecosystem contribution from the different sources likely was due to autumnal senescence of P. australis and Carex spp., which reduced CH₄ transport via herbaceous plants (van der Nat et al., 1998).

This study and findings reported by Pangala et al. (2013) provide conclusive evidence for the significance of tree-mediated CH₄ emissions in both tropical and temperate ecosystems. Interestingly, rates of tree-mediated CH₄ flux per hectare from mature trees were similar in the two studies (5.7 ± 0.6, summer fluxes in this study; 6.7 ± 0.7 g ha⁻¹ day⁻¹, Pangala et al., 2013), but the contribution of trees to ecosystem CH₄ flux differed greatly (9 to 27%, this study; 62 to 87%, Pangala et al., 2013). The difference results from the small contribu-

tion of nontree CH$_4$ emission sources in the tropical peat swamp forest where the understorey lacked the abundance of herbaceous plants present at Flitwick Moor.

Methane flux from nonvegetated hollows also contributed significantly to total ecosystem flux in Flitwick Moor because the upwelling hydrology of the system maintained a high water-table level, restricting methanotrophy to a thin (<5 cm) vadose zone. In contrast, up to 90% of soil CH$_4$ was oxidised in the SE Asian tropical forested wetland where the unsaturated zone was much thicker (0–50 cm), resulting in only small quantities of CH$_4$ being released at the soil surface (Couwenberg et al., 2010). Under such conditions, the contribution of tree-mediated CH$_4$ emissions to ecosystem flux became dominant (Pangala et al., 2013). Notably, measurements at Flitwick Moor demonstrating that young trees emit substantially more CH$_4$ than mature trees suggest that the contribution of tree-mediated CH$_4$ emissions to ecosystem flux estimated by Pangala et al. (2013) is a conservative estimate for tropical peat swamp forest as it was based primarily on measurements from mature trees.

Seasonal variations in stem CH$_4$ emission rates from $A$. glutinosa and $B$. pubescens were similar to emission characteristics for soil surfaces at Flitwick Moor and more generally, seasonal patterns reported for other temperate wetlands: CH$_4$ fluxes were highest in summer and low but detectable in winter (e.g. Dise et al., 1993; Alm et al., 1999; Kankaala et al., 2005). Tree-stem CH$_4$ emissions appear to be regulated strongly by temperature (Table S3, S5), which influences both soil CH$_4$ production (Hosono & Nouchi, 1997) and plant productivity (Kim et al., 1999; Kankaala et al., 2005). This assertion is supported by (i) a strong positive relationship between stem CH$_4$ emission rates and temperature (both soil and air) and pore-water CH$_4$ concentrations between 20 and 25 cm depths; (ii) enhanced CH$_4$ emission rates from $A$. glutinosa and $B$. pubescens in spring and early summer during the rapid growth phase; and (iii) decreased CH$_4$ emission rates during the dormant season (Fig. 1).

Methane emission rates from wetlands are influenced by water-table depth (e.g. Moore & Roulet, 1993; Waddington et al., 1996; Elberling et al., 2011). As a result, pore-water CH$_4$ concentrations measured in hummocks were smaller than hollows, which appeared to affect CH$_4$ emission rates at the peat surface (vegetated and nonvegetated hummocks), possibly as a result of greater CH$_4$ oxidation due to a larger aerobic unsaturated zone. However, water-table fluctuations had a minimal impact on stem CH$_4$ emission rates. The upwelling hydrology of Flitwick Moor is likely responsible for relatively high concentrations of CH$_4$ in hummocks between 30 and 40 cm depth (Fig. 4), which may have supported persistent CH$_4$ emissions from trees rooted in the hummocks. Methane may have entered extensive networks of lateral and vertical roots within the zone of CH$_4$ production or have been intercepted during upward migration via diffusion. Waddington et al. (1996) have demonstrated that the magnitude of plant-mediated CH$_4$ emissions under varying water-table conditions is dependent on plant rooting depth; however, the absence of a difference between stem CH$_4$ flux rates for trees rooted in hollows vs. hummocks, despite a higher pore-water CH$_4$ concentration in hollows (between 20 and 40 cm depth; Fig. 4), suggests that tree rooting depth and networks alone are insufficient to explain our observations at Flitwick Moor.

Environmental conditions experienced by $A$. glutinosa and $B$. pubescens were similar, but the two species displayed different rates and patterns of CH$_4$ flux, suggesting that physiological factors specific to tree species may influence stem CH$_4$ fluxes. For example, seasonal variation in stem CH$_4$ flux was less pronounced in $A$. glutinosa and an additional period of elevated CH$_4$ emission rates was observed in autumn after leaf loss when air and soil temperature were relatively low. An autumnal peak in CH$_4$ flux was not observed in $B$. pubescens and emissions decreased immediately after leaf loss (Fig. 1). The relationship between the stem height and CH$_4$ emissions also varied between $A$. glutinosa and $B$. pubescens with a linear relationship occurring for part of the year in the latter but not the former species (Table S1). Differences in stem CH$_4$ emission characteristics could result from a number of factors known to influence both pre- and postproduction of CH$_4$ (Sutton-Grier & Megonigal, 2011), involving complex above- and below-ground interactions.

First, different CH$_4$ transport mechanisms in plants, more specifically passive diffusion vs. convective transport, can influence rates of plant-mediated CH$_4$ flux (Whiting & Chanton, 1996; Sutton-Grier & Megonigal, 2011). Species-specific differences in modes of CH$_4$ transport are well documented for a number of wetland plants (e.g. Brix et al., 1992; Chanton et al., 1993; van der Nat et al., 1998; Kim et al., 1999). It is possible that $A$. glutinosa and $B$. pubescens utilise different CH$_4$ transport mechanisms or a combination of passive diffusion and convective transport. Pangala et al. (2014) reported no distinct diurnal pattern in stem CH$_4$ emissions from four-year-old $A$. glutinosa, suggesting that stem gas transport was driven mainly by passive diffusion. The young saplings also exhibited no relationship between stem CH$_4$ emissions and leaf physiological parameters. Gas transport primarily via passive diffusion through stems of $A$. glutinosa is consistent with the
absence of a decrease in stem CH$_4$ emissions after leaf loss. The sudden decrease in emissions from B. pubescens after leaf loss (Fig. 1) suggests physiological control on gas transport, most likely convective/transpiration driven gas transport; however, further work is required to identify the precise mechanisms involved.

Second, wetland vegetation can attenuate CH$_4$ production in the rhizosphere due to release of O$_2$ that stimulates methanotrophy (van der Nat et al., 1998; Jobasson & Christensen, 2001) and regeneration of alternate electron acceptors (Bouchard et al., 2007; Sutton-Grier & Mégonigal, 2011). A number of studies report the influence of different types of vegetation on CH$_4$ production and emission (e.g. Reay et al., 2005; Menyailo et al., 2012). Considering the limitations of this study (measurements not performed within close proximity of the trees during the observation period and no direct measurements of CH$_4$ oxidation), further work is required to identify the tree species-specific effect on CH$_4$ oxidation.

Third, release of labile carbon compounds and nutrients via root exudation, root turnover and leaf litter stimulating CH$_4$ production (Brix et al., 2001; Ström et al., 2003, 2005; Dorodnikov et al., 2011) is known to differ between different wetland plants. The type of organic compounds (e.g. organic acids, sugars, acetate, phenolics and amino acids), quality (e.g., C/N in root exudates, root tissues and leaf litter; Sjögersten et al., 2010; Sutton-Grier & Mégonigal, 2011) and quantity of these substrates also are known to be species dependent (Grayston et al., 1997). Although no direct evidence of species-specific differences in the release of substrates is available from this study, an increase in stem CH$_4$ emissions and pore-water CH$_4$ concentrations at 5–30 cm soil depth observed during autumn (Fig. 4) likely was due to increased substrate availability through autumal leaf fall and root turnover (Wilson et al., 1989).

Lastly, differences in wetland vegetation architecture (e.g. their anatomical, morphological and physiological properties) can affect both CH$_4$ production via differences in O$_2$ and carbon inputs (Grünfeld & Brix, 1999; Colmer, 2003a,b; Dinsmore et al., 2009) and CH$_4$ transport (Greenup et al., 2000; Henneberg et al., 2012). Species-specific differences in above- and below-ground biomass are known to be better predictors of CH$_4$ flux than abiotic factors (Greenup et al., 2000; Henneberg et al., 2012). Wood-specific density at different stem heights varied within and between the two tree species but on average was greater for B. pubescens than A. glutinosa. Nonetheless, wood-specific density displayed an inverse relationship with stem CH$_4$ emissions from both tree species at three sampling heights (Tables S4, S7). These observations offer a useful link between tree species traits and stem CH$_4$ emissions, suggesting that trees with increased pore spaces (i.e. as indicated by lower wood density) transport more CH$_4$. Notably, if wood-specific density was the key factor controlling species differences in stem CH$_4$ emission rates, then flux from A. glutinosa should have exceeded that of B. pubescens at all times. Total annual CH$_4$ emissions from A. glutinosa were greater, but stem CH$_4$ fluxes were higher from B. pubescens both in summer and during the one-off sampling from additional trees in August, suggesting no single factor exerted a dominant control on emission characteristics in these two tree species.

Our results indicate that tree-stem CH$_4$ emissions are controlled by more than temperature and the concentration of CH$_4$ dissolved in pore water. Tree-mediated CH$_4$ emissions contributed up to 27% of ecosystem CH$_4$ flux with significant stem CH$_4$ emissions observed even during the leafless season. Moreover, emissions from young trees exceeded that of mature trees by orders of magnitude. These results highlight the need for further work to accurately characterise and fully integrate the tree emission pathway into ecosystem and global CH$_4$ budgets. Furthermore, the response of tree-mediated CH$_4$ emissions in a changing environment (e.g. increased rainfall, thawing permafrost and increasing atmospheric CO$_2$) warrants further investigation. This is because it has been suggested that warming northern latitudes will promote enhanced tree growth and colonisation (Hartley et al., 2012), enhancing rates of carbon mineralisation (Dorrepaal et al., 2009) and ultimately CH$_4$ production. Further mechanistic studies of all CH$_4$ emission pathways, including tree-mediated CH$_4$ emissions in forested wetlands, are imperative for understanding the future response of CH$_4$ dynamics in wetlands to climate change.

Acknowledgements

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References


**Supporting Information**

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** The range of tree diameters measured at 1.3 m stem height within the 20 × 30 m study plot.

**Table S1.** Relationship between stem CH4 fluxes from mature trees and stem sampling height above the peat surface for A. glutinosa and B. pubescens.

**Table S2.** Relationship between stem CH4 fluxes from young trees and stem sampling height above the peat surface for A. glutinosa and B. pubescens.

**Table S3.** Relationship, between seasonal variation of the individual CH4 emission pathways (µg m⁻² h⁻¹) and environmental parameters.

**Table S4.** Relationship between stem CH4 fluxes (µg m⁻² h⁻¹), stem diameter, wood-specific density and pore-water CH4 concentrations at 20 to 30 cm soil depth measured within 1 m radius of trees under investigation.

**Table S5.** Results of stepwise multiple regression analysis of stem-CH4 emissions from A. glutinosa and B. pubescens measured at 20 to 50 cm stem height and all the independent variables measured.

**Table S6.** Results of stepwise multiple regression analysis of CH4 emissions from hollows (nonvegetated and vegetated), hummocks nonvegetated and vegetated and all the independent variables measured.

**Table S7.** Results of multiple regression analysis of stem-CH4 fluxes from A. glutinosa and B. pubescens measured at three stem heights, stem diameter and wood-specific density measured at corresponding stem heights, and pore-water CH4 concentrations measured at 20 to 30 cm soil depths within 1 m radius of the trees under investigation.