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Methane fluxes from tree stems and soils along a habitat gradient

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Abstract Forests are major sources of terrestrial CH_4 and CO_2 fluxes but not all surfaces within forests have been measured and accounted for. Stem respiration is a well-known source of CO_2, but more recently tree stems have been shown to be sources of CH_4 in wetlands and upland habitats. A study transect was established along a natural moisture gradient, with one end anchored in a forested wetland, the other in an upland forest and a transitional zone at the midpoint. Stem and soil fluxes of CH_4 and CO_2 were measured using static chambers during the 2013 and 2014 growing seasons, from May to October. Mean stem CH_4 emissions were 68.8 ± 13.0 (mean ± standard error), 180.7 ± 55.2 and 567.9 ± 174.5 $\mu g\ m^{-2}\ h^{-1}$ for the upland, transitional and wetland habitats, respectively. Mean soil methane fluxes in the upland, transitional and wetland were − 64.8 ± 6.2, 7.4 ± 25.0 and 190.0 ± 123.0 $\mu g\ m^{-2}\ h^{-1}$, respectively. Measureable CH_4 fluxes from tree stems were not always observed, but every individual tree in our experiment released measureable CH_4 flux at some point during the study period. These results indicate that tree stems represent overlooked sources of CH_4 in forested habitats and warrant investigation to further refine CH_4 budgets and inventories.

Keywords Trees · Methane · Wetland forest · Upland forest · C cycle

Introduction

Atmospheric methane (CH_4) concentrations have increased from 700 ppb to over 1800 ppb since the beginning of the industrial revolution and presently contribute 0.7 W m^{-2} or 25% of radiative forcing (IPCC 2013). Although the net balance of CH_4 sources and sinks is well constrained compared to trace gases other than CO_2, the relative contributions of individual sources and sinks are less certain (Kirschke et al. 2013; Saunois et al. 2016). Such uncertainty has made it difficult to explain phenomena such as changes in the globally averaged atmospheric growth rate and isotopic concentration of methane (Aydin et al. 2011; Nisbet et al. 2016) and exposed the limits of our current mechanistic understanding of CH_4 cycling. In

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response, the past decade has been a period of prospecting for novel CH_4 sinks and sources that might better describe CH_4 cycle dynamics.

Wetlands have always been considered a source of CH_4, which is emitted across both the soil–atmosphere interface and plant surfaces (Dacey and Klug 1979). Emission from herbaceous wetland plants is facilitated by aerenchyma tissue which allows rapid rates of gas exchange between soils and the atmosphere, supporting aerobic respiration but also diffusion and mass flow of CH_4 past oxic zones at the soil surface.

While whole-ecosystem (plant and soil) CH_4 emissions have been measured extensively in wetlands dominated by herbaceous plants (Conrad 2007; Dacey and Klug 1979), such data are generally lacking from woody plants such as trees because their large stature makes plant flux measurements difficult. Early studies demonstrated CH_4 emissions from woody wetland tree roots (Pulliam 1992; Rusch and Rennenberg 1998), and seedlings (Garnet et al. 2005; Vann and Megonigal 2003), but field measurements to quantify tree CH_4 emissions were conducted only in the last decade (Gauci et al. 2010; Pangala et al. 2015; Terazawa et al. 2007). The results indicate that tree-mediated CH_4 emissions have been overlooked and may account for 60–87% of total CH_4 efflux in tropical wetlands (Pangala et al. 2013) and 20% in temperate wetlands (Gauci et al. 2010). Given that forested wetlands represent 53% of total wetlands (Fung et al. 1987), these numbers are significant, yet have not been included global earth systems models and budgets (Saunois et al. 2016).

Upland forests have been generally considered net sinks of CH_4 based upon the assumption that the only surface in a forest that interacts with CH_4 is the soil. Studies have shown that CH_4 can be produced inside upland trees (Bushong 1907; Covey et al. 2012; Zeikus and Ward 1974), however, few in situ direct measurements have attempted to quantify net fluxes from trees (Machacova et al. 2016; Maier et al. 2017; Pitz and Megonigal 2017; Wang et al. 2016; Warner et al. 2017). Wang et al. (2016) estimated that tree CH_4 flux was sufficient to offset the soil sink by 5–10% on an annual basis. Machacova et al. (2016) suggested that depending on soil moisture, Scots pine CH_4 emission account up to 35% of soil uptake. Clearly, tree–atmosphere trace gas interactions cannot be ignored and have to be included in calculating CH_4 budgets in forested ecosystems.

The processes by which CH_4 is produced and emitted to the atmosphere through trees are poorly understood. Data are insufficient for developing a generalized conceptual model of tree CH_4 emissions that captures the wide range of species, ecosystems, and conditions. Studies in wetland forests generally show a positive relationship between tree emission rates and water table depth (Gauci et al. 2010; Pangala et al. 2015; Terazawa et al. 2007), suggesting that CH_4 produced under saturated, anaerobic conditions in groundwater becomes entrained in the transpiration stream or diffuses into plant tissue, where it is transported and eventually emitted to the atmosphere. In contrast, a more diverse set of mechanisms have been proposed in upland forests, including non-soil CH_4 sources such as UV-driven aerobic production (Keppler et al. 2008; Vigano et al. 2008) and anaerobic biological production in trunks associated with heart rot (Covey et al. 2012) or non-structural carbohydrates (Covey et al. 2016). Megonigal and Guenther (2008) hypothesized that groundwater is also a source of CH_4 emitted by upland forest tree species. In this case, deep roots growing in CH_4-rich groundwater or anoxic soil microsites could entrain CH_4 and transport it to the atmosphere, bypassing the oxic soil horizons where it would otherwise be consumed by methanotrophs. A growing list of studies indicates that a variety of plant-mediated CH_4 sources exist and that all ecosystems contain some surfaces that have the potential to emit CH_4.

Gradient studies can reveal insights into some of these processes as they vary across wetland and upland forests, but studies reported thus far have focused on only one habitat. In this study, we conducted the first CH_4 flux measurement along a soil moisture gradient from wetland to upland at the same location. The close proximity of upland and wetland allows potentially confounding variables such as climate, past land use, and, to some extent, plant community composition to be kept constant. We directly measured CH_4 fluxes from soils and stems from a variety of tree species that are common in mid-Atlantic deciduous forests.

The goals of this study were to: (1) quantify CH_4 emissions from trees growing across a soil moisture gradient in a temperate forest ecosystem, (2) compare the relative contribution of soils and trees in upland and wetland forests, and (3) relate these fluxes to environmental factors. We also report stem and soil CO_2 fluxes because CO_2 emissions from stem respiration are relatively well understood and thus help to interpret the pattern of CH_4 fluxes.

Methods

Study site

The study was conducted at the Smithsonian Environmental Research Center (SERC), a property of 1072 hectares (2650 acres) on the western shore of Chesapeake Bay in Maryland. Much of the site is forested with smaller areas of brackish tidal wetlands and farmland. Forests have been recovering for 70–150 years from different land use and disturbance histories such as logging, wind damage, and agricultural abandonment (Higman 1968; Yesilonis et al. 2016), with small patches that have no known history of land use. Our main study plot was in an upland forest that was most likely grazed before the Civil War and then abandoned (Higman 1968). Today the forest is dominated by Tulip poplar (*Liriodendron tulipifera*), American beech (*Fagus grandfolia*), and several species of oaks (*Quercus* spp.), and hickories *Carya* spp. The species composition is typical of the mature stage of a Tulip poplar association (Brown and Parker 1994; Brush et al. 1980) with a closed canopy and very little understory. Mean rainfall is 1146 mm and mean annual temperature is 13.0 °C (Correll, Jordan, and Duls, unpublished data). The mean annual maximum temperature is 19.0 °C and the mean minimum temperature is 8.0 °C (NCDC database, Annapolis Police Bar Station).

Soils at SERC are predominately fine sandy loams or sandy loams. Physical and chemical characteristics of surface soils reflect past land use history, forest age and non-native earthworm activity (Yesilonis et al. 2016). Our transect crossed three soil associations, with the upland and transitional sections in the Collington–Annapolis series and the Collington–Wist–Westphalia series, respectively. Soils in the wetland section transect were in the Widewater–Issue series (Natural-Resources-Conservation-Service 2016).

We established an approximately 150 m long transect along a soil moisture gradient (location 38.8878, − 76.5624). The elevation difference between the two end points of the transect was approximately 6 m. Based upon soil characteristics, elevation, and water table depth we divided the transect into three habitat types: upland (100 m), transitional (25 m) and wetland (25 m). Thirty-two trees selected for the study belonged to nine species (Table 1). Based upon stem counts, these nine species make up 80% of the mature stand adjacent to the transect (Parker and Tibbs 2004). *Liquidambar styraciflua* (sweetgum) occurred in all three habitat types, with the remaining species present in one or two habitats.

Stem and soil chambers, and flux measurements

Tree and soil measurements were made between May and November in 2013 and between May and September in 2014 using the closed chamber technique. A total of 32 trees were fitted with opaque rectangular chambers modified from Ryan (1990), originally designed to measure stem respiration. In 2013, 21 chambers were installed across the transect. In 2014, 10 additional trees were fitted with chambers in order to expand the upland section of the transect. Each tree was paired with a soil gas flux chamber placed within 1 m of the base. Sampling rounds differed among habitats with the upland habitat sampled more frequently in 2014 than the other two habitats, because our main interest was to quantify upland methane stem fluxes. Rectangular stem chambers were constructed of acrylic, permanently fixed to stems 30–60 cm above the soil, and were secured to the stem using elastic shock cord. Each chamber was 28 cm in height with varying depths and widths depending on the tree size. To create an airtight seal, closed-cell neoprene foam was placed between the chamber edge and the stem, and sealed with dental mold to create a non-VOC seal (Examix^{TM}, GC America, Alsip, IL, USA). Soil flux chambers were constructed out of 30.5 cm-diameter (12″) schedule 80 PVC pipe, machined into a 10-cm high ring and placed 5 cm into the soil surface. All chambers were in place for a minimum of 1 week before taking flux measurements, and once mounted they remained in place for the duration of the study.

In the 2 years of study we used two different instruments to analyze the gas samples from the headspace of the flux chambers. Gas samples from the headspace of the flux chambers were analyzed by gas chromatography (GC) in 2013 and by a more accurate and precise portable off-axis integrated cavity output

Table 1 Tree species used in the stem flux measurements at the Smithsonian Environmental Research Center

Latin name	Common name	Number	DBH[a] (cm) Mean ± SD	Range of DBH (cm)	Habitats found[b]	Wetland designation[c,d]
Fraxinus pennsylvanica	Green ash	4	24.7 ± 4.7	17.8–28.5	W	FACW
Liquidambar styraciflua	Sweetgum	8	39.6 ± 14.3	21.9–62.5	U, T, W	FAC
Carya tomentosa	Mockernut hickory	1	22.8	–	U	NI
Fagus grandifolia	American beech	8	45.1 ± 14.4	16.1–56.2	U, W	FACU
Liriodendron tulipifera	Tulip poplar	4	60.7 ± 26.7	31.8–92.6	U, T	FACU
Quercus velutina	Eastern black oak	1	65.8	–	U	NI
Quercus michauxii	Swamp chestnut oak	3	60.4 ± 18.4	39.9–75.5	U, T	FACW
Carpinus caroliniana	American hornbeam, Ironwood	1	12.5	–	W	FAC
Acer rubrum	Red maple	2	31.1 ± 14.6	17.0–46.2	U, W	FAC

[a] DBH: Diameter at breast height

[b] *U* upland, *T* transitional, *W* wetland

[c] Indicator status: *FACW* facultative wetland, *FAC* facultative, *FACU* facultative upland, *NI* no indicator assigned

[d] *Source* Tiner and Burke (1995)

spectroscope (OA-ICOS) (Ultra-Portable Greenhouse Gas Analyzer, Los Gatos Research, Mountain View, CA, USA) in 2014. The two instruments provided different amounts of data for each flux which required a different approach, described below, for the statistical analysis.

In 2013, gas concentrations in air samples were determined using a gas chromatograph. After closing the chamber lid, 12 mL samples were withdrawn by syringe at 0, 15, 30, 45, and 60 min. The air samples were immediately transferred from the syringe to a 12 mL, nitrogen-flushed exetainers (Labco, UK). The gas samples were analyzed for CH_4 and CO_2 on a Varian GC-450, equipped with a flame ionization detector (FID) and a thermal conductivity detector (TCD). The FID had a precision of 0.120 ppm for CH_4 and the TCD had a precision 5 ppm for CO_2.

In 2014, gas concentrations were measured using a portable OA-ICOS. The instrument is capable of measuring CH_4 within a range of 0.01–100 ppm with a precision of 0.002 ppm at 0.5 Hz. The OA-ICOS can also measure CO_2 in a range of 200–20,000 ppm with a precision of 0.3 ppm. The OA-ICOS was used as a closed system: headspace gas was drawn from the chamber, measured non-destructively for CH_4 and CO_2 concentration, and returned to the flux chamber as described in Baird et al. (2010). Changes in CH_4 and CO_2 concentration were measured over periods of approximately 5–30 min, during which the system generated ≥ 150 observations.

In 2013, five concentration data points were collected for each flux measurement. We occasionally dropped a concentration data point for two reasons; soil CH_4 ebullition or poor quality data from the GC. If a data point was dropped due to poor quality data from the GC, both CH_4 and CO_2 data had to support that conclusion. The slope of gas concentration change over time was determined by linear regression (SAS® procedure Proc Reg). In every case, the slope was based on ≥ 4 observations. For a slope to be determined as a quality data point, the R^2 had to be greater than 0.90. If the R^2 of a slope was less than 0.90, then the slope and flux was considered to be zero.

In 2014, the OA-ICOS provided concentration data at a rate of 0.5 Hz which required us to use a slightly different treatment of the data. When calculating the slope of gas concentration change over time, we ignored the first 20% of the observations, as those may produce false readings associated with closing the lid. The slope of gas concentration change was determined as described above (SAS® procedure Proc Reg). In every case, the slope was based on ≥ 120 observations.

Gas flux was calculated using the following equation:

$$F = \frac{d[CH_4]}{dt} \times \frac{PV}{ART}$$

where F is the flux in µg m^{-2} h^{-1}, P is atmospheric pressure, T is temperature, R is the universal gas constant, A is the collar surface area and V is the volume of the air enclosed by the chamber. Air temperature was measured by the OA-ICOS unit on gas circulating between the unit and the chamber. Atmospheric pressure was based on a nearby weather station (< 1 km). Flux units are reported in µg m^{-2} h^{-1} or mg m^{-2} h^{-1} to allow for direct comparison with stem flux data published by others.

Environmental data

Soil moisture was measured using a FieldScout TDR (Spectrum Technologies Inc., Aurora, Illinois, USA). Soil temperature was measured with a digital thermometer at 10 cm. Weather data was collected on site from the SERC weather station (Campbell Scientific, Utah, USA).

Water table depth or groundwater elevation along the transect was monitored using several monitoring wells. Four 5.08 cm diameter wells were installed (three in 2013, and one was added in 2014). One was installed in the wetland, one in the transitional zone, and two in the upland. The fourth well was added to the upland in 2014 when new trees were added to the transect. Wells were constructed of 5.08 cm PVC and screened with 152 cm sections of PVC with 0.25 mm slot size. Number #1 sand was used as a screen pack. Water table depth was recorded manually during each sampling event using a water level meter (Model 102 Water Level Meter, Solinist, Georgetown, Ontario, Canada). Well #2 in the transitional was monitored during the growing seasons in 2013 and 2014 (Fig. 1) using a groundwater elevation logger (Aqua Troll 200, In-Situ Inc., Fort Collins, Colorado, USA).

Statistical analysis

All statistical analyses on flux data were conducted using R v3.1.2 (R Core Team 2014), except gas fluxes that were calculated using SAS. Methane flux rates were Box–Cox transformed after increasing all values until the minimum value in the data set was 10 µg m^{-2} h^{-1} to avoid negative values after log transformation. Means and standard errors presented in the text, figures, and tables were calculated using non-transformed data. *P* values below 0.05 were considered significant; those between 0.05 and 0.1 were considered marginally significant. In this paper we report data on CH_4 and CO_2 fluxes from three habitat types (upland, transitional, and wetland) in 2013 and 2014. Upland stem and soil CH_4 flux data from 2014 were reported in Pitz and Megonigal (2017) but were combined in the present study for statistical analysis.

The mean CH_4 and CO_2 fluxes were calculated for each tree and the respective soil chambers and analyzed for the effects of habitats using analysis of variance (ANOVA) followed by the Tukey's HSD test for multiple comparisons. Mixed effect models were conducted using the lme4 package to evaluate the correlations between environmental factors and stem CH_4 flux, soil CH_4 flux, stem CO_2 flux, and soil CO_2 flux. Sampling round and tree identity were treated as random effects. Fixed effects included were habitat for all analyses, tree species and diameter at breast height (DBH) for stem fluxes, DTW, soil moisture and soil temperature for CH_4 fluxes, and soil moisture and soil temperature for CO_2 fluxes. These factors were evaluated in the models following the above order. Likelihood ratio tests were used to access significant differences between nested models, and were followed by the Tukey's HSD test for multiple comparisons using the multcomp package (Hothorn et al. 2008).

Results

A total of 470 flux measurements were made during the study, 235 measurements of tree stems and 235 of soils. Every tree stem emitted measurable CH_4 at least once during the two seasons of monitoring. Net CH_4 production was detected in all but two stem CH_4 measurements. Stem CH_4 fluxes ranged from − 8.1 to 1900 µg m^{-2} h^{-1} in the upland habitat, − 16.4 to 2146.2 µg m^{-2} h^{-1} in the transitional habitat and − 157.1 to 3757.6 µg m^{-2} h^{-1} in the wetland habitat of the transect (Fig. 2a). Soil was generally a CH_4 sink in the upland where 97% of the measurements showed net consumption, and a source in the wetland where

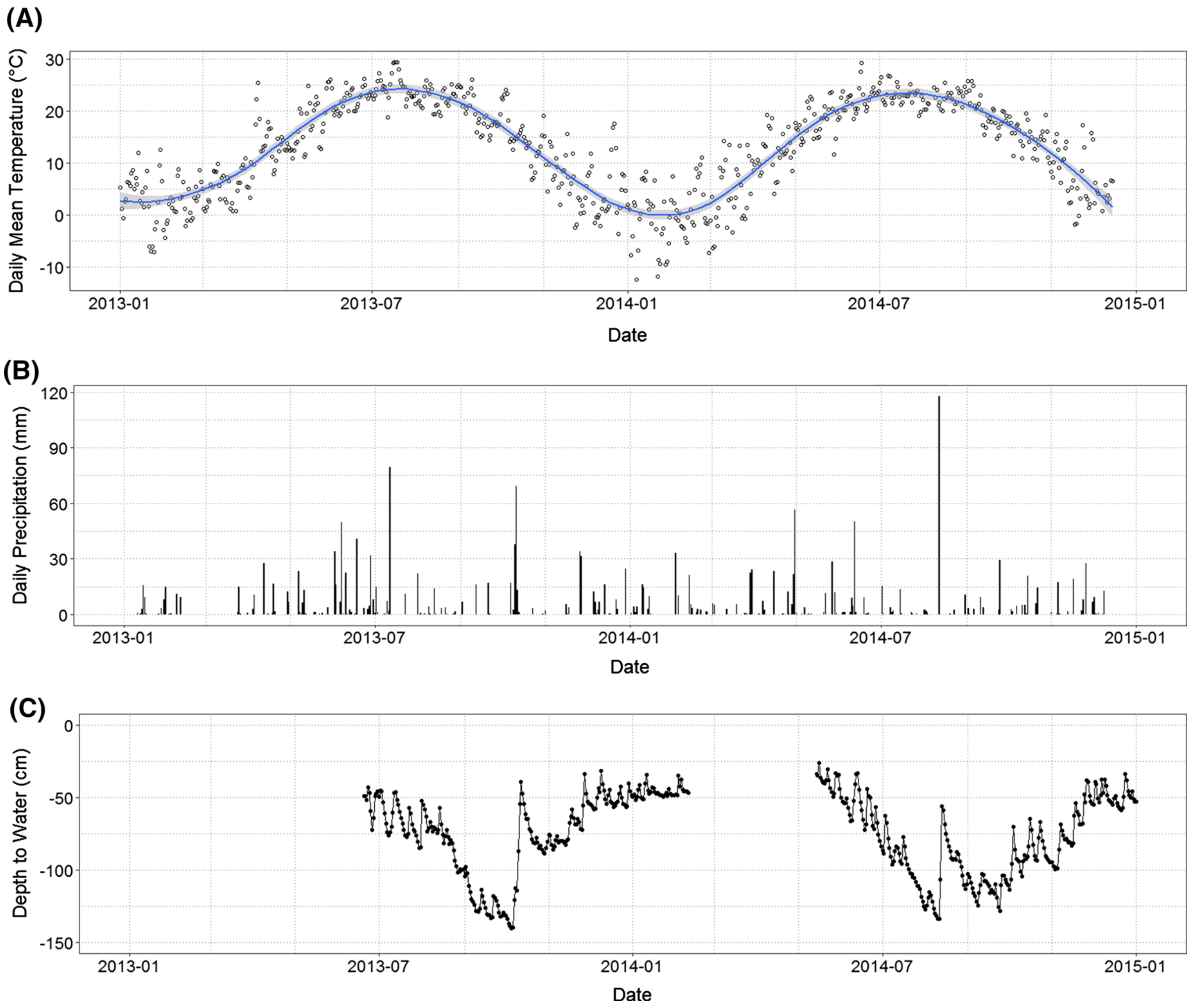

Fig. 1 Daily mean air temperature (**a**), daily precipitation (**b**) and groundwater elevation (**c**) at the SERC study site during 2013 and 2014. A continuous groundwater elevation data logger was placed in a well (Well 2) within the transitional habitat; groundwater elevation in the three other wells located within the study site were recorded manually (see "Methods"). The water table elevation data logger was removed for 3 months in the winter of 2014

80% of the measurements showed net production. The transitional segment of the transect fell in between, with 74% of the measurements demonstrating net consumption (Figs. 2a). Soil CH_4 fluxes ranged from $-$ 309.3 to 68.1 μg m^{-2} h^{-1} in the upland habitat, $-$ 167.4 to 651.4 μg m^{-2} h^{-1} in the transitional habitat and $-$ 33.3 to 4726.9 μg m^{-2} h^{-1} in the wetland habitat of the transect (Figs. 2a, 5b). Neither stem nor soil CH_4 fluxes exhibited a seasonal trend; rather high fluxes compared to average values were few and episodic (Fig. 2a).

Stem and soil CO_2 fluxes were consistently positive and three orders of magnitude higher than CH_4 fluxes (Fig. 2b). Both stem and soil CO_2 fluxes showed a seasonal trend with high values in the growing season and gradually declining values in the fall (Fig. 2b).

Combining all stem CH_4 measurements by habitat yielded mean (± SE) rates of 68.8 ± 13.0 μg m^{-2} h^{-1} (upland), 180.7 ± 55.2 μg m^{-2} h^{-1} (transitional) and 567.9 ± 174.5 μg m^{-2} h^{-1} (wetland). Stem CH_4 fluxes were significantly different in the three habitat types ($F_{2,\,29} = 5.80$, $P = 0.0076$), and were higher in wetlands than in uplands ($P = 0.006$, Tukey's HSD test) (Fig. 3a). Mean soil CH_4 fluxes were $-$ 64.8 ± 6.2 μg m^{-2} h^{-1} (upland), 7.4 ± 25.0 μg m^{-2} h^{-1} (transitional), and 190.0 ± 123.0 μg m^{-2} h^{-1}

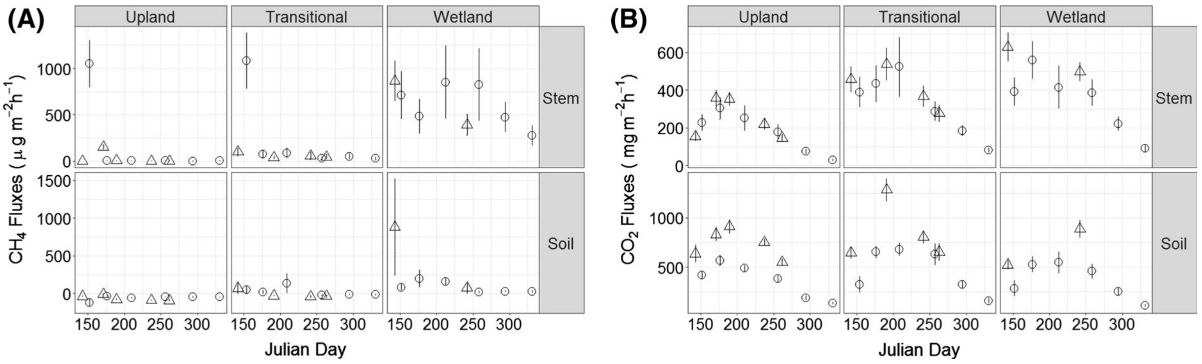

Fig. 2 Temporal changes of stem and soil CH_4 (**a**) and CO_2 (**b**) fluxes in the three habitat types. Data for 2013–2014 are combined. 2013 fluxes are represented by circles and 2014 fluxes are represented by triangles. Error bars are standard error. Note the different scales

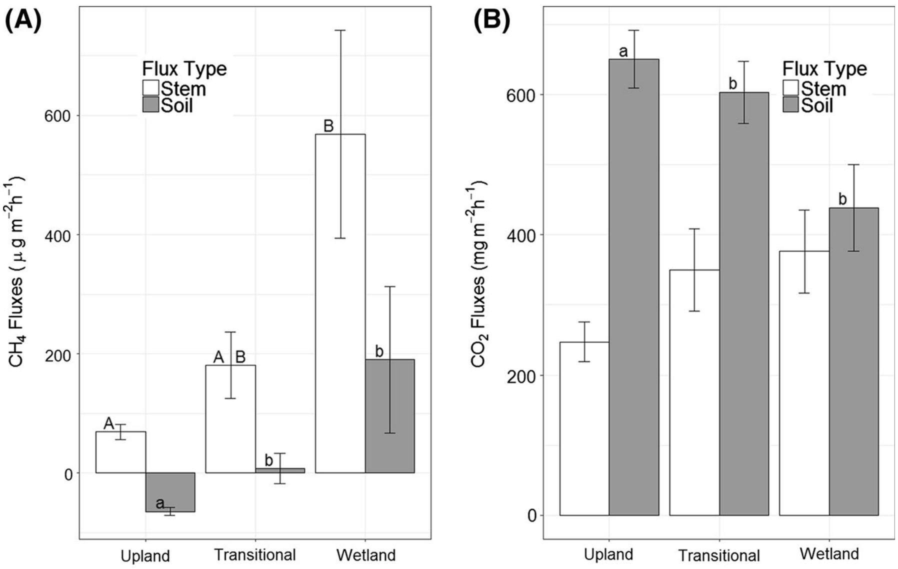

Fig. 3 Mean (± SE) stem and soil flux for CH_4 (**a**) and CO_2 (**b**) in the three habitat types at the SERC study site. Means with different letters are significantly different (Tukey's HSD, $P < 0.05$). Tests for stem and soil were run separately, and differences are indicated by upper and low case letters, respectively. Note the different units for CH_4 and CO_2 flux

(wetland). ANOVA showed significant differences in soil CH_4 flux among the three habitats types ($F_{2,\ 29} = 20.08$, $P < 0.001$), and significantly higher fluxes in wetland and transitional ($P < 0.001$ and $P = 0.012$, respectively) than in upland (Fig. 3a).

Stem CO_2 fluxes were only marginally affected by habitat types ($F_{2,\ 29} = 2.88$, $P = 0.073$). Contrary to CH_4, stem and soil CO_2 fluxes showed opposite trends across habitats. Soil CO_2 fluxes were significantly affected by habitat ($F_{2,\ 29} = 4.90$, $P = 0.015$), and were higher in upland than in wetland and transitional habitats ($P = 0.011$) (Fig. 3b). The significant effect of habitat was further supported by the mixed effect models (Table 2).

Stem CH_4 fluxes were marginally affected by tree species (Fig. 4), positively related to DBH and soil temperature, and negatively related to depth to water table (DTW) (Table 2). Soil CH_4 fluxes were negatively associated with DTW and positively associated with soil temperature. Both soil temperature and moisture showed significant positive relationships with stem and soil CO_2 fluxes (Table 2).

The range of stem CH_4 fluxes varied greatly by tree species (Online Resource 2). We detected the highest emissions from green ash and sweetgum, and the lowest from oak and ironwood (*Carpinus caroliniana*). Tree species identity was significant even after taking into account the confounding effect of habitat (Table 2), and comparing stem fluxes only in the

Table 2 Results of mixed effect models testing the effects of habitat, tree species, diameter at breast height (DBH), depth to water table (DTW), soil moisture, and soil temperature on methane and CO_2 fluxes

	Habitat		Tree species		DBH		DTW		Soil moisture		Soil temperature	
	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*
Stem CH_4	19.81	< 0.001	10.02	0.075	4.18	0.041	14.21	↓ < 0.001	ns	ns	4.03	0.045
Soil CH_4	22.31	< 0.001	–	–	–	–	49.51	↓ < 0.001	ns	ns	7.91	0.005
Stem CO_2	13.33	0.001	ns	ns	7.17	0.007	–	–	107.72	< 0.001	67.67	< 0.001
Soil CO_2	4.68	0.096	–	–	–	–	–	–	76.30	< 0.001	56.32	< 0.001

Both significant ($P < 0.05$) and marginally significant ($0.05 < P < 0.1$) effects were kept in the models; ↓, significant negative effects; – variables not analyzed; ns, non-significant variables excluded from the model

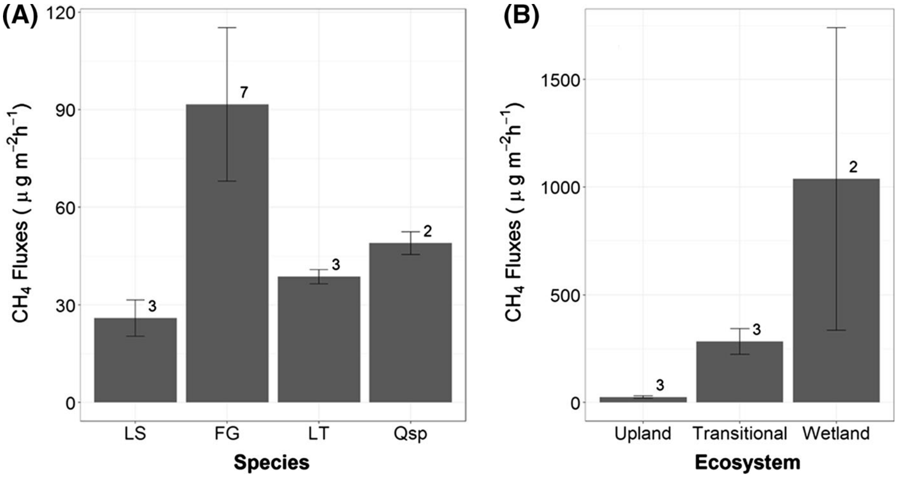

Fig. 4 Species and habitat effects on stem methane fluxes. **a** Four species in one habitat (upland); **b** One species (*Liquidambar styraciflua*, sweetgum) in three habitats. The species codes are LT (*Liriodendron tulipifera,* tulip poplar), FG (*Fagus grandifolia*, beech), LS (*Liquidambar styraciflua*, sweetgum), and Qsp (*Quercus sp.,* oak). Weighted mean (± SE) flux is shown (see "Methods"). Number of trees is shown on top of each column

upland habitat On the other hand, habitat effects are clearly shown for stem CH_4 fluxes for sweetgum, the only tree species found in all three habitat types (Fig. 4b).

Although there was a positive correlation between soil moisture and CH_4 flux in the upland soil (Fig. 5b), soil moisture in general was not a significant variable in the mixed effects model (Table 2). Soil moisture co-varies with habitat and DTW, and was added to the model as the last of these three variables.

Discussion

The present study is the first that simultaneously explores stem and soil trace gas fluxes along a soil moisture gradient (wetland, transitional and upland habitats) in close proximity to one-another. Habitat type is clearly the main driver of both CO_2 and CH_4 fluxes, but appears to more strongly affect the latter. To tease out the subset of abiotic and biotic factors that locally determines trace gas fluxes remains challenging.

We found large differences in the amount of CH_4 emitted from individual trees and from different species. Our data support other studies that report species differences in wetland (Pangala et al. 2015) and upland forests (Pitz and Megonigal 2017; Wang et al. 2016). Aspects of wood anatomy and tree physiology such as wood vessel structure, wood specific density, lenticel density, transpiration rates and sap flow rates may contribute to species level

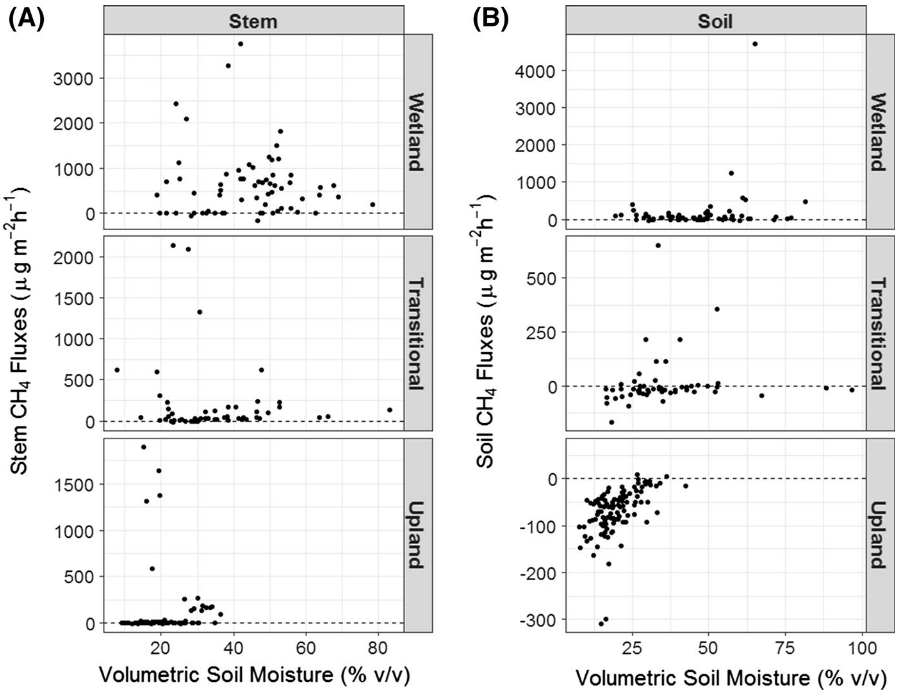

Fig. 5 Correlation between methane flux and soil moisture in the three habitats at SERC. Data for 2013–2014 are combined. Left panels: stem fluxes; right panels: soil fluxes. Note the different scales on the *y* axes

differences. While it has been shown that wood specific density and lenticel density affect stem CH_4 fluxes in wetland trees (Pangala et al. 2014, 2013), it is unclear how these other factors contribute to inter-specific CH_4 flux differences in upland trees. Among the four tree species we examined in the upland ecosystem, *Quercus* spp. have ring-porous vessel structure while the other three species are diffuse-porous. We did not detect any patterns that distinguish these morphological types. Future studies should incorporate these potential drivers into the experimental design.

The mixed effect model found stem CH_4 emissions to be positively related to DBH. This contrasts with Pangala et al. (2013) and Pangala et al. (2015) who found small diameter wetland trees emitted more CH_4 per unit area of stem than larger trees. There was little overlap between the DBH range of those studies (7.5–19.8 cm) and ours (16.1–92.6 cm). The mean stem diameter across all habitats in our study was 42.3 cm (Table 1), with only four trees out of 31 having DBH < 20 cm. Differences in root morphology and biomass between small and large trees may explain the contrasting results. Older and bigger trees have larger and deeper root systems and more likely have deep roots that tap into anaerobic soils or groundwater, both being potential sources of CH_4. Other potential CH_4 sources such as heart-rot and non-structural carbohydrates would result in a positive relationship between tree diameter and fluxes (Covey et al. 2012, 2016). Regardless of the mechanism, the data highlight the importance of tree size especially when scaling up plot-level studies to ecosystem-level estimates (Covey et al. 2016; Pangala et al. 2015). Future studies should address multiple tree size classes on a given species within one study site.

In the temperate region, stem CH_4 flux from trees has been shown to be related to temperature-dependent CH_4 production processes. In wetland forests, Pangala et al. (2015) reported a correlation between stem CH_4 emission and temperature, water-table depth, and CH_4 concentration in pore water. They concluded that CH_4 flux was driven by CH_4 production in water-logged wetland soil. By sampling a nearby spring, Wang et al. (2016) concluded that groundwater was not a source of CH_4 in an upland forest; rather, they attributed stem CH_4 flux to in situ CH_4 production in the heartwood. The trees in the present study were arranged along an upland-to-wetland gradient of groundwater depth. Our results showed a strong negative correlation between stem CH_4 flux and the depth to groundwater, and is consistent with a belowground CH_4 source hypothesis previously proposed for wetland trees (Pangala et al. 2015). We measured high stem CH_4 fluxes in the wetland habitat where soil CH_4 production is consistently high and lower but still positive stem CH_4 fluxes from upland trees even when adjacent soils are net CH_4 consumers. The observation that co-located upland soils act as CH_4 sinks while trees act as sources suggests that trees may provide a flux pathway through the woody tissue that bypasses the methanotrophs in the oxic soil layers (Megonigal and Guenther 2008).

Methane transport in plants can be via diffusion or transpiration (Megonigal and Guenther 2008; Pangala et al. 2014). The latter process has a strong diurnal pattern, suggesting that transpiration-driven CH_4 fluxes should exhibit a diel cycle. Pangala et al. (2014) reported only a weak positive relationship between emissions and transpiration, and Terazawa et al. (2015) did not observe diurnal patterns. Both studies concluded that diffusion is the major driver of stem CH_4 emissions. In an upland forest stand near our transect, Pitz and Megonigal (2017) demonstrated a strong diurnal pattern in stem CH_4 flux for American beech and tulip poplar, with a two-fold diurnal difference for the latter. This indicates that transpiration may play a significant role in stem emissions. Clearly, high frequency measurements for longer periods are necessary to reveal the relative importance of transpiration and diffusion in different habitats.

Soil moisture is considered a major driver of belowground biogeochemical processes, and is thus often reported as an abiotic variable. Usually soil moisture measurements reflect only the surface conditions. In a wetland, such data reflects conditions throughout the soil profile, but in the upland, surface conditions do not represent the steeper, more variable, vertical soil moisture gradient. Soil moisture was not a significant variable in our model of stem CH_4 fluxes (Table 2), which is consistent with root uptake from groundwater and transpiration as a mechanism for gas transport.

Soil CO_2 efflux decreased from upland to wetland, while stem respiration showed the opposite pattern (Fig. 3). Biological and physical processes may simultaneously explain this result. Lower soil CO_2 emissions in the wetland coincided with near-continuous flooding, which can be explained by several mechanisms. Flooding can decrease CO_2 respiration of stems by suppressing overall tree growth, and from roots by lowering both growth and root:shoot ratio (Megonigal et al. 1997). Similarly, flooding decreases microbial respiration both by suppressing overall microbial respiration and by lowering the CO_2:CH_4 ratio (Megonigal et al. 2004; Yu et al. 2008). Because stem CO_2 emissions were similar in the wetland and transitional zones, the most likely biological explanation for lower soil CO_2 emissions in the wetland is a decrease in microbial respiration as opposed to lower plant respiration. A purely physical explanation is that high soil moisture in the transitional and wetland habitats reduced gas diffusion rates through soil pore spaces (Davidson et al. 1998; Moyano et al. 2013; Suseela et al. 2012) favoring diffusion through woody tissues. These explanations are not mutually exclusive and may both have a role in explaining the cross-habitat patterns of soil and stem CO_2 emissions.

Tree CH_4 emission rates have now been measured in a variety of forest ecosystems (Table 3). Although the number of studies are few, it is noteworthy that during the growing season, the highest mean emissions from upland [190 μg m^{-2} h^{-1} (Covey et al. 2012)] and wetland stems (567.9 μg m^{-2} h^{-1} in the present study) are within the same order of magnitude. The observation that upland trees have the potential to emit CH_4 at rates comparable to wetland trees suggests the need for detailed mechanistic studies of CH_4 sources and sinks across all forest ecosystems.

Soil trace gas fluxes generally show high spatio-temporal variability and are often cited as examples for biogeochemical hotspots and hot moments (Hagedorn and Bellamy 2011; McClain et al. 2003; Ullah and Moore 2011). In such situations a single measurement can be several orders of magnitude higher than the mean (Kuzyakov and Blagodatskaya 2015). Our data also show high variability, especially in the wetland where soils and stems consistently emit CH_4. In this habitat, the coefficient of variation for soil flux (1.94) is twice as much as stem flux (0.92). Traditional soil trace gas measurement methods capture processes only in a small area, with large variations among individual measurements due to the existence of biogeochemical hot spots in a highly heterogeneous landscape. For a single tree, soil conditions around individual roots are highly heterogeneous, the entire root system spreads over a much larger area, and thus integrates widely varying conditions both vertically and horizontally (Schenk and Jackson 2002). Across

Table 3 Tree stem CH_4 flux comparisons from field experiments

Reference	Climatic region	Ecosystem	Tree species	Chamber method	CH_4 flux range (chamber height)[a] ($\mu g\ m^{-2}\ h^{-1}$)	CH_4 flux (mean ± SD)[a] ($\mu g\ m^{-2}\ h^{-1}$)
Terazawa et al. (2007)	Temperate	Floodplain	*Fraxinus mandshurica* var. *japonica*	Partial circumference	$164–212^m$ (15 cm) $76–118^m$ (70 cm)	176 97
Gauci et al. (2010)	Temperate	Wetland	*Alnus glutinosa*	Full circumference	3.22–126.5 (30 cm)	56.7 ± 52.7
Covey et al. (2012)	Temperate	Upland	Various	Modeled from internal concentration	4.24–181.3 (NA)	190 ± 34
Pangala et al. (2013)	Tropical	Wetland	Various	Full circumference	0.00–219 (35 cm)	103 ± 66
Pangala et al. (2015)	Temperate	Wetland	*Alnus glutinosa* *Betula pubescens*	Full circumference	$161–182^m$ (35 cm) $177–217^m$ (35 cm)	172 ± 8 196 ± 15
Terazawa et al. (2015)	Temperate	Floodplain	*Fraxinus mandshurica* var. *japonica*	Partial circumference	59–1514 (15 cm)	337 ± 419
Wang et al. (2016	Temperate	Upland	*Populus davidiana*	Full circumference	0–200 (30 cm)	85.3 (upper plot) 103.1 (lower plot)
Machacova et al. (2016)	Boreal	Upland	*Pinus sylvestris* L.	Full circumference	NA (20 cm)	0.005^{med}
Warner et al. (2017)	Temperate	Upland	Various	Partial circumference	56^b (130 cm)	6.3 ± 12
Maier et al. (2017)	Temperate	Upland	*Fagus sylvatica*	Full circumference	0–200 (40, 120, 200 cm)	30 ± 53
Present study	Temperate	Upland	Various	Partial circumference	− 8.1 to 1900 (45 cm)	68.8 ± 53.6
	Temperate	Transitional	Various	Partial circumference	− 4.0 to 2150 (45 cm)	180.7 ± 135.2
	Temperate	Wetland	Various	Partial circumference	8.6–3760 (45 cm)	567.9 ± 523.5

SD standard deviation (SD) not always available, *NA* not available, *m* mean of measurements, not an individual measurement, *med* median

[a] See Online Resource 3 for how data were derived from published studies

[b] Maximum value

all habitats pairwise measurements of stem CH_4 fluxes consistently exceeded soil CH_4 fluxes on an area basis, suggesting that the base of tree stems are a localized hot spot relative to the soil. In a few instances, we also recorded hot moments with extremely high (an order of magnitude higher than the mean) stem CH_4 fluxes (Fig. 2). It is important not to discard such data as outliers, even though data analysis becomes more challenging. Recent advances of continuous field trace gas measurement technology will allow high frequency sampling and thus to better characterize the sources, sinks and drivers of CH_4 fluxes in forests.

Despite the heightened interest following Keppler et al. (2006), to date only a handful studies convincingly documented trees as CH_4 sources (Table 3). Six of those, including our study, attempted to quantify CH_4 flux from live upland trees, and five directly measured stem fluxes in the field. Different studies report their data using incompatible approaches, including different methodologies to scale up data.

Studies have been conducted under different climatic conditions, from tropical rainforests to boreal forests. Chambers were closed from 6 min to 6 h for each measurement. The position of chambers above the ground, which has been shown to affect flux rates (Pangala et al. 2013), varied from 15 to 200 cm. One issue that we address here is the variations in stem flux chamber design used in direct field measurements. Some studies (Terazawa et al. 2007, 2015), ours included, employed a chamber that is mounted one side of a tree (i.e., partial-circumference design). The advantages of this design are that it allows measurements on large trees, maximizes the surface to volume ratio, allowing for relatively short measurement times. The design suited our goal of measuring emissions from a wide range of tree sizes and detecting small fluxes in upland forests. However, this type of chamber does not capture radially variation in emissions around the circumference of the tree and is difficult to fit on small trees. Other studies (Gauci et al. 2010; Pangala et al. 2013) have used a chamber that completely encloses the stem (i.e., full-circumference design). This chamber style results in a lower surface to volume ratio and may result in longer measurement times but it is well suited for small diameter stems. Recently Siegenthaler et al. (2016) developed a full-circumference design using low permeability, flexible material that significantly improves surface to volume ratios. This chamber style may ideally address some field, habitat, and tree diameter constraints. A systematic comparison between chamber styles and recommendations of standardized chamber designs and protocols will allow for interpretation and synthesis of stem flux measurements.

Conclusion

Forests cover about 30% of the global land surface (FAO 2016) and are important sinks of atmospheric carbon (IPCC 2013). The present and other studies indicate that upland trees emit CH_4 and thus have to be incorporated into forest carbon cycling models. Our data support a below ground CH_4 source, but this pathway probably works simultaneously with other mechanisms, such as CH_4 derived from internal microbial sources. Our study highlighted the many biotic and abiotic factors that influence tree mediated CH_4 fluxes. Future studies should focus on teasing apart the roles of tree size and species identity (physiology, wood structure, rooting depth), and a multitude of above- and below-ground environmental factors. Using high frequency measurements (Pitz and Megonigal 2017) will help determine drivers on diurnal, seasonal and annual scales, and identify hot moments. Considering evidence that the global warming potential of CH_4 is dramatically higher when being consumed from the atmosphere than emitted (sustained global warming potential of uptake = 203 vs emission = 45 over 100 years) (Neubauer and Megonigal 2015), systems such as upland forests where CH_4 is simultaneously produced and consumed are particularly important to evaluate from a whole-system perspective.

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