

Methane emission from stems of European beech (*Fagus sylvatica*) offsets as much as half of methane oxidation in soil

Katerina Machacova^{1*} , Hannes Warlo^{1,2*} , Kateřina Svobodová¹, Thomas Agyei^{1,3} , Tereza Uchytlová¹, Petr Horáček¹  and Friederike Lang² 

¹Global Change Research Institute of the Czech Academy of Sciences, 4a Belidla, CZ-60300 Brno, Czech Republic; ²Chair of Soil Ecology, Albert-Ludwigs-University, Bertoldstrasse 17, DE-79098 Freiburg, Germany; ³Department of Environmental Management, School of Natural Resources, University of Energy and Natural Resources, Box 214, Sunyani, Ghana

Summary

Author for correspondence:
Katerina Machacova
Email: machacova.k@czechglobe.cz

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- Trees are known to be atmospheric methane (CH₄) emitters. Little is known about seasonal dynamics of tree CH₄ fluxes and relationships to environmental conditions. That prevents the correct estimation of net annual tree and forest CH₄ exchange.
- We aimed to explore the contribution of stem emissions to forest CH₄ exchange. We determined seasonal CH₄ fluxes of mature European beech (*Fagus sylvatica*) stems and adjacent soil in a typical temperate beech forest of the White Carpathians with high spatial heterogeneity in soil moisture.
- The beech stems were net annual CH₄ sources, whereas the soil was a net CH₄ sink. High CH₄ emitters showed clear seasonality in their stem CH₄ emissions that followed stem CO₂ efflux. Elevated CH₄ fluxes were detected during the vegetation season. Observed high spatial variability in stem CH₄ emissions was neither explicable by soil CH₄ exchange nor by CH₄ concentrations, water content, or temperature studied in soil profiles near each measured tree. The stem CH₄ emissions offset the soil CH₄ uptake by up to 46.5% and on average by 13% on stand level.
- In Central Europe, widely grown beech contributes markedly to seasonal dynamics of ecosystem CH₄ exchange. Its contribution should be included into forest greenhouse gas flux inventories.

Introduction

Among natural forest ecosystems, temperate forest soils are the strongest sinks of the important greenhouse gas (GHG) methane (CH₄; $-4.79 \text{ kg ha}^{-1} \text{ yr}^{-1}$; Dalal & Allen, 2008). In well-aerated soils, CH₄ is oxidized and therefore consumed by methanotrophic bacteria under aerobic conditions, whereas under anaerobic conditions typical for flooded soils or anaerobic microsites, CH₄ is produced by methanogenesis (Smith *et al.*, 2003). At the soil surface, CH₄ can be exchanged with the atmosphere by gas diffusion, by advection driven by air pressure gradients, or, in the case of water-logged soils, by ebullition. Moreover, plants, including woody plants, are known to contribute to the forest CH₄ exchange by (1) transporting soil-produced CH₄ via roots, stems, and/or leaves into the atmosphere, thus preventing CH₄ molecules from being oxidized in well-aerated soil surface layers (Machacova *et al.*, 2013, 2016a); (2) producing CH₄ directly in plant tissues through plant's own physiological and microbial processes (Keppler *et al.*, 2006; Covey & Magonigal, 2019); (3) consuming CH₄ from the atmosphere by unknown processes (Sundqvist *et al.*, 2012; Machacova *et al.*, 2021); and (4) altering the carbon (C) turnover processes in

the rhizosphere and adjacent soil (Menyailo & Hungate, 2005). The CH₄ exchange by tree surfaces can be boosted further by the capability of cryptogamic stem covers (i.e. photoautotrophic organisms living on tree bark) to emit and consume CH₄ (Lenhart *et al.*, 2015; Machacova *et al.*, 2021), and by methane-oxidizing bacteria living in the tree bark (Jeffrey *et al.*, 2021a). The processes of gas production and consumption, gas transport, gas emission into the atmosphere, and gas uptake from the atmosphere take place simultaneously in the soil and plant systems, and their equilibrium determines whether the soil and tree surfaces constitute a net source or sink of CH₄ (Barba *et al.*, 2019a).

European beech (*Fagus sylvatica*) is a native and widely distributed deciduous tree species within temperate forests in Europe. Upland forests dominated by European beech trees cover c. 15 million ha in Europe and are predominantly found in Central and Southeast Europe (Brunet *et al.*, 2010). Beech trees grow on a wide range of soil types, both acidic and basic. The soils of beech forests are predominantly CH₄ sinks due to prevailing CH₄ oxidation by methanotrophs (Butterbach-Bahl & Papen, 2002; Maier *et al.*, 2018).

In addition to soils, European beech trees might themselves also contribute to the CH₄ exchange of beech forests. To our knowledge, however, only two studies are available on the CH₄

*These authors contributed equally to this work.

exchange potential of European beech trees. Machacova *et al.* (2013) detected CH₄ uptake potential by stems of beech seedlings grown under conditions of low soil water content and their CH₄ emission potential under short-term flooded conditions. Maier *et al.* (2018) identified mature beech stems in two temperate montane upland forests as possible CH₄ emitters. The tree fluxes showed very strong variability among five individually studied trees, however, and no potential environmental or physiological drivers of the tree fluxes could be identified due to the short measurement period (Maier *et al.*, 2018).

In general, the CH₄ exchange capacity of trees and their contribution to the forest CH₄ exchange seem to vary considerably among tree individuals, tree species, forest ecosystem types, and climatic zones and to depend on many aspects, such as soil and site parameters, tree size, age and health conditions, environmental conditions, and seasonal dynamics (Barba *et al.*, 2019a; Covey & Magonigal, 2019). Although recent research across all main climatic zones has identified woody plants as potential sources of atmospheric CH₄, common characteristics and mechanisms behind CH₄ exchange in the soil–tree–atmosphere continuum are still not well understood. One of the reasons consists in the lack of measurements focusing on the high spatial variability in CH₄ fluxes typical for trees of a single species (Maier *et al.*, 2018; Schindler *et al.*, 2020; Köhn *et al.*, 2021; Moldaschl *et al.*, 2021). Moreover, seasonal measurements of tree CH₄ exchange are rather rare, particularly during the dormant season. It remains unclear whether or not tree stem CH₄ exchange shows a clear seasonality, and whether it follows the tree's physiological activity (Pangala *et al.*, 2015; Wang *et al.*, 2016; Köhn *et al.*, 2021; Moldaschl *et al.*, 2021). Therefore, it is more than difficult to properly estimate the annual CH₄ fluxes, as their calculation is often based solely on the results of short measuring periods during the vegetation season. For correct interpretation of CH₄ fluxes in the soil–tree–atmosphere continuum, ecologically relevant whole-year studies are needed involving a substantial number of mature trees growing under natural field conditions and accompanied by environmental and physiological measurements (Machacova *et al.*, 2019). Determination of CH₄ fluxes of tree species common for Central Europe inclusive of the fluxes' temporal and spatial dynamics is of high importance for correctly estimating the European forest CH₄ budgets and therefore the global GHG flux inventories. Due to a continuing lack of detailed knowledge as to the role of trees in forest CH₄ exchange, the calculations of CH₄ fluxes between forest ecosystems and the atmosphere have mostly been limited to CH₄ exchange at the soil–atmosphere interface, thus excluding the exchange activity of trees and other vegetation. This approach can lead to a severe underestimation of the ecosystem fluxes (Barba *et al.*, 2019a) and needs to be improved in the near future.

Accordingly, the objective of our study was to quantify CH₄ exchange for stems of European beech trees (*F. sylvatica* L.). Seasonal and spatial CH₄ flux dynamics were determined on mature trees in a typical mountain beech forest (White Carpathians, Czech Republic) from November 2017 to December 2018. The measurements were accompanied by a parallel determination of stem CO₂ efflux (as an indicator of tree physiological activity)

and soil CH₄ and CO₂ fluxes, as well as numerous environmental parameters describing soil and atmospheric conditions (soil CH₄ and CO₂ concentrations, soil volumetric water content (VWC), soil temperature, air temperature, and photosynthetically active radiation (PAR)). We deliberately selected for our study, a long forest transect including plots with low soil water content and plots with temporarily stagnic properties and redoximorphic features. We aimed to investigate whether CH₄ emissions resulting from stagnic properties are associated with CH₄ emissions at the tree stem–atmosphere interface. We hypothesized that: (1) beech stems can emit large quantities of CH₄ under stagnic conditions, (2) the beech stem CH₄ exchange has substantial seasonal dynamics following the CH₄ production in soil, (3) the beech stems contribute significantly to the montane forest ecosystem's CH₄ exchange, and (4) the stem CH₄ fluxes are closely related to soil conditions directly or indirectly connected to CH₄ turnover in soil (i.e. soil CH₄ exchange, CH₄ concentrations and VWC at various soil depths, and soil temperature) rather than to tree physiological activity driven by environmental variables like temperature and PAR. The long-term analyses of CH₄ emissions from 20 mature beeches accompanied by the measurement of multiple environmental variables over 1 yr enabled us to investigate: (1) the seasonal dynamics of beech tree CH₄ exchange, (2) the trees' CH₄ exchange during winter dormancy, (3) the environmental and physiological controls of CH₄ fluxes, and (4) how trees contribute to the forest ecosystem CH₄ exchange at the annual scale.

Materials and Methods

Site description and experimental design

Measurements were conducted in a montane beech forest at the ecosystem research station near Štítná nad Vláří in the White Carpathians, Czech Republic (49°2'9.412"N, 17°58'12.154"E; elevation 550 m asl). The soil type is Eutric (Stagnic) Cambisol, and soil pH is 7.0 (FAO, 2006; Maier *et al.*, 2018). The organic surface horizon (L, F, H; humus type Mull) occurs at 0–3 cm, followed by Ah horizon (3–14 cm), Bvt (14–26 cm), Bv (26–70 cm), and BC horizon (70–88 cm; Darenova *et al.*, 2016). Annual mean temperature and precipitation are 7.5°C and 800 mm, respectively (Darenova *et al.*, 2016).

The forest is a c. 120-yr-old monoculture of European beech (*Fagus sylvatica* L.; current density of 283 trees ha⁻¹) with mean tree height of 32.2 m and mean stem diameter at breast height (DBH) of 0.35 m. The understory vegetation's composition is rather poor, with almost no herbal species. Smaller areas with small exemplars of *Impatiens noli-tangere* (L.) indicated generally higher soil water content with the presence of redoximorphic color patterns in the soil.

Within the forest site, we representatively selected a forest transect (approximate length and width of 200 and 120 m, respectively) horizontally located on a west–southwest 10° slope terrain with considerable small-scale heterogeneity in soil VWC. Within this transect, 20 small-scale forest plots ($n = 20$) were representatively chosen across the full available range of soil

VWC ranging between 0.14 and 0.47 $\text{m}^3 \text{m}^{-3}$ at 30 cm soil depth (median values per plot during the whole measurement period). One mature beech tree was selected for stem CH_4 and CO_2 flux measurements per each forest plot (in total 20 trees of average height and DBH, $n = 20$). In the vicinity of each studied tree, the soil CH_4 and CO_2 fluxes were determined (in total 20 soil positions, $n = 20$) together with soil CH_4 and CO_2 concentrations and VWC at four soil depths (10–20–30–40 cm) and soil temperature at 10 cm soil depth.

Stem and soil CH_4 and CO_2 fluxes were measured simultaneously at each plot to ensure measurements under similar environmental and climatic conditions. Stem fluxes were simultaneously determined in vertical stem profiles (*c.* 0.4, 1.2, and 2.0 m above the ground) at seven beech trees (numbered 1–7) accompanied by parallel measurements of the soil gas fluxes, soil VWC, and soil temperature. At these forest plots numbered 1–7, measurements were performed every 2–3 wk from November 2017 to December 2018. Stem gas fluxes at the remaining 13 plots (numbers 8–20) were quantified at the bottom part of the stems only (*c.* 0.4 m above the ground) and followed by all the aforementioned parallel soil measurements. These 13 trees and forest plots were investigated every 2–3 wk from April 2018 to December 2018, followed by parallel determination of CH_4 and CO_2 concentrations in vertical soil profiles in the vicinity of each of the 20 studied trees to examine spatial heterogeneity in tree and soil CH_4 fluxes and soil parameters in greater detail (Fig. 1).

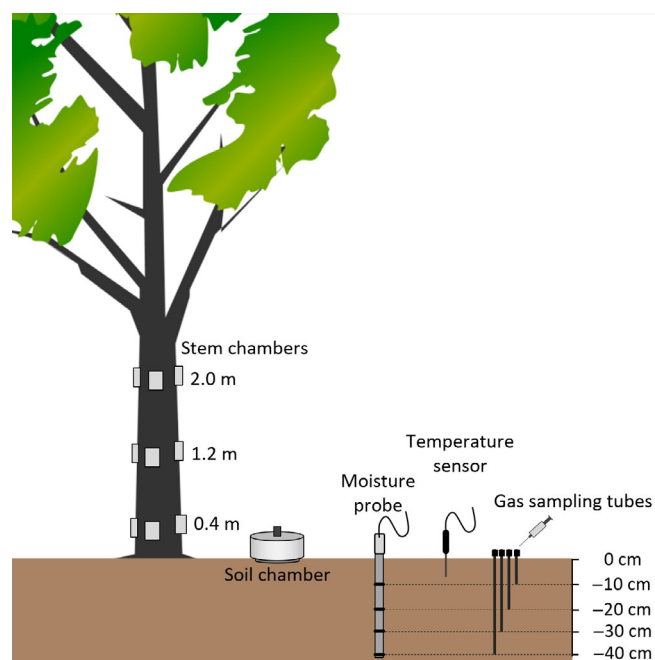


Fig. 1 Schematic overview of the experimental design. Measurements of gas fluxes at stem and soil surfaces, soil water content and soil gas concentrations within the vertical soil profile, and soil temperature at 10 cm soil depth are displayed. The scheme shows the stem chamber setup in the vertical stem profile for Beeches 1–7. For Beeches 8–20, the stem chambers were installed solely at 0.4 m height aboveground.

Measurements of CH_4 and CO_2 fluxes and concentrations

The fluxes of CH_4 and CO_2 from tree stems were measured manually using static stem chamber systems (see Supporting Information Table S1; Machacova *et al.*, 2015, 2017). The stem chambers consisted of transparent plastic boxes with removable airtight lids (Lock & Lock, Seoul, South Korea) and a neoprene sealing frame. They were gas-tightly affixed to the bark surface at least 2 wk before the first measurements were performed. The stem chambers installed at one height were interconnected into a single flow-through system using polyurethane tubes. Control measurements were performed to ensure that the observed fluxes did not originate from the chamber materials used. Gas-tightness of each individual stem chamber was regularly tested throughout the year by application of CO_2 as a tracer gas around all seals and connections. In case of a gas leak, a CO_2 concentration peak was monitored by a connected gas analyzer.

The gas fluxes of soil were measured using manual dark cylindrical soil chambers consisting of a collar constructed from a sewage pipe and a chamber hood constructed from a gas-tight stopper of a sewage pipe (Maier *et al.*, 2018; modified). The collars were installed into the soil *c.* 2 wk before the start of the first measurements to reduce the effect of soil disturbances. During measurements, the soil chambers were gas-tightly closed by the hood using a rubber seal and the headspace air temperature was recorded. The outer surface of the chamber hoods was covered by aluminum foil to minimize the heating of the chambers by the sun's radiation. In case of snow cover thicker than 10 cm, the uppermost snow layer above the soil collars was carefully removed to enable closing of the soil chambers.

All stem and soil chambers were left open between measurements. For the gas flux measurements, the chamber systems were closed and gas samples (each 20 ml) were regularly taken via a septum in the chamber lids (see Table S1) and stored in pre-evacuated gas-tight glass vials (Labco Exetainer, Labco, Ceredigion, UK) at 7°C until analysis.

The soil gas concentrations were determined at four soil depths (10, 20, 30, and 40 cm) close to each soil chamber and studied beech from April 2018 onwards to investigate production and consumption of CH_4 and CO_2 in the soil profile. Four stainless-steel pipes (inner diameter of 0.8 cm) of 20, 30, 40, and 50 cm length with open ends were installed into predrilled holes in vertical soil profiles. The four tubes were placed next to each other in one row with *c.* 10 cm distance between them. The pipes ended 10 cm above the soil in a three-way valve, which was closed between the measurements to ensure equilibration of air in the pipes with soil air. Gas samples were taken every 2–3 wk into pre-evacuated glass vials.

Gas analyses

All gas samples were analyzed for CH_4 and CO_2 concentrations using a Tracera gas chromatograph (Shimadzu, Kyoto, Japan) equipped with a barrier discharge ionization detector (BID), and Shin Carbon ST Micro column and fused silica capillary (Restek, Bellefonte, PA, USA). The BID, operating at 250°C,

was supplied with helium (80 ml min^{-1}), which was used also as a carrier gas (15 ml min^{-1}). The oven temperature program began at 70°C for 14 min and then was increased to 200°C for 1.5 min. The gas samples were automatically injected by a GX-271 autosampler (Gilson, Middleton, WI, USA). The CH_4 and CO_2 concentrations were calculated based on a four-point concentration calibration curve ($1.2, 2.3, 3.4, 4.5 \mu\text{mol CH}_4 \text{ mol}^{-1}$; $400, 667, 933, 1200 \mu\text{mol CO}_2 \text{ mol}^{-1}$). LabSolutions software (Shimadzu) was used to control the chromatography system and analyze the data. The detection limits of the Tracera gas chromatograph are $0.011 \mu\text{mol CH}_4 \text{ mol}^{-1}$ and $0.040 \mu\text{mol CO}_2 \text{ mol}^{-1}$.

Flux calculation

The stem and soil fluxes were calculated based on gas concentration changes in the chamber headspace over time while following Hutchinson & Livingston (2002) and applying robust linear regression (Maechler *et al.*, 2021) and then were expressed per m^2 of stem and soil surface area, respectively. Following Christiansen *et al.* (2015) and Nickerson (2016), we further calculated the minimum detectable flux (MDF) for CH_4 and CO_2 for large and small stem chamber systems, and vegetation and dormant period (Table S2). The comparison of the measured stem CH_4 and CO_2 fluxes with the MDF values was used as quality check

on chamber measurements and applied chamber closure time. The 84.1% and 96.9% of the stem CH_4 and CO_2 fluxes, respectively, measured over the whole year were above the MDF values of our analytical and measurement systems and applied methodology (Table S2). The small remaining portion of CH_4 fluxes below the MDF values was mostly related to the dormant season. These low, but expected stem CH_4 fluxes close to zero were left in the data set as their exclusion would lead to an incorrect overestimation of the overall CH_4 fluxes.

The fluxes were further scaled up to the ecosystem level (per hectare values) based on tree and forest characteristics (mean DBH of 0.35 m, mean tree height of 32.2 m, stand basal area of $33.7 \text{ m}^2 \text{ ha}^{-1}$, and tree density of $283 \text{ trees ha}^{-1}$). The upscaling procedure is described in Machacova *et al.* (2016a). Briefly, the stem surface area of each tree (mean area of 17.7 m^2 per tree) was calculated as the lateral surface area of a right circular cone using DBH and tree height. This area was further used to calculate the gas fluxes for the entire stem area of each tree using the gas fluxes measured at stem height of 0.4 m, as the vertical profiles of the CH_4 and CO_2 fluxes did not show a uniform trend across the studied trees (Figs 2, S1). We decided to use the mostly lower stem CH_4 fluxes measured near the ground (compared with higher fluxes at higher stem levels) in the upscaling procedure to avoid a potential overestimation of the upscaled stem CH_4 fluxes. The stem CH_4 and CO_2 fluxes from entire trees were further

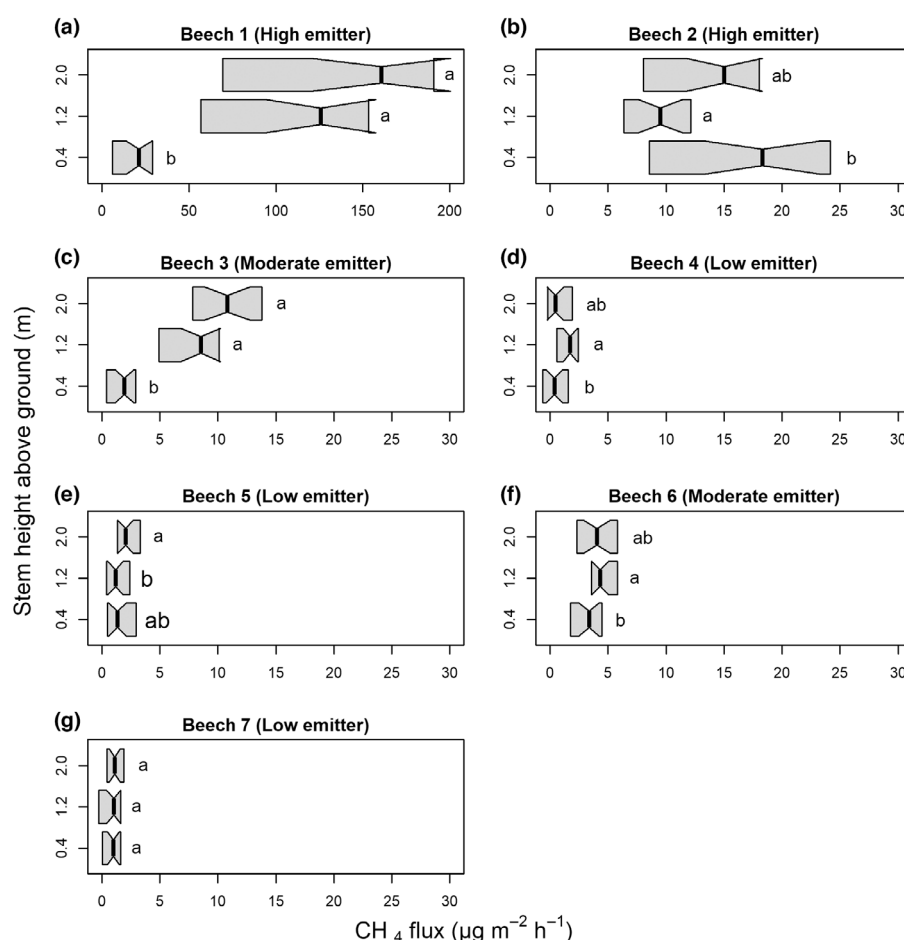


Fig. 2 Fluxes of CH_4 from vertical stem profiles of seven individual beech trees. The fluxes are expressed as medians of measurements from individual trees at three stem heights of c. 0.4, 1.2, and 2.0 m aboveground over the whole year (November 2017 to December 2018, Beeches 1–7; a–g). Division of the trees into the three groups according to CH_4 emission potential of all studied trees is labeled as follows: 'low CH_4 emitter', 'moderate CH_4 emitter', and 'high CH_4 emitter'. All fluxes are expressed per m^2 of stem area. Positive fluxes indicate trace gas emission; negative fluxes trace gas uptake. Box boundaries mark the 25th and 75th percentiles. Notches indicate 95% confidence intervals of medians. Statistically significant differences among fluxes at different stem heights at $P < 0.05$ are indicated by different letters next to bars (Dunn's test). Please note the different x-axis scale for Beech 1.

scaled up to a hectare of forest using the stand density. The gas fluxes originating from the forest floor were scaled up to hectare of forest after subtraction of the stand basal area from the forest area.

The monthly stem and soil fluxes for each forest plot were calculated as median daily fluxes of a given month multiplied by the number of days for each of the months. The annual cumulative fluxes were calculated as sums of monthly fluxes. The monthly stem and soil fluxes for groups of forest plots belonging to low, moderate, and high CH₄ emitters (for classification see 'Methane exchange of beech stems' in the Results section) were calculated as medians of measurements available per each month and group, as the beech trees and soil positions 1–7 measured all through the year were uniformly represented across all three studied groups. In the case of trees 8–20, fluxes for January, February, and March were calculated as median fluxes of trees 1–7, differentiated according to the classification in low, moderate, and high emitters. The annual fluxes were calculated as the sums of 12 monthly fluxes (January–December 2018) and the seasonal fluxes as the sums of fluxes over the vegetation season (April–October) and dormant season (November–March).

Ancillary measurements

Next to the studied tree and soil chamber at each forest plot, soil temperature and VWC were measured in parallel with gas flux measurements. Soil temperature at 10 cm soil depth was measured using a Testo 925 thermometer (Testo SE & Co., Lenzkirch, Germany). Soil VWC was determined at four soil depths (10, 20, 30, and 40 cm) using a PR2 Profile Probe and HH2 Moisture Meter (AT Delta-T Devices, Cambridge, UK). In addition, the following environmental parameters were continuously determined at the ecosystem research station in the vicinity of the studied transect and used for further correlation and regression analyses: PAR at 44 m height (i.e. above the canopy; quantum sensor EMS 12; EMS Brno, Brno, Czech Republic); air temperature at 12 m height within the forest stand and at 44 m height (air temperature probes EMS 33; EMS Brno); soil temperature at 5, 10, 20, 30, and 50 cm soil depth (temperature sensors Pt1000; Sensit, Roznov pod Radhostem, Czech Republic); and soil water content at 5, 10, 30, 60, and 90 cm soil depth (ML2x ThetaProbe; AT Delta-T Devices).

Statistics

All calculations and statistical analyses were made using R v.3.2.3 (R Foundation for Statistical Computing, Vienna, Austria). For gas flux calculations, robust linear regression models were applied from the ROBUSTBASE R package (Maechler *et al.*, 2021). Ninety-five per cent confidence intervals of medians were calculated according to McGill *et al.* (1978). Shapiro–Wilk test was used to check for normal distribution of flux data. The R package DUNN.TEST (Dinno, 2017) was used to test for significant differences between groups with Dunn's test for multiple comparisons. The *n*-values for statistical analyses are stated in the figure legends and in the 'Site description and experimental design' section.

Statistical significance of all tests was defined at $P < 0.05$. Relationships between stem flux data as dependent variable and environmental parameters as independent variables were tested with simple linear regression models, as in no case was there evidence of nonlinearity. Linear mixed effects modeling with the individual trees as random effect and variable selection based on Akaike information criterion and conditional R^2 did not increase the explained variance of the models compared with the simple regressions.

Results

Environmental parameters

Seasonal courses of accompanying environmental parameters continuously measured at the ecosystem research station (air and soil temperature, soil VWC, and PAR) during the period studied (November 2017 – December 2018) are shown in Fig. 3. The warmest month in this period was August, with mean daily air temperature within the forest stand of 20.3°C; the coldest month was on average February, with mean -3.8°C (Fig. 3a). Mean daily soil temperature at 30 cm soil depth was lowest in February and March (1.2°C and 1.4°C, respectively) and highest in August (16.9°C, Fig. 3b). A snow cover was present in the second half of January and from mid of February to mid of March 2018. Soil VWC at 30 cm soil depth (Fig. 3c) was highest between December 2017 and April 2018, and lowest between August and December 2018. The seasonal course for the daily sum of PAR (Fig. 3d) follows a pattern typical for temperate forest ecosystems. More details about environmental conditions for the flux measurement days only are shown in Fig. 3. The relationships between gas fluxes and measured environmental parameters are presented in Tables 1, S3, S4.

The concentrations of CH₄ in soil profile down to 40 cm soil depth were mostly below the ambient CH₄ concentration for all forest plots and soil depths and decreased with increasing soil depth (Fig. S2). The only notable exception was Plot 7, with 3.5 and 4.1 ppm CH₄ detected at 10 cm soil depth in November and December 2018, respectively. By contrast, the soil CO₂ concentrations showed an increasing trend with increasing soil depth (Fig. S3).

Methane exchange of beech stems

All beech trees studied were predominant stem CH₄ emitters (Figs 4a–c, S4). The detected stem CH₄ emissions were characterized by high interindividual and temporal variability and ranged between -4.37 and $173.97 \mu\text{g CH}_4 \text{ m}^{-2} \text{ stem area h}^{-1}$ (measured at 0.4 m stem height). The CH₄ emission potential of the studied trees showed positively skewed distribution, with approximately half of the trees being among the very low CH₄ emitters. The measured trees (and corresponding soil positions) were therefore classified into three groups based on their CH₄ emission potential (Fig. 4): Group 1 as 'low CH₄ emitters' ($n = 10$), Group 2 as 'moderate CH₄ emitters' ($n = 5$), and Group 3 as 'high CH₄ emitters' ($n = 5$). The stem CH₄ emissions

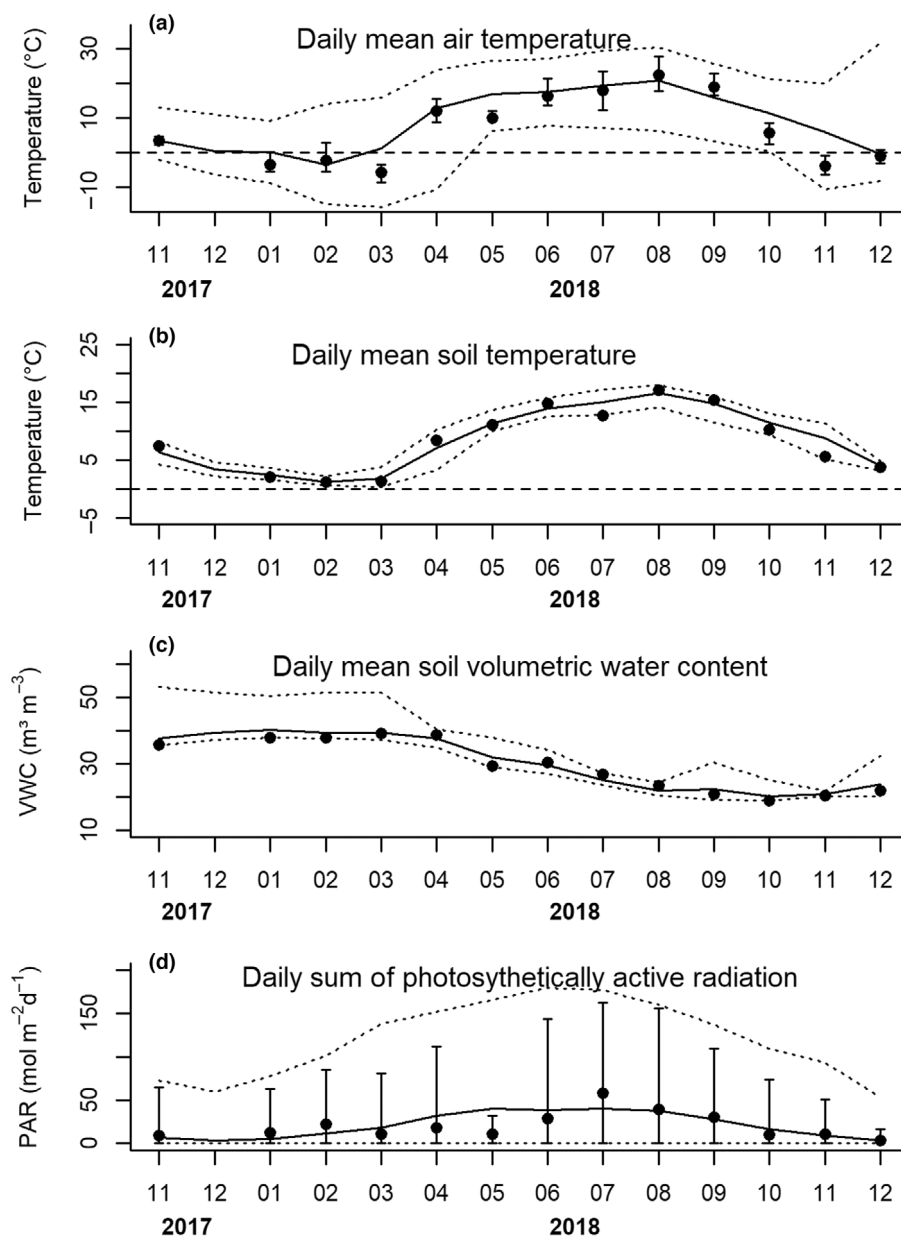


Fig. 3 Seasonal courses of basic environmental variables. Variables were measured at the ecosystem research station near Štítná nad Vláří in the White Carpathians, Czech Republic, from November 2017 to December 2018: (a) daily mean air temperature within the beech forest stand at 12 m height; (b) daily mean soil temperature and (c) soil volumetric water content (VWC), both at 30 cm soil depth; and (d) daily sum of photosynthetically active radiation (PAR). Solid lines represent monthly means \pm minimum/maximum (broken lines). Points represent mean values calculated for the flux measurement days only \pm minimum/maximum (error bars). Note that the variation in soil temperature and VWC in 30 cm depth at a specific day of each month is very low and therefore not visible as error bars.

significantly differed among the groups, with Group 3 showing up to two orders of magnitude higher CH_4 fluxes compared with Groups 1 and 2 (Fig. 4).

The vertical profile of stem CH_4 exchange was studied on seven trees uniformly distributed among the three groups over the whole year. No clear trends in stem CH_4 emissions were observed with respect to stem height aboveground in five trees (Fig. 2). However, Beech 1 belonging to high CH_4 emitters and Beech 3 from the moderate CH_4 emitters showed a significant increase in stem CH_4 emissions with increasing stem height (measured up to 2 m aboveground, Fig. 2a,c).

High CH_4 emitters within the studied beech trees showed substantial seasonality in their stem CH_4 emissions (Fig. 4c), with elevated CH_4 fluxes in the vegetation season. The fluxes decreased from October onwards, remained low but significant in relation to the annual totals during the dormant winter season,

and then increased again in March. The seasonal CH_4 emission dynamics of these trees clearly followed the stem CO_2 efflux ($R^2 = 0.79$, $P < 0.001$; Table 1). While the high CH_4 emitters displayed the most evident seasonal dynamics in their stem CH_4 fluxes, less pronounced CH_4 flux dynamics were observed for Groups 1 and 2 due to their low CH_4 exchange (Fig. 4a–c), and these were not linked to the stem CO_2 efflux ($R^2 = 0.06$, $P = 0.002$; $R^2 = 0.06$, $P = 0.02$; respectively; Table 1).

The majority of tested relationships among the stem CH_4 emissions of the individual tree groups over the year and the adjacent soil parameters, such as soil CH_4 flux, soil VWC, soil temperature, and soil CH_4 concentrations in the vertical profile, were only low ($R^2 \leq 0.2$) and/or nonsignificant ($P > 0.05$; Table 1). This was also evident when combined stem flux data including all three tree groups together were used in simple linear regression analysis (Table S3). Finally, multiple linear mixed models

Tree, soil, and environmental parameters	Stem CH ₄ flux			Stem CO ₂ efflux		
	Low CH ₄ emitters <i>R</i> ²	Moderate CH ₄ emitters <i>R</i> ²	High CH ₄ emitters <i>R</i> ²	Low CH ₄ emitters <i>R</i> ²	Moderate CH ₄ emitters <i>R</i> ²	High CH ₄ emitters <i>R</i> ²
Stem CO ₂ efflux	0.059**	0.064*	0.790***	—	—	—
Soil CH ₄ flux	0.002ns	0.134**	0.069*	0.008ns	0.021ns	0.095**
Soil CO ₂ flux	0.037*	0.000ns	0.000ns	0.253***	0.194***	0.021ns
Soil CH ₄ conc. 10 cm	0.020ns	0.004ns	0.209**	0.033ns	0.037ns	0.172*
Soil CH ₄ conc. 20 cm	0.014ns	0.004ns	0.070ns	0.011ns	0.010ns	0.066ns
Soil CH ₄ conc. 30 cm	0.003ns	0.000ns	0.002ns	0.001ns	0.027ns	0.004ns
Soil CH ₄ conc. 40 cm	0.005ns	0.015ns	0.000ns	0.022ns	0.001ns	0.023ns
Soil CO ₂ conc. 10 cm	0.075*	0.133*	0.029ns	0.177***	0.312***	0.010ns
Soil CO ₂ conc. 20 cm	0.031ns	0.207**	0.076ns	0.227***	0.386***	0.052ns
Soil CO ₂ conc. 30 cm	0.036ns	0.115ns	0.150*	0.264***	0.214*	0.197**
Soil CO ₂ conc. 40 cm	0.004ns	0.102ns	0.255**	0.220***	0.245**	0.255***
Soil VWC 10 cm	0.001ns	0.173**	0.010ns	0.025ns	0.027ns	0.024ns
Soil VWC 20 cm	0.002ns	0.319***	0.024ns	0.001ns	0.135**	0.080*
Soil VWC 30 cm	0.001ns	0.061ns	0.068ns	0.007ns	0.036ns	0.108*
Soil VWC 40 cm	0.000ns	0.036ns	0.106ns	0.010ns	0.004ns	0.128*
Soil temperature	0.000ns	0.006ns	0.066ns	0.383***	0.405***	0.052ns
Air temperature	0.033*	0.022ns	0.128**	0.389***	0.356***	0.071*

The 20 studied trees were classified into three groups according to their stem CH₄ emission potential: 'low CH₄ emitters' (*n* = 10), 'moderate CH₄ emitters' (*n* = 5), and 'high CH₄ emitters' (*n* = 5). Stem CO₂ efflux and soil CH₄ and CO₂ fluxes were measured simultaneously with stem CH₄ fluxes from November 2017 to December 2018. Remaining environmental parameters were determined in parallel with gas flux measurements from April to December 2018. Significance levels are expressed as follows: ns, not significant; *, *P* < 0.05; **, *P* < 0.01; ***, *P* < 0.001. VWC, volumetric water content.

incorporating tree individuals as a random effect did not explain stem CH₄ fluxes better than simple regression (Table S4).

Based on the clear seasonal dynamics in stem CO₂ efflux (Fig. S5a–c), the period from November to March was identified as the dormant season, and the period from April to October as the vegetation season. In addition to stem CH₄ emissions during the vegetation season, our study revealed that all the studied beech trees exchanged CH₄ even during the dormant season (Fig. 5a–c). The stem emissions were significantly lower over the dormant season compared with the vegetation season and contributed 20.6%, 19.3%, and 15.2%, respectively, to the annual CH₄ emissions from stems of trees belonging to low, moderate, and high CH₄ emitters.

The beech stems were net annual sources for atmospheric CH₄, with trees from Group 3 being the strongest CH₄ sources per year (146.3 ± 12.1 mg CH₄ m^{−2} stem area and 0.73 ± 0.06 kg CH₄ ha^{−1} ground area; median ± 95% confidence interval; Fig. 6). At the individual scale, Beech 10 was the strongest CH₄ emitter among all studied trees, and Beech 19 was the weakest emitter (Figs S4, S6).

Methane exchange of soil

The soil was a predominant sink of atmospheric CH₄ (Figs 4e–g, S7) but characterized by substantial spatial flux variability. Fifteen soil positions showed clear CH₄ uptake and five positions CH₄ emissions. According to the CH₄ emission potential of the

trees, the corresponding soil positions were classified into three groups (Fig. 4). The soil near trees characterized as low CH₄ emitters (i.e. Group 1) showed elevated CH₄ uptake, whereas the soil in the vicinity of the high tree CH₄ emitters (i.e. Group 3) was a significantly lower CH₄ sink (Fig. 4e–h). The five soil positions showing CH₄ emissions were, however, equally distributed across all three groups including also two positions next to trees characterized as low CH₄ emitters (Fig. S7). Overall, there was only a weak correlation between CH₄ fluxes of stems and soil (*R*² = 0.07, *P* < 0.001) and between CH₄ fluxes of stems and CH₄ concentrations in the soil profile (max. *R*² = 0.04, *P* < 0.05, in 10 cm depth; Table S3).

The soil CH₄ exchange at forest plots near low tree CH₄ emitters exhibited clear seasonality, with lower CH₄ uptake detected in the winter dormant season and elevated CH₄ uptake in the vegetation season (Fig. 4e). The highest CH₄ uptake was detected in August and September. The soil adjacent to trees belonging to Groups 2 and 3 showed no clear seasonal flux patterns (Fig. 4f, g). In all three groups, the CH₄ uptake in the vegetation season significantly exceeded the CH₄ uptake in the dormant season (Fig. 5d–f). The soil CH₄ uptake in the dormant season therefore contributed 21.4%, 24.8%, and 31.6%, respectively, to the annual soil CH₄ uptake for Groups 1, 2, and 3 (Fig. 5d–f).

At annual scale, soil in the vicinity of low tree CH₄ emitters consumed atmospheric CH₄ at the highest rates (−261.6 ± 19.9 mg CH₄ m^{−2} soil area yr^{−1}, −2.61 ± 0.20 kg CH₄ ha^{−1} ground area yr^{−1}; median ± 95% confidence interval; Fig. 6).

Table 1 Relationships between stem CH₄ fluxes and stem CO₂ efflux and environmental parameters detected next to each individual studied tree using linear regression analyses.

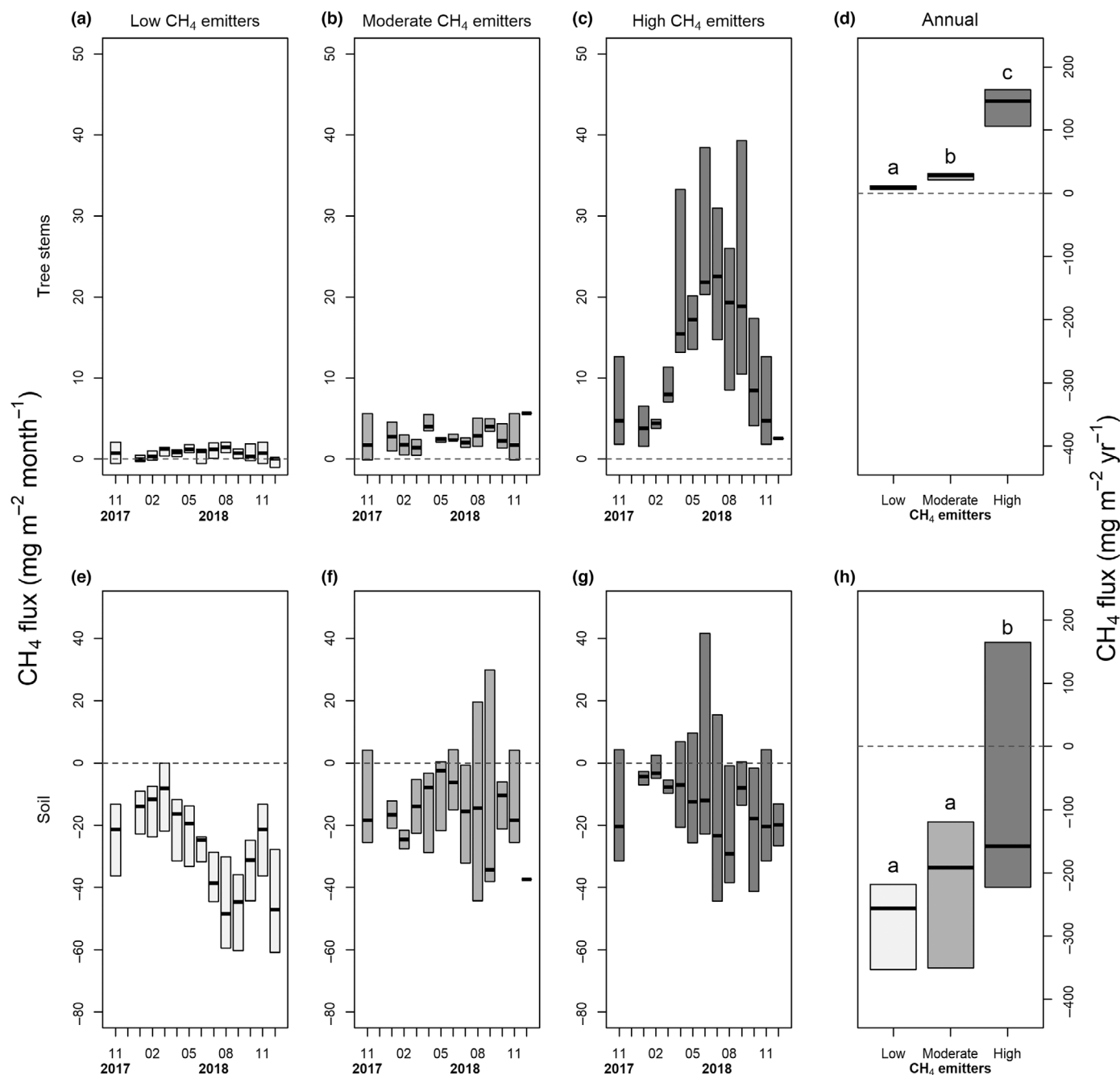


Fig. 4 Stem and soil CH₄ fluxes. Seasonal courses of monthly CH₄ fluxes (mg m⁻² month⁻¹) and net annual CH₄ fluxes (mg m⁻² yr⁻¹) from beech stems (a–d), and soil (e–h). The 20 studied trees were classified into three groups according to their CH₄ emission potential: Group 1 as ‘low CH₄ emitters’ (*n* = 10), Group 2 as ‘moderate CH₄ emitters’ (*n* = 5), and Group 3 as ‘high CH₄ emitters’ (*n* = 5). The soil positions were separated into the same three groups based on the CH₄ emissions of the tree stems in their vicinity. The fluxes are expressed per m² of stem and soil area, respectively. The CH₄ fluxes measured at stem height of 0.4 m aboveground were applied. Monthly stem and soil fluxes were calculated as medians of measurements available per each month and group. Annual fluxes were calculated as the sums of 12 monthly fluxes (January to December 2018). Positive fluxes indicate CH₄ emission, negative fluxes CH₄ uptake. Solid line within each box marks the median value and box boundaries the 25th and 75th percentiles. Statistically significant differences in annual fluxes among the three groups at *P* < 0.05 (Dunn's test) are indicated by different letters above bars.

The soil near high tree CH₄ emitters showed the lowest uptake rates (-158.0 ± 80.6 mg m⁻² yr⁻¹, -1.57 ± 0.81 kg ha⁻¹ yr⁻¹). The contribution of tree stem CH₄ emission to the soil CH₄ uptake (equal to -100%) amounted to 1.5%, 7.5%, and 46.5%, respectively, for Groups 1, 2, and 3 (Fig. 6b).

Carbon dioxide exchange of beech stems

The measured CO₂ exchange of tree stems and soil is an ancillary parameter (i.e. an indicator of physiological activity) helping to understand the CH₄ exchange in the soil–tree–atmosphere

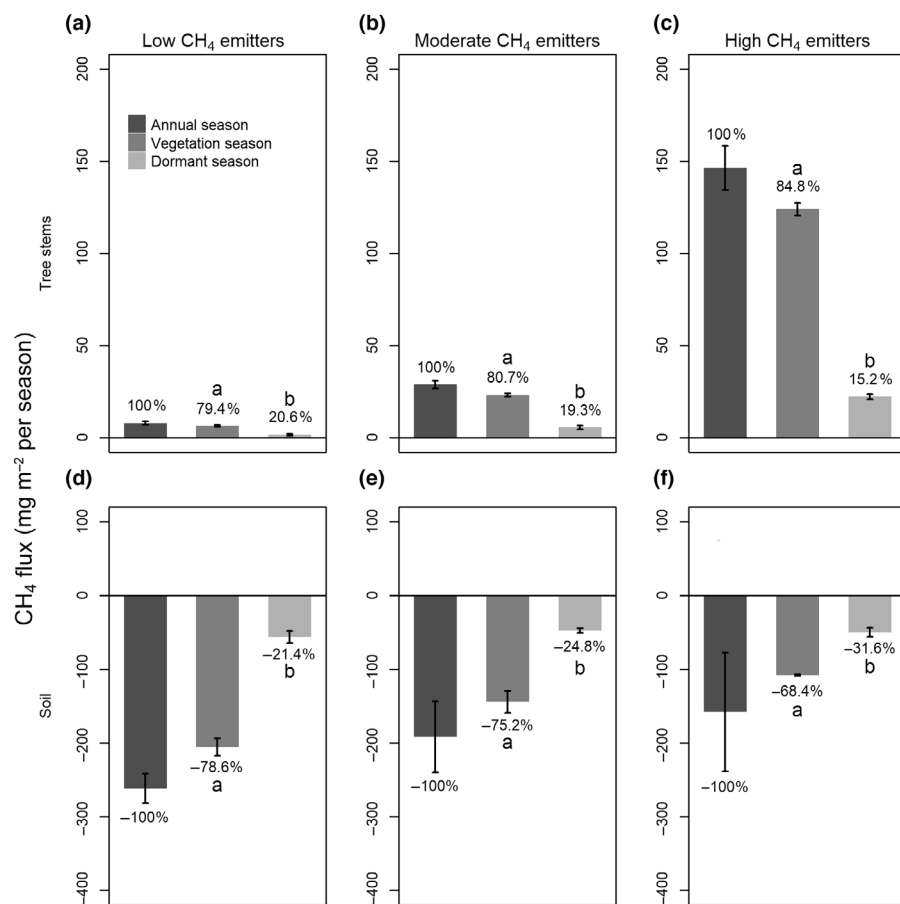


Fig. 5 Seasonal CH₄ fluxes in tree stems and soil. Fluxes of beech stems (a–c) and in soil (d–f) are presented at annual scale (dark gray columns), for vegetation season (April–October, gray columns), and for dormant season (November–March, light gray columns). The 20 studied trees and soil positions were classified into three groups according to the CH₄ emission potential of the tree stems: Group 1 as ‘low CH₄ emitters’ ($n = 10$), Group 2 as ‘moderate CH₄ emitters’ ($n = 5$), and Group 3 as ‘high CH₄ emitters’ ($n = 5$). The fluxes (medians \pm 95% confidence interval) are sums of CH₄ exchanged over 1 yr, vegetation season, or dormant season, respectively, and are expressed per m² of stem or soil area. The CH₄ fluxes measured in stem height of 0.4 m aboveground were applied. Positive flux values indicate CH₄ emission, negative values CH₄ uptake. Statistically significant differences between fluxes over vegetation and dormant season at $P < 0.05$ (Dunn’s test) are indicated by different letters. Percentage contributions of fluxes over the vegetation and dormant season to the annual fluxes (defined as 100%) are indicated above or below the bars.

continuum. The tree stems emitted CO₂ into the atmosphere, and their CO₂ efflux was uniform across the tree groups as defined based on their stem CH₄ emissions (Figs S5a–d, S8) and across the vertical stem profile (Fig. S1). The stem CO₂ efflux exhibited clear seasonal dynamics (Fig. S5a–c) following seasonality in the environmental parameters air and soil temperature and PAR (Fig. 3). The relationships between the stem CO₂ efflux and measured environmental parameters are visible in Table 1. Significant differences in stem CO₂ efflux between the vegetation and dormant seasons were detected in all studied trees (Fig. S9a–c), with the dormant CO₂ efflux accounting for between 4.6% and 13.3% of the annual CO₂ efflux. At annual scale, the tree stems emitted in total 0.83, 0.73, and 0.90 kg CO₂ m⁻² and 4.1, 3.6, and 4.5 Mg CO₂ ha⁻¹ yr⁻¹ for low, moderate, and high CH₄ emitters, respectively (Fig. S10).

Carbon dioxide exchange of soil

Soil was a net source of CO₂, with significantly higher CO₂ emissions detected close to trees from Group 1 (Fig. S5e–h). Soil CO₂ emissions of all forest plots followed a clear seasonal trend, with the highest emissions observed from June to August, and the lowest emissions detected in February and March (Fig. S5e–g). Even though the CO₂ emissions from soil remained low during winter dormancy, they nevertheless contributed as much as 16.4% to the annual totals (Fig. S9d–f). At annual scale, the soil

adjacent to trees characterized as low, moderate, and high CH₄ emitters, respectively, emitted in total 2.94, 2.02, and 2.09 kg CO₂ m⁻² and 29.3, 20.1, 20.8 Mg CO₂ ha⁻¹ yr⁻¹ (Fig. S10).

Discussion

Stems of beech trees as CH₄ emitters

The mature beech trees were identified predominantly as sources of atmospheric CH₄, whereas soil was predominantly a sink for atmospheric CH₄ over the whole year (Fig. 4). Both stem and soil CH₄ fluxes were characterized by high spatial flux variability. The experimental site is located on a sloped terrain, characterized by strong heterogeneity in soil properties such as soil water content (and thereby of air-filled soil pore space and soil aeration). That makes the site a most appropriate place to test the hypothesis whether soil water content controls CH₄ emission by trees. Nonetheless, the strong spatial heterogeneity in stem CH₄ emissions could neither be explained by water content and CH₄ and CO₂ concentrations in the soil profile and soil temperature nor by the soil CH₄ and CO₂ exchange itself (Tables 1, S3, S4). Even the five soil positions with observed CH₄ emissions were equally distributed near trees characterized as low, moderate, and high CH₄ emitters (Fig. S7). It seems the CH₄ emissions from stems of European beech are not closely related to or controlled by soil parameters directly or indirectly connected to soil CH₄ turnover.

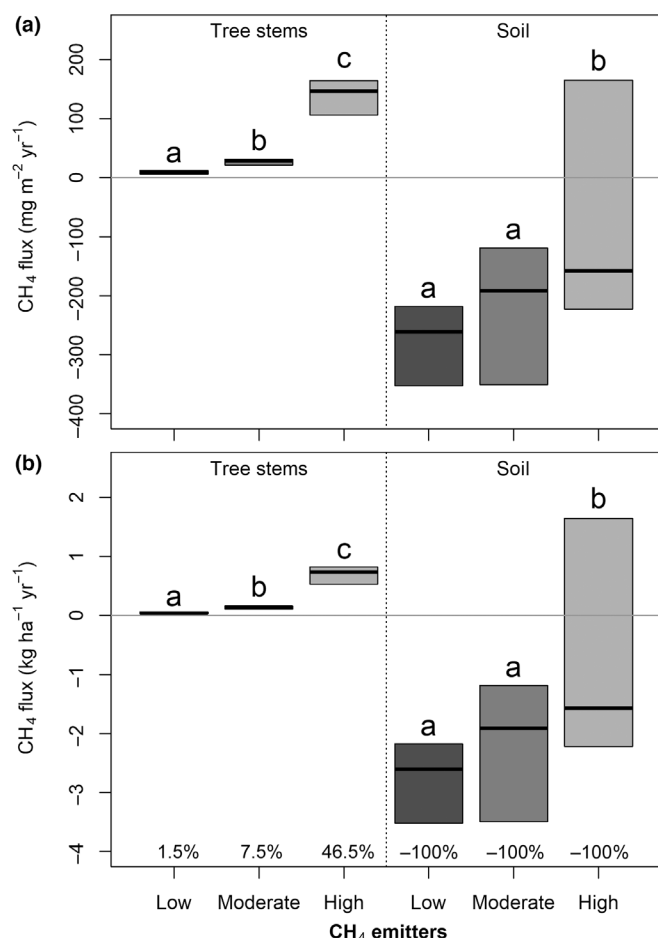


Fig. 6 Annual CH₄ fluxes in tree stems and soil. Fluxes are expressed per stem or soil area unit (a) and scaled up to a unit ground area of temperate forest (b). Fluxes are expressed as medians (solid line) of measurements from three groups of trees and soil positions classified according to the CH₄ emission potential of the studied trees: Group 1 as 'low CH₄ emitters' ($n = 10$), Group 2 as 'moderate CH₄ emitters' ($n = 5$), and Group 3 as 'high CH₄ emitters' ($n = 5$). Annual fluxes were calculated as the sums of 12 monthly fluxes (January to December 2018). Positive fluxes indicate CH₄ emission, negative fluxes CH₄ uptake. Box boundaries mark 25th and 75th percentiles. Statistically significant differences in annual stem and soil fluxes among the three groups at $P < 0.05$ (Dunn's test) are indicated by different letters above boxes. Contributions of stem fluxes to soil CH₄ fluxes within emission groups (equal to -100% , minus sign underlines the different flux direction) are expressed as percentages of the soil flux.

High spatial variability in stem CH₄ fluxes, which cannot easily be explained by a single influential factor, is known for various temperate upland and wetland tree species (Terazawa *et al.*, 2015; Wang *et al.*, 2016; Pitz & Megonigal, 2017; Warner *et al.*, 2017; Pitz *et al.*, 2018; Köhn *et al.*, 2021). Similar to our observations, Moldaschl *et al.* (2021) found no relationship between stem CH₄ emissions of *Populus alba* and *Fraxinus excelsior* and soil CH₄ concentrations or soil CH₄ flux, but they did detect a positive correlation with water-filled pore space of the soil. Such positive effect of soil water content has been detected mostly for wetland tree species only (Machacova *et al.*, 2013, 2016b; Pangala *et al.*, 2013; Schindler *et al.*, 2020; Köhn *et al.*, 2021; Mander *et al.*, 2022), whereas in the case of upland

trees, stem CH₄ emissions could not be often explained by soil water content or by soil and air temperature (Pitz & Megonigal, 2017; Warner *et al.*, 2017; this study).

Origin of CH₄ emitted from tree stems

The main question is whether the CH₄ emitted from the beech stems is produced in the soil and transported with the transpiration stream and/or by diffusion, or whether it is produced within the stems. A case study (Maier *et al.*, 2018) conducted in the same forest on five beeches in July 2015 proposed a soil origin of the emitted CH₄. In 2018, however, the CH₄ concentrations within the soil profiles near all 20 studied trees were sub-ambient and mostly decreased with increasing soil depth (Fig. S2), indicating CH₄ oxidation by methanotrophs rather than CH₄ production by methanogens up to at least 40 cm soil depth. Yet, we cannot fully exclude that CH₄ is produced in deeper soil layers and is transported via the root and stem tissue as a preferential transport system into the atmosphere. On the contrary, the densest fine root layer in the studied forest is located only 10 cm deeper (c. 50 cm depth; Krupková *et al.*, 2019) than the maximum measurement depth in our study, so that a significant source of CH₄ available for root uptake seems unlikely. Likewise, CO₂ concentrations in the soil were barely higher than 1%, indicating aerobic conditions and sufficient soil aeration (Fig. S3). A similar situation has been found in upland *Populus davidiana*, where high stem CH₄ emissions were accompanied by sub-ambient CH₄ concentrations within the soil and by strong soil CH₄ uptake, suggesting no or low contribution of soil-produced CH₄ to the net stem CH₄ emissions (Wang *et al.*, 2016).

Methane can also be produced in tree tissues via abiotic aerobic pathways from plant compounds such as pectin, lignin, cellulose, methionine, and ascorbic acid (Keppler *et al.*, 2006; Viganò *et al.*, 2008), or by methanogens living in tree tissues (Wang *et al.*, 2017; Yip *et al.*, 2019; Feng *et al.*, 2022). The precursors for microbial CH₄ production can be nonstructural carbohydrates, such as free sugars and starches transported to tree stems and stored in wood (healthy wood; Wang *et al.*, 2016; Li *et al.*, 2020), or wood degradation products of complex biopolymers, such as cellulose and pectin (infected wood; Zeikus & Ward, 1974; Covey *et al.*, 2012). Elevated CH₄ concentrations have been detected not only in wet heartwood of healthy stems, but also from trees suffering wood decay, and the internal wood's CH₄ production is expected to be one source of CH₄ emitted from the tree stems (Mukhin & Voronin, 2009, 2011; Covey *et al.*, 2012; Wang *et al.*, 2016, 2017; Jeffrey *et al.*, 2021b).

Even though we neither measured CH₄ concentrations in the stems nor ran microbial analyses of the wood, we suggest that CH₄ emitted from mature beech stems might be mostly produced from nonstructural carbohydrates in heartwood (facultative heartwood formation is known for beech; Knoke, 2003) and released into the atmosphere through sapwood and bark. As the investigated trees are c. 120 yr old and some of them are growing in conditions of elevated soil water content, internal wood decay could contribute further to CH₄ production. This assumption was confirmed by test wood coring at Beech 1 belonging to high

CH₄ emitters, where wet heartwood saturated with stem water was detected. Variations in the wet heartwood distribution and thereby wood internal CH₄ production might explain differences in stem CH₄ emissions between the studied beech individuals and the observed decoupling of the stem CH₄ emissions from soil CH₄ fluxes. Wang *et al.* (2017) detected large spatial variability in both CH₄ concentration and water content in heartwood among various upland trees, and this can be mirrored in the CH₄ emissions at the stem surface. Moreover, Covey *et al.* (2012) and Wang *et al.* (2016) showed that *in situ* CH₄ production and concentrations in the stem wood and the stem CH₄ emissions were not related to soil hydrologic parameters.

The atypical pattern of stem CH₄ emissions observed for Beeches 1 and 3 (Fig. 2) might also be related to CH₄ formation within the stem. Instead of an expected clear decrease in stem emissions with increasing stem height, commonly explained by the transport of soil-produced CH₄ via roots to the lower stem part followed by its release into the atmosphere (i.e. trees as conduits of soil-produced CH₄; Pangala *et al.*, 2015; Barba *et al.*, 2019b; Jeffrey *et al.*, 2020, 2021b; Sjögersten *et al.*, 2020; Köhn *et al.*, 2021), an opposite trend was evident. No stem surface anomalies were observed within the vertical stem profile of these two trees. However, test wood coring by Beech 1 caused several minutes long outflow of stem water from the wet heartwood at stem heights of 1.2 and 2.0 m, which showed as well similarly high stem CH₄ emissions (Fig. 2). By contrast, no wet heartwood was detected at 0.4 m stem height, characterized by low stem CH₄ emissions only. Vertical variation in the wet heartwood distribution and therefore in the expected internal wood's CH₄ production could also explain substantial differences in stem CH₄ emissions with tree height. Moldaschl *et al.* (2021) observed a similar pattern for *F. excelsior*, as the lowest CH₄ emissions were detected at the stem base and fluxes were gradually increasing up to the maximum measurement height of 3.6 m. This atypical pattern was explained as being due to formation of wet heartwood and the presence of moldered trunk parts. The volume and distribution of wet heartwood, its density, the wood water, and oxygen content, as well as the density of lenticels are known to vary with stem height of individual trees (Pangala *et al.*, 2014, 2015; Wang *et al.*, 2016, 2017).

Seasonality in tree stem CH₄ emissions, fluxes in dormant season

Considering the limited number of whole-year studies in temperate forests and their contradictory findings, it is unclear whether observed seasonality in the stem CH₄ fluxes of high emitters is or is not a general phenomenon for trees (Pangala *et al.*, 2015; Wang *et al.*, 2016; Barba *et al.*, 2019a, 2021; Köhn *et al.*, 2021; Moldaschl *et al.*, 2021).

The seasonal dynamics of the beech stem CH₄ emissions clearly followed stem CO₂ efflux ($R^2 = 0.79$, $P < 0.001$; Table 1). That supports our assumption for coupling of stem CH₄ exchange with tree physiological activity. Similar to our study, CH₄ production in wood and CH₄ emissions from stems of birch, pine, and bird cherry have been observed to follow wood

respiratory activity with coinciding temperature maxima (Mukhin & Voronin, 2011). Wang *et al.* (2017) found that stem CH₄ emissions of various upland tree species follow the seasonal patterns of wood CH₄ concentration. Moreover, increased availability of nonstructural carbohydrates during periods of high physiological activity together with oxygen depletion within the stem could promote CH₄ production by methanogenic archaea (Li *et al.*, 2020).

The beech trees showed lower but still clearly detectable CH₄ fluxes during the dormant season. That is in agreement with contributions of *Betula* sp. (31%) and *Pinus sylvestris* (19%) during dormancy (K. Machacova *et al.*, unpublished). Similarly, the soil CH₄ uptake remained low but clearly detectable and significant to the annual totals during winter dormancy, which is in agreement with findings from other beech forests in Europe (Butterbach-Bahl & Papen, 2002; Borken *et al.*, 2003; Guckland *et al.*, 2009). This points out on still ongoing gas diffusion and microbial CH₄ oxidation in the soil, even though the soil was snow covered and the upper soil layers were frozen. Therefore, it is highly crucial to consider winter tree and soil flux measurements in long-term studies to achieve accurate estimates of the CH₄ budget of forest ecosystems. The exclusion of our winter tree and soil flux measurements would lead to an underestimation of the net annual ecosystem CH₄ fluxes by 24.8%.

Net annual CH₄ exchange by tree stems and soil

The observed CH₄ emissions of beech stems (0.074–1.269 $\mu\text{mol m}^{-2} \text{ h}^{-1}$) lie in the lower quadrant of the broad range of stem CH₄ emission rates detected for upland tree species (mean fluxes between 0.001 and 6.5 $\mu\text{mol m}^{-2} \text{ h}^{-1}$; Machacova *et al.*, 2016a; Wang *et al.*, 2016; Warner *et al.*, 2017; Pitz *et al.*, 2018; Barba *et al.*, 2019b, 2021; Plain *et al.*, 2019). Despite the apparently low CH₄ emission of the investigated beech trees, they substantially reduced the CH₄ uptake potential of the whole forest ecosystem by 1.5%, 7.5%, and 46.5%, depending on their emission class. By comparison, the contribution of stem CH₄ emissions of *Quercus petraea* to soil CH₄ uptake has been reported at only 0.1% (Plain *et al.*, 2019), of *P. sylvestris* and *Picea abies* between 0.1% and 0.4% (K. Machacova *et al.*, unpublished), and of various temperate upland trees of North America in the range of 1–6% (Pitz & Magonigal, 2017; Warner *et al.*, 2017). To our knowledge, the greatest potential of upland trees to offset soil CH₄ uptake has been detected for *Carya cordiformis* (42–70%; Barba *et al.*, 2019b) and *P. davidiana* (30–90%; Wang *et al.*, 2016).

When scaled up to 1 ha of the studied beech forest, the stems belonging to high, moderate, and low CH₄ emitters, respectively, release into the atmosphere 0.73 ± 0.06 , 0.14 ± 0.01 , and $0.04 \pm 0.01 \text{ kg CH}_4 \text{ ha}^{-1} \text{ ground area yr}^{-1}$ (median $\pm 95\%$ confidence interval). The adjacent soil consumed CH₄ at rates of -1.57 ± 0.81 , -1.91 ± 0.48 , and $-2.61 \pm 0.20 \text{ kg CH}_4 \text{ ha}^{-1} \text{ yr}^{-1}$, respectively. If we regard the ratio of the emission classes of trees and soil positions to occur as high group 25%, moderate group 25%, and low group 50% (i.e. 1 : 1 : 2), then the averaged net annual CH₄ exchange of beech stems and soil in the studied

forest can be roughly estimated at 0.24 and $-1.92 \text{ kg ha}^{-1} \text{ yr}^{-1}$, respectively. The estimated soil CH_4 uptake lies within the uptake rates reported for temperate beech forests ranging between -0.08 and $-5.4 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (table 3 in Guckland *et al.*, 2009). As the CH_4 emissions of beech stems seem to be independent from soil water content and stagnic soil properties and are rather a consequence of internal CH_4 production in tree stems, they can be assumed relevant across all beech forests in the temperate zone. Assuming universality of our results and coverage of *c.* 15 million ha in Europe by upland European beech forests (Brunet *et al.*, 2010), the stems of beech trees all across Europe would emit *c.* 3600 Mg $\text{CH}_4 \text{ yr}^{-1}$, whereas the soil of beech forests would consume *c.* $-28\,800 \text{ Mg CH}_4 \text{ yr}^{-1}$. Disregarding stem fluxes would therefore result in an overestimation of the CH_4 sink strength of beech forests by *c.* 13%.

Conclusion and future perspectives

We conclude that CH_4 production in stem tissues seems to be the most likely process to explain significant CH_4 emissions from beech stems, since stem fluxes were barely connected to soil parameters. This leads to the general assumption that in Central Europe widely spread European beech trees contribute markedly to seasonal dynamics of the ecosystem CH_4 exchange, and their contribution should be included in forest GHG emission inventories. The still-practiced exclusion of the CH_4 emission potential of beech from the beech forests' CH_4 budgets can lead to severely overestimating those forests' CH_4 sink capacity. More studies on beech trees in forest ecosystems across Europe characterized by various environmental conditions are needed in order to understand the mechanisms behind the stem CH_4 production and emissions and to look for hidden CH_4 sources. The nighttime measurements would account for diurnal variability. In future work, also leaves should be considered as potential CH_4 emitters in order to accurately determine the GHG budget of forest stands. Microbial community characterization of tree stem tissues and wood incubation assays would help to understand the CH_4 turnover in the tree stems.

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Competing interests

None declared.

Author contributions

KM had the idea for the study. KM designed the study. TA, TU and KM carried out the field measurements. KS analyzed the gas

samples using gas chromatography. HW analyzed the data and prepared all graphic outputs. KM, HW, FL and PH contributed to writing the manuscript. KM and HW contributed equally to the manuscript.

ORCID

Thomas Agyei  <https://orcid.org/0000-0002-4606-3117>
Petr Horáček  <https://orcid.org/0000-0002-7097-4877>
Friederike Lang  <https://orcid.org/0000-0002-2327-1044>
Katerina Machacova  <https://orcid.org/0000-0002-8289-169X>
Hannes Warlo  <https://orcid.org/0000-0002-1767-0399>

Data availability

The datasets generated and analyzed during this study are available from the authors upon reasonable request.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Fluxes of CO₂ from vertical stem profiles of seven individual beech trees.

Fig. S2 Concentrations of CH₄ in vertical soil profile at 20 forest plots.

Fig. S3 Concentrations of CO₂ in vertical soil profile at 20 forest plots.

Fig. S4 Monthly and cumulative stem CH₄ fluxes.

Fig. S5 Stem and soil CO₂ fluxes.

Fig. S6 Monthly and cumulative stem and soil CH₄ fluxes scaled up to the ground area units, their comparison.

Fig. S7 Monthly and cumulative soil CH₄ fluxes.

Fig. S8 Monthly and cumulative stem and soil CO₂ fluxes scaled up to the ground area units, their comparison.

Fig. S9 Seasonal CO₂ fluxes in tree stems and soil.

Fig. S10 Annual CO₂ fluxes in tree stems and soil.

Table S1 Detailed information about measurements of CH₄ and CO₂ fluxes from tree stems and soil.

Table S2 Minimum detectable flux (MDF) for measurements of CH₄ and CO₂ fluxes from beech stems under usage of the applied analytical and measurement systems and protocols, and the fraction of measured stem gas fluxes exceeding the MDF.

Table S3 Relationships between stem CH₄ fluxes and stem CO₂ efflux and environmental parameters detected next to each individual studied tree using linear regression analyses.

Table S4 Relationships between stem CH₄ fluxes and stem CO₂ efflux and environmental parameters detected next to each individual studied tree using linear mixed effects models.

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