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ORIGINAL ARTICLE

A Topographic Gradient Drives Spatial Variability of Stem CH_4 Fluxes in a Temperate Alder Stand

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Abstract

Tree stems in both wetland and upland forests are a potentially significant source of the greenhouse gas methane (CH_4). Stem CH_4 emissions are assumed to play an important role on a global scale. Yet, uncertainties regarding temporal and spatial variability as well as transport processes of stem emissions remain high. Here, we assess the spatial variability and range of CH_4 egress from 28 black alder (*Alnus glutinosa* (L.) Gaertn.) trees based on data we recorded during three measurement campaigns in a mature alder carr in spring 2019. Fluxes varied significantly in time and space. The overall temporal variability during the three campaigns was larger than the spatial variability. The fluxes ranged from less than 1 μg m^{-2} h^{-1} to 450 μg m^{-2} h^{-1} with an average overall flux of 25 ± 59 μg m^{-2} h^{-1} (± SD). Stem CH_4 fluxes were highest (61.6 ± 104.5 μg m^{-2} h^{-1}) during higher soil temperatures in spring, with increasing sap flux density and an intermediate water level just above the surface (+ 2.7 ± 0.3 cm). Morphological properties of the trees, including diameter at breast height, their position on hummocks or hollows and height of the measurement on the stem, largely failed to explain variability in stem CH_4 fluxes. Large-scale topography (overall elevation gradient) within the study site and CO_2 flux were the best predictors of stem CH_4 emissions, but inundation and leaf out also significantly influenced stem CH_4 fluxes. Thus, large-scale factors such as topography as an indirect indicator for water level can potentially facilitate upscaling of tree stem CH_4 emissions.

Key words: Peatland; Methane; CH_4; Trees; Stem; Temperate; Black alder; Alnus; Glutinosa.

Highlights

- Stem CH_4 fluxes show large variability within a small spatial range.
- Stem CH_4 fluxes respond quickly to changing environmental conditions.
- Stem CH_4 fluxes show time-consistent spatial patterns which are strongly associated with large scale topographic elevation.

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Introduction

Methane (CH_4) emissions from tree stems have been commonly observed in forested wetlands (Jeffrey et al. 2020, 2023; Petaja et al. 2023; Rusch and Rennenberg 1998) and upland forests (Pitz et al. 2018; Warner et al. 2016). Still, the magnitude of stem CH_4 emissions is considered to be a major knowledge gap in the global carbon cycle (Barba et al. 2018). Relative to soil emissions, stem emissions have been reported to be either of low importance (Köhn et al. 2020) or of intermediate or even high importance in ecosystem CH_4 budgets (Jeffrey et al. 2023; Pangala et al. 2017, 2015). Just recently, studies in both boreal, temperate and tropical forests found tree stems to be CH_4 sinks of potentially global importance (Gauci et al. 2024; Machacova et al. 2021; Sundqvist et al. 2012). Very high variability has been found in stem CH_4 emissions, both seasonally (Jeffrey et al. 2023; Köhn et al. 2021) and spatially (Terazawa et al. 2015). The spatial variability is thought to be coupled to water table depth (ibid.), which ultimately depends on the topography of the studied site. Most often, an increase in stem CH_4 emissions has been found to be associated with increasing water tables (Jeffrey et al. 2023; Petaja et al. 2023; Pitz et al. 2018; Schindler et al. 2020; Terazawa et al. 2021) which is generally the case in temperate alder forests and holds true for both soil CH_4 fluxes (Mander et al. 2008; Soosaar et al. 2011) and stem CH_4 fluxes (Schindler et al. 2020). More precisely, peaks of stem CH_4 emissions were associated with water tables just above the soil surface, and a further increase in water levels did not increase CH_4 fluxes (Jeffrey et al. 2023). Increasing temperature is another important factor that can explain rising stem CH_4 fluxes (Barba et al. 2018; Sakabe et al. 2021; Terazawa et al. 2021). Generally, studies of stem CH_4 fluxes have shown high variability which can also partly be explained from different measurement settings. Upland forests often show low fluxes and low contributions to overall CH_4 emissions (Machacova et al. 2016; Pangala et al. 2015), while very high fluxes with very high contributions to the overall ecosystem CH_4 budgets have repeatedly been reported from tropical and/or systems with water-logged or permanently wet soils (Pangala et al. 2017, 2013).

Two most likely origins of the emitted CH_4 are discussed in the literature: 1) production in the soil and subsequent uptake by the roots and transport within the tree, either actively in the sap or passively by diffusion in air-filled spaces. This theory is supported by several studies reporting the highest emissions of the relevant gases from the lowest parts of the trees (Barba et al. 2018; Köhn et al. 2020; Pangala et al. 2017, 2013; Sjögersten et al. 2020; Terazawa et al. 2007). Thus, the topographic location of the tree itself may influence stem CH_4 emissions (that is, trees located at lower elevation are more often connected to the anoxic layer in the soil resulting in higher stem CH_4 emissions). 2) Production within the stem and subsequent radial diffusion to the atmosphere: Here, heart-wood rot is thought to be a possible driver of stem CH4 emissions (Covey et al. 2012; Wang et al. 2016) which will, however, not be considered further in this study as neither wood samples nor microbiology samples were taken and the focus lies on rather large-scale variability.

Regardless of the origin of the CH4, transport mechanisms inside the tree play an important role and are themselves strongly dependent on the abiotic and biotic environment. CH_4 from the soil can be transported solely by diffusion, which is indicated by decreasing CH_4 emissions with increasing stem height (Pangala et al. 2013). Further, pressurized ventilation can cause variable CH_4 emissions in time, due to changes in air and surface temperature of the plant which in turn are caused by increasing solar irradiation (Chanton et al. 1993). Also, CH_4 transport through the xylem can be driven by transpiration; thus, increased transpiration during higher temperatures is likely to increase CH_4 emissions from plants (Garnet et al. 2005; Pangala et al. 2015), which however is species dependent (Pangala et al. 2015).

The spatial and temporal variability of CH_4 emitted from tree stems adds uncertainties when upscaling CH_4 emissions in forested ecosystems. Here, we address the temporal and spatial patterns of stem emissions in a temperate alder wetland. We include spatial factors such as the height of the measurement relative to the stem base and the relative orthometric height of the tree base in comparison with the overall topography and temporal factors such as the varying environmental conditions (that is, water table fluctuations, air temperature and sap flux density). Thus, for our study we formulate the following hypotheses:

- General elevation (that is, orthometric height of the tree base) explains, at least in part, the spatial variability of stem CH_4 emissions.
- The effect of small-scale topography (hummocks, hollows) plays a minor role compared to large-scale topography (general elevation).
- Stem CH_4 emissions increase with an increase in biological activity (that is, sap flux in trees due to

increased evapotranspiration and increased activity of microorganisms in the soil due to increasing soil temperatures)
- The water level is the prime factor influencing the temporal variability of stem CH_4 flux.

Materials and Methods

The study site, a temperate Black alder (*Alnus glutinosa* (L.) Gaertn.) forest with fluctuating water tables, is located in northeastern Germany (54° 7′ 36.27″ N, 12° 28′ 55.5″ E; see Figure 1). The site was drained in the past, and the trees were logged before the site was gradually rewetted in 1998, with the final water level establishing in 2004. The site is located at an elevation of approx. 40 m a.s.l. and is situated within a local depression. It is characterized by hummocks covered by trees and hollows that are inundated for a few months a year. The average annual precipitation and temperature are 627 mm and 8.5 °C, respectively (derived from the 1 km grid product of the German Weather Service, Krähenmann et al. 2016, reference period: 1981–2010). Black alder (*Alnus glutinosa*) is the only tree species at the site, while the understorey is dominated by sedges (*Carex acutiformis* Ehrh., *Carex riparia* Curtis), Featherfoil (*Hottonia palustris* L.) and Bitter nightshade (*Solanum dulcamara* L.). At the time of study, the forest had a uniform age of approximately 40 years and the trees had an approximate stem height of 15–20 m. The diameter at breast height (DBH) was 34.6 ± 6.2 (SD) cm. For more details see (Jurasinski et al. 2020).

Study Setup

Within the stand 28 trees were chosen that were located within a depression with high water table variability. Further, the trees were chosen based on their location on large, elevated hummocks (n = 10), smaller hummocks (n = 11) and trees that were not located on a hummock (n = 7).

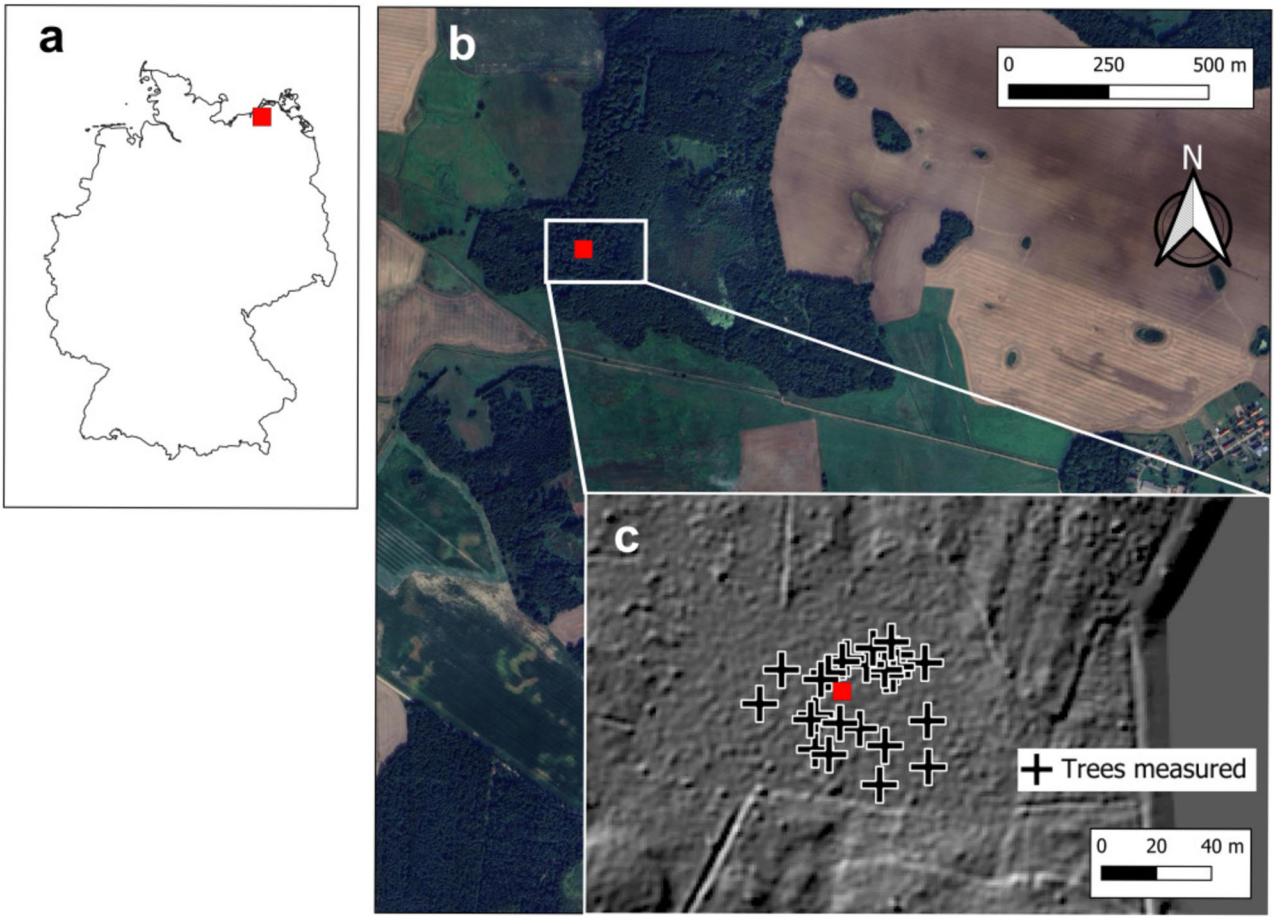


Figure 1. **a** Study location in Germany, **b** aerial view of the study location. © Bing Aerial Maps and **c** location of trees where stem CH_4 flux was measured, background depicts the DEM

One chamber per tree was permanently installed with adhesive synthetic sealant (plastic fermit ©) at between 30 and 80 cm above the stem base, depending on feasibility due to the surface roughness of the bark. Yet the chambers were located as low on the stem as possible as we expected the highest fluxes in this height. These closed dynamic chambers (non-steady-state through-flow) (Livingston and Hutchinson 1995; Pavelka et al. 2018) were constructed from polypropylene containers from which the bottom was cut out (V = 0.001 m^3 EMSA ©). All 28 chambers were installed in early March 2019, and measurement campaigns were carried out on April 24th, 2019, May 14th and May 28th, 2019. The dates of the campaigns were chosen to cover the period in which Black alder leafs out suggesting an increase of the physiological activity of the trees and a change of environmental conditions.

Flux Measurements

To perform a measurement with a stem chamber, a lid with a rubber gasket was mounted on top of the chamber to make it gas tight. The chamber was connected to a GHG analyzer via PVC tubing. During chamber closure, we simultaneously measured CO_2 and CH_4 concentrations inside the chamber with laser-based gas analyzers (either an Ultra-portable Greenhouse Gas Analyzer (Los Gatos Research Inc.) or a GasScouter (Picarro Inc.)) with measurement frequencies of 1 and 2 Hz, respectively. The Ultra-portable Greenhouse Gas Analyzer was used exclusively on the first campaign and the GasScouter exclusively during the other two campaigns. Raw data from both analyzers were treated equally, and the process of flux estimation was identical. Both analyzers were considered to have equal precision and accuracy (Jurasinski et al. 2019). We used a closing time of 3 min because changes in gas concentrations inside the chambers were quickly visible in trial measurements. However, when concentration changes were slow, we prolonged the closure time up to 7 min. We estimated fluxes with the *fluxx* function of the package flux for R (Jurasinski et al. 2014) and opted for median-based regression to estimate the fluxes. Here, the slopes between concentration values are calculated in a moving window fashion and subsequently, the median of all slope values provides the slope to estimate the flux (Siegel 1982). Fluxes are then derived by using the determined slope in the following equation:

$$f = \left(\frac{MpV}{RT}\right) * \left(\frac{1}{A}\right) * \left(\frac{\partial c}{\partial t}\right)$$

with f the CH_4 flux in mg m^{-2} r^{-1}, M the molar weight of CH_4, p the atmospheric pressure [hPa], V the volume of the chamber [m^3], R the gas constant (R = 0.0821), T the air temperature in Kelvin,

A the base area of the chamber (stem area) and $\partial c/\partial t$ the change of CH_4 concentration over time. All subsequent statistical analyses were carried out using R version 4.0.2 (R Core Team 2021).

Environmental Variables

Soil temperatures were measured and logged automatically every 15 min at three locations in two depths (5 and 15 cm) (HOBO UA001-64, Onset Computer Cooperation, MA. USA). A weather station located 500 m SE of the study site monitored air temperature, precipitation, relative humidity and photosynthetically active radiation (PPFD (photosynthetic photon flux density)) in µmol m^{-2} s^{-1}). Water level was monitored at an interval of 1 min at a central location in the stand using a SEBA © CS457 dipper connected to a CR300 logger (Campbell Scientific ©). Furthermore, we used a digital elevation model (DEM) with 1 m horizontal and 0.25 m vertical resolution (©GeoBasis-DE/M-V 2015) to derive the topographic wetness index (TWI) by calculating the slope and specific catchment area (Böhner and Selige 2002) with QGIS and SAGA (Conrad et al. 2015). The TWI is used to estimate lateral water transport and can, thus, be used as a predictor for water accumulation.

We assumed that the vertical position of the trees relative to the ground could be of high importance for the measured fluxes. However, the vertical resolution of the DEM was not accurate enough for this purpose. Therefore, we recorded the exact vertical positions (orthometric height) of all tree stem bases with a tachymeter at the site with a vertical precision of better than 1 cm. In this context the vertical position depicts the highest point of a hummock (if a tree was located on a hummock) and was defined as the spot where the visible part of the tree above the soil begins. This exact point was also used as the base point from where the additional variable height above stem base (HASB) was measured. Additionally, the diameter at breast height (DBH) was recorded. Moreover, the tachymeter measurements were used to measure the relative orthometric soil height at distinct points (n = 24) between all trees monitored. This information was then used to interpolate the soil

surface using IDW interpolation. For each tree a soil height value was then sampled from the interpolated raster.

To obtain interpolated water level values across the stand the difference between the orthometric height of the ground water well and the sampled points in the stand was calculated. On the base of the recorded ground water level (daily average of each campaign day) and the height difference between the ground water well and the sampled heights from the raster, an interpolated water level could be calculated. This was used to add a categorical variable *inundated* that entered statistical analyses stating if the tree base was most likely inundated or not. An additional categorical variable *leaf.out* stated if the measurement was taken prior or post leaf out. Leaf out was determined visually in the field.

Further, sap flux density was measured at three representative black alder trees with the heat field deformation method (HFD) with a pair of permanently installed thermocouples on each tree (Type SF- G, Ecomatik GmbH, Dachau, Germany). We calculated the sap flux density with the following formula:

$$U = 0.714 * \left(\frac{\Delta Tmax - \Delta T}{\Delta T}\right)^{1.231} * 60$$

with U the sap flux density in [ml m^{-2} s^{-1}], $\Delta Tmax$ the maximum value of ΔT every day and ΔT the temperature difference between the pair of thermocouples installed in the tree.

All data analyses and visualizations were done using R (R Core Team 2021; Wickham 2016). To test for significant differences of stem GHG exchange between measurement campaigns, the entire flux data set was tested for normality using Shapiro–Wilk test. As the flux data set was not normally distributed, Wilcoxon–Mann–Whitney test was used to determine statistically significant differences between the campaigns.

Linear mixed effect models were used to find the variables having the strongest effect on stem CH_4 fluxes. Prior to analyses using linear mixed effect models, all numerical variables were centered and scaled. The best performing model was chosen by manual backward selection, e.g., successively leaving out the variable with the lowest t-value. Subsequently, the conditional R^2 was calculated using the *performance* package in R (Lüdecke et al. 2021). This procedure was done as long as R^2 did not decrease. The final model incorporated the individual tree as a random effect and orthometric height, CO_2 flux, TWI, leaf out, HASB and inundated as fixed effects. An ANOVA was carried out on the final model parameters in order to obtain levels of significance. Averages are given ± 1 standard deviation (SD).

Results

Environmental Parameters

Environmental parameters varied significantly over the course of the measurement period. Generally, air temperatures increased from the second campaign onward and precipitation was relatively low. During the week preceding each measurement campaign, average air temperatures were 10.8 °C, 8.8 °C and 12.6 °C, for campaign one, two and three, respectively. Total precipitation during the week preceding each campaign was 0.1 mm, 6.2 mm and 0.2 mm for campaign one, two and three, respectively (Figure 2).

Water levels dropped from above the soil surface to below soil surface during the study period, overall averaging + 4.5 ± 5.5 cm. Soil temperatures gradually increased and on average were 10.1 ± 2.3 °C and 9.6 ± 2.1 °C at 5 and 15 cm depth, respectively Figure 3. The third campaign differed quite strongly from the first and second campaigns in that soil temperatures were approx. 3 °C higher and water levels were lower (-5 cm in contrast to water levels above ground surface during the first and second campaign) Figure 3. Additionally, all three campaigns differed in their meteorological conditions (Figure 3). All three campaigns were characterized by sunny weather with gradually increasing solar radiation (268 ± 301 µmol m^{-2} s^{-1}, 293 ± 315 µmol m^{-2} s^{-1}, 317 ± 328 µmol m^{-2} s^{-1} for the first, second and third campaign, respectively). The air temper-

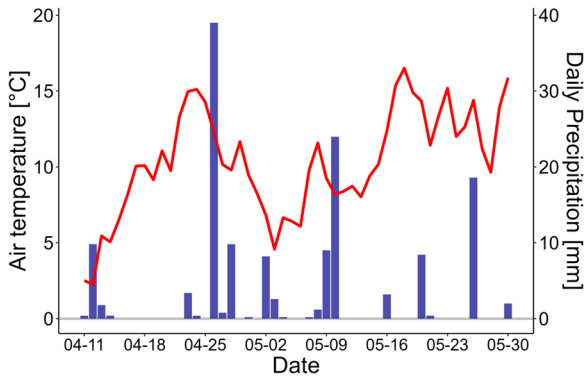


Figure 2. Air temperature recorded at the weather station close to the study site and precipitation data obtained from the DWD (German weather service) grid data.

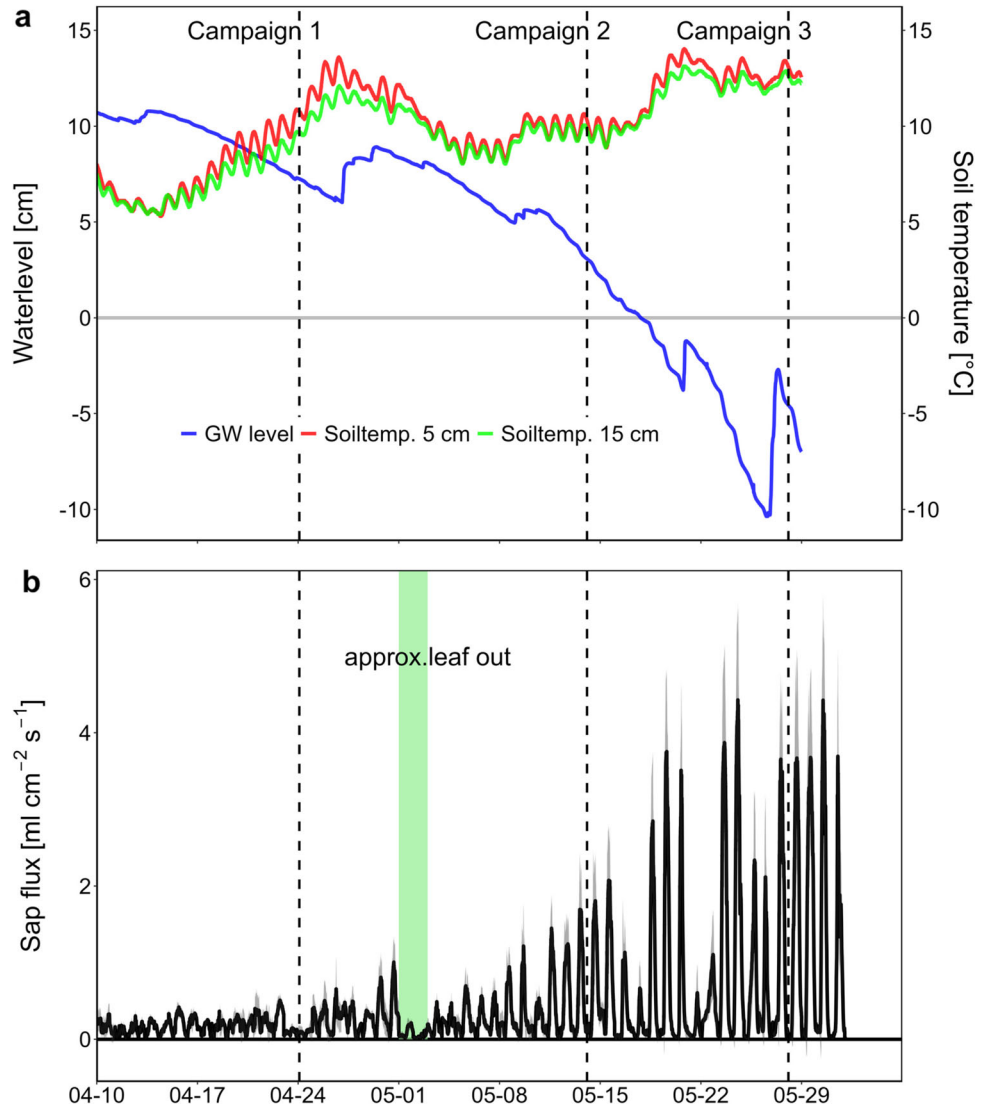


Figure 3. **a** Average soil temperature at 5 and 15 cm depth measured at three spots within the stand and water level measured at one spot, **b** sap flux density (shading represents standard deviation).

ature did not differ significantly during the campaigns ($p = 0.5$). However, sap flux increased strongly from the first to the third campaign (0.1 ± 0.02 ml m^{-2} s^{-1}, 0.7 ± 0.6 ml m^{-2} s^{-1}, 1.4 ± 1.4 ml m^{-2} s^{-1}, for the first, second and third campaign, respectively, $p < 0.01$) (Figure 4). This indicates a strong increase in physiological activity of the trees during the course of the three campaigns.

Tree Stem CH_4 and CO_2 Exchange

All tree stems that we monitored ($n = 28$) were at least temporarily a source of CH_4 during the three campaigns, and we did not measure noteworthy CH_4 uptake (Figure 5). Generally, CH_4 fluxes ($n = 252$) were low across the stand with few maxima. Fluxes varied significantly between campaigns ($p = 0.02$), averaging 16 ± 25 µg m^{-2} h^{-1} on April 24th, 64 ± 106 on May 14th and 15 ± 20 µg m^{-2} h^{-1} on May 28th. The highest fluxes of each campaign were 83 µg m^{-2} h^{-1}, 452 µg m^{-2} h^{-1} and 77 µg m^{-2} h^{-1}, respectively. Notably, six trees acted as high emitters showing much higher emissions than the majority of the other trees (Figure 5).

The tree stems acted as a source for CO_2. CO_2 fluxes also differed significantly during the cam-

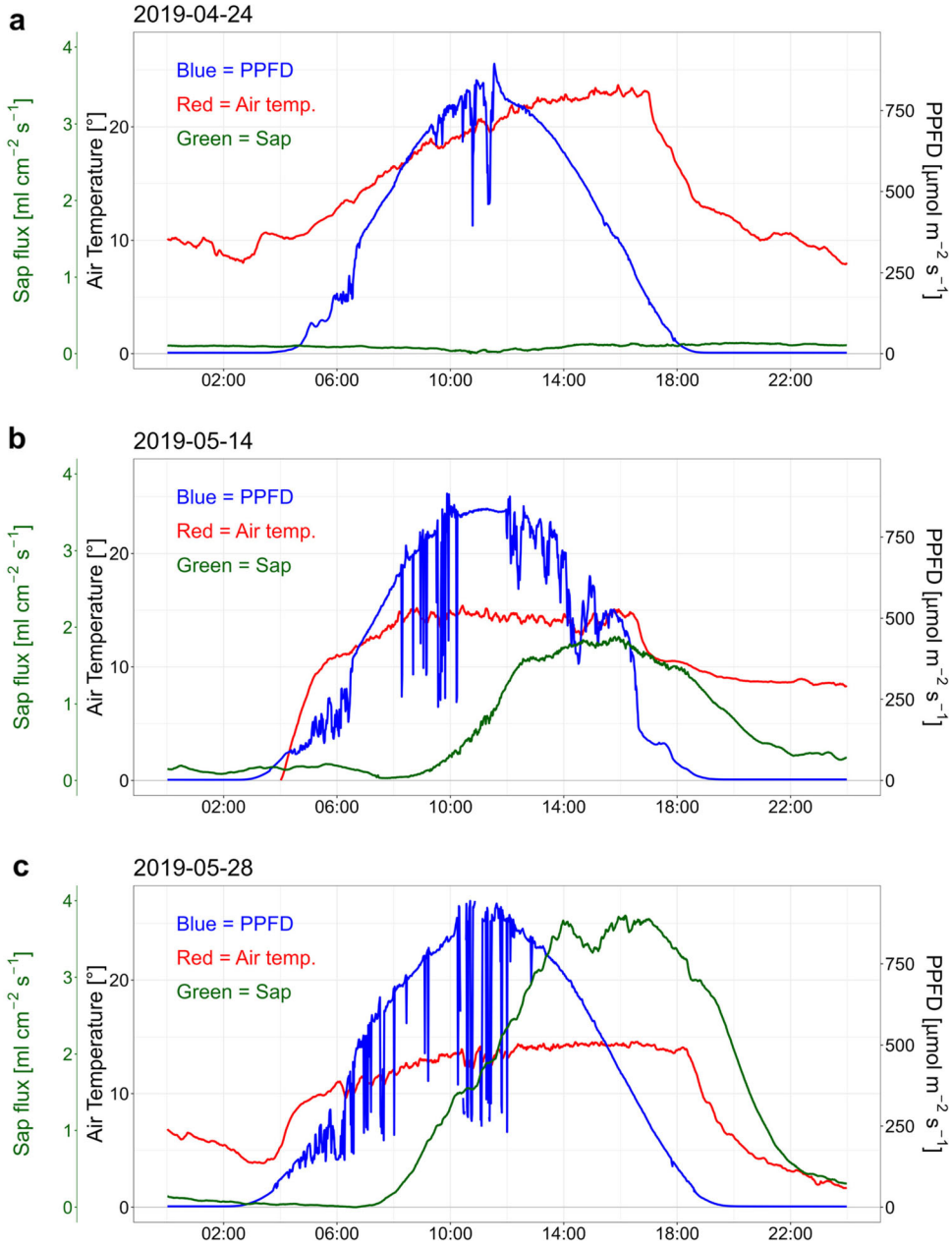


Figure 4. **a** Air temperature, sap flux density and photosynthetic photon flux density during each measurement campaign **a–c**, on April 24th, May 14th and May 28.[th]).

paigns (p = 0.01); however, not as many outliers were apparent as were in the CH_4 fluxes. Further, the magnitude of the CH_4 fluxes was much lower than that of the CO_2 fluxes. The overall mean stem CO_2 flux was 57.1 ± 37.3 mg m^{-2} h^{-1}. The average CO_2 fluxes by campaign were 53.8 ± 33.1 mg m^{-2} h^{-1}, 49.4 ± 33.1 mg m^{-2} h^{-1} and 65.3 ± 44.4 mg m^{-2} h^{-1} for the campaigns one to three, respectively. The highest measured flux was 234.2 mg m^{-2} h^{-1} on May 28th.

Topography

The range of the TWI (topographic wetness index) within the stand was relatively small (3 to 8.9) compared to the overall data set (0–27). Thus, the TWI may be limited in giving explanations regarding the topographic setting of the trees. The orthometric height that was measured within the site revealed variable microtopography with a minimum of 36.85 m and a maximum of 37.44 m above sea level.

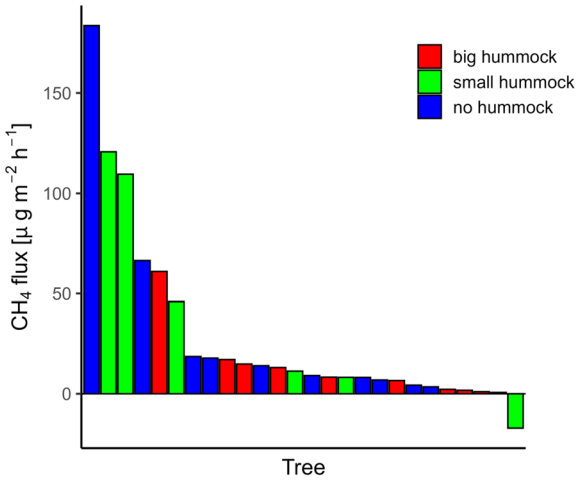


Figure 5. Average stem CH_4 fluxes ordered by their magnitude. Color depicts the location of the tree on big, small or no hummock.

Controlling Factors of Stem CH_4 and CO_2 Fluxes

Neither DBH (diameter at breast height) nor the vertical position of the tree base (hummock, hollow) significantly explained differences in stem CH_4 flux, nor did the soil temperature measured in the middle of the stand. The vertical position of the chamber (HASB = height above stem base) and CH_4 fluxes were only significantly related for the first and last campaign ($R^2 = 0.25$, $p = 0.006$ and $R^2 = 0.23$, $p = 0.009$, respectively). When fluxes generally increased during the second campaign, the relationship was barely significant ($R^2 = 0.11$, $p = 0.084$). However, CO_2 fluxes and CH_4 fluxes were significantly positively related to each other on all measurement days ($R^2 = 0.19$, $p < 0.01$). However, the strength of the relationship varied strongly between campaigns (campaign 1: $R^2 = 0.67$, $p < 0.01$; campaign 2: $R^2 = 0.52$, $p < 0.01$; campaign 3: $R^2 = 0.57$, $p < 0.01$) and was caused by only very few fluxes (Figure 6).

In simple linear regression, the TWI showed no significant relationship with the CH_4 flux. The orthometric height showed a weak, yet significant, overall negative relationship with CH_4 emissions ($R^2 = 0.14$, $p < 0.001$), which was strongest during the second measurement campaign (Figure 6) ($R^2 = 0.29$, $p < 0.01$).

After manual backward selection of linear mixed effect models, the final best performing model consisted of six variables.

According to the interpretation of standardized regression coefficients (Cohen 1988) the effect of the variables *inundation* and *leaf out* can be considered large and that of CO_2 medium (Table 1).

CH_4 fluxes showed a distinct spatial pattern (Figure 7) with the southern half of the trees constantly showing higher CH_4 fluxes than the trees of the northern half. Overall elevation seems to have had an effect on stem CH_4 fluxes, as higher orthometric height was spatially associated with lower stem CH_4 fluxes.

Discussion

In general, our results confirm that Black alder (*Alnus glutinosa* (L.) Gaertn.) stems can act as sources for CH_4 emissions, as we have shown with long-term data from the site elsewhere (Köhn et al. 2020). Stem CH_4 fluxes measured in this study were in the lower range of fluxes reported in other studies from temperate wetlands (Gauci et al. 2010; Köhn et al. 2020; Mander et al. 2022; Terazawa et al. 2007), but rather fall into the range of fluxes reported from upland forests (Covey et al. 2012; Wang et al. 2016). The CH_4 fluxes on the second measurement day with favorable conditions for CH_4 production, however, were comparable to those from other wet temperate alder (Gauci et al. 2010) and dry upland beech forests (Machacova et al. 2023).

Spatial Variation of CH_4 Fluxes

CH_4 emissions from the 28 measured trees showed considerable spatial variability. Moreover, this variation was stable over time, with the same trees showing the highest emissions on all days. Clearly, six trees acted as high emitters with distinctively higher fluxes than all other trees (Figure 5). This suggests that either physiological/morphological traits or abiotic factors such as temperature or water level in proximity of the tree influence CH_4 formation and emission. Topographic position of trees has been shown to be a good indicator of stem CH_4 emissions (Pitz et al. 2018; Terazawa et al. 2007). This is not surprising since water level is an important driver of CH_4 production (Jeffrey et al. 2020; Sakabe et al. 2021; Schindler et al. 2020; Sjögersten et al. 2020). Water-level differences of 20 cm can make a large difference for CH_4 production and oxidation (Dinsmore et al. 2009), which lies in the typical range of height differences a hummock can make, suggesting lower CH_4 production and emissions from alder trees on hummocks. On the other hand, hummocks, protruding slightly out of the water, can also have much higher soil temperatures in spring than the low-

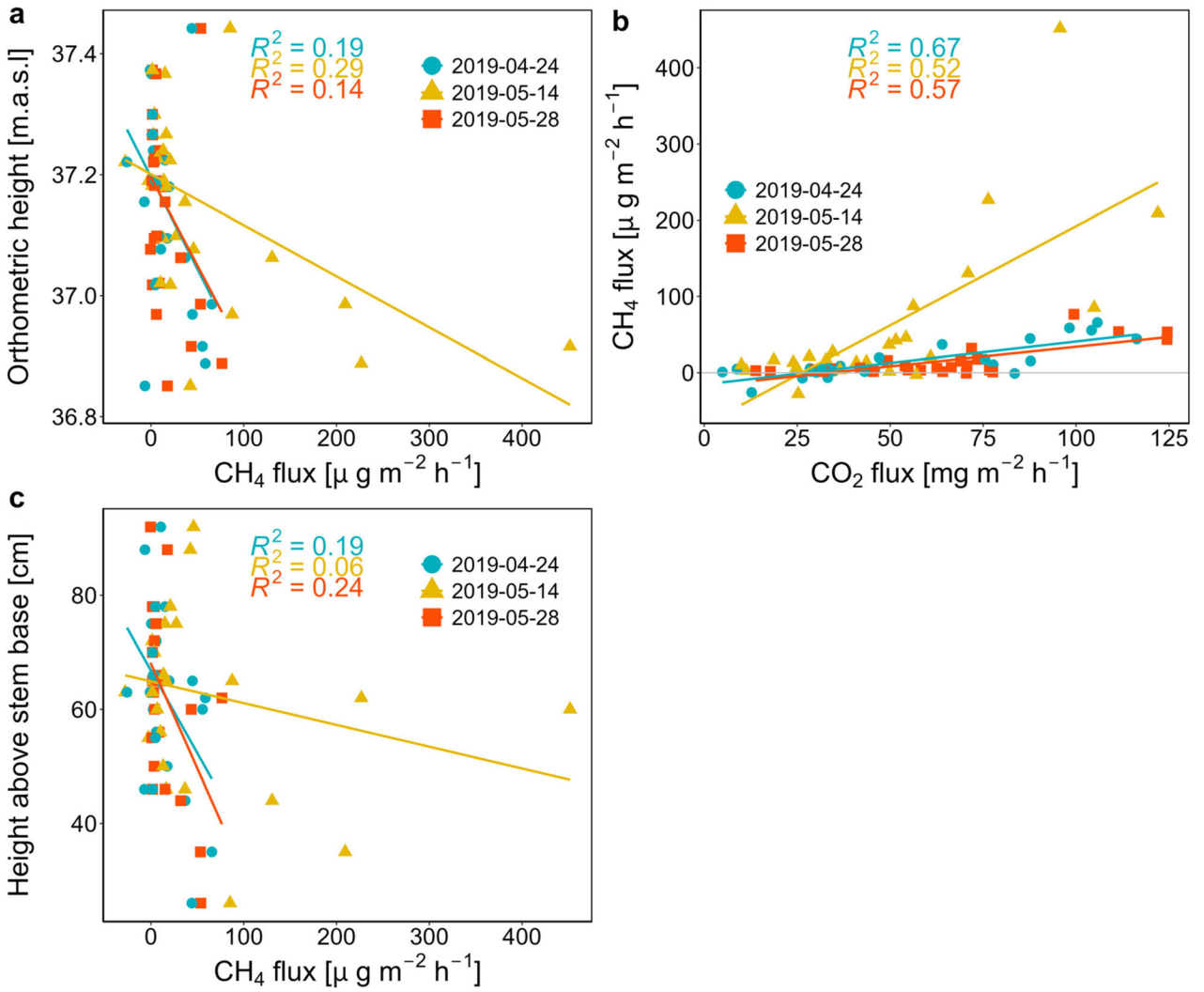


Figure 6. Relationships between **a** stem CH_4 flux orthometric height, **b** CH_4 flux and CO_2 flux and **c** between CH_4 flux and height above stem base (HASB).

Table 1. Summary Statistics of a Linear Mixed Effect Model with the Highest Explanatory Power after Manual Backward Selection

Variable	Effect size	p-value	t-statistic
Orthometric height	− 0.23	0.02	− 2.1
CO_2 flux	0.38	< 0.01	3.6
Leaf out	0.71	0.07	− 3.5
TWI	− 0.17	< 0.01	1.8
HASB	− 0.11	0.28	− 1.1
Inundation	0.80	< 0.01	3.8

Standard Coefficient as Effect Size was Calculated with the R-Package ***Effect Size*** *(Ben-Shachar et al. 2020)*

lying, water-covered areas. This in turn can increase production of CH_4 since methanogenesis is, like all microbial processes, strongly temperature dependent (Aben et al. 2017; Christensen et al. 2003; Koebsch et al. 2015). Against this background, it is unexpected that neither the topographic wetness index nor the categorical position variable (high hummock, low hummock, no hummock) was significantly related to stem CH_4 fluxes in our data set.

One reason for this might be the fact that there is a slight elevation gradient across the site. Although the 28 trees are all situated in a depression, the southern part of the study area is located a bit lower than the northern half, which potentially leads to a longer duration of inundation. Indeed, CH_4 emissions from trees in the southern half of the study

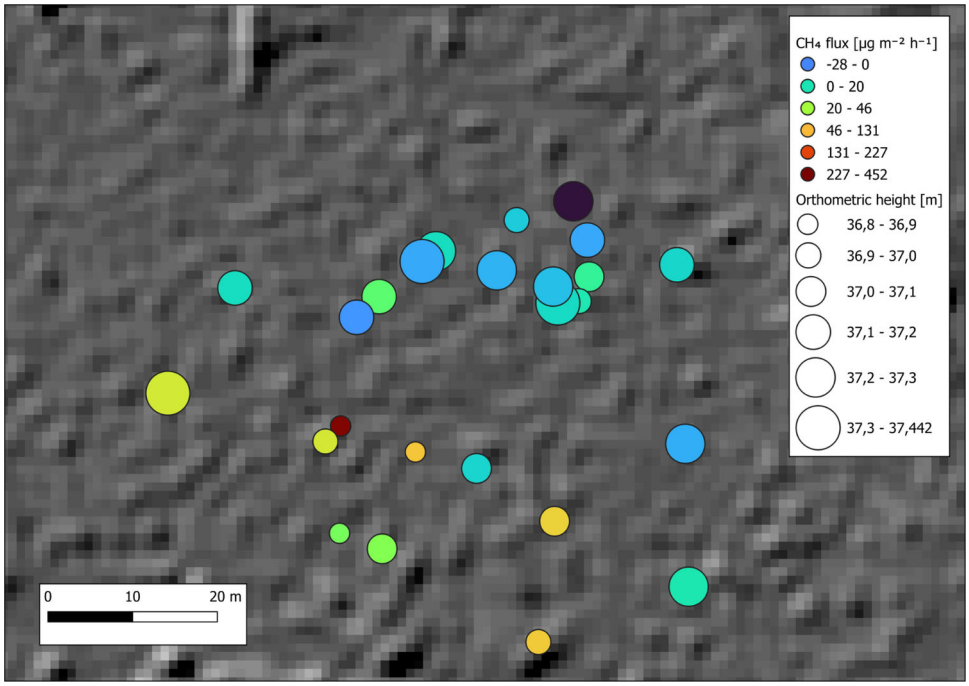


Figure 7. Visual overview of the spatial variability of stem CH_4 fluxes (colors) and orthometric height (size of circles).

area were generally higher throughout the measurement campaigns. Our findings indicate that the large-scale topographic position of the trees is of importance and can function as a proxy for the relative water table position. This explanation is further supported by the fact that the interpolated water level was the variable having the strongest effect on stem CH_4 fluxes and that stem CH_4 fluxes were significantly correlated with the orthometric height of the tree base. The topographic gradient, however, may lead to subsurface water movement, potentially altering the redox conditions in the soil, the CH_4 production and hence the uptake rates by the roots of the tree. As the porewater CH_4 concentration has a great influence on stem CH_4 emissions (Sakabe et al. 2021), it should be included in future analyses. The fact that the calculation of the Terrain Wetness Index did not yield satisfying results may further be because the area was probably slightly inundated at the time of laser scanning, creating a leveled-out area instead of the real surface area. The acquisition of the highly precise vertical position of each tree could yield an appropriate indicator for the CH_4 egress from each stem. Nevertheless, it has to be noted that both the DEM and the orthometric height are variables with a **1.** small range of values within the study area, making conclusions difficult and **2.** relatively high uncertainty. Firstly because the remotely sensed DEM has a limited resolution and secondly the in situ measurement of the orthometric height depends on the definition of the stem base which may vary and not be easily comparable depending on how the tree and the hummock is shaped, thus, the approach of using orthometric height or remotely sensed information from DEMs should be assessed in potentially more suitable settings with greater elevation gradients in combination with constantly wet parts. In addition, this study was undertaken in a Black alder stand with relatively low stem emissions and also low overall ecosystem contribution of stem fluxes to the overall CH_4 budget (Köhn et al. 2020). Hence, a trial with the methods presented here is potentially more informative in a stand with constantly high stem CH_4 fluxes. In conclusion, orthometric height as a proxy for stem CH_4 fluxes is promising because of its simplicity but has to be trialed in a more suitable environment.

Temporal Variation of CH_4 and CO_2 Fluxes During Spring

We conducted three campaigns during the transition from winter senescence to leaf out. Thereby we covered a range of important abiotic and physiological factors that are potential drivers of stem CH_4 emissions (that is, water level (Schindler et al. 2020; Sjögersten et al. 2020)) and mainly increasing temperatures (Koebsch et al. 2015; Sakabe et al. 2021; Yvon-Durocher et al. 2014).

During our measurement period soil temperatures increased notably, while the water level dropped by at least 20 cm. The stem CH_4 fluxes followed neither of the variables directly. However, the interaction between stem CH_4 fluxes and influential variables is most likely not that straightforward and CH_4 concentrations in the porewater which are a prime influencing factor (Pangala et al. 2013; Sakabe et al. 2021) were not monitored. Further, soil water content is another potential proxy that may be a more direct predictor of stem CH_4 fluxes, especially over longer periods of time (Mander et al. 2022) that could make scaling of stem CH_4 fluxes more precise. However, a central limitation of this study is that the campaigns rather represent snapshots in time and the derivation of dynamic proxies such as soil moisture, soil temperature and water level could not really beaccounted for. CH_4 emissions were highest in the second campaign, which may have been caused by low temperatures being a limiting factor for methanogenesis *before* the second campaign and oxic soil conditions limiting methanogenesis *after* the second campaign. Thus, it seems likely that Alder stands with more stable water tables will show higher sustained CH_4 emissions when higher water levels are also associated with higher temperatures (Köhn et al. 2020). Notably, leaf out had a profound impact on stem CH_4 fluxes, which is just a proxy for a multitude of underlying factors such as soil temperature, radiation or physiological activity. Hence, it remains difficult to disentangle these factors.

Sap flux intensity in the adjacent trees and CO_2 release from the stems increased strongly from the first to the third campaign. Both can be interpreted as proxies for the physiological activity of the trees. Since CH_4 fluxes did not follow the same pattern, abiotic factors such as water level and soil temperature seem to have been more important than the physiological activity of the trees. As an alternative explanation, the effect of physiological activity on stem CH_4 emissions may not have been visible because of low CH_4 production rates in the soil. Since CH_4 emissions ceased with a decrease in water table, despite increasing soil (and air) temperatures, CH_4 production either by heartwood rot (Zeikus and Ward 1974) or production in plant material itself (Keppler et al. 2006) is rather unlikely. This is further supported by negative relationships between stem CH_4 emissions and height above stem base (Figure 6). This relationship has already been found in other studies with saplings (Rusch and Rennenberg 1998) as well as with mature Black alder trees (Pangala et al. 2015; Schindler et al. 2020) et al., indicating that the source of the CH_4 is in the soil.

Additionally to limited CH_4 production rates, methanotrophy within the tree has to be considered. Studies in several ecosystems from boreal to tropical settings have found tree stems to be CH_4 sinks with potentially global importance (Gauci et al. 2024). Uptake rates were as high as 498 $\mu g\ m^{-2}\ h^{-1}$ in tropical settings (ibid.) or 11 $\mu g\ m^{-2}\ h^{-1}$ on average in boreal ecosystems (Sundqvist et al. 2012). An increase in the CH_4 sink function of tree stems with increasing stem height was observed despite the trees not being located in a permanently dry ecosystem (Gauci et al. 2024) which could mean that also in this study an uptake of CH_4 further up on the stem is possible. Measurements in this study only took place at the lowest part of the stem which potentially leads to a disproportional representation of stem CH_4 *emissions*. Only 2% of the fluxes were negative with rates between -25 and $-27\ \mu g\ m^{-2}\ h^{-1}$, all stemming from the same tree located relatively high. Jeffrey et al. (2021) showed that methanotrophic bacteria inhabit the bark of subtropical tree species and Gauci et al. (2024) found CH_4 oxidizing capacity in wood cores of several tree species. This shows that it is likely that tree stems, especially at greater stem heights, could constitute an important CH_4 sink. This sink may furthermore be dependent on the GPP (gross primary productivity) or PAR (photosynthetically active radiation) which was discussed as a potential indirect indicator for enhanced activity of methanotrophic bacteria by Sundqvist et al. (2012).

Thus, the absence of a straightforward relationship between abiotic controls and CH_4 emissions may be explained by in increase of methanotrophic activity within the stem at higher temperatures. In conclusion it must be noted that firstly, CH_4 uptake also takes place in a periodically wet ecosystem, secondly, that methanotrophic activity in the stem must be considered in studies assessing stem CH_4 emissions and, lastly, that the overall contribution of stems to the ecosystem CH_4 budget may be overestimated if a setup is used as it was in this study.

Regarding the transport mechanisms of CH_4 produced in the soil conclusions are still hard to make. Teskey and McGuire 2004 have shown that stem CO_2 efflux can be directly linked to CO_2 concentration in the sap. This could mean that CH_4 dissolved in the pore water could be absorbed by the roots and transported in the xylem sap. Barba et al. (2019) point out that simultaneous measurements of sap flux intensity and stem emissions

could yield important information regarding the transport processes of the gas. A relationship between sap flux and stem CH_4 emissions has already been found in temperate *Alnus japonica* forests (Sakabe et al. 2021; Takahashi et al. 2022). As the thermo-osmotic gas transport in Black alder is strongly dependent on radiation levels Schröder (1989), it could be expected that a slight increase in radiation over the course of the campaigns would firstly lead to increased stem CH_4 fluxes or secondly to strong diurnal variability of the fluxes which was found in a study from a temperate *Alnus japonica* stand where this variability was connected to sap flux (Takahashi et al. 2022). Pangala et al. (2014) found no distinctive diurnal pattern. An increase in stem emissions due to elevated radiation is not likely due to water level and moisture overriding any potential other variable Evans et al. (2021). Further, an intensive 18-h campaign in the same stand did not reveal any diurnal variability (Köhn et al. 2020).

In our study, the recorded increase in sap flux from the first through the second and third campaign was associated with a decrease in CH_4 emissions. Thus, despite this apparent increase in physiological activity of the trees and the absence of an congruent increase in stem CH_4 flux it is likely that decreasing water levels and/or soil moisture (not measured) limited methanogenesis, that the CH_4 is simply not transported in the sap or that methanotrophy within the stem increased leading to lower emissions. For future studies it could be beneficial to monitor more trees within a stand with water levels constantly at or above soil surface, since these ecosystems emit the largest amounts of stem-mediated CH_4 (Jeffrey et al. 2020; Köhn et al. 2020). Further, it is of importance to monitor CH_4 fluxes at higher stem heights or even within the canopy.

Variability of CH_4 Emissions in Space and Time—What is More Important?

Despite the fluxes included here being relatively small, variability in space and time was high which supports the assumption that alder stem emissions of CH_4 must not be neglected. According to our analyses, spatial variability of stem CH_4 fluxes shows temporally constant patterns which are most likely related to patterns of surface elevation which act as an indicator for inundation. The scale of the horizontal spatial variability lies within a few meters but is most likely best visible at stand scale of several 10 or 100 m. Vertically, the spatial variability is visible at the decimeter or even centimeter scale. However, larger vertical differences in topography would likely make this relationship more pronounced. As the temporal period in this study was rather short and focused on the changing environmental boundary conditions, it is not possible to clearly state whether temporal or spatial variability is to be considered more important. However, stand-scale topographic factors such as elevation generally show a strong relationship with stem CH_4 emissions (Jeffrey et al. 2023). With a combination of such easy to obtain proxies and the knowledge of emission patterns of different tree species, it could be possible to make an assumption on global variability of stem CH_4 emissions. Thus, focusing on spatial variability may be more beneficial in order to close apparent gaps in the global CH_4 budget.

Conclusion

In our study we focused on the spatial and temporal variability of stem CH_4 emissions from Black alder (*Alnus glutinosa* L. Gaertn). We found that the majority of trees in a temperate alder forest were sources of CH_4, with fluxes varying over three orders of magnitude. Secondly, we found that spatial patterns could be explained by the general topographic elevation (that is, orthometric height) of the tree rather than microtopography such as hummocks and hollows. The stand-scale topography likely served as a proxy for the duration of inundation which presumably can be considered as the most important factor directly influencing stem CH_4 emissions. The influence of the water level may override other factors such as air and soil temperature or the physiological activity of the tree (that is, sap flux density) which leads us to the conclusion that a general increase in physiological activity does not necessarily result in increased stem CH_4 emissions and must be considered against the backdrop of spatial patterns in elevation.

To further address the spatial variability, larger-scale studies in homogeneous stands with constant water levels and ideally continuous flux measurements (that is, automatic chambers) would be needed. Additionally, linking stem CH_4 fluxes to topographical characteristics of the landscape and tree species could facilitate upscaling or prediction of CH_4 emissions with remote sensing in the future. Annual budgets of CH_4 emissions from Alder stands should be based on spatially and temporally dense measurements from the entirety of the stem, potentially including leaves and twigs of the canopy to be reliable. And we need more of such measurements from a wider variety of stands to

develop trustworthy proxies for upscaling emissions.

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DATA AVAILABILITY

The data are available at https://zenodo.org/records/14676949.

Declarations

Conflict of interests The authors declare that they have no conflict of interest.

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