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Tree stem CH_4 and N_2O fluxes
in various forest ecosystems

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Tree stem CH$_4$ and N$_2$O fluxes in various forest ecosystems

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ORIGINAL PUBLICATIONS

This thesis is based on the following publications, referred to in the text by Roman numerals. Published papers are reproduced in print with the permission of the publisher.

I. **Schindler, T**., Mander, Ü., Machacova, K., Espenberg, M., Krasnov, D., Escuer-Gatius, J., Veber, G., Pärn, J., Soosaar, K. 2020. Short-term flooding increases CH_4 and N_2O emissions from trees in a riparian forest soil-stem continuum. *Scientific Reports* 10, 3204. https://doi.org/10.1038/s41598-020-60058-7

II. Mander, Ü., Krasnova, A., Escuer-Gatius, J., Espenberg, M., **Schindler, T**., Machacova, K., Pärn, J., Maddison, M., Megonigal, P., Pihlatie, M., Kasak, K., Niinemets, Ü., Junninen, H., Soosaar, K. 2021. Forest canopy mitigates soil N_2O emission during hot moments. *npj Climate and Atmospheric Science.* In press

III. Mander, Ü., Krasnova, A., **Schindler, T.,** Megonigal, P., Escuer-Gatius, J., Espenberg, M., Machacova, K., Maddison, M., Pärn, J., Ranniku, R., Pihlatie, M., Kasak, K., Niinemets, Ü., Soosaar, K. 2021. Tree stem and soil fluxes driven by soil moisture dynamics determine methane budget in a riparian forest. To be submitted.

IV. **Schindler, T**., Machacova, K., Mander, Ü., Escuer-Gatius, J., Soosaar, K. 2021. Diurnal tree stem CH_4 and N_2O flux dynamics from riparian alder forest. *Forests* 12, 863. https://doi.org/10.3390/f12070863

V. Moldaschl, E., Kitzler, B., Machacova, K., **Schindler, T**., Schindl-bacher, A. 2021. Stem CH_4 and N_2O fluxes of *Fraxinus excelsior* and *Populus alba* trees along a flooding gradient. *Plant and Soil.* https://doi.org/10.1007/s11104-020-04818-4

VI. Soosaar, K., **Schindler, T**., Pärn, J., Machacova, K., Fachin-Malaverri, L.M., Rengifo-Marin, J.E., Alegría-Muñoz, W., Jibaja-Aspajo, J.L., Negron-Juarez, R., Zárate-Gómez, R., Garay-Dinis, D.J., Arista-Oversluijs, A.G., Tello-Espinoza, R., Pacheco-Gómez, T., Mander, Ü. 2021. High CH_4 emission from palm stems and N_2O from the soil in a Peruvian Amazon peat swamp forest. To be submitted.

VII. Machacova, K., Borak, L., Agyei, T., **Schindler, T.,** Soosaar, K., Mander, Ü., Ah-Peng, C. 2021. Trees as net sinks for methane (CH_4) and nitrous oxide (N_2O) in the lowland tropical rain forest on volcanic Réunion Island. *New Phytologist* 229(4), 1983–1994. https://doi.org/10.1111/nph.17002.

Author's contribution to the articles denotes: '*' a minor contribution, '**' a moderate contribution, '***' a major contribution.

	Articles						
	I	II	III	IV	V	VI	VII
Original idea	**	**	**	***	*	*	*
Study design	***	**	**	***	*	**	*
Data processing and analysis	***	**	**	***	**	**	*
Interpretation of the results	***	**	**	**	**	**	*
Writing the manuscript	***	*	*	***	*	*	*

ABBREVIATIONS AND ACRONYMS

ANOVA	analysis of variance
a.s.l.	above sea level
C	carbon
CH_4	methane
CO_2	carbon dioxide
CP	control plot
CRDS	cavity ring-down spectroscopy
DBH	tree stem diameter 1.3 m above ground
DO	dissolved oxygen
ECD	electron capture detector (Gas chromatograph)
FID	flame ionization detector (Gas chromatograph)
FP	flooded plot
FTIR	Fourier-transform infrared spectroscopy
GHG	greenhouse gas
GC	Gas Chromatograph
IPCC	The Intergovernmental Panel on Climate Change
N	nitrogen
N_2O	nitrous oxide
PAR	photosynthetically active radiation
PVC	polyvinyl chloride
QCLS	quantum cascade laser absorption spectrometer
s.d.	standard deviation
s.e.	standard error
SWC	soil water content

ABSTRACT

The understanding of global warming and climate change are strongly related to our knowledge about greenhouse gases (GHG) such as methane (CH_4) and nitrous oxide (N_2O). Terrestrial ecosystems play a significant role in the global carbon (C) cycle, regulating climate and climate change. In particular, temperate and tropical forests significantly contribute to the CH_4 and N_2O exchange with the atmosphere. Previous investigations usually excluded the gas exchange potential of the vegetation. However, plants, especially trees, can be essential sources or sinks of CH_4 and N_2O. Although the general importance of tree gas exchange is accepted, their specific role is still largely unknown. The complexity of various climatic zones, forest ecosystem types, and tree species with individual characteristics such as soil and site parameters, health and environmental conditions, and seasonal dynamics cause a challenge to quantify and identify processes, mechanisms, and pathways behind the fluxes. This thesis investigates the role of CH_4 and N_2O fluxes from tree stems in different temperate and tropical forests and further examines the impact of several environmental conditions on these fluxes. The objectives were to (I) analyze the impact of flooding, (II) investigate the temporal flux dynamics, (III) analyze tree stem fluxes in temperate riparian forests, a tropical palm swamp forest and a tropical rain forest on a lava flow, and (IV) estimate the contribution of stem fluxes within ecosystem fluxes.

The flooding impact was analyzed in temperate forests in Estonia and the Danube river basin in Austria, showing enhanced CH_4 and N_2O emissions from tree stems at higher soil water content, especially at the lower segments of the tree stems. When adding the findings of the field study on palms and boarwood in a tropical Amazonian forest, it seems plausible that trees demand stable hydrological regimes to form and maintain aerenchyma that are required for the gas exchange between the tree above the water and the submerged tissues. Short-lived diurnal changes of CH_4 and N_2O fluxes were not found, although seasonal adaptations were identified at the temperate study sites.

The tree stems over wet soil were CH_4 emitters and turned into a weak sink under dryer conditions in temperate forests. However, additional observations in the tropics revealed likely specific physiological and morphological parameters in the role of trees of being a source or sink: (i) palm trees in Amazonia formed pseudobark in the lower stem zones inhibiting the radial gas exchange, and (ii) the CH_4 and N_2O exchange of trees with the atmosphere at the volcanic island of La Reunion was less linked with adjunct soils, but cryptogamic stem covers seemed to play a dominating role.

Conclusively, the role of tree stems in GHG exchange is highly variable in forest ecosystems. Different soil conditions, water regimes, the origin of the investigated CH_4 and N_2O, and the gas exchange processes between trees and the atmosphere reflect a dominant role of tree stems in particular forests. Investigating GHG fluxes from tree stems is far more complex, and multiple and interdisciplinary approaches are required in the future. Identifying microorganisms and biochemical pathways to improve the understanding of the origin of CH_4 and N_2O emitted from trees is evident for reliable estimation and modelling of the GHG process dynamics.

1. INTRODUCTION

Trace gases are important actors in the atmosphere and influence the environment and the climate, causing phenomena like global warming. Methane (CH_4) and nitrous oxide (N_2O) are both climate-forcing trace gases and contribute 16% and 6% to global warming (IPCC, 2014). Both gases have high global warming potential, with known sources from traffic, industry, and urban areas. However, the terrestrial biosphere can be seen as a net source of greenhouse gases (GHG) to the atmosphere (Tian *et al.*, 2016). Thus, the interest in climate change and its associated carbon (C) cycle has increased, similar to the acceleration of global warming (Cox *et al.*, 2000).

Forests play a dominant role in the global C cycle while regulating climate and climate change. Temperate and tropical forests are essential carbon dioxide (CO_2) sinks but show an important contribution to the CH_4 and N_2O exchange with the atmosphere (Bonan, 2008; Pan *et al.*, 2011). Riparian forests are known to be important sources of CH_4 because of their predominant CH_4 production in their soils. Upland forest soils are natural sinks of CH_4 and natural emitters of N_2O (Ambus *et al.*, 2006; Dalal & Allen, 2008; Carmichael *et al.*, 2014; Saunois *et al.*, 2016). Early investigations usually excluded the exchange potential of the vegetation when estimating the forest ecosystem exchange (Smith *et al.*, 2000; Megonigal & Guenther, 2008; Covey & Megonigal, 2019). However, plants, especially trees, can be essential sources of CH_4 (e.g. Keppler *et al*. 2006; Pangala *et al*. 2013; Dalva *et al*. 2001) and N_2O (Baldocchi, 2014) even if their role is still largely unknown (U.S. EPA, 2010).

The potential impact of trees in GHG dynamics is an ongoing investigation, as recent studies uncovered their importance in various forest ecosystems (Terazawa *et al.*, 2007; Pangala *et al.*, 2015; Welch *et al.*, 2019; Machacova *et al.*, 2021).

In particular, typical tree species in wetland and upland ecosystems in the temperate zone seem to be consistent emitters of CH_4 and N_2O (Pitz & Megonigal, 2017; Machacova *et al.*, 2019; Vargas & Barba, 2019; Moldaschl *et al.*, 2021). However, in some upland ecosystems, even N_2O uptake has been detected (Machacova *et al.*, 2017). In general, deciduous trees tend to emit more CH_4 than coniferous ones (Covey *et al*., 2019; Pitz *et al*., 2018; Machacova *et al.*, 2016; Wang *et al.*, 2017). Furthermore, at least drained soils in upland ecosystems act as CH_4 sinks (Le Mer & Roger, 2001; Saunois *et al.*, 2016).

Trees under tropical and subtropical climates are supposed to be high CH_4 emitters (Pangala *et al.*, 2015, 2017). However, first studies reveal the potential that tropical forest ecosystems have as a CH_4 sink (Machacova *et al.*, 2021). Few reports showed the N_2O exchange of mature trees (Díaz-Pinés *et al.*, 2016; Machacova *et al.*, 2017, 2019; Wen *et al.*, 2017), but information for tropical forest sites is even more limited (Welch *et al.*, 2019). However, Pärn et al. (2018) in their study "Nitrogen-rich organic soils under warm, well-drained conditions are global nitrous oxide emission hotspots" stressed the need to deeper investigate

the tree-soil-atmosphere-continuum. Thus, the known potential of biological surfaces like tree stems and leaves to emit or consume CH_4 (Carmichael *et al.*, 2014) in forests should be extended to further investigations about N_2O flux dynamics at tree stems.

Methane is produced under strictly anaerobic conditions by methanogenic archaea and can be oxidized by aerobic or anaerobic methanotrophs (Smith *et al.*, 2018). On the other hand, N_2O is a natural product of several N turnover processes under different water content conditions: aerobic nitrification, anaerobic denitrification, and dissimilatory nitrate reduction to ammonium in suboxic conditions (Klemedtsson *et al.*, 1988; Espenberg *et al.*, 2018). Even if both gases are released into the atmosphere by gas diffusion, advection, or ebullition at the soil surface (Joabsson *et al.*, 1999), studies revealed that trees might contribute to ecosystem GHG exchange by i) gas uptake from the soil via their root system, transport into the transpiration stream or aerenchyma systems to aboveground tree tissues and emission into the atmosphere (Rusch & Rennenberg, 1998; Machacova *et al.*, 2013); ii) uptake of CH_4 and N_2O from the atmosphere by a non-specified mechanism (Sundqvist *et al.*, 2012; Machacova *et al.*, 2017, 2019), iii) in-situ production of CH_4 and N_2O in plant tissues (Zeikus & Ward, 1974; Smart & Bloom, 2001; Keppler *et al.*, 2006; Flanagan *et al.*, 2021) or iv) alternation of gas turnover processes in adjacent soils (Machacova *et al.*, 2013, 2017; Maier *et al.*, 2018).

Anaerobic soil conditions that are required for biosynthetic processes as described before change with the water regime. Their respective gas transportation could become modified and, consequently, may change the potential trace gas emissions (Unger *et al.*, 2009a,b; Niinemets *et al.*, 2017). However, field experiments investigating such stress exposition on an ecosystem scale are scarce.

Even though there is a consensus about the general importance of tree gas exchange within the soil-tree-atmosphere-continuum, the trees' capacity and contribution vary among climatic zones, forest ecosystems, tree species, and individual trees. Characteristics such as soil and site parameters, tree size, age, and health conditions, environmental conditions, and seasonal dynamics define the particular role of trees and soils in the CH_4 and N_2O exchange (Barba *et al.*, 2019a; Covey & Megonigal, 2019; Machacova *et al.*, 2019, 2021; Vargas & Barba, 2019). However, the role of woody plants in GHG dynamics within the soil-plant-atmosphere-continuum is still far away from being quantified, and detailed knowledge to identify processes, mechanisms and pathways is still lacking.

Therefore, **the main objectives of the thesis are to estimate the CH_4 and N_2O fluxes from adult tree stems and analyze the impact of different environmental conditions on these fluxes in the soil-tree-atmosphere continuum.**

The detailed objectives of the current thesis are to,

– analyze the <u>impact of flooding</u> (**Article I and V**) on tree stem gas exchange with the atmosphere;
– determine the <u>temporal dynamics</u> of tree stem fluxes from a multi-seasonal (**Article II and III**) and diurnal (**Article IV**) perspective;
– analyze tree stem fluxes in different climatic zones: <u>temperate riparian forests</u> (**Articles I–V**), a <u>tropical palm swamp forest</u> (**Article VI**) and a <u>tropical rain forest on a lava flow</u> (**Article VII**)
– estimate the contribution of stem fluxes within ecosystem fluxes.

The hypotheses of the study were:
– high soil water content enhances CH_4 and N_2O emissions from tree stems
– CH_4 and N_2O fluxes from tree stems show a seasonal and diurnal pattern
– the lowest parts of the tree stems show the highest CH_4 and N_2O fluxes
– the role of tree stems in CH_4 and N_2O exchange is highly variable in forest ecosystems.

2. MATERIALS AND METHODS

The fieldworks were conducted in a riparian forest in eastern Estonia, a river floodplain forest along the Danube, Austria, a palm swamp in the Peruvian Amazon, and a tropical lowland forest on the volcanic island of La Reunion, France (*Figure 1*). Dominant tree species in the selected regions characterized by different climate and hydrological conditions were investigated for their respective CH_4 and N_2O dynamics.
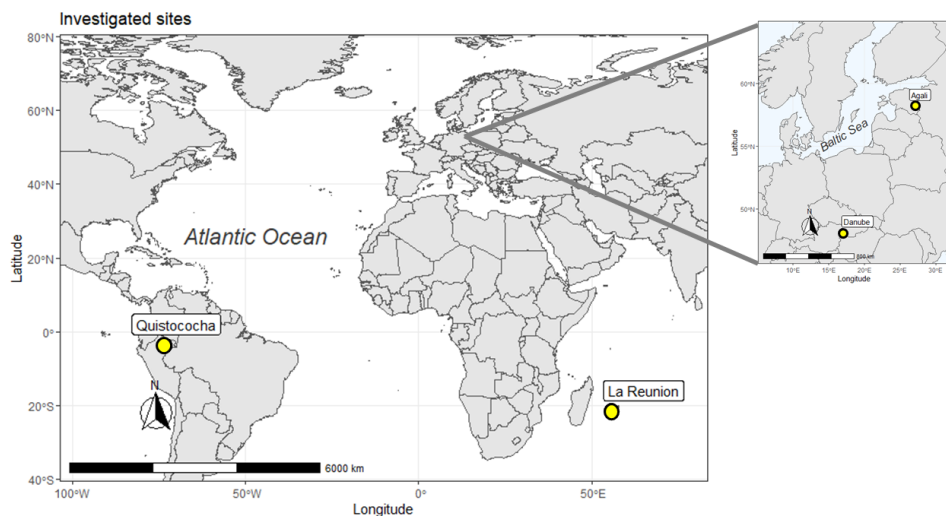

Figure 1. Location of study sites.

2.1. Description of study sites

The tree stem fluxes in a 40-year hemiboreal *Filipendula* type grey alder (*Alnus incana* (L.) Moench) forest stand on a former agricultural gleysol were studied in **Articles I–IV**. The experimental FluxGAF (Biogeochemical Fluxes in Grey Alder Forest) site of Agali (58°17'13"N; 27°17'01"E; 32 m a.s.l.) is situated in eastern Estonia, 10 km west of Lake Peipus. The mean height of the forest stand was 19.2 ± 1.4 m (mean ± s.d.), with an average stem diameter at breast height (DBH) of 0.15 ± 0.04 m. In **Article I**, a flooding experiment mimicking the impact of intensive rain at the FluxGAF site with different periods: pre-, mid-, and post-experimental was carried out in summer 2017. **Articles II and III** focused on long-term the CH_4 and N_2O fluxes at the FluxGAF site from an ecosystem perspective within 2.5 years from 2017 until December 2019. In **Article IV,** the diurnal pattern of stem fluxes at noon and midnight during three periods (summer 2017, spring and summer 2018) were analyzed.

The study in **Article V** was conducted from April 2018 to March 2019 in the Danube National Park along the Danube River in Austria (48°08'40"N, 16°53'04"E). The area is locally characterized as an alpine stream with up to seven meters of fluctuating water table. The three selected sites in a temperate floodplain forest with fluvisol soils were chosen along a ~1km long transect line – a non-flooded upland (147 m a.s.l.), a rarely flooded, mid-elevated site within the dike (146 m a.s.l.) and a frequently flooded site (440 m a.s.l.). Dominant tree species were common ash (*Fraxinus excelsior* (L.), DBH 0.26 ± 0.13 m, tree height 18.8 ± 8.1 m at the non-flooded site, and silver poplar (*Populus alba* (L.) at the infrequently (DBH 0.34 ± 0.16 m, tree height 27.2 ± 6.9 m) and the frequently flooded site (DBH 0.36 ± 0.14 m, tree height 23.6 ± 5.2 m),

The study in a palm peat swamp in the southwest of Iquitos in the Peruvian Amazon (3°50'03"S, 73°19'08"W; 101 m asl.), carried out from September 2019 to March 2020, and the results are presented in **Article VI.** Excessive rainfalls around the year determined a humid tropical climate in the region. Aguaje palm (*Mauritia flexuosa* (L. f.)) (DBH 0.293 m, height 21.3 m) and boarwood (*Symphonia globulifera* (L.)) (DBH 0.166 m, height 15.1 m) trunks, both dominant plant species in this transition zone between the minerotrophic and ombrotrophic peat zones, were chosen for the study.

For a field expedition in a tropical lowland rain forest with dry and humid seasons, a mixed forest on 400 years old volcanic bedrock in the Mare Longue Nature Reserve (21°21'28"S, 55°44'37"E, 180–200 m a.s.l.) in the southeast of the Réunion Island (**Article VII**) was selected. The stem fluxes of six dominant, mostly endemic tree species were studied (*Table 1*) from October 8 to November 7, 2018.

Table 1. Selected tree species, DBH and tree height, La Reunion study, **Article VII.**

Species	DBH (m)	Tree height (m)
Syzygium borbonicum J. Guého et A.J. Scott	0.33 ± 0.08	18.8 ± 4.4
Doratoxylon apetalum (Poir.) Radlk *var. apetalum*	0.25 ± 0.05	13.9 ± 2.7
Antirhea borbonica J.F. Gmel	0.16 ± 0.02	13.1 ± 1.9
Homalium paniculatum (Lam.) Benth	0.43 ± 0.23	16.0 ± 7.8
Mimusops balata (Aubl.) C.F. Gaertn	0.42 ± 0.17	23.7 ± 9.4
Labourdonnaisia calophylloides Bojer	0.54 ± 0.21	28.5 ± 10.6

2.2. Gas sampling from tree stems and field analyses

The exchange of CH_4 and N_2O from tree stems was measured with closed chamber systems in all field studies. Rectangular chambers were made of transparent plastic containers with airtight lids; in the workshop, the bottom was cut, the resulting frame hot-glued with a neoprene band (Machacova *et al.*, 2017). At least

one week before sampling, the prepared chambers were mounted airtight to the tree stems at up to three different heights fitting the chambers to the shape of the investigated trees (*Table 2*). For the manual sampling, four samples were collected from each chamber system via septum in a 0/60/120/180 min sequence (**Article I–IV, VI**) and a 0/30/60/90 min sequence (**Article V**), respectively. The gas samples were stored in pre-evacuated (0.3 bar) coated gas-tight vials (LabCo International, United Kingdom) and consequently analyzed at laboratories using gas chromatographs equipped with an electron capture detector (ECD) for detection of N_2O and a flame ionization detector (FID) for CH_4, respectively. A mobile Fourier transform infrared (FTIR) analyzer (DX-4015, Gasmet Technologies Oy, Finland; Warlo *et al.*, 2018) was used during the campaign at La Reunion (**Article VII**). With this, every single measurement of tree stem flux lasted c. 45 min.

Table 2. Chamber dimensions and gas sample analysis.

	Article I–IV	**Article V**	**Article VI**	**Article VII**
Chamber area [m²]	0.0108	0.018	0.0108	0.0108*
Chamber volume [m³]	0.00119	0.00196	0.00119	0.0021*
Installed height [m] above ground	0.1/0.8/1.7	0.3/1.6/ (3.6)	0.3/0.8/1.7	0.4/1.1/1.8
Number of investigated trees	12	18	10	24
Sampling and analysis	Manual GC GC-2014, Shimadzu, Tokyo, Japan	Manual GC Agilent 6890 N, Santa Clara, CA, USA	Manual GC GC-2014, Shimadzu, Tokyo, Japan	Through flow Mobile FTIR analyser Gasmet DX-4015, Gasmet, Vantaa, Finland

* *S. borbonicum*: A = 0.0162 m², V = 0.0028 m³

2.3. Soil flux measurements

At the Agali studies (**Article I–IV**), close to each investigated tree, simultaneously with stem flux measurements, soil fluxes were measured using an automated dynamic closed chambers system. A closed-loop system equipped with 12 opaque soil chambers (A = 0.16 m², V = 0.032 m³, polymethyl methacrylate – Plexiglas), multiplexer, and a G2508 analyzer (Picarro Inc., Santa Clara, CA, USA) was used to determine the gas concentration changes sequentially within each chamber. This cavity ring-down spectroscopy (CRDS) technology continuously monitored CH_4 and N_2O gas concentrations.

Static soil chambers close to the measured trees were used for studies at the Danube National Park (**Article V**) and the Peruvian Amazon (**Article VI**), with a basal area/volume of 0.071 m²/0.007 m³ (cylindric) and 0.196 m²/0.065 m³ (truncated conic), respectively. Four samples were taken in a 0/5/10/20 min sequence from 12 chambers in Austria and in a 0/20/40/60 min sequence from 10 chambers in Peru. The gas samples were stored in pre-evacuated gas-tight bottles and consequently analyzed at the laboratories as the tree stem samples before.

The soil fluxes at La Reunion (**Article VII**) were measured with static soil chambers (A = 0.0083 m², V = 0.0015 m³) using a portable FTIR analyzer (DX-4015, Gasmet Technologies Oy, Vantaa, Finland). To determine CH_4 and N_2O fluxes from basaltic lava flows, the chambers were installed directly on the volcanic surfaces, covering an enclosed rock area of 0.0054 m² with a volume of 0.0013 m³, connected to the Gasmet DX-4015 FTIR gas analyzer.

2.4. Ancillary data

Soil temperature at different depths and soil moisture from the upper soil layer was determined manually or automatically logged. Precipitation, air temperature, and relative humidity were measured automatically at Agali (**Article I–IV**) and manually at the short-termed campaigns in Peru (**Article VI**) and La Reunion (**Article VII**) or obtained from closely located weather stations (the Danube, **Article V**). Groundwater level was measured in Agali automatically and manually in Peru. In Agali and Peru, soil samples were collected and analyzed for physical and chemical parameters at Estonian University of Life Sciences in Tartu.

2.5. Calculations and statistical analyses

Gas fluxes were quantified on a linear approach according to change of CH_4 and N_2O concentrations in the chamber headspace over time, using the equation according to Livingston and Hutchinson 1995. In general, a data quality control was applied based on linear fit for CO_2 measurements. If the adjusted coefficient of determination (R^2) of the linear fit for CO_2 efflux was above 0.9, both CH_4 and N_2O fluxes were accepted regardless of their R^2 values. If the R^2 value did not meet the criteria, the chamber session was discarded; values below the limit of detection (GC) were assigned as zero if the regression line was horizontal.

Over time, a decreasing gas concentration indicated a gas uptake, i.e., a negative flux; an increasing gas concentration indicated gas emission, i.e., a positive flux. Further, stem fluxes were roughly upscaled to a hectare of soil surface area according to Machacova *et al.* (2016), based on tree and forest characteristics (DBH, tree height, tree density).

The normality of distribution was verified using the Shapiro-Wilk, Kolmogorov-Smirnov, and Lilliefors tests. The distribution of the gas fluxes deviated from the normal distribution; hence non-parametric tests were used. The Mann-

Whitney rank-sum test, the Kruskal-Wallis (One-way ANOVA on ranks) test, and the Spearman's Rank-Order Correlation were used to determine the significance of differences and the strength and direction of the relationships. Statistical analyses were carried out using Sigmaplot software (v11, v 14), Microsoft Office Excel and R v.3.1.2 / 3.6.1. Statistical significance of $p < 0.05$ was defined and accepted in all cases.

3. RESULTS AND DISCUSSION

3.1. Impact of flooding on stem CH₄ and N₂O flux dynamics in a riparian grey alder forest (Article I)

By mimicking an intensive rain-induced overland flow, 55–70 m³ daily of pond water irrigated the flooded plot at the FluxGAF site in summer 2017. The CH₄ and N₂O emissions from stems and soils showed diverging patterns in the studied plots (flooded plot – FP, control plot – CP) and the experimental periods. However, both soil and stem surfaces were net emitters of CH₄ and N₂O (*Figures 2* and *3*) in principle.
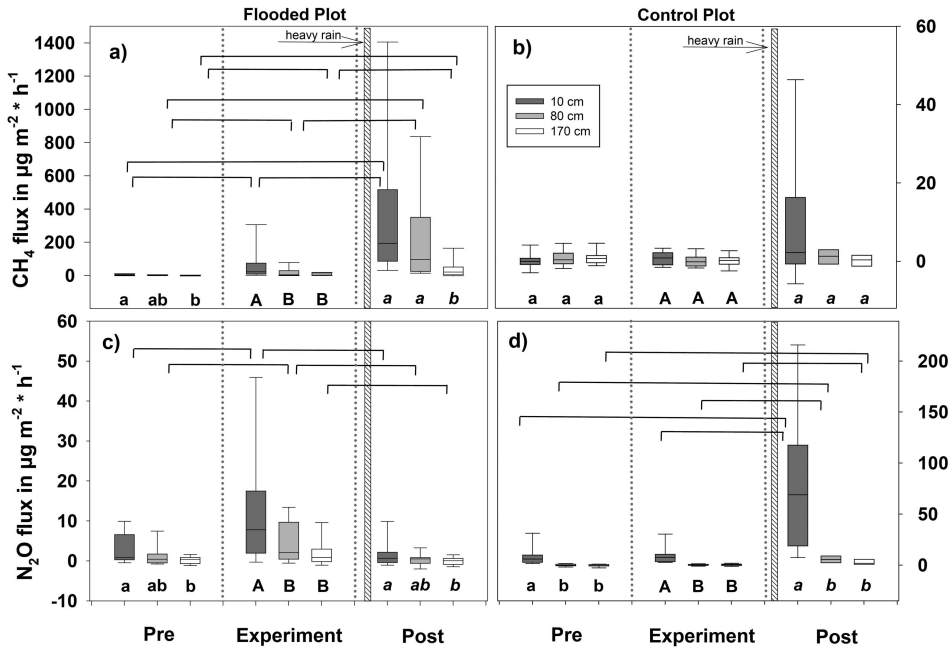

Figure 2. Stem fluxes of CH₄ (a, b) and N₂O (c, d) during the study periods at 10, 80 and 170 cm heights ($\mu g\ m^{-2}\ h^{-1}$). Stem fluxes in soil surface area equivalent. Letters below bars indicate statistically significant differences in fluxes of each stem height among the periods, differences in fluxes between adjunct periods are marked with brackets. Notice the scale difference in the flooded and control plots. The solid line within each box marks the median value, box boundaries the 25th and 75th percentiles, whiskers the 10th and 90th percentiles. Adapted from **Article I**.

3.1.1. CH₄ and N₂O fluxes at the experimental periods

In the pre-experimental period, set as a reference, no significant differences were detected in CH_4 emissions between the flooded and the control plot. At the flooded plot, stem CH_4 fluxes increased substantially from the pre- to the post-experimental period (*Figure 2a*). CH_4 fluxes from the soil (*Figure 3a*) in the flooded plot were steadily increasing from a weak consumption (-0.2 ± 1.7 µg m^{-2} h^{-1}, mean ± s.e.) at the pre-experiment to emission (12.8 ± 2.1 µg m^{-2} h$^{-1)}$) at the post-experiment period (*Figure 3a*).

Very few significant differences in N_2O emission from tree stems appeared between flooded and control plot before and during the experiment. Fluxes of N_2O from tree stems increased significantly along with the flooding experiment and declined at the post-experimental period. However, N_2O emissions from all stem heights were significantly lower in the flooded plot than the control plot during the post-experimental period ($p < 0.001$ in all cases). Nevertheless, the intensive rain forced occasional peaks with significant effect at the post-experimental period (*Figure 2d*). Soil N_2O fluxes did not differ significantly between the periods or plots (*Figure 3b*).
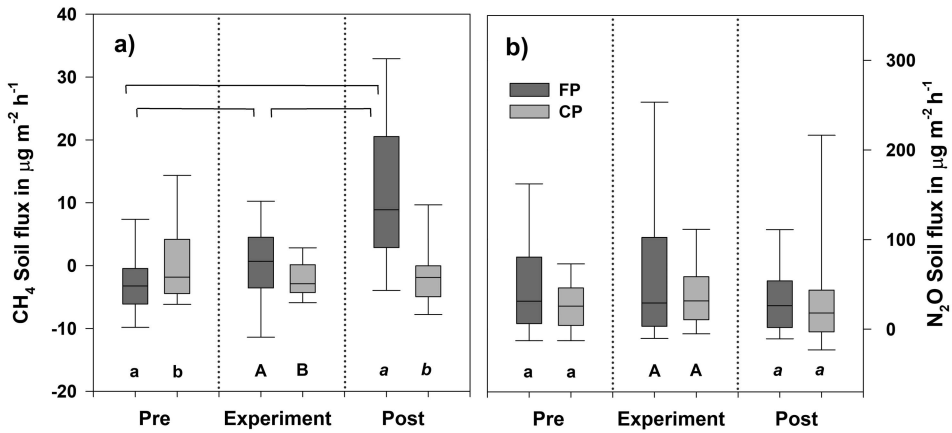

Figure 3. CH_4 (a) and N_2O (b) fluxes from the soil surface at the study period in µg m^{-2} h^{-1}. The letters below the bars indicate statistically significant differences. The solid line within each box marks the median value, box boundaries the 25th and 75th percentiles, whiskers the 10th and 90th percentiles. Flooded plot – FP, control plot – CP. Adapted from **Article I.**

3.1.2. Fluxes along the vertical tree stem profile

A significant decline ($p < 0.05$) of CH_4 fluxes along the overall vertical stem profile was found at the flooded plot during and after the experiment (*Figure 2a*) although no changes were observed at the control plot (*Figure 2b*).

The N_2O fluxes, on the other hand, showed a diminishing trend within the first meter of tree height (*Figure 2c*). Tendentially higher N_2O fluxes at the 10 cm level were observed, although a general decrease with increasing stem height was missing ($p > 0.1$). A significant difference in the control plot was noted only before and after the experimental period at the 10 cm level (*Figure 2d*), most likely caused by the heavy rain event.

3.1.3. Contribution of stems and soil

Stem fluxes were upscaled to the ground area of the forest and compared with the soil fluxes (*Figure 4*). Flood-induced CH_4 emissions from tree stems dominated with up to 88% contribution to the total CH_4 fluxes (i.e., the sum of stem and soil flux) but low uptake rates from soil surfaces balanced with stem emissions at the control area (*Figures 4a, b*).

The stems and soils were N_2O emitters, while no consumption was observed. Soil dominated the N_2O flux ratio on both plots with up to 99% contribution. However, stem fluxes contributed 12% at the control plot's post-experimental period (*Figures 4c, d*).

Known drivers such as soil water content and soil temperature (Le Mer & Roger, 2001; Terazawa *et al.*, 2015) determined the most variation of CH_4 fluxes from stems and soils also in this study. Further, aerobic nitrification and anaerobic denitrification, known as N_2O-producing processes, depend on N availability and soil water content (Butterbach-Bahl *et al.*, 2013; Pärn *et al.*, 2018). In soils holding $0.5–0.6 \ m^3 \ m^{-3}$ water, both nitrification and denitrification may contribute to N_2O (Klemedtsson *et al.*, 1988; Bateman & Baggs, 2005).

The flooding experiment observed both CH_4 and N_2O emissions from the tree stems and soils simultaneously during a reliable timeframe. Analogous experiments under laboratory conditions from three years old black alder (*Alnus glutinosa* (L.) Gaertn.) seedlings considered no effect on CH_4 emission and an increase of N_2O emissions immediately after flooding had started, although vice versa results after 40 days (Rusch and Rennenberg, 1998) which is likewise coherent with our outcomes. In the same study and our flooding experiment, CH_4 and N_2O emission decreased with stem height from 0 to 2 m. Another laboratory mesocosm experiment with *Alnus glutinosa* seedlings (Machacova *et al.*, 2013) found the same trends. In contrast, the N_2O emissions from tree stems in Agali were much lower (f~10 instead of 740), and the CH_4 emissions were up to 100 times higher. The pulsing groundwater level study in a grey alder forest (Mander *et al.*, 2015) found an increase in soil CH_4 emissions but a decrease in N_2O emissions after flooding.
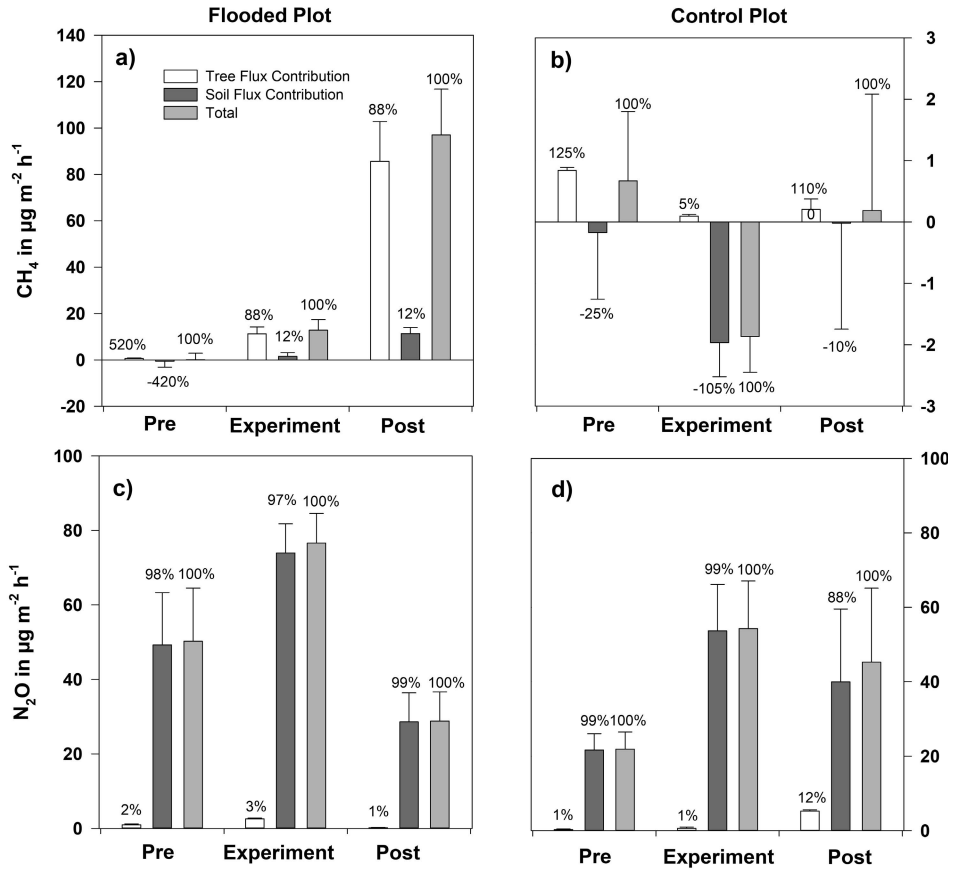
Figure 4. Contribution of sources at the pre-experimental (pre), experimental, and post-experimental (post) periods from the stems and soil in µg m^{-2} h^{-1}, scaled to a unit of the ground area of forest. Positive values indicate emission, negative fluxes gas uptake. The columns represent fluxes as means ± standard error. The stem and soil flux contributions are expressed as percentages of the sum of stem and soil fluxes. Adapted from **Article I.**

However, the recent field flooding experiment in Agali indicated a similar "chimney effect" reported earlier (Joabsson *et al.*, 1999; Rice *et al.*, 2010). Additionally, the lowland tree study with decreasing CH$_4$ emissions with stem height (Jeffrey *et al.*, 2020) supports the flooding experiment's results, i.e. CH$_4$ is produced by soil microbes and transported via roots, stems, and leaves to be released to the atmosphere.

3.2. Long-term dynamics of stem CH_4 and N_2O fluxes in a grey alder forest (Articles II and III)

The relative contribution of CH_4 and N_2O fluxes from tree stems to GHG exchange of a hemi-boreal forest ecosystem was investigated during 52 campaigns from September 2017 to December 2018. The riparian *Alnus incana* forest in Agali was a slight annual sink of CH_4 (–24.0 ± 3.3 mg CH_4-C m^{-2} y^{-1};), according to eddy covariance measurements. Average stem fluxes were the highest during the wet period from mid-September 2017 until the beginning of February 2018. They showed relatively low values during the rest of the study period (*Figure 5a*). During the wet period, fluxes from tree stems contributed 81% of CH_4 measured above the canopy. The main drivers determing CH_4 was the soil water content and soil temperature (details see **Article III**). Apparently, significant CH_4 emissions from tree stems were relatively short-lived but intensive and occurred after wetter or inundated periods. However, the time cluster was determined mainly by soil water content and soil temperature conditions and physiological activity *(Figure 5a)*, in line with other studies (Barba *et al.*, 2019; Köhn *et al.*, 2021).

For the whole study period, about 40% of ecosystem CH_4 flux originated from stems. On the other hand, in the wet period, 81% of the ecosystem CH_4 emissions contributed to the tree stems (*Figure 5b*)
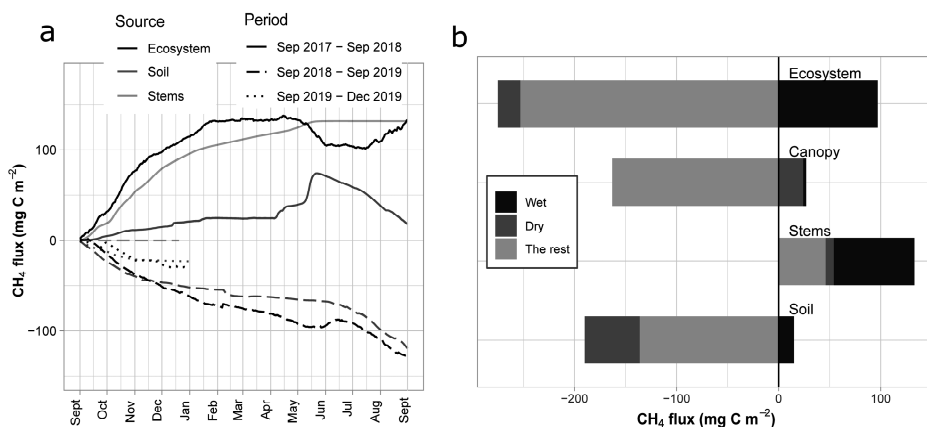

Figure 5. Cumulative CH_4 fluxes from soil, stems, and ecosystem (eddy covariance above the canopies). (a) Fluxes during two full years (Sept. 2017 – Sept. 2019) and one-third year (Sept. – Dec. 2019). Notice that the stem fluxes have been measured from Sept. 2017 to Dec. 2018. (b) The share of different sources in the CH_4 flux over the whole study period. Adapted from **Article III.**

The correlation between dissolved oxygen (DO) from groundwater and CH_4 stem fluxes at the three measured stem heights was substantial (*Figure 6*). It is possible that the CH_4 is produced in deeper (< 40cm) soil zones, where the tree roots might be disconnected from the water-saturated soil layers. In this case, molecular diffusion and bulk flow are aerating submerged organs, stipulating the CH_4 transport to the atmosphere (Joabsson *et al.*, 1999). On the other hand, aerenchyma tissues built by following strongly anoxic soil conditions provide a quick gas transport between soil and the atmosphere and, thus, supplying oxygen to the roots (Covey & Megonigal, 2019). However, the discussion is hypothetical and remains unproven.
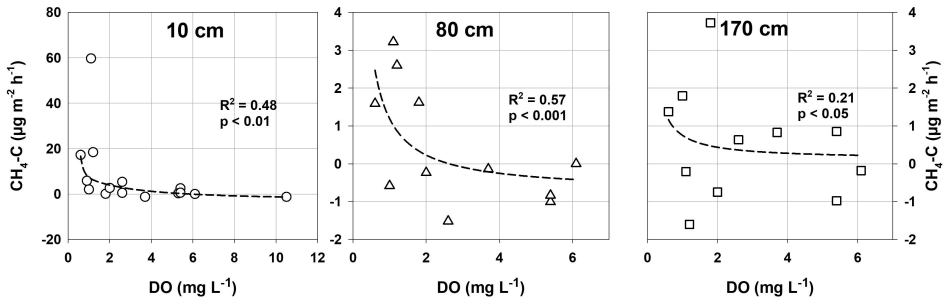

Figure 6. Relationship between the groundwater dissolved oxygen (DO) content and the CH_4 stem flux at the heights of 10, 80 and 170 cm. Mean ± standard deviation values are shown. Adapted from **Article III.**

Averaged over all measured heights and expressed per m^2 of the soil surface, the N_2O exchange from tree stems varied between a weak -0.00028 mg N m^{-2} h^{-1} uptake and low emission of 0.0228 mg N m^{-2} h^{-1}. The highest N_2O emissions were measured on the lowest position of tree stems. In contrast, slight consumption was observed at higher positions (170 cm above the ground), following a decreasing vertical profile and indicating a soil origin of N_2O.

During the 1.5 years of measurements, the cumulative flux from alder stems was 3.53 mg N m^{-2}, which constituted only 0.8% of cumulative soil fluxes (for details, see **Article II**). Thus, fluxes from tree stems in this particular ecosystem can be neglected on an annual scale and from the ecosystem perspective (*Figure 7*). However, the stepwise increase of N_2O fluxes from tree stems seems to be linked with an increase of SWC during these periods, although magnitudes lower than from soil. The high water solubility of N_2O may explain the low relevance of tree stems in this particular ecosystem (Dowdell *et al.*, 1979). The more relevant exchange of N_2O from soil and canopy with the atmosphere suggests a transport role of trees without release to the atmosphere. However, this remains speculative.
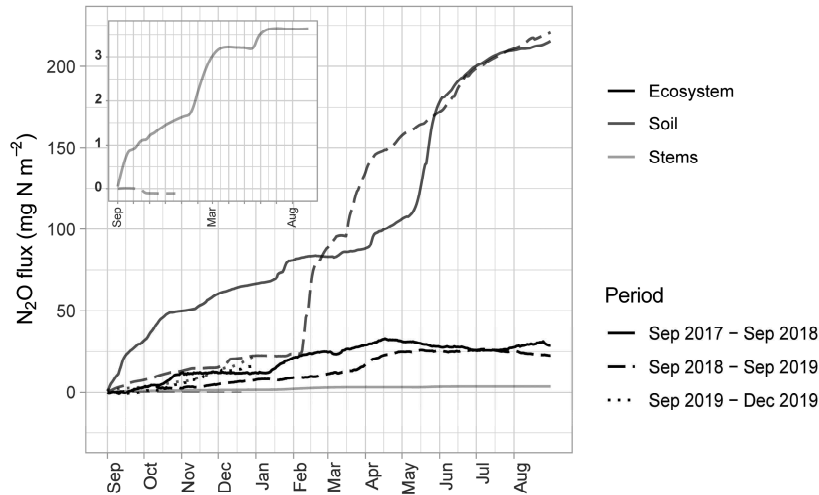
Figure 7. Cumulative fluxes of N_2O from soil, stems, and the ecosystem (eddy covariance above the canopies) during two full years (September 2017 –September 2019) and one-third year (September – December 2019). Due to significantly lower values, the stem fluxes are also plotted in the inset. Notice that the stem fluxes have been measured from Sept. 2017 to Dec. 2018. Adapted from **Article II.**

3.3. Diurnal pattern of CH_4 and N_2O fluxes from stems (Article IV)

Based on expected climate characteristics, anticipated seasonal plant activities, and consequential CH_4 and N_2O fluxes, diurnal measurement campaigns at noon and midnight were performed in the grey alder (*Alnus incana*) FluxGAF forest. A diverging day-night pattern of air (*Figures 8a–c*) and soil temperature (*Figures 8d–f*), and photosynthetically active radiation (PAR) was determined during all three investigated periods. There was no significant difference in volumetric SWC between day – and nighttime. The SWC declined during all investigated periods, although intermediately rising in summer 2017. (*Figures 8g–i*). Further, the soil water table was in good accordance with SWC, underlining the impact of intense precipitation events on the water table in August 2017 (*Figure 8j–l*).

The tree stems were emitters of CH_4 with lower flux rates in summer 2017 and much higher ones in spring 2018. In contrast, the stems had a fluctuating CH_4 uptake in summer 2018 (*Figure 9a–c*). Diurnal CH_4 fluxes from the tree stems noon and midnight were not significantly different, regardless of the periods. The CH_4 exchange from soils was varying seasonally. Principal CH_4 uptake was observed in summer 2017 and 2018, both day- and nighttime; however, the pre-dominant CH_4 emissions were detected in the spring 2018 (*Figure 9d–f*). Despite single campaigns, no statistically significant differences between the day and nighttime soil fluxes were observed (*Table 3, Figure 9*).
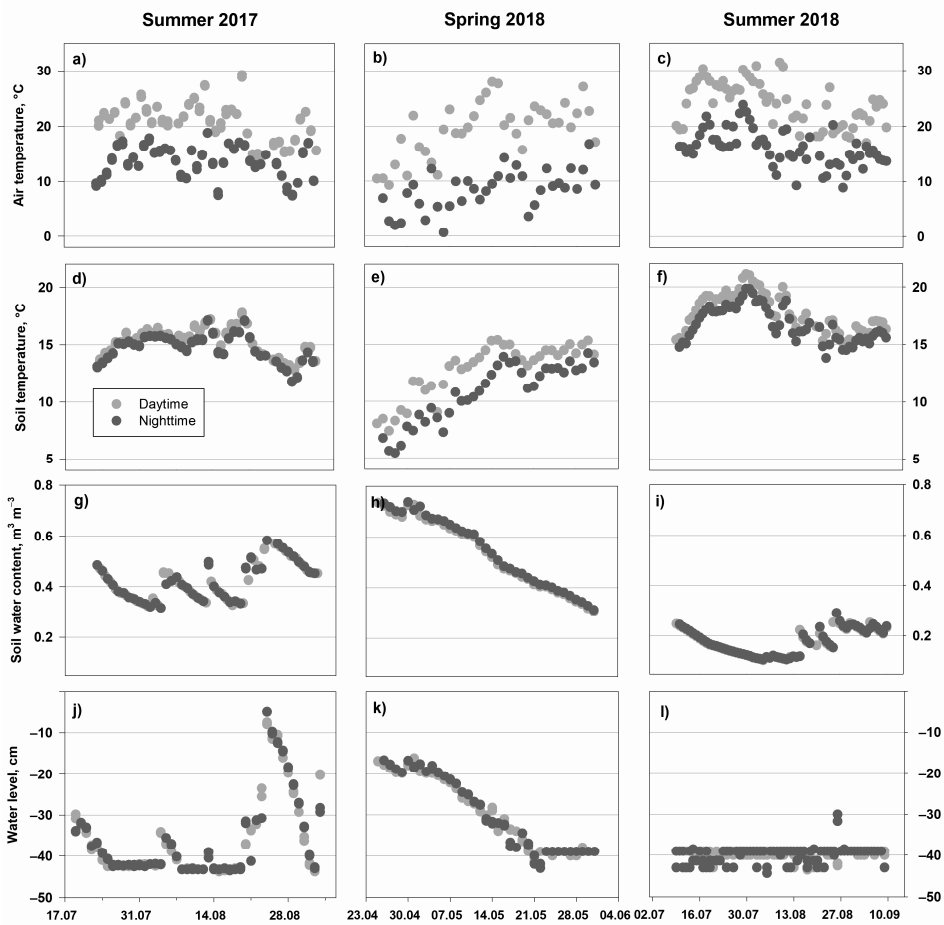
Figure 8. Environmental parameters at three studied periods: (a–c) air temperature, (d–f) soil temperature at 5 cm depth, (g–i) soil volumetric water content (SWC) at 5 cm depth, (j–l) soil water level. Adapted from **Article IV.**

Table 3. Diurnal CH_4 and N_2O stem fluxes, values as mean ± s.e.

	Stem CH_4 µg C m^{-2} h^{-1}		N_2O µg N m^{-2} h^{-1}	
	Daytime	Nighttime	Daytime	Nighttime
Summer 2017	4.63 ± 1.42	2.96 ± 0.88	14.9 ± 4.90	11.2 ± 3.56
Spring 2018	164.1 ± 33.9	168.5 ± 33.6	3.30 ± 0.83	2.39 ± 0.56
Summer 2018	−0.21 ± 0.06	−0.40 ± 0.05	0.11 ± 0.08	−0.04 ± 0.22

Tree stems were net emitters of N_2O in the summer of 2017 and spring of 2018 with lower rates. Small N_2O exchange was determined in the summer of 2018 with minor uptake and emissions. The soil was also dominantly a net emitter of N_2O, with the highest fluxes detected in the spring of 2018 (*Figure 9j–l*). Differences between the day- and nighttime were not statistically significant for either stem or soil N_2O fluxes.
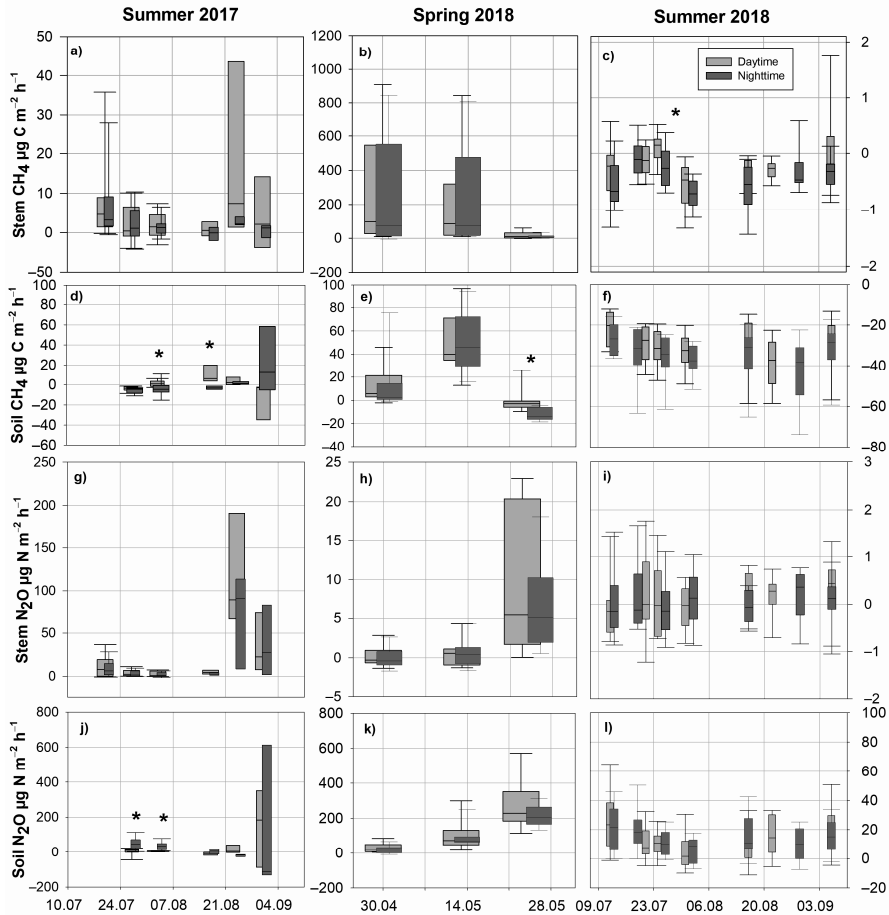

Figure 9. Stem CH_4-C (a–c) and N_2O-N (g–i) fluxes in µg m^{-2} stem surface area h^{-1}, and soil fluxes of CH_4-C (d–f) and N_2O-N (j–l) in µg m^{-2} soil surface area h^{-1} during the three studied periods, each at daytime (12:00–16:00) and nighttime (0:00–04:00). Please note different flux scales. Significant difference of stem fluxes between day- and nighttime marked with an asterisk. The solid line within each box marks the median value, the box boundaries mark the 25th and 75th percentiles, the whiskers mark the 10th and 90th percentiles. Adapted from **Article IV.**

Regardless of the tree stem flux direction (gas emission or uptake) and the gas exchange rates, which considerably differed for each study period, no significant

difference between the day- and nighttime stem CH_4 and N_2O fluxes were revealed. Similarly, the soil fluxes of CH_4 and N_2O mostly did not significantly vary between the day- and nighttime.

Various studies have shown a seasonal stem GHG pattern (Pangala *et al.*, 2015; Barba *et al.*, 2019a; Machacova *et al.*, 2019), initiated by changing environmental conditions such as temperature and soil water conditions and physiological activity of trees. The few existing investigations detected either no (Pangala *et al.*, 2014; Köhn *et al.*, 2021) or a high diurnal flux variability (Pangala *et al.*, 2015; Barba *et al.*, 2019a,b; Jeffrey *et al.*, 2020) while reported as "not consistent throughout the growing season". Such diurnal variability could not be found in our 12 hours' time-shifted experiment.

Methane in soils is produced under anoxic conditions and known controlling factors are temperature and SWC (Mikkelä *et al.*, 1995; Le Mer & Roger, 2001). Unlike previous diurnal studies on CH_4 emissions at different soils (Mikkelä *et al.*, 1995; Koch *et al.*, 2007; Flanagan *et al.*, 2021), we could not observe a significant difference within our studied periods, although moderate diurnal changes of soil temperature and SWC were detected. Even the observed impact of heavy precipitation on the soil water table showed no significant effect on the diel CH_4 flux ratio, indicating the anaerobicity within the soils was less affected in the short terms. However, the dependency of fluxes on the availability of water and temperatures detected in our study confirmed the seasonal trends in CH_4 fluxes, which is also described in the literature both for soils (Oertel *et al.*, 2016) and stems (Barba *et al.*, 2019a).

The positive correlation of PAR and photosynthesis rates with CH_4 emissions (Whiting & Chanton, 1992) from vascular plants, updated by Joabsson et al. (1999), was associated with the interactions of belowground ventilation and soil microbial processes. However, our hypothesized independence of tree stem CH_4 fluxes from tree physiological activity such as photosynthetic rates, expressed by PAR measurements, was confirmed since our study did not show any fast response of CH_4 emissions to increased solar radiation within the 12 hours time slots. However, wetland tree species, in particular *Alnus incana*, are assumed to passively transport soil-produced CH_4 via gas diffusion through the aerenchyma system and exchange it with the atmosphere later (Rusch and Rennenberg., 1998; Machacova *et al.*, 2013; Jeffrey *et al.*, 2020).

Nitrous oxide is produced under aerobic (nitrification) or anaerobic (denitrification) conditions (Butterbach-Bahl *et al.*, 2013); hence soil water content influences both of these processes in the soil (Klemedtsson *et al.*, 1988; Bateman & Baggs, 2005). Investigations about the changes in soil water conditions and their impact on N_2O fluxes revealed the importance of a specific range of SWC rather than a temporal dependence (Christiansen *et al.*, 2012). Our study confirms that diurnal differences of SWC and soil temperature are minor in compliance with these findings, and they affect the N_2O fluxes neither from the tree stems nor the soils. However, similarly to the recently reported study by Machacova *et al.* (2019), we found that seasonally changing soil water regime and soil temperature influence N_2O fluxes from soil and stems. Further, we observed an inter-

and intraseasonal influence of low SWC level on N_2O emissions. A similar impact has been mentioned by (Barrat *et al.*, 2020). Further analysis of anaerobicity, substrate conditions and microbial communities are needed to explain the temporal dynamics of N_2O fluxes from stems.

Our results suggest a transport role of tree stems for soil produced CH_4 and N_2O, rather than a production of CH_4 and N_2O in tree tissues, even if this cannot be excluded. Based on our results detecting no differences in tree stem fluxes in daytime and nighttime, the tree stem CH_4 and N_2O fluxes commonly measured in the daytime can be used alone to estimate the daily, monthly, and annual fluxes in riparian alder forest. However, further detailed research and modelling approach could provide more deep-going insights into this topic and contribute to the solution.

3.4. Stem CH_4 and N_2O flux dynamics from deciduous riparian trees along a flooding gradient (Article V)

The investigated *Populus alba* and *Fraxinus excelsior* showed different GHG flux patterns along with the vertical stem profile: CH_4 and N_2O fluxes from Poplar tree stems decreased significantly with increasing stem height, while CH_4 fluxes from Ash tree stems increased. No relationship of N_2O fluxes with respect to stem height was found. Decreasing efflux rates are coherent with the "pathway-theory", determining tree stems as conduits for soil produced GHGs (Pitz and Megonigal 2017). The highest CH_4 emissions from ash at 3.6 m height could indicate methanogenic microbes within the stem (Covey *et al.*, 2012; Yip *et al.*, 2019). Heartwood with higher water content was observed at the studied trees, which could imply preferential production conditions for CH_4 (Kerr, 1998). However, this particular explanation remained speculative in this study, together with the possibility of hollow or mouldered trunks.

Table 4. Comparison of annual mean stem and soil flux data measured at three sites (upland site *Fraxinus excelsior*, mid-elevation site *Populus alba*, flooded site *Popolus alba*) after upscaling to unit ground area. Fluxes are expressed as mean ± s.e.

	CH_4 flux		N_2O flux	
	Soil	Stem	Soil	Stem
	(kg CH_4-C ha^{-1} yr^{-1})		(kg N_2O-N ha^{-1} yr^{-1})	
upland	−5.11 ± 0.72	0.028 ± 0.036	0.27 ± 0.08	0.009 ± 0.011
mid-elevation	−2.85 ± 0.76	0.031 ± 0.046	0.32 ± 0.06	0.012 ± 0.015
flooded	−0.83 ± 1.02	0.11 ± 0.174	0.39 ± 0.21	0.007 ± 0.010

After extrapolating the tree stem fluxes to the forest ground areas, the CH_4 stem emissions increased with the soil water gradient. A similar trend was found for the soil fluxes, whereas all sites were CH_4 sinks, and their CH_4 uptake decreased with the soil wetness (*Table 4*). Consequentially, tree stems offset the soil's CH_4 sink capacity by 1.2% (upland), 1.1% (mid-elevation) and 30% (flooded). Tree stems emitted N_2O across all sites and contributed 5.1% (flooded), 3.1% (mid-elevation) and 7.4% (upland) of soil emissions.

Overall, the studied floodplain forest tree stems were moderate net emitters of CH_4 at all sites, comparable to temperate upland forests (Pitz *et al.*, 2017; Warner *et al.*, 2017; Maier *et al.*, 2018) and lower than waterlogged temperate wetlands (Gauci *et al.*, 2010; Pitz *et al.*, 2018). This pattern was likely related to the well-draining Danube soils and short inundation times of 1–3 days, inhibiting long-lasting anaerobic conditions. Furthermore, there was no short-termed inundation impact of gas fluxes observed, which is required to establish and maintain anaerobic conditions for the microbial methanogen population and significant CH_4 production (Machacova *et al.*, 2013).

The tree stems were net N_2O emitters at all sites and in a similar range as observations from temperate upland forests (Díaz-Pinés *et al.*, 2016; Wen *et al.*, 2017). Periodical uptake was observed in the Danube study and some non-flooded forests (Machacova *et al.*, 2017; Barba *et al.*, 2019b).

In summary, the investigated typical tree species in floodplain forests of Central Europe are annual net emitters of CH_4 and N_2O. The highest stem emissions of CH_4 were found from poplars growing in moist and periodically flooded soils. A clear seasonal trend could not be followed, although water-filled pore space and soil temperature were identified as environmental factors controlling the stem fluxes.

3.5. Stem CH_4 and N_2O fluxes
in a tropical Amazonian palm swamp (Article VI)

The mean CH_4 fluxes from the palm stems were significantly larger than from the boarwood stems, being the highest at 80 cm stem height (961 µg C m^{-2} h^{-1}), while the boarwood stem showed the highest fluxes from the lowest measurement level of 30 cm (6.71 µg C m^{-2} h^{-1}). Significant differences in fluxes between the stem heights of palms were detected, while a slight insignificant decrease of fluxes with increasing stem height was found on the boarwood stems (*Figure 10a, b*). The CH_4 flux peak at 80 cm height of palm stems might likely result from an effect of pseudobark formed at the lower (0–50 cm) part of the palm stem. Pseudobark is detached from the cortex and functional stem tissues due to the growth of adventitious roots from the root initialization zone (functional stem tissues) below the bark (Tomlinson *et al.*, 2011). Fluxes of N_2O were low on both species without significant changes along stem height (*Figure 10c, d*).
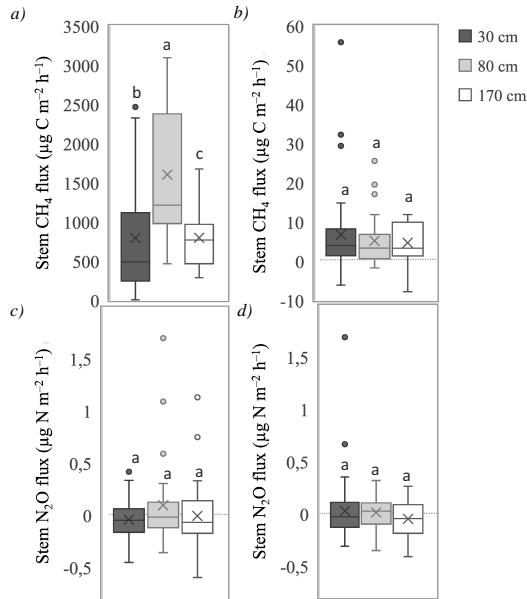
Figure 10. Stem CH_4 and N_2O fluxes measured at three stem heights (30, 80, and 170 cm) above the ground. (a) CH_4 from the aguaje palms (*Mauritia flexuosa*), (b) CH_4 from the boarwood (*Symphonia globulifera*), (c) N_2O from the aguaje palms, and (d) N_2O from the boarwood. Significant differences are marked with letters above the columns. The dashed line marks the median, the cross inside the box marks the mean, the box boundaries mark the 25th and 75th quartiles, the whiskers mark the min and max values, and the outliers (dots) are shown. Adapted from **Article VI.**

The mean soil CH_4 flux was 3,496 µg C m^{-2} h^{-1} and varied from −103.8 to 19,476 µg C m^{-2} h^{-1}. The CH_4 emissions were slightly lower close to the palms. The mean soil N_2O fluxes were higher close to the palms (143 µg N m^{-2} h^{-1}) and lower close to the boarwood trees (*Figure 11*).

Roughly upscaled to m^2 per soil, fluxes from palm and boarwood stems contributed approximately 4% to the total CH_4 emissions and almost no N_2O.

The mean soil CH_4 fluxes were within the range reported from Brazilian flooded swamp forests. However, the upscaled palm stem CH_4 emissions in Quistococha, adding a mean of 135 µg C m^{-2} h^{-1} to the soil fluxes, were an order of magnitude lower than the stem CH_4 fluxes detected in various tree species in Brazilian Amazonia basin by Pangala *et al.* (2017). The relatively dry study period with a variation of the water table from −12.5 cm to +8 cm (Griffis *et al.*, 2020) was in contrast with the 8 m difference of water table in the Brazilian floodplain during the flood and non-flooding period. Thus, the relatively high CH_4 fluxes from the palm stems, compared to soil emissions, was related with the aerated upper soil layer, egressing CH_4 from deeper anoxic soil layer through the palm roots and stems. Further, the aerenchymous palm root and stem tissues may explain the differences between the palms and boarwood tree fluxes. The palms have intercellular (lacunose) spaces, which can serve as transport conduits for soil produced CH_4 into the palm stems (van Lent *et al.*, 2019).
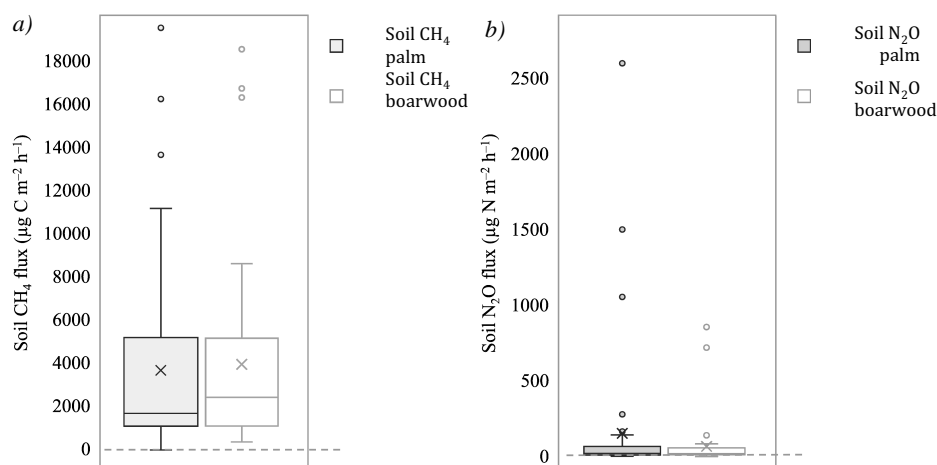
Figure 11. Soil CH₄ (a) and N₂O (b) fluxes in the palm swamp forest. No significant differences between adjacent soil to palm and boarwood stems were found. The dashed line marks the median, the cross inside the box marks the mean, the box boundaries mark the 25th and 75th quartiles, the whiskers mark the min and max values, and outliers (dots) are shown. Adapted from **Article VI.**

In Amazonian palm swamps, no previous studies on N₂O stem fluxes are known. However, the mean N₂O soil fluxes in this study were 2.5–7 times higher than model-predicted emissions of 21 µg N m^{-2} h^{-1} for the Amazon Basin (Guilhen *et al.*, 2020) but still lower than N₂O emissions from floodplain soils in the Brazilian Amazon (Figueiredo *et al.*, 2019).

To conclude, aguaje palm (*Mauritia flexuosa*), a dominant plant species in West Amazonian peatlands, can emit a large amount of CH₄ from stems, being significantly higher CH₄ emitter than boarwood (*Symphonia globulifera*) stems. On the other hand, no difference was found in the very low stem N₂O fluxes. Furthermore, the mean soil CH₄ flux was significantly higher than mean CH₄ fluxes from all studied stems. The stem CH₄ emission was about a magnitude lower than reported previously for trees in the Amazon floodplain.

3.6. Trees as CH₄ and N₂O sinks in a tropical upland forest in a volcanic island (Publication VII)

At the studied tropical forest of the volcanic La Reunion Island, all the investigated forest compartments – tree stems, cryptogams, adjunct soils, and volcanic surfaces of a basalt lava flow – were sinks of CH₄. The irregularly spread shallow soil layers and volcanic rocks seemed equally distributed and showed similar CH₄ consumption. The studied mature tree stems were net sinks from the atmosphere

$(-15.6 \pm 2.0\ \mu g\ CH_4\ m^{-2}\ h^{-1}$ (stem area)) without significant species-specific variability (*Figure 12a*). Furthermore, no significant changes in stem CH_4 fluxes were observed on the studied vertical stem profile.

The determined stem CH_4 flux rates were upscaled to ecosystem level (*Figure 13a,b*) and the stems of the six studied trees consumed in total -59.0 ± 17.9 mg $CH_4\ ha^{-1}\ h^{-1}$ (ground area, mean $\pm$ s.e.). Stem fluxes contributed 7.1% to the soil CH_4 uptake (-833.1 ± 97.5 mg $CH_4\ ha^{-1}\ h^{-1}$; *Figure 13a, b*). Assuming similar CH_4 uptake potential for the > 80 tree species present in the studied forest, the overall stem contribution might be 41%. Thus, the stems seem to be strong CH_4 sinks at the beginning of the rainy season.
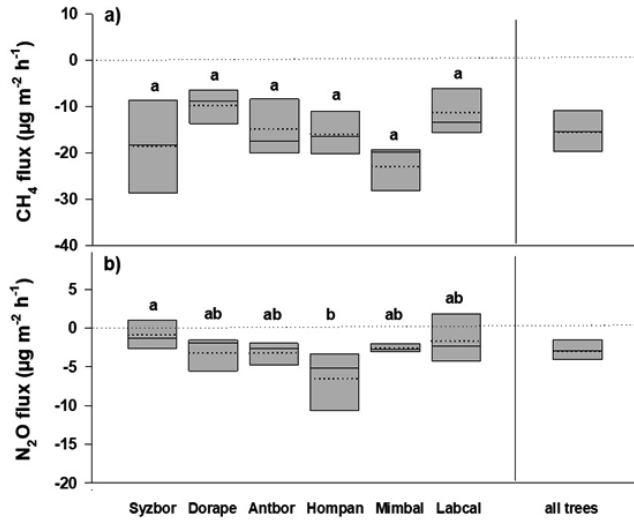

Figure 12. Fluxes of CH_4 (a) and N_2O (b) from stems of six individual tree species (Syzbor – *Syzygium borbonicum*, Dorape – *Doratoxylon apetalum*, Antbor – *Antirhea borbonica*, Hompan – *Homalium paniculatum*, Mimbal – *Mimusops balata*, Labcal – *Labourdonnaisia calophylloides*, from all studied trees/tree species ("all trees"). Significant differences among fluxes in individual tree species are marked with different letters above bars. The solid line within each box marks the median, the dotted line marks the mean, the box boundaries mark the 25th and 75th percentiles. Adapted from **Article VII.**

The soil was a weak source of N_2O ($1.8 \pm 2.5\ \mu g\ N_2O\ m^{-2}\ h^{-1}$), the detected exchange potential of volcanic surfaces of basaltic lava flows was negligible ($0.024 \pm 0.871\ \mu g\ N_2O\ m^{-2}\ h^{-1}$). Both showed high spatial heterogeneity without any clear trend, including meager consumption and emission of N_2O. In contrast, tree stems have shown an evident uptake of N_2O from the atmosphere ($-3.0 \pm 0.8\ \mu g\ N_2O\ m^{-2}\ h^{-1}$; *Figure 12b*). Like CH_4, no significant changes in stem N_2O fluxes were observed on the studied vertical tree stem profile.

The N_2O consumption by the tree stems was upscaled (-11.9 ± 6.3 mg $N_2O\ ha^{-1}\ h^{-1}$), representing -64% of the soil N_2O emissions (18.4 ± 25.2 mg-$N_2O\ ha^{-1}\ h^{-1}$; *Figures 13c, d*), and, thus, decreasing the weak source strength of the soil.

Assuming similar uptake rates from all 80 tree species in the forest, the overall N_2O uptake potential might represent –374% of the soil N_2O exchange, thus turning the tropical rain forest into a N_2O sink.

The irregular and thin soil (Kirman *et al.*, 2007), the steep slope, and the high porosity of volcanic bedrocks, typical for volcanic, contribute to rapid water runoff and prevent forming of anaerobic soil conditions required for methanogenic CH_4 production, moreover supporting methanotrophic CH_4 oxidation (Smith *et al.*, 2000).
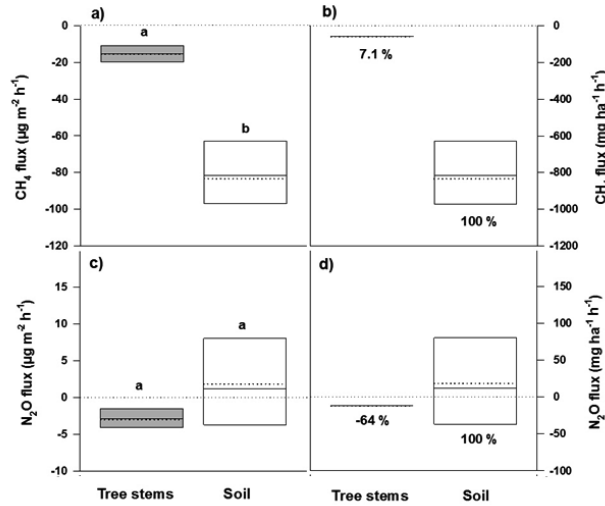

Figure 13. Fluxes of CH_4 (a, b) and N_2O (c, d) from tree stems and adjacent soil expressed per stem or soil surface area unit (a, c) and scaled up to unit ground area of tropical rain forest (b, d). The contributions of stem fluxes of six tree species to the soil fluxes (equal to 100%) are expressed as percentages of the soil flux. Significant differences in fluxes are indicated by different letters above the bars. The solid line within each box marks the median, the dotted line marks the mean, the box boundaries mark the 25th and 75th percentiles. Adapted from **Article VII.**

The field study at the tropical forest of La Reunion clearly revealed all mature tree stems as net CH_4 sinks. In contrast, tree stems were determined to be net emitters from soil produced CH_4 in tropical Amazonia (Pangala *et al.*, 2017; Welch *et al.*, 2019; Sjögersten *et al.*, 2020). Stem uptake potential was observed on boreal trees in the dormant season and was rather negligible (Machacova *et al.*, 2016). Irregular CH_4 uptake by the stem of *Simarouba amara* was observed in a tropical upland forest in Panama during the transition from dry to wet season (Welch *et al.*, 2019). Those authors assumed a diffusion gradient from the atmosphere via tree stems into the soil with predominant CH_4 oxidation, resulting in tree stem uptake of trace gases. Cryptogam stem covers are likely involved in the observed CH_4 uptake (Lenhart *et al.*, 2015, this study).

The studied tree stems were identified as N_2O sinks. Most likely, limited N availability in the thin soil layer and young lava flow may result in a weak N_2O exchange potential. However, few studies observed a link between N_2O exchange

and tree physiological activity in boreal trees, particularly CO_2 uptake and release (Machacova *et al.*, 2019). Like CH_4, biocrusts such as cryptogams covering tree stems (Machacova *et al.*, 2017; Lenhart *et al.*, 2019) may also explain the low N_2O exchange, although these processes need future investigations.

3.7. Synthesis of the primary outcomes

The impact of flooding under artificial (**Article I**) and natural conditions (**Article V**) focused on measurements of both CH_4 and N_2O emissions from tree stems and soils simultaneously. Stem emissions have shown a solid correlation to soil water content. Within two weeks of inundation at the Agali site, the stem CH_4 fluxes increased with the flooding but rose more sharply after the flooding and were the highest when the soil was not inundated but still saturated in the post-flooding period. The anoxic soil conditions enhanced the formation of aerenchyma, a tree-mediated pathway to transport the CH_4 produced in the soil and exchange it with the atmosphere(Henneberg *et al.*, 2012). Consequently, the recent field flooding experiment in Agali indicated a similar "chimney effect" reported earlier (Joabsson *et al.*, 1999; Rice *et al.*, 2010). Tree stem N_2O fluxes raised with the soil inundation and decreased afterwards. However, N_2O tree flux was up to two orders of magnitudes lower than the CH_4 flux.Nevertheless, the experimental flooding significantly enhanced complementary aerobic nitrification and anaerobic denitrification processes in the adjunct soils.

On the other hand, natural flooding of few days as investigated at the Danube basin (**Article V**) showed that shorter time slots prevent long-lasting anaerobic conditions required to establish and maintain anaerobic conditions for the methanogens and significant CH_4 production. Furthermore, the higher elevated plots with lower SWC emitted less CH_4. The N_2O fluxes from tree stems varied and were also magnitudes less than CH_4. The soil water content must most likely reach a certain critical value and maintain it before a relevant change of stem emissions occurs (Köhn *et al.*, 2021). This aspect is also essential to explain the temporal pattern of stem fluxes in the riparian alder forest. Missing diurnal changes of stem CH_4 and N_2O fluxes (**Article IV**) clearly determine the soil as a source of these trace gases, caused by the time demand to provide sufficient anaerobic system conditions to establish and maintain aerenchyma for gas ebullition (Covey & Megonigal, 2019; Covey *et al.*, 2021). The investigated seasonal changes (**Article II and III**) of stem CH_4 and N_2O fluxes followed the changing soil water and temperature regime. Furthermore, the soil flux dynamics within this particular forest ecosystem underline the aerenchyma relevance. Up to 40% of the annual CH_4 ecosystem fluxes (eddy covariance) and up to 83% during the wetter periods contribute to the tree stems. N_2O fluxes follow the dynamic trend, too. However, the much lower extend with magnitudes less than CH_4 force the N_2O stem fluxes to play a negligible role within this forest ecosystem on an annual scale.

Decreasing CH_4 and N_2O fluxes with increasing stem height were found at the alder trees in Agali (**Article I**) and poplars at the Danube (**Article V**), likely an outcome of passive diffusion of soil-microbe produced gases that are transported via aerenchyma and roots, stems, and leaves to be released to the atmosphere. The irregular vertical pattern at ashes (**Article V**), palms and boarwood in Amazonian Peru (**Article VI**) remains speculative. Methanogenic microbes within the ash stem might explain the highest CH_4 emissions at 3.6 m height (Covey *et al.*, 2012; Yip *et al.*, 2019). Further, the possibility of hollow or moulded trunks, together with observed heartwood with higher water content indicates preferential conditions for in-situ CH_4 production (Kerr, 1998). The effect of pseudobark, formed at the 0–50 cm segment of the palms stems in Amazonian Peru (**Article VI**), likely explains the higher fluxes at 80 cm height. Pseudobark is detached from the cortex and functional stem tissues due to the growth of adventitious roots from the root initialization zone (functional stem tissues) below the bark (Tomlinson *et al.*, 2011). The homogenous vertical profile from tree stems at La Reunion (**Article VII**) is likely caused by missing aerenchyma for gas uptake from the thin soil layer on lava flow but the biocrust stem cover. Moreover, the shallow soil layer is aerated and soil-produced methane is questionable. Although several studies on tropical forest clearly demonstrate higher GHG emissions from lower parts of stems (Pangala *et al.*, 2017; Sjögersten *et al.*, 2020) the relevance of biocrusts (e.g cryptogams or algae) both at tree stems and within the porous basalt lava rocks seem to be more evident in this unique ecosystem (see Lenhart *et al.*, 2015).

4. CONCLUSIONS

Methane and nitrous oxide are known to be processed by microbes under certain conditions, either aerobic, anaerobic, or anoxic. In principle, water conditions within soils are the dominant drivers. The analysis of the flooding impact at the riparian alder forest and in the Danube basin, linked with the field study at the tropical forest site in the Peruvian Amazon, confirms the first hypothesis of enhanced CH_4 and N_2O emissions from tree stems under higher soil water content. However, the duration of stable hydrological regimes needs to be understood as a precondition for plants at hypoxic soils to form and maintain aerenchyma to fulfil their role on behalf of the gas exchange between the tree above the water and the submerged tissues. Consequentially, such relatively slow processes were reflected in the temporal pattern: short-termed, diurnal changes were not identified. However, seasonal adaptations with both soil water and temperature impact were found at the temperate study sites. Thus, the second hypothesis can be confirmed partly.

In cases where the dominant CH_4 and N_2O sources can be found in the soils, and these GHG are axially transported via the tree stems, the pressure-dependent gas diffusion results in higher stem emissions close to the ground. Thus, at least for the studied tree species in the temperate zone in general, the third hypothesis can be confirmed: the lowest parts of tree stems show the highest GHG fluxes. The fluxes at the investigated palms in tropical Amazonia were higher at stem heights of 80 cm, resulting from the pseudobark formed in the lower stem zones, inhibiting the radial gas.

Conclusively, the fourth hypothesis can be confirmed: the role of tree stems in GHG exchange is highly variable in forest ecosystems. Different soil conditions, water regimes, the origin of the investigated CH_4 and N_2O, and the gas exchange processes between trees and atmosphere cause a dominant role of tree stems as seen for CH_4 exchange in forest ecosystems in Agali and La Reunion, a moderate role at the Danube basin and the Peruvian Amazon, but a negligible role for N_2O exchange at all sites except the tropical La Reunion.

Investigating greenhouse gas fluxes from tree stems is far more complex, and multiple and interdisciplinary approaches are required in the future. Identifying microorganisms and biochemical pathways to improve the understanding of the origin of CH_4 and N_2O fluxes from trees calls for adequate availability and use of microbiological methods. Local trace techniques and measurements from leaves and within the canopy would enhance the knowledge from a plant physiology perspective. The forest compartments' ecosystem relevance, including the specific role of trees, might be investigated when using remote sensing. Further, intensive data collection at a higher frequency and long-termed, preferably with automatic measurement systems, is important for reliable modelling of the GHG process dynamics.

The obtained results convince us that the tree stem CH_4 and N_2O exchange should be included in forest ecosystem GHGs budgets and forest-ecosystem process models. In addition, extreme climate events (flooding, drought) significantly alter the soil and the stem fluxes. However, emission from tree stems of different species may vary significantly, and further studies are needed for comprehensive flux estimates for different forest types.

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SUMMARY IN ESTONIAN

Puutüvede metaani- ja naerugaasivood erinevates metsaökosüsteemides

Globaalse soojenemise ja kliimamuutuste mõistmine on oluliselt seotud meie teadmistega kasvuhoonegaaside (KHG), näiteks metaani (CH_4) ja dilämmastik-oksiidi ehk naerugaasi (N_2O) kohta. Mõlemad on ohtlikud kasvuhoonegaasid, kusjuures naerugaas on tanapäeval peamine inimtekkeline gaas, mis hävitab Maa elustikku UV-kiirguse eest kaitsvat stratosfäärset osoonikihti Maaismaaökosüsteemidel on globaalses süsiniku- ja lämmastiku ringes suur roll, reguleerides kliimat ja mõjutades kliimamuutusi. Seejuures reguleerivad parasvöötme ja troopilised metsad ökosüsteemide ja atmosfääri vaheliste CH_4 ja N_2O voogude dünaamikat. Varasemad uuringud ei ole tavaliselt käsitlenud taimestiku osatähtsust selles regulatsioonis ehkki taimed, eriti puud, võivad olla CH_4 ja N_2O olulised allikad või sidujad. Vaatamata viimasel dekaadil intensiivistunud uuringutele puude gaasivahetuse tähtsuse selgitamiseks pole puude spetsiifiline roll metsade gaasivahetusrežiimis siiani suures osas teada. Erinevate kliimavöönidite ja metsaökosüsteemide lõikes varieeruvad gaasivahetust mõjutavad tegurid (nt puuliikide erinevad omadused, mulla temperatuur ja niiskusrežiim ning nende sesoonne dünaamika) suurtes piirides. Seetõttu on gaasivahetust mõjutavate protsesside ja mehhanismide üldistamine ja modelleerimises rakendamine tõsiseks väljakutseks.

Käesolevas töös analüüsiti puutüvede metaani- ja naerugaasivoogude osatähtsust erinevates parasvöötme ja troopilistes metsades ning selgitati keskkonnatingimuste mõju puude ja atmosfääri vahelisele gaasivahetusrežiimile. Töö eesmärkideks olid: (I) analüüsida üleujutuste mõju puutüvede ning uuritava ala metsamulla metaani- ja naerugaasivoogudele, (II) selgitada nende voogude ajalist dünaamikat, (III) analüüsida puude tüvevooge parasvöötme kaldametsades, troopilises palmisoometsas Amasoonase madalikul Peruus ja laavavoolul kasvavas troopilises vihmametsas Réunioni saarel ning (IV) hinnata tüvevoogude osakaalu ökosüsteemi voogudes.

Üleujutuse mõju analüüsiti kaldaäärsetes metsades Eestis (hall-lepik Agalis Järvseljal) ja Austrias (papli ja saare enamusega lammimets Doonau lammil). Seal ilmnes mulla kõrgema veesisalduse korral puutüvedest CH_4 ja N_2O heitkoguste selge suurenemine, eriti puutüvede alumises osas. Troopilise palmisoo uuringutes mõõdeti väga kõrge metaanivoog *aguaje* palmi (*Mauritia flexuosa*) tüvedest, kuid domineeriva puuliigi *Symphonia globulifera* tüvedest oli see nulli-lähedane. Parasvöötme kaldametsades oli mulla metaaniemissioon suhteliselt madal ja kuival perioodil valdavalt negatiivne, mis tähendab metaani oksüdeerimist vastavate mikroorganismide poolt. Troopilises palmisoos oli metaanivoog mullast (turbast) ühtlaselt kõrge. Naerugaasi emissioonid puutüvedest olid väga madalad nii parasvöötme kaldametsades kui ka troopilises palmisoos. Mulla N_2O emission oli seevastu aga mõlemates metsades perioodiiti väga kõrge, kusjuures

Eesti hall-lepikus metsa kohal vaatlustornist mõõdetud voog oli oluliselt väiksem. Puuvõrade roll metaani, kuid eriti just naerugaasi voogude dünaamikas on veel seni lõplikult lahendamata. Laavavoolul kasvavas troopilises vihmametsas oli aga nii puutüvedest kui mullast mõlema gaasi voog madal ja enamikul mõõtmistest ilmnes puutüvedes gaasi sidumine.

Üldistades nii parasvöötme kaldametsade kui troopilise palmisoometsa tulemusi võib öelda, et puude ja mulla vahel esineb metaani emissioonis tõenäoliselt dünaamiline tasakaal, mis on määratud peamiselt mulla veesisalduse poolt. Märjal mullal suurenes puutüvedest CH_4 emissioon, mis osaliselt kahandas metsamuldade metaani sidumisefekti. Teatud tingimustes võib puutüvede emissioon ületada metsamullas sidumise. Antud tööst ilmnes ka, et tõenäoliselt juhivad puud juurtega sügavalt mullast ülesvõetud metaani puutüvedesse ja võrasse, ilma et see saaks oksüdeeruda ülemises hapnikurikkas mullakihis. Puud etendavad niisiis selgelt täiendava metaani emissioonikanali rolli. Seejuures ei saa antud uuringud kinnitada teistvõimalikku seletust, et metaan moodustub püütüves endas anaroobsete mikroorganismide vahendusel.

Puutüvede KHG voogude puhul ilmnesid selgelt pikaajalised sesoonsed erinevused: parasvöötmes nii temperatuuri kui mullaniiskuse muutuste mõjul, troopikas aga sademeterohkete ja -vaeste perioodide vaheldumisest tingituna. Lühiajalisi ööpäevaseid muutusi seevastu ei leitud.

Detailsem analüüs aitas selgitada liigispetsiifilisi füsioloogilisi parameetreid, mis määravad puude/palmide allikaks või sidujaks olemise rollis: (i) *aguaje* palmidel on moodustnud tüvede alumises maapinnaga kontaktis olevas osas nn pseudokoor, mis pidurdas radiaalset gaasivahetust ja (ii) kasvuhoonegaaside vahetus Réunioni vulkaanilise saare puude ja atmosfääri vahel oli tõenäoliselt vähem õhukesest ja kohati lausa puuduvast mullakihist sõltuv ning domineeriv kasvuhoonegaaside allikas oli tõenäoliselt tüvedel kasvav samblike, sammalde, vetikate nn krüptogaamne kate.

Kokkuvõtteks võib öelda, et puutüvede roll kasvuhoonegaaside vahetuses atmosfääriga on metsaökosüsteemides väga erinev. Erinevad mullatingimused, veerežiim, CH_4 ja N_2O päritolu ning puude gaasivahetusprotsessi analüüs võimaldab aga väita, et puud etendavad metsade CH_4 ja N_2O režiimis domineerivat rolli

Puutüvedest pärit kasvuhoonegaaside voogude uurimine on tehniliselt keerukas protsess ning tulevikus on vaja pikaajalist ja interdistsiplinaarset lähenemist. Kasvuhoonegaaside dünaamika usaldusväärseks hindamiseks ja modelleerimiseks on vajalik mikroorganismide ja biokeemiliste radade tuvastamine, mõistmaks paremini puude CH_4 ja N_2O voogude päritolu ning lisandamaks teavet KHG paremaks sidumiseks metsaökosüsteemides.

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PUBLICATIONS

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