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Dry and wet periods determine stem and soil greenhouse gas fluxes in a northern drained peatland forest

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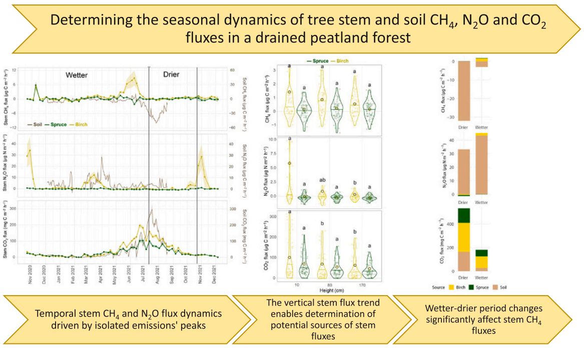
HIGHLIGHTS

- Birch stems more important in annual peatland forest GHG dynamics than spruce stems
- Temporal stem CH_4 and N_2O flux dynamics driven by isolated emissions' peaks
- Sustained higher or lower water table depth determines net stem and soil CH4 flux
- Rapid changes in soil hydrologic conditions, e.g. freeze-thaw, drive N_2O emissions
- Stem CH_4 emissions can offset nearly half of the soil sink during the wetter period

GRAPHICAL ABSTRACT



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ABSTRACT

Greenhouse gas (GHG) fluxes from peatland soils are relatively well studied, whereas tree stem fluxes have received far less attention. Simultaneous year-long measurements of soil and tree stem GHG fluxes in northern peatland forests are scarce, as previous studies have primarily focused on the growing season. We determined the seasonal dynamics of tree stem and soil CH_4, N_2O and CO_2 fluxes in a hemiboreal drained peatland forest. Gas samples for flux calculations were manually collected from chambers at different heights on Downy Birch (*Betula pubescens*) and Norway Spruce (*Picea abies*) trees (November 2020–December 2021) and analysed using gas chromatography. Environmental parameters were measured simultaneously with fluxes and xylem sap flow was recorded during the growing season. Birch stems played a greater role in the annual GHG dynamics than spruce stems. Birch stems were net annual CH_4, N_2O and CO_2 sources, while spruce stems constituted a CH_4 and CO_2 source but a N_2O sink. Soil was a net CO_2 and N_2O source, but a sink of CH_4. Temporal dynamics of stem CH_4 and N_2O fluxes were driven by isolated emissions' peaks that contributed significantly to net annual fluxes. Stem CO_2 efflux followed a seasonal trend coinciding with tree growth phenology. Stem CH_4 dynamics were significantly affected by the changes between wetter and drier periods, while N_2O was more influenced by short-term changes in soil hydrologic conditions. We showed that CH_4 emitted from tree stems during the wetter period can offset nearly half of the soil sink capacity. We presented for the first time the relationship between tree stem GHG fluxes

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and sap flow in a peatland forest. The net CH_4 flux was likely an aggregate of soil-derived and stem-produced CH_4. A dominating soil source was more evident for stem N_2O fluxes.

1. Introduction

Peatlands – wetland ecosystems with predominantly waterlogged conditions – occupy about 3 % of the global land surface (Xu et al., 2018). Peatland soils constitute a globally significant reserve of carbon (C) and nitrogen (N), storing about a third of global soil C and 12–21 % of global soil organic N (Frolking et al., 2011; Limpens et al., 2006). The destabilisation of these C and N pools could have substantial effects on the local biogeochemical cycles and global climate, altering the dynamics of key greenhouse gases (GHG) such as carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O). GHG dynamics in pristine peatland soils are typically characterised by small atmospheric CO_2 uptake, moderate release of CH_4 and low emissions of N_2O to the atmosphere (Frolking et al., 2011; Hugelius et al., 2020). However, drainage for forest productivity enhancement affects soil hydrology, which is considered the most critical factor governing GHG balances of peatlands (Korkiakoski et al., 2019; Lohila et al., 2011; Pihlatie et al., 2010). The switch from anaerobic to aerobic soil conditions after lowering the groundwater table can turn peatland soils from a CO_2 sink to a source, decrease CH_4 emissions, and elevate N_2O release (Korkiakoski et al., 2019; Lohila et al., 2011; Pihlatie et al., 2010).

Tree stems also play a substantial role in the ecosystem GHG balances of forestry-drained peatlands, exchanging CO_2, CH_4, N_2O with the atmosphere (Barba et al., 2019a; Machacova et al., 2016; Wang et al., 2019). However, due to the spatio-temporal variability and uncertainty of stem flux dynamics, as well as difficulties with upscaling stem fluxes to the ecosystem level, they are disregarded in most GHG models and assessments (Barba et al., 2019a; Barba et al., 2019b; Machacova et al., 2019).

While numerous long-term studies have monitored the seasonal variations in soil GHG fluxes, stem flux measurements displaying annual dynamics are rare (Jeffrey et al., 2023b; Machacova et al., 2019; Mander et al., 2022). Previous studies have primarily focused on short measurement periods during the growing season (Barba et al., 2021; Gauci et al., 2010; Wen et al., 2017). However, emerging evidence of prevailing stem fluxes in the winter (Machacova et al., 2019) and the large contribution of autumn and spring fluxes to cumulative stem N_2O emissions (Mander et al., 2021), highlight the need to further examine the seasonal variability of stem fluxes and their specific environmental drivers.

A variety of biophysical mechanisms drive soil and stem GHG production and consumption. In forest soils, CH_4 is produced by anaerobic microbial methanogenesis but also consumed by aerobic methanotrophy (Ni and Groffman, 2018). N_2O is produced by microbial nitrification and denitrification (Butterbach-Bahl et al., 2013), and CO_2 by respiration of plant roots and microorganisms (Jiang et al., 2020). Furthermore, microbial CH_4 and N_2O production can occur inside tree stems (Barba et al., 2019a; Gauci et al., 2010; Keppler et al., 2006) and CH_4 production has also been demonstrated on stem bark (Lenhart et al., 2015). In addition, stem CO_2 efflux is influenced by photosynthesis and respiration processes in the stem (Gansert and Burgdorf, 2005; Salomón et al., 2021).

A combination of various environmental factors and processes regulate how these GHG are exchanged between the soil, stems, and the atmosphere. The production of gases and their solubility in the soil are controlled by several factors such as soil temperature, soil water content (SWC), water table depth (WTD) and nutrient availability (Barba et al., 2019a; Pitz and Megonigal, 2017; Teskey et al., 2008). The subsequent absorption of the dissolved gases by plant roots depends on the density of the root system (Puhe, 2003). Gas transport within tree stems is governed by xylem sap flow, as gases are moved up the stem via the xylem due to the pressure gradient (Gansert and Burgdorf, 2005). In addition, axial upward gas diffusion has recently been shown to also occur between bark layers, independent of the transpiration stream, in trees with laminar bark layers (Jeffrey et al., 2023a). The final diffusion or transpiration of gases from the stems to the atmosphere is controlled by aspects of stem morphology and tree physiology, such as wood density, lenticel abundance and bark characteristics (Pangala et al., 2013; Pitz et al., 2018; Teskey et al., 2008).

As xylem sap flow is a key process governing gas transport within tree stems, it is pivotal to study how much of the final GHG flux is determined by sap flow rates in stems. However, in-situ evidence of relationships between sap flow and stem CH_4 fluxes is scarce (Takahashi et al., 2022), and relationships with stem N_2O fluxes have only been shown in upland forests (Barba et al., 2021). There also remains uncertainty in the knowledge around the relationship between internal xylem CO_2 transport and the final efflux to the atmosphere, and the relative contribution of diffusive CO_2 flux to the forest C budgets (Barba et al., 2021; Kunert, 2018).

Investigating the vertical profile of stem fluxes can give insight into the origin of the released gases. An indication of fluxes primarily originating from the soil is a decreasing vertical flux trend, whereby the magnitude of fluxes is higher at the bottom part of the stem and diminishes with increasing stem height (Barba et al., 2019b; Machacova et al., 2019; Pitz and Megonigal, 2017). If the vertical trend does not occur, microbial production of CH_4 and N_2O likely occurs inside tree stems (Barba et al., 2021; Pitz and Megonigal, 2017). On the other hand, stem CO_2 flux is a combination of stem respiration and xylem-mediated flux. Therefore, irregular vertical patterns may suggest a higher proportion of the flux being related to respiration, which is predominantly determined by meteorological variables, such as air temperature (Barba et al., 2021; Kunert, 2018).

Peatland soil C and N retention capabilities and the associated GHG dynamics are extremely vulnerable to changes in hydrological regimes brought on by climate warming (Hugelius et al., 2020). As soil water status also plays a primary role in driving stem fluxes, changes related to potential shifts in hydrologic extremes due to climate change can also impact stem flux patterns. Expected climate change effects in northern hemisphere peatlands, such as increased precipitation and accelerated snowmelt in spring (IPCC, 2021), can lead to wetter conditions and raised groundwater levels. Flooding has been shown to increase stem fluxes of CH_4 and N_2O in a riparian forest (Schindler et al., 2020) and the contribution of stem CH_4 fluxes to total ecosystem fluxes has been shown to be significantly higher during the wet period compared to the dry period when stem emissions remained low (Jeffrey et al., 2023a; Mander et al., 2022). However, there is a lack of information for different forest types and tree species. Conversely, elevated temperatures could heighten evapotranspiration rates and increase the frequency and severity of droughts, which in turn could lower groundwater levels. Thus, these combined effects can disrupt the onset and duration of wet and dry periods in northern peatlands, influencing the general hydrologic regime and GHG fluxes.

Further examination of these dynamics and quantification of stem flux contributions to total ecosystem fluxes during different hydrologic periods is needed to better understand how GHG dynamics on an ecosystem level may react to the changing climate. In this study, we looked at annual patterns of CO_2, CH_4 and N_2O fluxes in a northern drained peatland forest. We examined the possible origin of tree stem fluxes by simultaneously measuring stem and soil fluxes with a high sampling frequency, and exploring the relations between the stem fluxes, soil environmental and chemical parameters, and sap flow rates. We hypothesise that higher CH_4 and N_2O stem fluxes occur during the wetter period of the year, that stem CH_4 fluxes during the wetter period make a significantly higher contribution to total soil and stem fluxes compared to the drier period, and that stem GHG fluxes are driven by xylem sap flow rates.

2. Methods

2.1. Site description and study design

The study was carried out in the eastern part of Estonia at a drained peatland forest site (58°17′N, 27°17′E; 38 m.a.s.l.; 1.72 ha, Supplementary Fig. 1). The research site belongs to the warm summer humid continental climate zone according to the Köppen classification (Köppen, 1936), and to the hemiboreal vegetation zone, serving as a transitional region between temperate and boreal climates (Ahti et al., 1968). The region experiences an average annual precipitation of 650 mm, with temperatures averaging 17 °C in July and − 6.7 °C in January, and a growing season lasting 175–180 days (Kupper et al., 2011). In comparison, our study year (October 2020 – October 2021) was slightly warmer and drier than the long-term average, with an average precipitation of 545 mm and average temperatures of 22.6 °C in July and − 2.5 °C in January.

The forest soil was drained in the early 1970s through an open-ditch network drainage system (Clément et al., 2020). Currently, the *Oxalis*-type (Lõhmus, 1984) drained peatland forest is covered mainly by downy birch (*Betula pubescens* Ehrh.) and Norway spruce (*Picea abies* (L.) H. Karst.) trees. Tree stand characteristics are brought out in Table 1. The soil at the study site was classified as Drainic Eutric Histosol (IUSS Working Group WRB, 2015), featuring low dry bulk density, high organic C content, and low pH, and a peat layer thickness of 100 cm (Becker et al., 2018; Clément et al., 2020). Soil chemical parameters are summarised in Supplementary Table 1. Sampling was performed from twelve representative monitoring points located in a 50 × 70 m study plot within the total study area. Six points consisted of one birch and one spruce tree with installed stem chambers and one automatic dynamic soil chamber. The remaining six monitoring points were set pairs of one birch tree and one soil chamber. A detailed scheme of the study site is presented in Supplementary Fig. 1.

2.2. Stem and soil greenhouse gas sampling and analyses

Manual collection of gas samples from static stem chamber systems installed on the stems of birch ($N = 12$) and spruce ($N = 6$) trees took place weekly (60 campaigns in total) from October 2020 to December 2021. A chamber system consisted of two chambers per height profile, placed randomly across 180° (total area of 0.0108 m^2 stem surface, total volume of 0.00119 m^3) (Machacova et al., 2016). Stem chambers constituted transparent rectangular plastic containers (Lock & Lock, Seoul, South Korea) that had their bottoms removed and secured with a neoprene band using hot glue. The chambers were sealed with removable airtight lids for sampling sessions. Chambers were installed to the smoothed stem surface at heights of 0.1, 0.8 and 1.7 m above the ground to measure the vertical profile of the stem flux, except for six birch trees with chambers only at the lowest height. During sampling between 09:00 and 13:00, four mixed 25 ml gas samples were collected in pre-evacuated (0.3 bar) gas-tight vials from each chamber system in 60-min intervals. Gas samples were analysed at the Biochemistry lab at University of Tartu using gas chromatography (GC-2014, Shimadzu, Kyoto, Japan), equipped with a flame ionisation detector for CH_4 and an electron capture detector for CO_2 and N_2O concentrations.

Table 1
Tree stand characteristics. Based on Becker et al. (2018).

Tree species	Number of trees (#/ha^{-1})	Average stand height (m)	Average stem diameter at breast height 1.3 m (cm)	Basal area (m^2 ha^{-1})	Tree biomass stock (m^3 ha^{-1})
Downy birch	1660	15	14.0	24.5	193
Norway spruce	942	17	18.4	25	208

Soil gas fluxes were measured between 4 December 2020 and 19 August 2021 using twelve automated dynamic chambers (area of 0.16 m^2 soil surface, volume of 0.032 m^3), one on each monitoring point. The closing time of the chamber during the measurement was nine minutes, followed by a one-minute flushing period with ambient air. Air was sampled from the closed chamber's headspace and analysed with a gas analyser (G2508, Picarro Inc., Santa Clara, California, United States), which uses cavity ring-down spectroscopy technology to measure CO_2, CH_4 and N_2O concentrations. Automated soil gas sampling was performed for a shorter period than manual stem gas sampling due to system malfunction. Therefore, for statistical comparisons between soil and stem fluxes, only stem flux data from the period where soil and stem measurements ran simultaneously was used.

2.3. Flux calculations and data quality check

Stem and soil CO_2, CH_4 and N_2O flux rates were calculated according to the linear regression fit of the chamber headspace gas concentration change over time using the following equation (Eq. (1)):

$$F = \frac{\mathrm{M} \times \mathrm{P} \times \mathrm{V} \times \sigma\mathrm{v}}{R \times T \times t \times A \times f^{1}} \tag{1}$$

where F = gas flux rate (μg C m^{-2} h^{-1} or μg N m^{-2} h^{-1}), M = molecular mass of the gas (M_{CO2} = 44 g mol^{-1}, M_{CH4} = 16 g mol^{-1}, M_{N2O} = 44 g mol^{-1}), P = air pressure (101,300 Pa), V = chamber volume (V_{stem} = 0.00119 m^3, V_{soil} = 0.032 m^3), σv = the slope of linear regression gas concentration change in chamber headspace during the sampling time (ppm(v)), R = gas constant (8.314 m^3 Pa K^{-1} mol^{-1}), T = temperature in the laboratory (293.15 K), t = time ($t = 1$ h), and A = soil or stem surface area covered by the chamber (A_{stem} = 0.0108 m^2, A_{soil} = 0.16 m^2), f^1 = ratio of an element in the compound.

The quality of the manual stem chamber measurement session was validated using the adjusted R^2 value of the linear regression for the CO_2 measurements, which certifies chamber closure quality. Flux values were accepted if the R^2 value exceeded 0.9. All stem flux measurements were accepted. Quality of the automated soil flux measurements was determined by visual inspection of all sessions, removing measurements that indicated a clear leak in the chamber closure, i.e. rapid concentration changes. This led to removal of 0.13 % (CH_4), 0.03 % (N_2O) and 0.01 % (CO_2) of fluxes. To compare the contribution of soil and stem CH_4 and N_2O fluxes, stem fluxes averaged across the three heights were upscaled to a hectare of ground area, calculated based on tree stand characteristics brought out in Table 1, assuming a cylindric shape of the tree, according to methods used by previous papers (Jeffrey et al., 2019), particularly a study done in an adjacent riparian forest (Schindler et al., 2020).

2.4. Environmental parameters

Soil and air temperature, SWC and WTD were continuously measured during the study period for each chamber. Soil temperature (107 temperature probe, CAMPBELL SCIENTIFIC. INC, Logan, Utah, USA) and soil moisture sensors (ML3 ThetaProbe, Delta-T Devices, Cambridge, United Kingdom) were placed vertically at 0.1 m soil depth inside the soil chambers. The soil water level was observed in groundwater wells using automatic data loggers (Hobo U20L-04, Onset Computer Corporation, Bourne, Massachusetts, USA). Precipitation data was acquired from a meteorological station located approximately 2 km from the study site.

2.5. Soil physiochemical parameters

Soil physical and chemical parameters were analysed using soil samples collected during twelve monthly sampling campaigns from November 2020 to October 2021. Soil samples were collected from 0 to 10, 10–20 and 20–40 cm below ground from each of the 12 monitoring points adjacent to the automatic soil chambers ($N = 144$). Three soil cores from each sampling point were collected and pooled to form a composite sample. Plant-available phosphorus (P) and potassium (K^+) were determined from a NH_4-lactate extraction solution using the FiaStar5000 flow-injection analyser (FOSS, Hilleroed, Denmark) and the flame photometric method, respectively. Plant-available magnesium (Mg^{2+}) was determined from a 1 M ammonium-acetate solution with a titanium-yellow reagent on the flow-injection analyser and calcium (Ca^{2+}) was analysed from the same solution by a flame-photometrical method. Soil pH was determined from a 1 M KCl solution. Soil ammonium ($NH_4^+{-}N$) and nitrate ($NO_3^-{-}N$) were determined from a 2 M KCl extract by flow injection analysis c. Total N contents of air-dried samples were determined by a dry-combustion method on a varioMAX CNS elemental analyser (Elementar Analysensysteme GmbH, Germany). The soil organic matter content of dry matter was determined by loss on ignition at 550 °C. The helium atmosphere (He—O) soil incubation method was used to measure potential N_2 fluxes from soil cores ex-situ, as described in Butterbach-Bahl et al. (2002) and Mander et al. (2014).

2.6. Xylem sap flow

The xylem sap flow of birch ($N = 3$) and spruce ($N = 3$) trees was recorded with six sap flow systems of EMS81 (EMS Brno, Brno, Czech Republic) from 29 May until 10 September 2021. The sensors were mounted at 2–2.5 m from the ground level. The stem sap flow rate (kg/h) was divided to stem xylem area (cm^2) at the sensor height to calculate sap flux density (g h^{-1} cm^{-2}). The sap flow data was recorded every minute and stored as a 10-min average. In addition, stem temperature (°C) of the sample trees was measured under the weather shield of the sap flow gauge.

2.7. Statistical analysis

Statistical analysis was performed using R version 4.0.3 (R core team, 2020). The normality of data distribution was examined using the Kolmogorov-Smirnov test. As flux data were not normally distributed, non-parametric tests were used for analysis. Kruskal–Wallis one-way analysis of variance was used to determine the significance of temporal variability of gas fluxes and differences between stem fluxes at different heights and during the wetter and drier periods. Dunn's multiple comparison, corrected with the Bonferroni method, was conducted as a post hoc test to determine which groups differed. Spearman's rank correlation was used for correlation analysis. A significance level of $p < 0.05$ was used. Mean and standard error (SE) are used for characterisation of variability across all calculations.

3. Results

3.1. Temporal dynamics of stem fluxes

Tree stems were a net annual source of CH_4 for both species. Birch trees emitted 1.12 ± 0.121 (mean ± SE μg C m^{-2} h^{-1} and spruce trees 0.231 ± 0.05 μg C m^{-2} h^{-1}), on average during the study period. The full study year was divided into wetter and drier periods based on the SWC values. The drier period was defined by sustained daily average SWC values below 0.3 m^{3}m^{-3} (13 July 2021–20 October 2021) and thus the wetter period with SWC above this value (22 October 2020–12 July 2021). Table 2 presents average fluxes for the full study period, as well as drier and wetter periods of the year. The temporal dynamics of tree stem CH_4 fluxes showed fluctuations between small emissions and uptake throughout most of the year (Fig. 1B). An increase in both birch and spruce stem emissions occurred in November (daily means up to 5.58 ± 1.48 μg C m^{-2} h^{-1} for birch and 5.87 ± 1.53 μg C m^{-2} h^{-1} for spruce stems). Birch emissions increased in early summer and peaked in June, with daily mean value reaching 8.47 ± 3.14 μg C m^{-2} h^{-1}. The combined flux during these peak emissions' periods accounted for 66.9 % of the total flux from birch stems. However, no such increase was observed for spruce fluxes. Statistically significant vertical patterns were not observed for stem CH_4 fluxes for either species (Fig. 2A). Correlations between fluxes and relevant meteorological and soil chemical parameters are presented in Table 3. Supplementary Fig. 2 illustrates the results of a Principal Component Analysis of fluxes and environmental parameters. Supplementary Fig. 3 further shows the annual temporal patterns of the soil $NO_3^-{-}N$ and $NH_4^+{-}N$ contents. Across the study period, birch CH_4 fluxes were significantly related to SWC ($r = 0.18$), soil temperature ($r = 0.15$) and WTD ($r = 0.11$). Spruce CH_4 fluxes did not show statistically significant correlations with any of the measured meteorological parameters on an annual scale. However, spruce fluxes correlated with stem temperature ($r = 0.37$) measured simultaneously with sap flow during the growing season (Table 3). Birch CH_4 also correlated with soil N compounds $NO_3^-{-}N$ ($r = -0.40$), $NH_4^+{-}N$ ($r = 0.27$) and N_2 flux ($r = 0.29$), while spruce CH_4 flux only correlated with soil N_2 flux ($r = 0.31$) (Table 3).

Table 2
Average (mean ± SE) fluxes of CH_4 (μg C m^{-2} h^{-1}), N_2O (μg N m^{-2} h^{-1}) and CO_2 (mg C m^{-2} h^{-1}) from birch stems, spruce stems and soil, averaged for the full study period (October 2020–December 2021 for stem fluxes and December 2020–August 2021 for soil fluxes), the wetter period (22 October 2020–12 July 2021) and the drier period (13 July 2021–20 October 2021 for stem fluxes and 13 July 2021–19 August 2021 for soil fluxes). The drier period was defined by SWC being continuously <0.3 m^{3}m^{-3}.

	CH_4 (μg C m^{-2} h^{-1})	N_2O (μg N m^{-2} h^{-1})	CO_2 (mg C m^{-2} h^{-1})
		Full period	
Birch	1.12 ± 0.12	2.50 ± 0.38	92.1 ± 3.2
Spruce	0.231 ± 0.050	−0.242 ± 0.031	61.4 ± 2.1
Soil	−6.44 ± 0.21	42.4 ± 1.8	43.1 ± 1.5
		Wetter period	
Birch	1.40 ± 0.16	3.28 ± 0.49	79.9 ± 3.8
Spruce	0.226 ± 0.072	−0.107 ± 0.035	54.7 ± 52.49
Soil	−3.04 ± 0.18	43.6 ± 2.0	26.9 ± 1.1
		Drier period	
Birch	0.353 ± 0.077	0.308 ± 0.387	126.0 ± 5.7
Spruce	0.244 ± 0.083	−0.62 ± 0.06	80.1 ± 3.9
Soil	−32.2 ± 1.2	33.4 ± 3.0	165.0 ± 6.5

Birch stems were a net annual emitter of N_2O (2.50 ± 0.379 μg N m^{-2} h^{-1}), whereas spruce stems showed small uptake of atmospheric N_2O (−0.242 ± 0.031 μg N m^{-2} h^{-1}). While spruce stem fluxes fluctuated around zero between small release and uptake throughout the year, birch stem fluxes showed more pronounced temporal variability (Fig. 1C). The largest emissions occurred in autumn, both in 2020 and 2021, with maximum values of 34.3 ± 11.9 μg N m^{-2} h^{-1} in October 2020 and 28.7 ± 0.455 μg N m^{-2} h^{-1} in November 2021. A smaller peak of up to 12.4 ± 3.22 μg N m^{-2} h^{-1} occurred in early spring (Fig. 1C). Fluxes during periods of peak N_2O emissions accounted for 94.9 % of the total birch stem flux. Birch stem N_2O fluxes showed a statistically significant decreasing trend with increasing stem height (Fig. 2B). Across the study period, mean fluxes were 5.86 ± 0.883 μg N m^{-2} h^{-1} at 10 cm, 0.888 ± 0.215 μg N m^{-2} h^{-1} at 80 cm and 0.328 ± 0.105 μg N m^{-2} h^{-1} at 170 cm stem height. No vertical trend was observed for spruce N_2O fluxes. Birch N_2O fluxes showed positive correlations with WTD ($r = 0.39$), SWC ($r = 0.21$) and growing season stem temperature ($r = 0.53$), but negative correlations with air ($r = -0.37$) and soil temperatures ($r = -0.33$), and soil $NO_3^-{-}N$ content ($r = -0.17$). Similarly, spruce N_2O fluxes were positively correlated with WTD ($r = 0.41$) and SWC ($r = 0.23$), and negatively with air ($r = -0.54$) and soil temperatures ($r =$

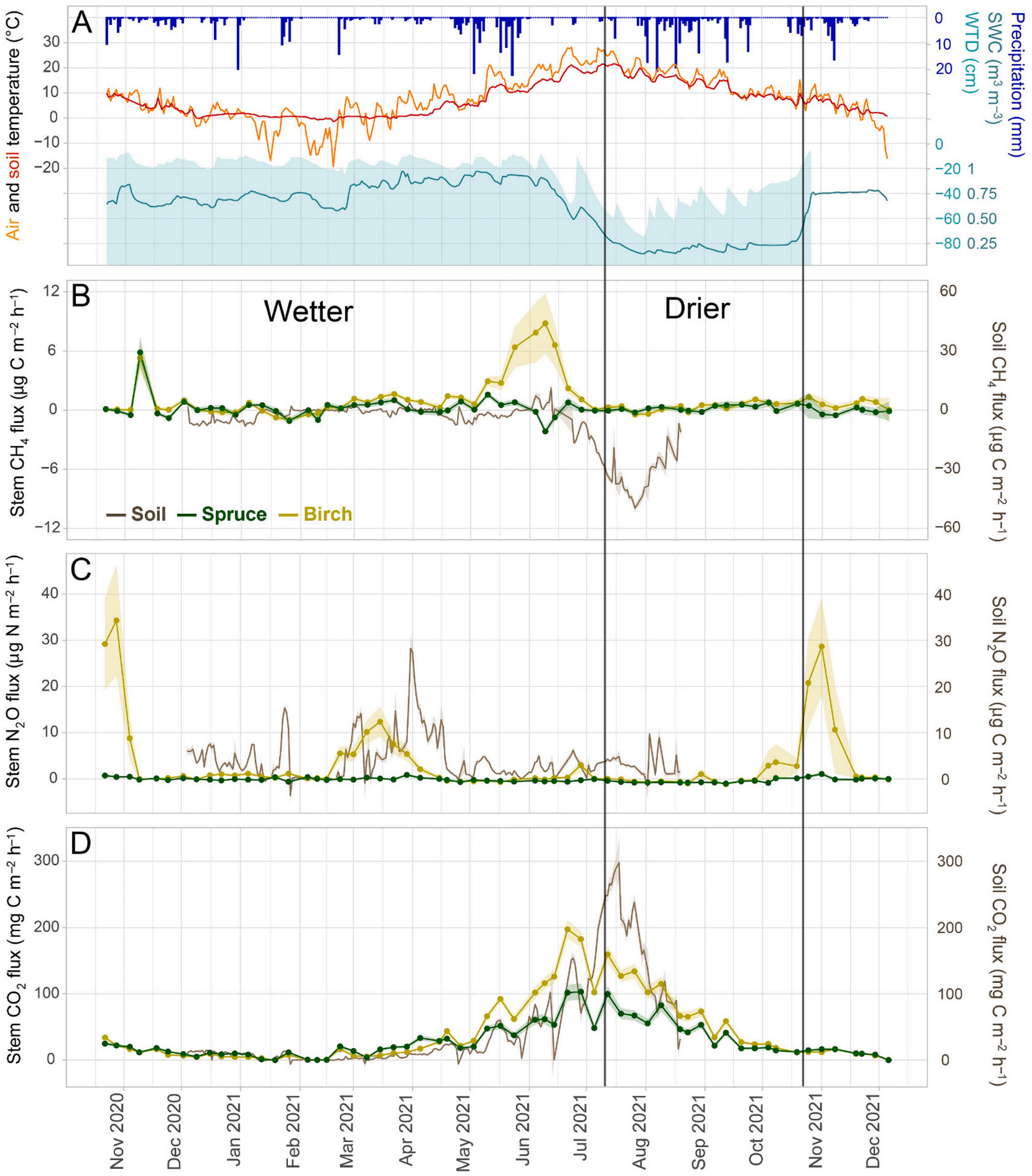

Fig. 1. Temporal dynamics of soil and stem CH_4, N_2O and CO_2 fluxes and environmental parameters in the drained peatland forest. (A) Daily mean air and soil temperatures (°C), soil water content (SWC, $m^3\ m^{-3}$), water table depth (WTD, cm), and daily sum precipitation (mm) (October 2020–December 2021); daily mean soil (December 2020–August 2021) and stem (October 2020–December 2021) (B) CH_4 (μg C m^{-2} h^{-1}), (C) N_2O (μg N m^{-2} h^{-1}) and (D) CO_2 (mg C m^{-2} h^{-1}) fluxes with standard error as the shaded area. Stem fluxes are expressed in units per m^2 of stem bark surface area. Soil fluxes are expressed in units per m^2 of soil surface area. Drier and wetter periods of the year are emphasised by grey vertical lines. The drier period was defined by SWC being continuously <0.3 $m^3 m^{-3}$. Drier period: 13 July 2021–20 October 2021; wetter period: 22 October 2020–12 July 2021.

−0.37) (Table 3).

Both birch and spruce stems had a net positive CO_2 flux throughout the year, with an average of 92.1 ± 3.23 mg C m^{-2} h^{-1} for birch and 61.4 ± 2.13 mg C m^{-2} h^{-1} for spruce. Daily average stem fluxes for both tree species were much lower during the dormant season, beginning a gradual increase during spring months (Fig. 1D). Fluxes were higher in the summer, with daily averages reaching 394.9 ± 26.7 mg C m^{-2} h^{-1} (birch) and 206.3 ± 24.8 mg C m^{-2} h^{-1} (spruce) at the end of June. A gradual decrease of fluxes occurred towards autumn months (Fig. 1D). Birch stem CO_2 fluxes displayed a vertical trend where fluxes were significantly higher from the lowest part of the stem (101.2 ± 4.58 mg C m^{-2} h^{-1}) and decreased to 68.9 ± 5.12 mg C m^{-2} h^{-1} at 80 cm and to 63.0 ± 4.78 mg C m^{-2} h^{-1} at 170 cm stem height. The difference was not statistically significant between CO_2 fluxes at 80 and 170 cm stem height (Fig. 2C). No clear trend was observed for spruce CO_2 fluxes. Birch and spruce CO_2 efflux was highly dependent on air ($r = 0.95$ for birch and $r = 0.94$ for spruce) and soil temperatures ($r = 0.88$ and $r = 0.73$), as well as growing season stem temperatures ($r = 0.61$ and 0.54). Birch CO_2 fluxes also had significant relationships with WTD ($r = -0.52$), SWC ($r = -0.23$), and soil NO_3^-–N ($r = -0.18$) and NH_4^+–N ($r = 0.20$) contents. Spruce CO_2 flux also had a significant negative correlation with WTD ($r = -0.40$) (Table 3).

Xylem sap flow rates measured in the growing season and the calculated sap flow density were, on average, higher for birch trees (0.963 ± 0.045 kg/h and 4.83 ± 0.033 g/h/cm^2, respectively) than for spruce trees (0.453 ± 0.030 kg/h and 2.26 ± 0.018 g/h/cm^2, respectively). Daily average flow density was higher in late June and early July and decreased towards the end of the growing season (Supplementary Fig. 4). Birch N_2O and CO_2 and spruce CO_2 flux rates correlated positively with birch xylem sap flow density, whereas other correlations

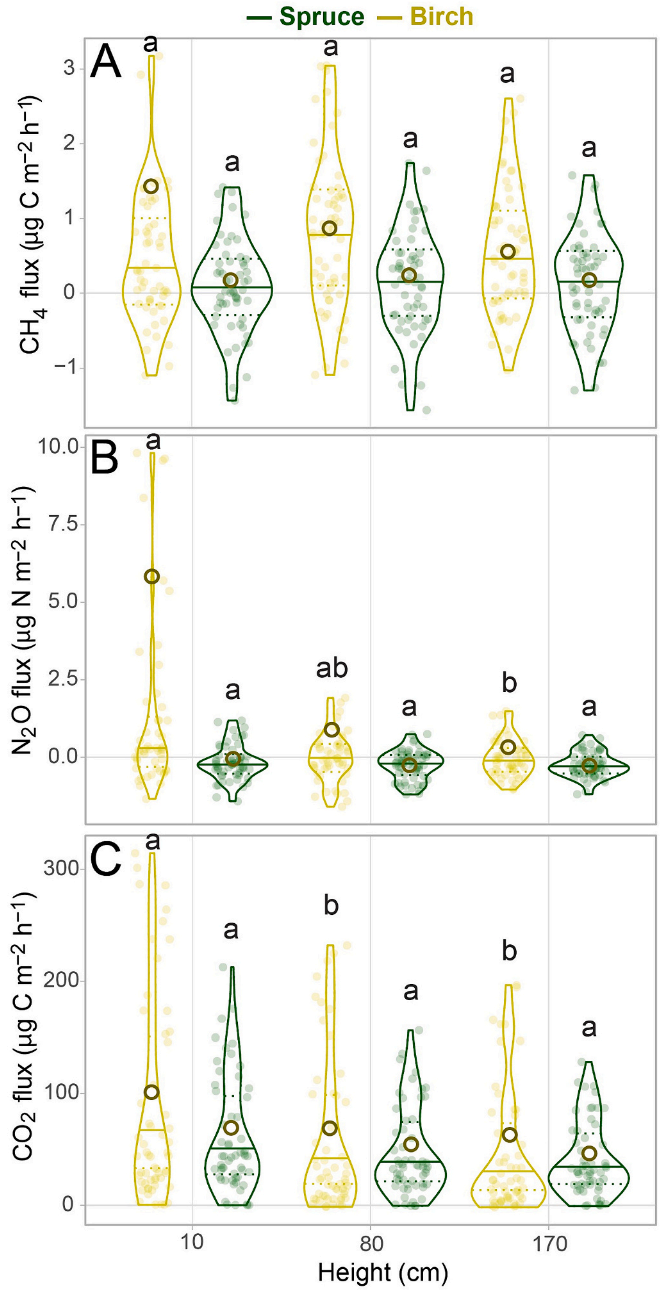

Fig. 2. Vertical profile of (A) CH_4, (B) N_2O and (C) CO_2 stem fluxes at 0.1 m ($N = 349$), 0.8 m ($N = 174$) and 1.7 m (N = 174), averaged across all plots and throughout the study period. Different letters above bars indicate statistically significant differences between fluxes at different heights within species, according to a Kruskal-Wallis one-way analysis of variance followed by a post-hoc Dunn test ($p < 0.05$). The solid line within each box marks the median value, circles the mean value and dotted lines the 25th and 75th percentiles.

were non-significant (Fig. 3).

3.2. Temporal dynamics of soil fluxes

Soil at the study site was a net sink of CH_4 (−6.44 ± 0.21 µg C m^{-2} h^{-1}) from the atmosphere, and a source of N_2O (42.4 ± 1.84 µg N m^{-2} h^{-1}) and CO_2 (43.1 ± 1.49 mg C m^{-2} h^{-1}) during the measurement period. The temporal dynamics of soil CH_4 fluxes were characterised by near-zero fluctuations in the dormant season and substantial uptake in the summer months, peaking in late-July (daily average − 49.5 ± 5.07 µg C m^{-2} h^{-1}) (Fig. 1B). Average soil fluxes for the wetter and drier periods have been brought out in Table 2. Soil CH_4 fluxes were positively related to WTD ($r = 0.48$), SWC ($r = 0.46$) and N_2 flux ($r = 0.22$), and negatively to soil temperature ($r = -0.47$), air temperature ($r = -0.35$) and $NO_3^-{-}N$ ($r = -0.37$) (Table 3). Soil N_2O fluxes' temporal dynamics displayed peaks of different magnitudes, mainly in the winter and spring periods. Maximum emissions were reached in late March and early April (daily means up to 279.3 ± 82.7 µg N m^{-2} h^{-1}). Soil N_2O fluxes were positively correlated with air ($r = 0.16$) and soil ($r = 0.15$) temperatures. Soil CO_2 fluxes showed a clear seasonal trend of near-zero fluxes during the dormant season (Fig. 1D). Emissions increased in spring and peaked in mid-July (maximum daily average 297.8 ± 35.8 µg C m^{-2} h^{-1}), after which emissions decreased again towards the end of summer. Soil CO_2 fluxes displayed the positive correlations with air ($r = 0.87$) and soil ($r = 0.83$) temperatures and $NH_4^+{-}N$ ($r = 0.32$), and negative correlations with WTD ($r = -0.51$) and SWC ($r = -0.38$). Comparing stem CH_4, N_2O and CO_2 fluxes to the soil fluxes of the respective gas showed that birch stem fluxes have positive correlations with soil CH_4 ($r = 0.24$), N_2O ($r = 0.18$) and CO_2 ($r = 0.76$) fluxes. However, for spruce stem fluxes, significant correlations only occurred with soil CO_2 fluxes ($r = 0.64$).

3.3. Contributions of stem and soil fluxes to total fluxes

When these net average fluxes were upscaled to m^2 of forest ground area and only stem fluxes that temporally coincided with soil flux measurements (4 December 2020–19 August 2021) were used, the percentage partitioning of total fluxes between stem and soil fluxes was calculated (Fig. 4). Upscaled birch and spruce stem CH_4 release during the total measurement period offset the soil CH_4 sink by 25.9 % and 1.9 %, respectively. Stem fluxes from both species accounted for 3.0 % of the combined soil and stem N_2O emissions. Birch emissions added 3.5 % to the total emissions, while spruces were a sink that offset total emissions by 0.5 %. Birch and spruce CO_2 fluxes respectively accounted for 52.4 % and 28.6 % of total soil and stem CO_2 release, while the soil added 19 %.

Results showed that there were significant differences in fluxes of all three gases between the wetter and drier periods of the year. CH_4 fluxes showed great variability in flux partitioning between drier and wetter periods. During the drier period, stem CH_4 fluxes were negligible and offset the soil sink by 0.3 %. However, during the wetter period, stem emissions increased while soil uptake diminished, which resulted in a 40.6 % offset of the soil sink by stem emissions (Fig. 4A). The contribution of stem N_2O fluxes to the total soil and stem flux was low during both drier and wetter periods. During the drier period, combined stem fluxes were net consumers of atmospheric N_2O, counteracting soil emissions by 4.1 %, whereas during the wetter period, stem fluxes combined added 3.9 % to soil emissions (Fig. 4B). Although net CO_2 release from all sources were higher during the drier period, the total contribution of stem fluxes was higher during the wetter period (69.2 % and 85.2 % during the drier and wetter periods, respectively), with birch fluxes contributing more than spruce fluxes (Fig. 4C). Soil fluxes thus accounted for 30.8 % and 14.8 % of the total CO_2 fluxes during the drier and wetter periods, respectively.

4. Discussion

Compared to our results of stem CH_4 release, previous studies have shown higher values on an annual scale from various broadleaved tree species. However, these studies have been conducted in wetter soils than on our site, for example in a riparian forest (Mander et al., 2022), floodplain forest (Moldaschl et al., 2021), and forested wetlands (Jeffrey et al., 2023b; Pangala et al., 2015). Long-term measurements from forests with drier conditions, which could provide more comparable results with our drained forest, are lacking. Higher SWC and WTD are commonly associated with higher stem CH_4 emissions, providing anaerobic conditions needed for methanogenesis in the soil, leading to more CH_4 readily available for pick-up by tree roots (Barba et al., 2019a). Across the year, soil and tree stem CH_4 flux dynamics were

Table 3
Spearman's correlations between birch, spruce and soil CH_4, N_2O and CO_2 fluxes, and soil environmental parameters, as well as chemical parameters from the topsoil layer (0–10 cm) during the whole measurement period. Statistically significant correlations have been marked in bold ($p < 0.05$).

	CH_4 ($\mu g\ C\ m^{-2}\ h^{-1}$)			N_2O ($\mu g\ N\ m^{-2}\ h^{-1}$)			CO_2 ($mg\ C\ m^{-2}\ h^{-1}$)		
	Birch	Spruce	Soil	Birch	Spruce	Soil	Birch	Spruce	Soil
Soil water content ($m^3 m^{-3}$)	**0.18**	−0.03	**0.47**	**0.21**	**0.23**	−0.03	**−0.23**	−0.07	**−0.38**
Water table depth (cm)	**0.11**	−0.02	**0.52**	**0.39**	**0.41**	−0.02	**−0.52**	**−0.40**	**−0.51**
Soil temperature (°C)	**0.15**	−0.06	**−0.46**	**−0.33**	**−0.37**	**0.15**	**0.88**	**0.73**	**0.81**
Air temperature (°C)	0.26	−0.15	**−0.35**	**−0.37**	**−0.54**	**0.16**	**0.95**	**0.94**	**0.87**
Stem temperature (°C)[1]	−0.04	**0.37**		**0.53**	0.19		**0.61**	**0.54**	
NH_4^+-N (mg/kg)	**0.27**	0.08	0.08	0.14	−0.01	0.18	**0.20**	0.19	**0.32**
NO_3^--N (mg/kg)	**−0.40**	−0.04	**−0.37**	**−0.17**	0.06	0.04	**−0.18**	−0.21	0.01
Soil N_2 flux (μg N m-2 h-1)	**0.29**	**0.31**	**0.22**	0.01	0.10	−0.11	0.15	0.04	−0.02
Sap flow density ($g/h/cm^2$)[1]	−0.01	−0.20		**0.38**	0.31		**0.56**	0.28	
Soil CH_4 flux ($\mu g\ C\ m^{-2}\ h^{-1}$)	**0.24**	0.10	**1**	**0.18**	**0.21**	**−0.26**	**−0.36**	**−0.34**	**−0.56**
Soil N_2O flux ($\mu g\ N\ m^{-2}\ h^{-1}$)	−0.02	−0.03	**−0.26**	**0.18**	0.04	**1**	**0.16**	0.09	**0.37**
Soil CO_2 flux ($mg\ C\ m^{-2}\ h^{-1}$)	0.07	−0.11	**−0.56**	**−0.31**	**−0.29**	**0.37**	**0.76**	**0.64**	**1**

[1] Note that sap flow and stem temperature were only measured during the growing season (29 May–10 September 2021). The presented correlations are based on stem flux data corresponding to this period.

primarily driven by changes in soil hydrological conditions and temperature (Table 3; Supplementary Fig. 2). It is likely that the significant correlations between soil and stem CH_4 fluxes and soil N contents and N_2 flux are also connected to changes in soil hydrology, as anaerobic conditions lead to reduction of NO_3^--N and release of N_2 through denitrification. Although sap flow is responsible for the consequent upward transport of soil-produced CH_4 in the xylem (Anttila et al., 2023), we did not find a relationship between sap flow and stem CH_4 flux. Sap flow may not lead to gas efflux from the stem if the initial concentrations of the respective gas dissolved in the sap are low. Further investigation into these relationships is crucial to understand the upward transport processes of gases dissolved in soil water that have been taken up by tree roots. In addition to CH_4 produced in the soil, CH_4 could also be produced inside or on the stem. The exact differentiation between these sources of CH_4 is still contested (Barba et al., 2019a; Jeffrey et al., 2021; Pitz and Megonigal, 2017). Our results suggested that the net CH_4 flux was likely an aggregate of soil and stem derived CH_4. Stem CH_4 fluxes had significant relationships with soil environmental parameters, as well as soil CH_4 flux (Table 3), indicating a potential soil source. However, as xylem sap flow was not driving CH_4 fluxes during the growing season (Fig. 3A), and a vertical stem flux profile trend was missing (Fig. 2A), CH_4 emitted through stems could also be produced microbially inside or on the tree stem. As the soil constituted a net CH_4 sink while the stems remained a source of CH_4, the soil-derived CH_4 must have originated from deeper soil layers, where conditions are more anaerobic and methanogenesis prevails (Machacova et al., 2023; Pitz et al., 2018; Ranniku et al., 2023). The temporal dynamics of tree stem CH_4 fluxes were characterised by isolated emissions' peaks but near-zero fluctuations for most of the year. We observed peaks in stem CH_4 emissions for both tree species in November, following an increase in SWC (Fig. 1A and B). A more pronounced peak for birch emissions occurred in early summer, coinciding with the end of the wetter period, where sustained higher water levels together with increasing soil temperatures likely created optimal conditions for methanogenesis in the soil (Fig. 1A and B) (Pangala et al., 2015). On average, stems emitted more CH_4 during the wetter period of the year, mostly driven by the peaks. The wetter period peak emissions also suggest that the baseline stem emissions may be a combination of fluxes of soil and stem origin, whereas the peaks themselves are driven by changes on soil hydrology, and therefore soil-originated CH_4 is responsible for driving the peaks.

Net annual birch N_2O emissions measured in this study exceeded those from birch and spruce trees in a boreal forest (Machacova et al., 2019), from alder trees in a hemiboreal riparian forest (Mander et al., 2021), and from ash and poplar in a temperate floodplain forest (Moldaschl et al., 2021). Consumption of N_2O, as observed from spruce stems in this study, has previously only been reported for broadleaved tree species in temperate upland forests during the growing season (Barba et al., 2019b; Machacova et al., 2017). N_2O uptake could be related to a stem-atmosphere concentration gradient where the atmospheric concentrations exceed those in the stem (Barba et al., 2019b), or to the presence of cryptogamic stem covers (Machacova et al., 2017), which were not, however, prevalent on our measured spruce trees. While annual spruce stem N_2O fluxes were negligible, temporal dynamics of birch stem fluxes were driven by emissions' peaks in autumn and spring (Fig. 1C), governed by changes in SWC and WTD. The spring-time peak also coincided with a substantial increase in soil N_2O emissions, defined as a hot-moment of emissions related to soil freeze-thaw (Kazmi et al., 2023; Ranniku et al., 2023). During freeze-thaw events, dead cells of microorganisms, fine roots, and mycorrhiza in the soil, destroyed by freezing, can rapidly decompose during thawing, increasing nitrate availability for N_2O production by microbes (Groffman et al., 2006; Teepe et al., 2001). We observed increased nitrate content (Supplementary Fig. 3) directly prior to the spring-time peak of soil and stem N_2O emissions (Fig. 1C). A combination of heightened soil NO_3^--N and SWC likely led to the peak N_2O emissions, as increased NO_3^--N can stimulate denitrification in anaerobic soil conditions. As the N pool is depleted, the denitrification process is subdued and fluxes decrease. However, the monthly soil sampling frequency may have been insufficient to account for faster changes in soil N content related to N_2O fluxes that would have provided more direct relationships. Furthermore, the short-lived peaks indicate that stem N_2O emissions can be induced by rapid changes in soil hydrological conditions, such as freeze-thaw or flooding events or wet and dry period transitions (Mander et al., 2021; Ranniku et al., 2023; Schindler et al., 2020). Higher-frequency measurements are needed for more precise timing of these emissions' peaks to adequately estimate the total contribution of stem fluxes on the annual forest GHG budgets (Barba et al., 2019b; Barton et al., 2015). Stem N_2O fluxes had an inverse relationship with soil and air temperatures, potentially owing to peak emissions occurring in the autumn months when temperatures are lower. Thus, changes in soil water status play a greater role in driving stem N_2O fluxes than temperature dynamics. A dominating soil source for stem N_2O fluxes was evidenced by relatively strong relationships between fluxes, soil environmental parameters and sap flow rates, as well as the decreasing vertical stem flux trend. Although we found that sap flow was one of the driving factors of stem N_2O fluxes during the growing season, this relationship has not been thoroughly investigated before.

Our results of net annual birch and spruce stem CO_2 fluxes were roughly 10 times higher than those measured from European beech in a temperate upland forest (Machacova et al., 2023) and from Scots pine in a boreal forest (Kolari et al., 2009). Both tree stem and soil CO_2 fluxes followed a seasonal trend, with lower values during the dormant season

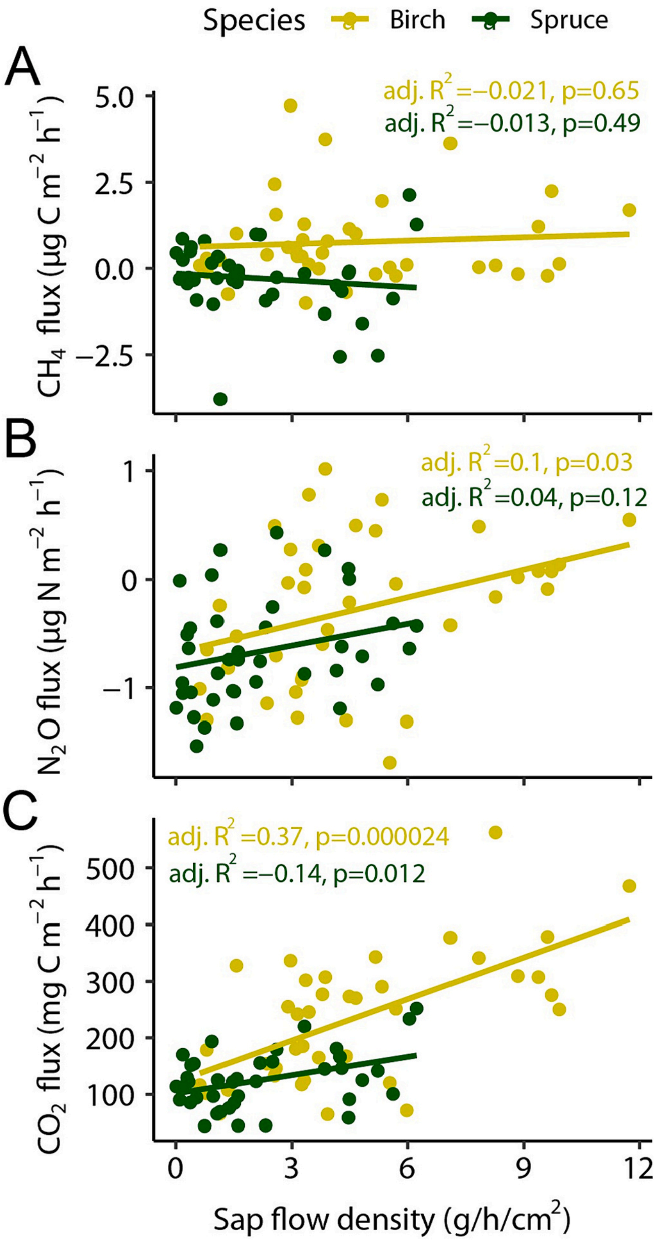

Fig. 3. Relationship between sap flow density and birch ($N = 39$) and spruce ($N = 39$) stem (A) CH_4, (B) N_2O and (C) CO_2 fluxes during the growing season (04 June 2021–06 September 2021). Adjusted R^2 and p-values of the relationships have been calculated according to the linear regression model.

and increased fluxes during the growing season (Fig. 1D). Similar stem flux trends coinciding with tree growth phenology have been shown in Norway spruce at a subalpine site (Etzold et al., 2013), Scots pine in a boreal forest (Kolari et al., 2009) and European beech in a temperate upland forest (Machacova et al., 2023). Conversely to CH_4 and N_2O dynamics, average stem and soil CO_2 release was higher during the drier period, and the main determinant of the efflux was temperature, rather than hydrologic conditions (Table 3; Supplementary Fig. 2). This has also been shown in previous studies (Barba et al., 2019b; Ojanen et al., 2010; Takahashi et al., 2022), mainly related to temperature sensitivity of stem and forest floor respiration processes and diffusion rates (Teskey et al., 2008). Increased CO_2 efflux during drier periods has also been associated with reduced transpiration, leading to higher concentrations of gaseous CO_2 in the stem (Salomón et al., 2016). The negative relationship with soil water parameters can be explained by higher stem water content in wetter conditions, leading to increased resistance to radial diffusion (Bowman et al., 2005; Gansert and Burgdorf, 2005; Salomón et al., 2016). Stem-emitted CO_2 is primarily a combination of root respiration, respiration inside the stem and, to a lesser extent, root-uptake of CO_2 dissolved in the soil water (Aubrey and Teskey, 2009; Bloemen et al., 2013). However, the disentangling of the origin of stem CO_2 efflux is of continuous scientific debate due to several complexities. Our results suggested that stem-emitted CO_2 may more likely be driven by root respiration and root-uptake of CO_2, evidenced by higher fluxes from lowest part of the stem and significant relationships with xylem sap flow. However, previous studies have shown varied vertical stem CO_2 flux gradients, as CO_2 produced by woody-tissue respiration can also dissolve and be transported away from the production location (Salomón et al., 2024). As both sap flow rates and CO_2 efflux from the stems are highly dependent on air temperature (Hölttä and Kolari, 2009), relationships between the two should be further investigated independently of the temperature effect. Moreover, it is vital to quantify stem CO_2 fluxes higher along the vertical gradient and determine the stem and bark anatomical effects on stem GHG diffusion rates.

The inter-species variance in temporal stem flux patterns demonstrates that the processes driving GHG fluxes need to be contextualised depending on tree species. Firstly, site-level differences in microtopography can bring about flux variations between trees by creating variations in SWC and WTD. Thus, trees growing in depressions with potentially higher water availability for roots may emit more CH_4 and N_2O (Jeffrey et al., 2020; Terazawa et al., 2015). Birch trees are known to be better adapted to wetter conditions than spruces, and may prefer such locations as their habitat within the forest ecosystem (Kozlowski, 1997). The quantities of dissolved gases transported up the xylem may also depend on the spatial variability of gas concentrations in the soil water (Machacova et al., 2016; Machacova et al., 2019). Moreover, root depth and density can vary between tree species. The fine root density of spruce is generally higher closer to the soil surface. Thus, only birch roots may reach the deeper soil layers to facilitate water uptake and gas transport, particularly for CH_4 that may originate from deeper soil layers where methanogenesis occurs (Puhe, 2003; Ranniku et al., 2023). Stem morphology and tree physiology differ between broadleaved and coniferous trees, leading to variations in transpiration and gas diffusion rates (Pitz and Megonigal, 2017; Salomón et al., 2021; Teskey et al., 2008). Higher GHG fluxes may be assumed from conifers, as they generally have lower wood density compared to broadleaved trees (Machacova et al., 2019; Zhang et al., 2020). However, our results suggest that stem density did not play a significant role in the flux variability, with birch emissions surpassing spruce fluxes for all gases. The same tendency was found for CH_4 fluxes from birch and spruce trees in a boreal forested fen (Vainio et al., 2022). Furthermore, the differences in xylem structures results in variations in sap flow rates. Conifers use tracheids for water transport within the xylem, while broadleaved trees have wider vessels, facilitating upwards water transport from roots more efficiently (Zhang et al., 2020). Additionally, birch trees exhibit bark characteristics favourable for potential axial bark-mediated gas diffusion, as demonstrated in lowland *Melaleuca quinquenervia* trees with laminar paper-like layers (Jeffrey et al., 2023a). However, studies demonstrating how wood and bark anatomy influence stem GHG fluxes are scarce and there remains a need for a more mechanistic understanding of how species-specific variations in tree physiology and stem anatomy affect mediating gas transport in the soil-tree-atmosphere continuum.

Tree stem GHG fluxes can substantially contribute to the sum of soil and stem fluxes. Neglecting stem fluxes from forest GHG inventories can lead to under- or overestimation of the budget of the respective gases (Machacova et al., 2023; Ranniku et al., 2023). Across the whole study period, birch and spruce stem CH_4 emissions offset the soil sink by 25.9 % and 1.9 %, respectively (Fig. 4A). The varying potential of trees to offset the soil CH_4 sink has primarily been shown in temperate upland forests (Machacova et al., 2023; Pitz and Megonigal, 2017; Wang et al.,

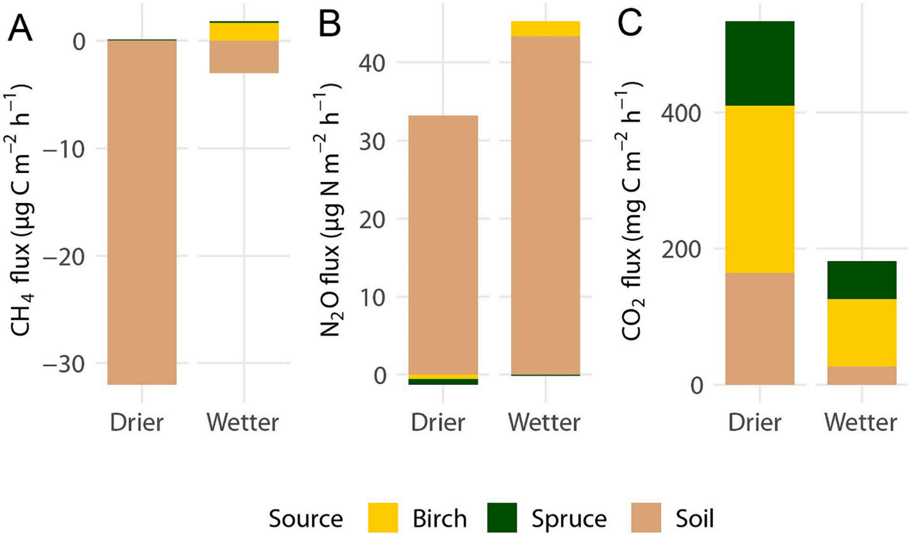

Fig. 4. Contributions of average tree stem (birch and spruce) and soil (A) CH_4, (B) N_2O and (C) CO_2 fluxes during the drier and wetter periods of the year, scaled to a unit of ground area of forest. The drier period was defined by SWC being continuously $<0.3\ m^3m^{-3}$. Wetter period: 4 December 2020–12 July 2021; drier period: 13 July 2021–19 August 2021. Note that both stem and soil flux data from these date ranges were used for contributions' calculations as soil flux data was only available between 4 December 2020–19 August 2021. Positive flux values indicate gas emission, negative values uptake. The boxes represent mean fluxes across all measurement points.

2016), whereas in ecosystems with wetter soils where soil is a net CH_4 source, stem emissions have been shown to add up to 83 % to the total soil source in different wetland forests (Jeffrey et al., 2023b; Mander et al., 2022; Pangala et al., 2015). The contribution of stems to total N_2O emissions was relatively low, with stem fluxes adding 3.0 % to the soil N_2O source, almost entirely associated with birch emissions (Fig. 4B). Low contributions have also been estimated from a boreal forest (birch 0.75 % and spruce 2.5 %) (Machacova et al., 2019), and a riparian forest (alder 0.8 %) (Mander et al., 2021). Stem fluxes were a significant contributor to the CO_2 balance of the ecosystem, accounting for 81 % of total CO_2 release (Fig. 4C). Although long-term stem CO_2 flux monitoring in forest ecosystems is rare, studies during the growing season have shown stem flux contributions of 28.4 % in a temperate upland forest (Warner et al., 2017). However, it is crucial to highlight that the upscaling procedure of chamber measurements, most commonly performed at the bottom parts of the stems, to tree-level fluxes is one of the key uncertainties in stem flux studies (Barba et al., 2024), potentially leading to inaccuracies in quantifying the contribution of stem fluxes to total ecosystem fluxes.

Our results suggested substantial differences in the contributions of stem fluxes to total fluxes between wetter and drier periods of the year. However, these differences markedly varied depending on the respective gas. During the drier period, when the soil became a large CH_4 sink, stem CH_4 emissions were negligible. However, during the wetter period, stem CH_4 emissions increased while soil uptake decreased (Fig. 4A). Consequently, stem emissions offset the soil sink by 40.6 %. Mander et al. (2022) demonstrated that stem emissions can result in a riparian forest ecosystem becoming a net emitter of CH_4 during the wet period. These dissimilarities between wetter and drier period stem CH_4 fluxes further emphasise the strong effect of soil hydrological conditions on stem CH_4 dynamics. On the other hand, stem N_2O fluxes' contributions remained relatively low, regardless of the wetter and drier periods (Fig. 4B). The small variance further highlights that stem N_2O fluxes may be more responsive to short-term changes in hydrological conditions, such as freeze-thaw events, flooding and drought (Mander et al., 2021; Schindler et al., 2020), rather than seasonal wet and dry periods. Total CO_2 efflux from soil and stems was much higher during the drier period, whereas the relative contribution of stem fluxes was more prevalent during the wetter period (Fig. 4C). It is likely that as temperature is a stronger determinant of stem CO_2 dynamics, the changes in hydrologic conditions have a secondary effect on these dynamics (Etzold et al., 2013; Kolari et al., 2009).

5. Conclusions

Birch stems played a greater role in annual GHG dynamics in the northern drained peatland forest than spruce stems. The temporal dynamics of tree stem CH_4 and N_2O fluxes were characterised by isolated emissions' peaks but near-zero fluctuations for most of the year. These peak events resulted in higher average CH_4 and N_2O emissions during the wetter period of the year. On the other hand, stem CO_2 fluxes showed a seasonal trend coinciding with tree growth phenology, with higher average stem fluxes during the drier period. We concluded that hydrological changes played a greater role in stem CH_4 and N_2O dynamics, whereas CO_2 fluxes were primarily driven by temperature changes. Furthermore, stem CH_4 dynamics were significantly affected by the seasonal changes between wetter and drier periods, while N_2O was more influenced by short-term changes in SWC and WTD, such as freeze-thaw events in the spring. Our results demonstrated that there can be significant differences in the contributions of stem fluxes to total stem and soil fluxes between wetter and drier periods of the year. We showed that CH_4 emitted from tree stems during the wetter period can offset nearly half of the soil sink capacity. Therefore, if only soil fluxes are accounted for in regional budgets, the net CH_4 sink can be overestimated. Furthermore, the significance of stem CH_4 emissions during the wet period is of particular importance considering the potential increase in hydrologic extremes related to climate change. We showed for the first time the relationship between tree stem CH_4, N_2O and CO_2 fluxes and sap flow in a peatland forest. These relationships, as well as correlations with other environmental parameters and the vertical stem flux trend, enabled the determination of the potential sources of stem fluxes. The net CH_4 flux was likely an aggregate of soil-derived and stem-produced CH_4. A dominating soil source was more evident for stem N_2O fluxes. Root respiration may have dominated over stem respiration in higher parts of the stem to determine the net stem CO_2 flux. More high-frequency and longer-term measurements are needed to quantify stem and soil GHG fluxes more accurately in different ecosystems and estimate the total contribution of stem fluxes in annual forest GHG budgets.

CRediT authorship contribution statement

Reti Ranniku: Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation. **Ülo Mander:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Conceptualization. **Jordi Escuer-Gatius:** Writing – review & editing, Visualization, Formal analysis. **Thomas Schindler:** Writing – review & editing, Methodology, Investigation. **Priit Kupper:** Writing – review & editing, Methodology, Investigation. **Arne Sellin:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Kaido Soosaar:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.172452.

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