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Long-term dynamics of soil, tree stem and ecosystem methane fluxes in a riparian forest

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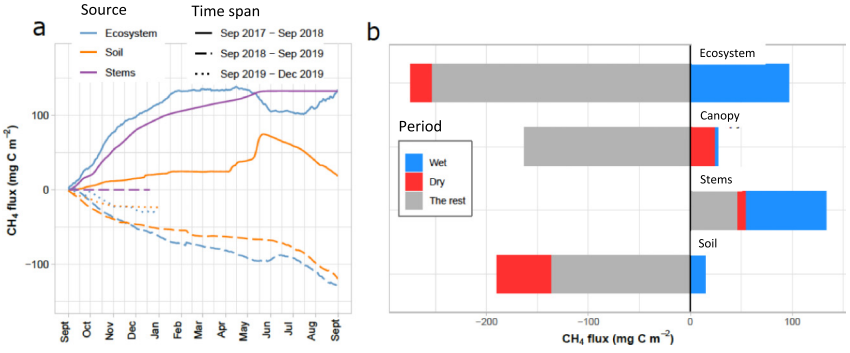
HIGHLIGHTS

- Significant difference in CH_4 fluxes between the wet and dry periods
- Wet period: 83% of ecosystem CH_4 emission moves through the tree stems
- Dry period: CH_4 consumed in the soil and emitted from the canopy
- Strong positive correlation of soil and stem CH_4 fluxes with soil water content
- In a long term, riparian alder forests constitute a minor CH_4 sink

GRAPHICAL ABSTRACT

During the 2.5 –yr study the forest was a CH4 sink. However, in the wet period (Sep-Dec 2017) 83% of CH_4 was emitted from the tree stems whereas in the dry period CH_4 was consumed in the soil and stem emission was very low.



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ABSTRACT

The carbon (C) budgets of riparian forests are sensitive to climatic variability. Therefore, riparian forests are hot spots of C cycling in landscapes. Only a limited number of studies on continuous measurements of methane (CH_4) fluxes from riparian forests is available. Here, we report continuous high-frequency soil and ecosystem (eddy-covariance; EC) measurements of CH_4 fluxes with a quantum cascade laser absorption spectrometer for a 2.5-year period and measurements of CH_4 fluxes from tree stems using manual chambers for a 1.5 year period from a temperate riparian *Alnus incana* forest.

The results demonstrate that the riparian forest is a minor net annual sink of CH_4 consuming 0.24 kg CH_4-C ha^{-1} y^{-1}. Soil water content is the most important determinant of soil, stem, and EC fluxes, followed by soil temperature. There were significant differences in CH_4 fluxes between the wet and dry periods. During the wet period, 83% of CH_4 was emitted from the tree stems while the ecosystem-level emission was equal to the sum of soil and stem emissions. During the dry period, CH_4 was substantially consumed in the soil whereas stem emissions were very

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spectrometer
Soil fluxes
Soil water content
Stem fluxes

low. A significant difference between the EC fluxes and the sum of soil and stem fluxes during the dry period is most likely caused by emission from the canopy whereas at the ecosystem level the forest was a clear CH_4 sink. Our results together with past measurements of CH_4 fluxes in other riparian forests suggest that temperate riparian forests can be long-term CH_4 sinks.

1. Introduction

Methane (CH_4) is a greenhouse gas (GHG) with a global warming potential 28 to 45 times that of carbon dioxide (CO_2) (IPCC, 2014; Neubauer and Megonigal, 2015). Atmospheric CH_4 is responsible for approximately 20% of global warming since the preindustrial era (Kirschke et al., 2013). In ecosystems, CH_4 is primarily produced in anaerobic environments by methanogens and oxidised to CO_2 in aerobic environments by methanotrophs (Megonigal et al., 2004).

Forests are the most important ecosystems in the global terrestrial carbon cycle, maintaining 86% of the standing plant carbon (C) pool and 73% of the soil C pool (Pan et al., 2011). Upland forest soils are dominant terrestrial components in the global CH_4 budget as a sink of atmospheric CH_4 (Dutaur and Verchot, 2007; Dlugokencky et al., 2011; Saunois et al., 2020). Of the total CH_4 consumed in soils at the global scale, 60% corresponds to forest ecosystems with the yearly uptake estimated at 9.16 Tg CH_4 y^{-1} (Dutaur and Verchot, 2007; Yu et al., 2017). However, because of the joint effects of climate change and land-use changes, a decline in soil CH_4 uptake has been identified in forests across the globe (Ni and Groffman, 2018; Han and Zhu, 2020). On the other hand, wetland forest soils are significant CH_4 sources (Salm et al., 2012; Turetsky et al., 2014; Covey and Megonigal, 2019). Drainage can turn wetland forest soils from sources to sinks (Minkkinen et al., 2007; Ojanen et al., 2010; Abdalla et al., 2016; Viru et al., 2020; Carter et al., 2012; Tan et al., 2020), although this is not always the case (Petrescu et al., 2015). Large emissions have been measured from the soils of tropical wetland forests (Sakabe et al., 2018; Wong et al., 2018; Dalmagro et al., 2019; Griffis et al., 2020; Liu et al., 2020).

Forest CH_4 fluxes are the net balance of production, oxidation and transport of CH_4 through the ecosystem (Saunois et al., 2016; Covey and Megonigal, 2019; Flanagan et al., 2020). Methane may be produced in anaerobic soil layers and transported by trees to the atmosphere by several mechanisms including diffusion (Pangala et al., 2014; Megonigal et al., 2019), pressurized ventilation (Große and Schröder, 1984; Schröder, 1989), and mass flow as a solute in the transpiration stream to the atmosphere (Covey and Megonigal, 2019). These transport mechanisms create a bypass for CH_4 avoiding its oxidation that may occur in upper layer of soils during diffusion of methane through the soil columns (Maier et al., 2018). In addition to plants acting as conduits for methane produced in soil substrates, methane can be directly produced in situ in some tree stems (Zeikus and Ward, 1974; Barba et al., 2019; Yip et al., 2019; Barba et al., 2021). Emission of methane from living tree stems in upland forests can be of the same magnitude as the methane sink in soils for brief periods of time (Pitz and Megonigal, 2017) or an annual basis (Wang et al., 2017), offsetting a portion of the soil CH_4 sink capacity of these ecosystems (Rice et al., 2010; Covey et al., 2012). Yet, CH_4 consumption by soils is the only process that has been regularly included in methane budgets for upland forest ecosystems (Saunois et al., 2016; Warner et al., 2017; Covey and Megonigal, 2019). Accounting for tree emissions can dramatically increase estimates of the amount of CH_4 emitted by forested wetlands (Pangala et al., 2013, 2015; Liu et al., 2020).

Numerous studies have considered methane fluxes from soils and tree stems in upland forests (Pitz and Megonigal, 2017; Warner et al., 2017; Barba et al., 2018; Maier et al., 2018; Covey and Megonigal, 2019; Machacova et al., 2021), and wetland and floodplain forests (Gauci et al., 2010; Pangala et al., 2013, 2015, 2017; Terazawa et al., 2015; Moldaschl et al., 2021), whereas a limited number of investigations have focused on riparian forests (Flanagan et al., 2020; Schindler et al., 2020). Riparian forests provide important ecosystem services (Riis et al., 2020) such a provisioning of water quality (Sweeney et al., 2004; Mander et al., 2017), and GHG regulation (Flanagan et al., 2020; Schindler et al., 2020). Grey alder (*Alnus incana* (L.) Moench.) forests are widely distributed in Europe and North America (Caudullo et al., 2017), often dominating riparian zones (Clerici et al., 2013). In Europe the area covered by *Alnus incana* subsp. *incana* forests reaches 15,000 km^2 (Caudullo et al., 2017). This is one reason why several tree-stem scale CH_4 studies have focused on *Alnus* species (Gauci et al., 2010; Machacova et al., 2013; Pangala et al., 2014; Schindler et al., 2020; Köhn et al., 2021).

Most studies of CH_4 emission and consumption by trees have focused on the main tree stem, however some studies report emission from shoots and leaves (Machacova et al., 2016). Ecosystem-level studies using the eddy covariance (EC) technique suggest that tree canopies contribute to the ecosystem CH_4 budget (do Carmo et al., 2006). Eddy covariance measurements of CH_4 fluxes have been conducted in boreal forests (Iwata et al., 2015; Nakai et al., 2020), temperate forests (Wang et al., 2013; Hommeltenberg et al., 2014; Shoemaker et al., 2014; Flanagan et al., 2020), and tropical/sub-tropical forests (do Carmo et al., 2006; Dalmagro et al., 2019; Griffis et al., 2020; Liu et al., 2020). In addition, data are available from FLUXNET network sites in Finland, Switzerland, Russia and Indonesia. The temperate and boreal EC stations are present both in upland and wetland forests whereas the tropical EC stations are mostly located in wetland forests. However, most previous studies did not separate soil versus tree stem sources or sinks which is needed to understand and model CH_4 cycling processes in forests. Thus, there is a gap in the forest CH_4 literature between whole-ecosystem (EC) studies that do not partition fluxes between soils and tree surfaces, and bottom-up studies that measure tree stems but not canopies.

Scaling and modelling forest CH_4 dynamics requires an understanding of the key environmental drivers of variability. It is well established that soil moisture is a primary determinant of CH_4 fluxes in both forest soils (negative relationship) and wetland soils (positive relationship) (Del Grosso et al., 2000; Smith et al., 2000; Dutaur and Verchot, 2007; Jungkunst et al., 2008; Shoemaker et al., 2014; Sakabe et al., 2018). There is evidence that soil moisture has similar effects on CH_4 fluxes across tree stems (Pitz et al., 2018; Barba et al., 2019; Schindler et al., 2020) and at the ecosystem-level (Hommeltenberg et al., 2014; Iwata et al., 2015; Wong et al., 2018; Nakai et al., 2020). The effects of soil moisture interact with temperature, which generally increases CH_4 fluxes, to determine the spatial and temporal patterns of CH_4 fluxes from forest soils (Itoh et al., 2008; Courtois et al., 2018) and tree stems (Vargas and Barba, 2019; Covey and Megonigal, 2019),

This paper aimed to analyse long-term ecosystem exchange of CH_4, partition CH_4 exchanges between soils and tree stems, and relate CH_4 fluxes to key environmental factors in a representative temperate riparian grey alder forest. In particular, we sought to separate the contributions of tree stems and soil to overall ecosystem CH_4 fluxes. The second objective was to establish the factors responsible for temporal variations in CH_4 fluxes, in particular the impacts of

variation in soil-moisture and temperature. We tested the following hypotheses: (1) this riparian forest ecosystem is a net CH_4 sink, (2) ecosystem level (EC) CH_4 fluxes are equal to the sum of soil and stem fluxes, (3) soil moisture dynamics determine the long-term pattern of CH_4 fluxes, and (4) the tree stems are a bypass of soil CH_4 emissions i.e., we assume the stem emissions are positively correlated with soil emissions.

2. Material and methods

2.1. Study site description and location of eddy tower and soil chambers

The studied riparian forest is a 40-year *Filipendula* type grey alder (*A. incana* (L.) Moench) stand grown on former agricultural land (Fig. 1). It is situated in the Agali hamlet (58°17' N; 27°17' E) in eastern Estonia in the Lake Peipsi Lowland (Varep, 1964).

The area is characterised by flat relief with an average elevation of 32 m a.s.l., formed in the bottom of former periglacial lake systems. It is slightly inclined (1% slope) towards a tributary of the Kalli River. The soil is Gleyic Luvisol. The thickness of the humus layer was 15–20 cm. The content of total carbon (TC), total nitrogen (TN), Ca and Mg per dry matter in 10 cm topsoil was 2.42, 2.89, 1487 and 283 mg kg^{-1}, respectively. This translated to a TC and TN contents of 3.8% and 0.33%, respectively. The abundance of these elements decreased precipitously below 20 cm dropping by 2–8 times in concentration (Supplementary Table 1).

The average annual precipitation of the region during the last 30 years is 650 mm (Kupper et al., 2011). Average annual air temperature is 5.8 °C whereas in July and January the mean air temperatures are 17.0 °C and − 6.7 °C, respectively. The duration of the growing season is typically 175–180 days from mid-April to October (Kupper et al., 2011).

The mean height of the forest stand is 17.5 m, the mean stem diameter at breast height is 15.6 cm and the growing stock is 245 m^3 ha^{-1} (based on Uri et al. (2014) and Becker et al. (2015)). In the forest floor, the following herbs dominate: *Filipendula ulmaria* (L.) Maxim., *Aegopodium podagraria* L., *Cirsium oleraceum* (L.) Scop., *Geum rivale* L., *Crepis paludosa* (L.) Moench,), shrubs (*Rubus idaeus* L., *Frangula alnus* L., *Daphne mezereum* L.) and young trees (*A. incana*, *Prunus padus* L.) dominate. In the moss-layer *Climacium dendroides* (Hedw.) F. Weber & D. Mohr, *Plagiomnium* spp. and *Rhytidiadelphus triquetrus* (Hedw.) Warnst. are common.

2.2. Soil flux measurements

Soil fluxes were measured using 12 automatic dynamic chambers located close to each studied tree and installed in June 2017. The chambers were made from polymethyl methacrylate (Plexiglas) covered with non-transparent plastic film. Each soil chamber (volume of 0.032 m^3) covered a 0.16 m^2 soil surface. To avoid stratification of gas inside the chamber, air with a constant flow rate of 1.8 L min^{-1} was circulated within a closed loop between the chamber and gas analyser unit during the measurements by a diaphragm pump. The air sample was taken from the top of the chamber headspace. For the measurements, each soil chamber was closed automatically for 9 min. Flushing time of the whole system with ambient air between measurement periods was 1 min. Thus, there were approximately 12 measurements per chamber per day. A Picarro G2508 (Picarro Inc., Santa Clara, CA, USA) gas analyser using cavity ring-down spectroscopy (CRDS) technology was used to monitor CH_4 gas concentrations at a frequency of approximately 1.17 Hz. The chambers were connected to the gas analyser using a multiplexer.

The whole 9 min period of chamber closure consisted of an initial 2 min period for stabilization of the trend. Thus, only 5 min of the linear trend of CH_4 concentration change was used for soil flux calculations. After the quality check we were able to use 105,500 (98% of total possible) of the soil CH_4 fluxes collected during the whole study period. Although plants were inside the chambers, we prefer to use the term "soil fluxes" instead of "floor fluxes".

2.3. Stem flux measurements

The tree stem fluxes were measured manually with a frequency of once per week from September 2017 until December 2018. Twelve representative mature grey alder trees were selected for stem flux measurements and equipped with static closed tree stem chamber systems for stem flux measurements (Machacova et al., 2017). The tree chambers were installed in June 2017 on tree stems at approximately 10, 80 and 170 cm above the ground. The rectangular shaped stem chambers were made of transparent plastic containers, including removable airtight lids (Lock & Lock Co Ltd., Seoul, Republic of Korea). For chamber preparation see Machacova et al. (2017) and Schindler et al. (2020). Two chambers per each measurement height on tree stem were set randomly across 180° and interconnected with tubes into one system (total volume of 0.00119 m^3) covering 0.0108 m^2 of

Fig. 1. Location and research set-up of the riparian grey alder forest in Agali, Estonia. Automated soil chambers, eddy tower and its footprint area are shown. Illustrations on the instrumental setup are presented in Supplementary Fig. 1.

stem surface. A pump (model 1410VD, 12 V; Thomas GmbH, Fürstenfeldbruck, Germany) was used to homogenize the gas concentration in paired chambers prior to sampling. Chamber systems remained open between each sampling campaign. During 60 measurement campaigns, four gas samples (each 25 mL) were collected from each chamber system via a septum at 60 min intervals in a sequence of 0/60/120/180 min and stored in pre-evacuated (0.3 bar) 12 mL gas-tight vials coated with pierceable chlorobutyl septum (LabCo International, Ceregidion, UK). In 16 campaigns both daytime (between 12:00 and 16:00) and nighttime (00:00–04:00) samples were taken. The gas samples were analysed in the laboratory at University of Tartu within a week using a gas chromatograph (GC-2014; Shimadzu, Kyoto, Japan) equipped with a flame ionization detector for CH_4. The gas samples were injected automatically using Loftfield autosampler (Loftfield Analytics, Göttingen, Germany). For gas-chromatographical settings see Soosaar et al. (2011).

2.4. Soil and stem flux calculations

Changes in CH_4 concentration in the chamber headspace over time were used to quantify the stem and soil fluxes as quantified by the linear approach of Livingston and Hutchinson (2015). A data quality control for the stem flux values was applied based on R^2 values of linear fit for CO_2 measurements. When R^2 of CO_2 efflux was >0.9, the CH_4 fluxes were used regardless of their R^2 values.

To compare the contribution of the soil and stems, the stem fluxes were upscaled to m^2 of ground area based on average stem diameter, tree height, stem surface area, tree density, and stand basal area. A cylindric shape of tree stem was assumed. To estimate average stem emissions per tree, non-linear regression curves were fit between stem emissions and height for each measurement campaign as previously done by Schindler et al. (2020).

2.5. Eddy covariance instrumentation

The eddy-covariance system was installed on a 21 m high scaffolding tower. A fast 3-D sonic anemometer Gill HS-50 (Gill Instruments Ltd., Lymington, Hampshire, UK) was used to obtain three wind components. Air was sampled with the 30 m Teflon inlet tube and analysed by a quantum cascade laser absorption spectrometer (QCLAS) (Aerodyne Research Inc., Billerica, MA, USA) for CH_4 concentrations. The QCLAS was installed in a heated and ventilated cottage near the tower base. A high-capacity free scroll vacuum pump (Agilent, Santa Clara, CA, USA) guaranteed air flow rate of 15 L min^{-1} between the tower and QCLAS gas analyser during the measurements. Air was filtered for dust and condensed water. All measurements were done at 10 Hz and the QCLAS reported concentrations per dry air (mixing ratios).

2.6. Eddy-covariance flux calculation and data quality control

The fluxes of CH_4 were calculated using the EddyPro software (v.6.0–7.0, Li-Cor) as a covariance of the gas mixing ratio with the vertical wind component over 30-min periods. De-spiking of the raw data was performed following Mauder et al. (2013). Anemometer tilt was corrected with the double axis rotation. Linear detrending was chosen over block averaging to minimize the influence of a possible fluctuations of a gas analyser. Time lags were detected using covariance maximisation in each time window (5 ± 2 s was chosen based on the tube length and flow rate). The water vapor correction was performed by the Aerodyne TDLWintel software, which reported mixing ratios. Both low and high frequency spectral corrections were applied using fully analytic corrections (Moncrieff et al., 1997, 2004).

Calculated fluxes were filtered out in case they were coming from the half-hour averaging periods with at least one of the following criteria: more than 1000 spikes, half-hourly averaged mixing ratio out of range (1.8–2.5 ppm), quality control (QC) flags higher than 7 (Foken et al., 2004).

Footprint area was estimated using Kljun et al. (2015) implemented in TOVI software (Li-Cor Inc.). Footprint allocation tool was implemented to flag the non-forested areas within the 90% cumulative footprint and fluxes appointed to these areas were removed from the further analysis.

Storage fluxes were estimated using point concentration measurements from the eddy system, assuming the uniform change within the air column under the tower during every 30 min period (calculated in EddyPro software). In the absence of a better estimate or profile measurements, these estimates were used to correct for storage change. Friction velocity threshold of 0.29 ms^{-1} was applied to eliminate low air mixing periods from the analysis (Papale et al., 2006). Total flux values that were higher than eight times the standard deviation were additionally filtered out (following Wang et al. (2013)). Overall, the quality control procedures resulted in 61% data coverage.

To obtain the continuous time-series and to enable the comparison to chamber estimates over hourly time scales, gap-filling of CH_4 fluxes was performed using marginal distribution sampling method implemented in ReddyProcWeb online tool (https://www.bgc-jena.mpg.de/bgi/index.php/Services/REddyProcWeb) (described in detail in Wutzler et al. (2018).

MATLAB (ver. 2018a-b, Mathworks Inc., Natick, MA, USA) was used for all the eddy fluxes data analysis.

2.7. Ancillary measurements

Air temperature and relative humidity were measured within the canopy at 10 m height using the HC2A-S3 – Standard Meteo Probe / RS24T (Rotronic AG, Bassersdorf, Switzerland) and Campbell CR100 data logger (Campbell Scientific Inc., Logan, UT, USA).

Soil temperature (Campbell Scientific Inc.) and soil water content (SWC) sensors (ML3 ThetaProbe, Delta-T Devices, Burwell, Cambridge, UK) were installed at 0–10 cm soil depth close to the studied trees. Near-ground air temperature sensors were installed directly on the ground. During six campaigns from August to November 2017 composite topsoil samples were taken with a soil corer from a depth of 0–10 cm for physical and chemical analysis using standard method (APHA-AWWA-WEF, 2005). In the groundwater of piezometers installed close to each analysed tree, dissolved O_2 concentration was measured using a handheld YSI Professional Plus Multiparameter Water Quality Instrument with a Quatro field cable (YSI Incorporated, Yellow Springs, OH, USA).

2.8. Analysis of eddy covariance CH_4 data from global network

Worldwide, the network of research stations measuring CH_4 fluxes from ecosystems using the EC method is rapidly increasing. Most of the sites are included in FLUXNET, AMERIFLUX, ICOS and other regional networks (Knox et al., 2019). According to this source about 200 stations were listed where the EC method for CH_4 flux can be potentially used. We found 9 FLUXNET stations in forests from where the CH_4 flux data are available. Together with published papers, 21 data sources were available for the comparison with our results (Supplementary Table 2).

2.9. Data analysis

R version 4.0.2 was used to examine, analyse and visualise the data. The significance level considered for all the tests was 0.05. The “akima” package version 0.6–2.1 was used to create interpolated contour plots representing a three-dimensional surface (Akima et al., 2016) by plotting soil temperature and SWC against soil CH_4 emissions as the independent variable. Linear regression models were fitted for soil temperature, SWC and soil CH_4 flux in Fig. 6. For Figs. 7, 9 and

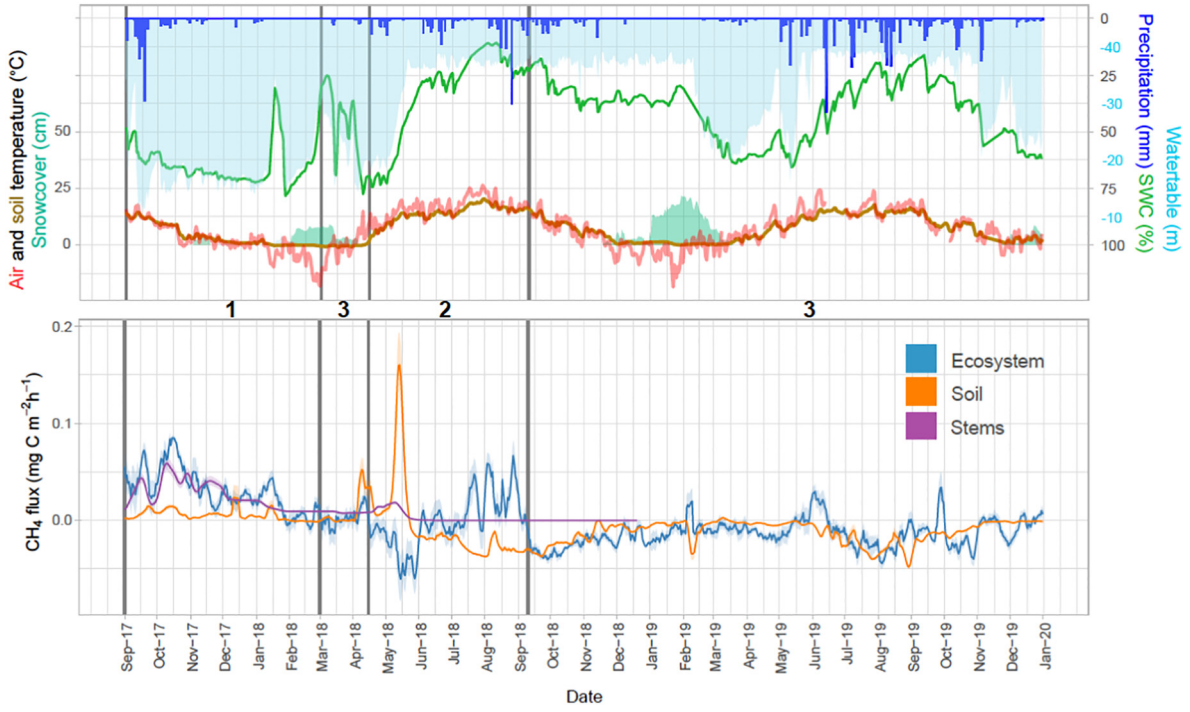

Fig. 2. Dynamics of environmental characteristics (above) and CH_4 fluxes at the soil (n = 105,000), stem (n = 2145) and ecosystem level (EC; below; n of gap-filled 1.5-h averaged values = 43,680) in the Agali grey alder forest during the Sept. 2017 – Dec. 2019 study period. Lines of CH_4 fluxes denote 5-day median values, the shaded area shows 25th and 75th percentiles. Periods of interest (borders marked with vertical lines): 1 - wet (2017-09-01 … 2018-02-28), 2 - dry (2018-04-15… 2018-09-10), and 3 – the rest (2018-03-01…2018-04-14 and 2018-09-11…2019-12-31).

supplementary Fig. 4, a workflow for the nonlinear regression analysis was used (Archontoulis and Miguez, 2015) and regression models were fitted in R using functions nls or loess.

Based on high fluxes of CH_4 (both emission and consumption), and dynamics of SWC and near-ground air temperature, we identified three periods of interest (see numbers in Fig. 2): 1 - wet (2017-09-01 … 2018-02-28), 2 - dry (2018-04-15… 2018-09-10), and 3 – the rest of the study (2018-03-01…2018-04-14 and 2018-09-11…2019-12-31).

3. Results

3.1. General proportion of fluxes and CH_4 budget

CH_4 fluxes varied remarkably during the study (Fig. 2), displaying patterns that we divided into two periods of interest: wet and dry (Fig. 2). Average CH_4 fluxes from the soil varied from −68 to 210 μg CH_4-C m^{-2} h^{-1} and from tree stems −1.6 to 60 μg CH_4-C m^{-2} h^{-1} (units for both soil and stem are per ground area), being the highest during the wet period and the onset of dry period whereas the dry period was characterised with low CH_4 fluxes from both soil and stems (Fig. 2).

During the wet period, average ± standard error (SE) CH_4 stem fluxes (224.4 ± 6.3 mg CH_4-C m^{-2} yr^{-1}) contributed 83% of CH_4 measured above the canopy by EC technique (Table 1; Fig. 2), and ecosystem-level emissions were nearly equal to the sum of soil and stem emissions (Table 1). Consequently, during the whole year from September 2017 to September 2018, the cumulative stem CH_4 flux was following the ecosystem-level measured cumulative flux curve, exceeding the soil flux negative value at the end of the period (Fig. 3a). In the dry period, average soil CH_4 flux was negative, however in the beginning of the period both soil and stems emitted CH_4 quite remarkably (up to 30 and 40 μg CH_4-C m^{-2} h^{-1} on 5-days average, respectively; Fig. 3a, Supplementary Fig. 2). However, throughout the rest of dry period the soil CH_4 flux was negative and the stem emission close to zero (Fig. 2). A significant difference between the EC fluxes and the sum of soil and stem fluxes during the dry period was most likely caused by the emission from the canopy (Fig. 3b).

The EC measurements showed the forest was a slight annual sink of CH_4 across the whole study period (−53.6 ± 3.4 mg CH_4-C m^{-2} y^{-1}; Table 1).

Comparison of different years of the study demonstrates significance differences (Supplementary Table 3; Fig. 2): wet period with high soil and stem CH_4 fluxes at the end of 2017, significant drought period with fluctuating soil and ecosystem level fluxes CH_4 fluxes in 2018, and the rest of the study with relatively low soil and EC fluxes in 2019.

The main environmental factor determining CH_4 fluxes from all compartments was the soil water content which showed a strong positive correlation between the soil, tree stem and ecosystem-level fluxes; the Spearman's ρ correlations were 0.82, 0.75, and 0.33, respectively (Fig. 4). Soil temperature was the second most important environmental factor determining methane fluxes: Spearman's ρ values for soil and tree stem fluxes were − 0.57 and − 0.48, respectively.

Table 1
Average ± SE fluxes of CH_4 (mg CH_4-C m^{-2} yr^{-1}) from all sources during the periods of interest and the whole study. See breakdown of periods in Fig. 2.

Source	Wet period (1)	Dry period (2)	Rest of the study (3)	Whole study
Soil	48.0 ± 4.6	−77.2 ± 17.4	−82.2 ± 2.6	−53.6 ± 3.4
Stems	224.4 ± 6.3	20.8 ± 1.7	29.6 ± 1.6	101.6 ± 2.8[a]
Ecosystem (EC)	270.1 ± 14.8	4.0 ± 2.6	−108.6 ± 6.6	−24.0 ± 6.7

[a] Measured for the period of 487 days (from 2017 to 09-01 to 2018-12-31).

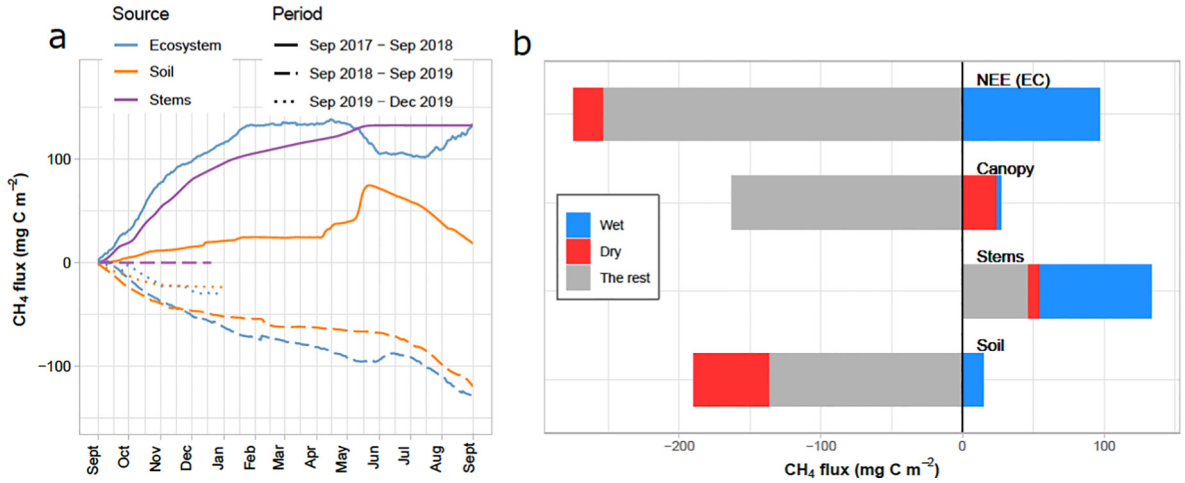

Fig. 3. Cumulative CH_4 fluxes from the soil, stems and ecosystem (eddy covariance above the canopies). (a) Fluxes during two full years (Sept. 2017 –Sept. 2019) and one half-year (Sept. – Dec. 2019). Notice that the stem fluxes have been measured from Sept. 2017 to Dec. 2018 only. (b) The proportion of different CH_4 sources and sinks in the wet and dry period and over the whole study. Canopy flux was calculated as a difference between the eddy covariance (EC) fluxes, and the sum of soil and stem fluxes. NEE – net ecosystem exchange.

Throughout the whole study, tree stem CH_4 flux showed a significant positive Spearman's ρ correlation with ecosystem-level fluxes (Fig. 4), whereas during the wet period the correlation was stronger (Figs. 3a and 4). There was no significant correlation between the ecosystem-level fluxes and either air or soil temperature. Likewise, precipitation did not correlate with any of the CH_4 flux categories analysed. There was a strong positive Spearman's ρ correlation between the air and soil temperatures as expected but also a negative correlation between the soil temperature and soil water content ($\rho = -0.56$; Fig. 4). At low but significant Spearman's ρ correlation values ($\rho < 0.5$) we were cautious interpreting these results.

3.2. Soil fluxes

CH_4 fluxes varied from −61 to 210 μg CH_4-C m^{-2} h^{-1}. The heatmap in Supplementary Fig. 2 presents spatial and temporal variation of these values, showing that across the whole study period, no remarkable differences between the values measured in individual chambers were observed. However, chambers 2, 7, and 9 located in lower positions (10–15 cm from the average soil surface) showed somewhat higher values. Throughout the whole study soils were net consumers of methane (Fig. 5) with an average flux of −14.3 ± 0.6 μg CH_4-C m^{-2} h^{-1} (Table 1). The temporal pattern of soil CH_4 fluxes showed seasonal variation, being remarkably higher during the wet period from September 2017 to February 2018 (average flux about 45 μg CH_4-C m^{-2} h^{-1}) as well as in winter 2018/2019 and late autumn 2019 (Fig. 5). The highest average flux values (60 μg CH_4-C m^{-2} h^{-1}) were observed in a few days in the beginning of dry period in May 2018 (Fig. 2). During the wet period, a majority (>90%) of individual chambers showed daily average flux >0 mg CH_4-C m^{-2} h^{-1} (Supplementary Fig. 2). The autumn (September–October) soil CH_4 fluxes were significantly higher in 2017 than those in following autumns (Fig. 5). This was caused by higher SWC in autumn 2017 (Fig. 2).

In most months during the whole study, differences between the daytime and nighttime CH_4 soil fluxes were not significant. At the beginning of the dry period (April–May 2018), somewhat higher fluxes in daytime were measured but these differences were not significant either (Supplementary Fig. 3).

The soil CH_4 flux was primarily determined by the soil water content and soil temperature (Fig. 6). Most emissions occurred under relatively high SWC (0.6–0.75 m^3 m^{-3}) whereas higher peaks were measured below 14 °C and SWC range 0.4–0.6 m^3 m^{-3}, and in freezing-thawing conditions (−1 to 1.5 °C at SWC range 0.35–0.75 m^3 m^{-3}; Fig. 6a). However, the monthly average values from the freeze-thaw period in February 2019 did not show any remarkable increase in soil CH_4 fluxes (Figs. 2; 5; Supplementary Fig. 2).

The linear regression model of soil temperature and CH_4 fluxes showed a significant negative relationship ($R^2 = 0.12$, $p < 0.001$) although the above-mentioned peaks at lower (−1 to 1.5 °C) and higher (13-14 °C) temperature values were noticeable (Fig. 6b). According to the linear regression model of SWC and CH_4 fluxes, this relationship was positive ($R^2 = 0.33$, $p < 0.001$). Here, remarkably higher values of CH_4 flux were measured at the SWC range 0.4–0.6 m^3 m^{-3} (Fig. 6c). A non-linear curve with an optimal SWC range was obtained by a generalised additive model linking daily CH_4 fluxes from soil with SWC ($R^2 = 0.29$, $p < 0.001$; Supplementary Fig. 4).

3.3. Stem fluxes

CH_4 stem fluxes were the highest during the wet period and the onset of dry period (April 2018) reaching 60 μg CH_4-C m^{-2} h^{-1} (calculated per m^2 of forest ground). CH_4 consumption by the stems was negligible. Median values of stem fluxes from the lowest parts of tree stems (10 cm from ground) were remarkably higher than those from the 80 and 170 cm (7.8, 3.0 and 1.0 μg CH_4-C m^{-2} h^{-1}, respectively).

For all the stem height sections we found a negative correlation between the dissolved oxygen concentration in groundwater and the CH_4 stem flux.

No significant differences between the daytime and nighttime CH_4 fluxes from tree stems were found ($p > 0.05$).

A significant positive correlation (Spearman's $\rho = 0.74$) was found between the soil and tree stem methane fluxes (Fig. 4).

3.4. Ecosystem fluxes (eddy covariance)

The average ecosystem-level CH_4 flux from the grey alder forest for the whole study was −0.07 mg CH_4-C m^{-2} d^{-1} whereas weekly average CH_4 fluxes varied between −2.4 and 3.1 mg CH_4-C m^{-2} d^{-1}; Fig. 8). In wet period and following spring in 2018 the forest varied from a weak sink of CH_4 to a source, with weekly averages of −0.05 to 3.1 mg CH_4-C m^{-2} d^{-1}. During the dry period largest fluctuations in CH4 fluxes were observed, from consumption (down to −2.3 mg CH_4-C m^{-2} d^{-1}) in the beginning of the period to high emission (up to 1.0–1.2 mg CH_4-C m^{-2} d^{-1}) at the second part of the period (Figs. 2 and 8). The latter has been considered as the heatwave (see Krasnova et al., 2022) lasting from July until mid-September 2018 and causing a

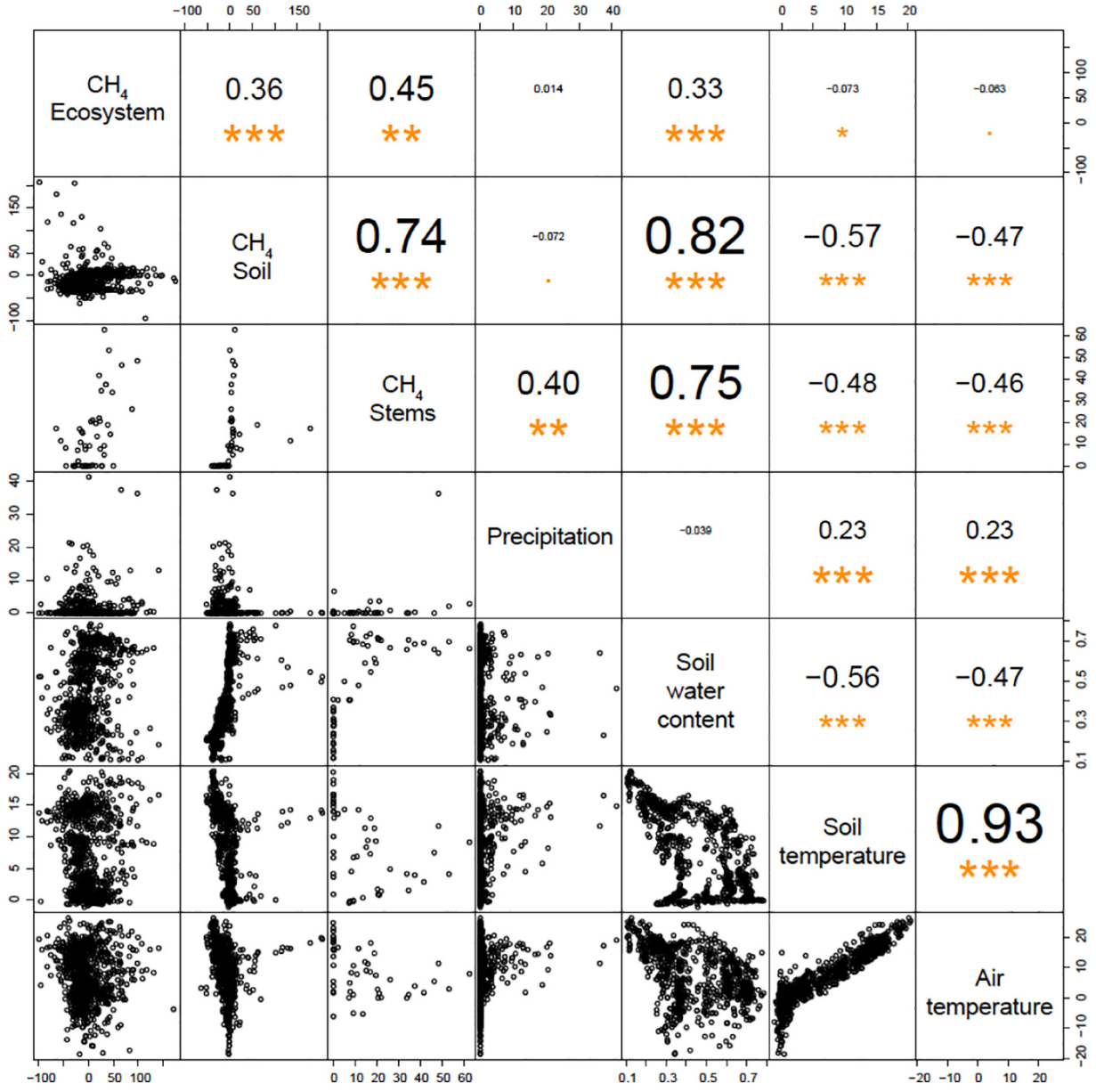

Fig. 4. Correlogram of Spearman's rank correlation coefficients (ρ) between the soil, stem, and ecosystem (EC) CH_4 fluxes and key environmental factors. p values: * - <0.05, ** – <0.01, *** – <0.001, *** – <0.0001. Units for parameters: CH_4 flux – μg C m^{-2} h^{-1}, precipitation – mm d^{-1}, soil water content – m^3 m^{-3}; soil and air temperature - ºC.

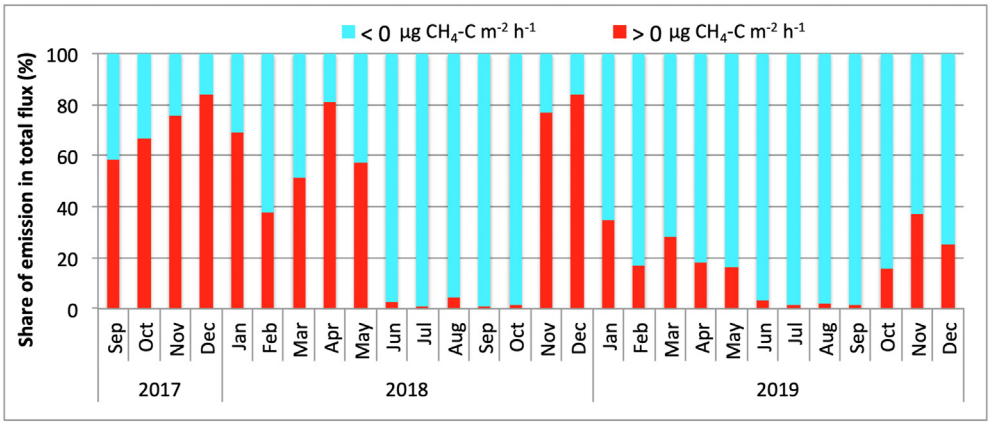

Fig. 5. Temporal pattern of soil CH_4 fluxes. A value of "0" separates consumption ("-" values) from emission ("+" values). Maximum possible number of measurements per month after quality check was between 228 and 372.

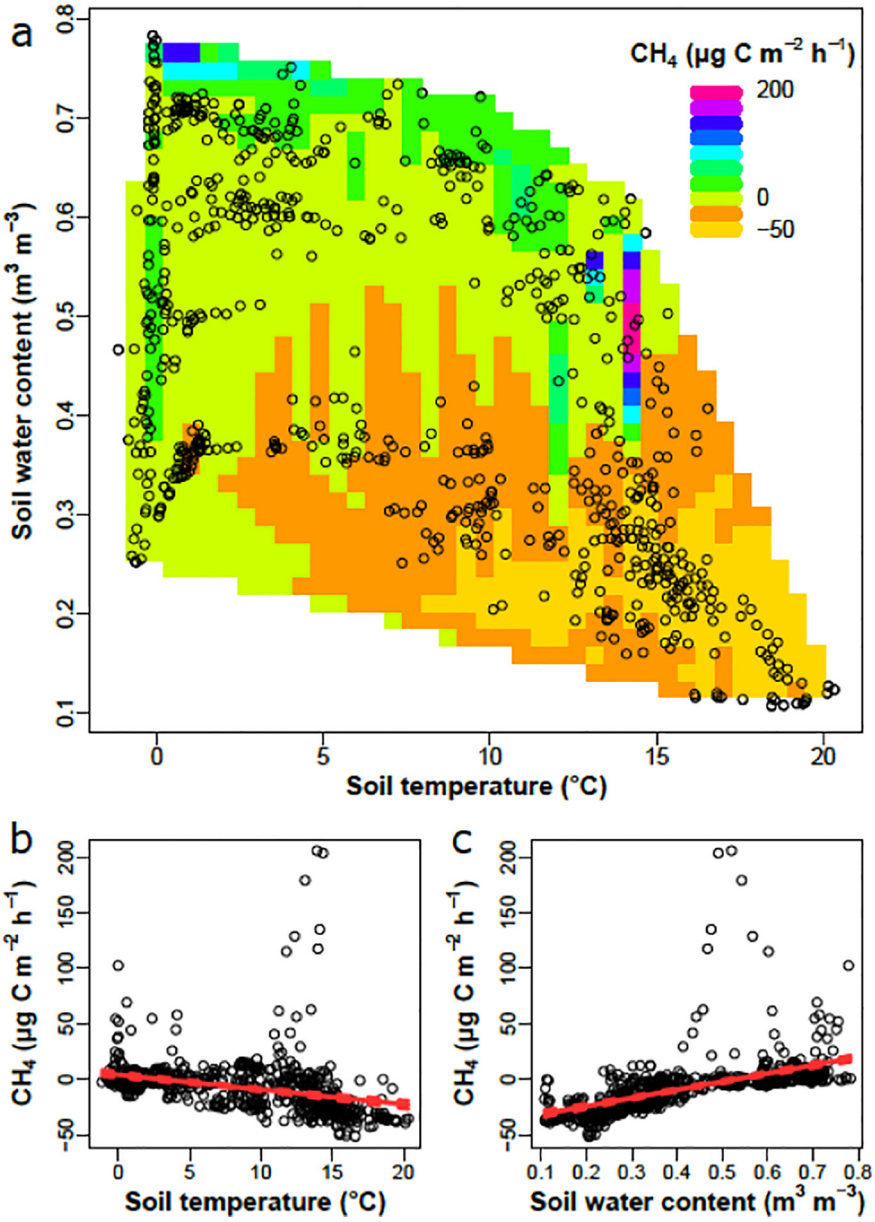

Fig. 6. Relationships between soil temperature, soil water content (SWC) and soil CH_4 flux over the whole study period. (a) Contour plot showing relationships between soil temperature, SWC and CH_4 fluxes ($n = 755$). Using linear fitted regression, the variability of the CH_4 fluxes ($R^2 = 0.33$, n = 755) were determined mainly by soil moisture ($p < 0.001$) and less by soil temperature ($p > 0.05$). (b) Regression curve of soil temperature vs CH_4 flux. Linear fitted regression of soil temperature (ST) and CH_4 flux ($R^2 = 0.12$, p < 0.001, $n = 756$). $CH_4 = 4.11 + (-1.33) \times ST$. (c) Regression curve of SWC vs CH_4 fluxes. Linear fitted regression of SWC and CH_4 flux ($R^2 = 0.33$, $p < 0.001$, $n = 757$). $CH_4 = -38.82 + 73.61 \times SWC$. The dashed red lines represent 95% confidence intervals for the regression line. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

remarkable consumption in soil but an unexpected short-lived emission from the whole ecosystem (Fig. 2). During the rest of the study period slight CH_4 consumption prevailed whereas in the freeze-thaw period in February 2019 slight increase in CH_4 emission was measured. Among the EC data about 25% were gap-filled (Fig. 8).

During the growing season (April–October) eddy covariance CH_4 fluxes showed a clear dependence on soil water content with the highest fluxes at a SWC value of 0.7 m^3 m^{-3} (Supplementary Fig. 5).

A literature analysis of eddy covariance CH_4 measurements across forest ecosystems in different climate conditions showed that in regions with average annual air temperature < 10 °C (non-tropical areas mainly) the temperature dependence of CH_4 fluxes is unclear (Supplementary Table 2). In tropical regions (>20 °C) a rapid increase in CH_4 emission with air temperature can be observed (Fig. 9).

4. Discussion

Due to the strong CH_4 oxidation capacity of soils, upland forests and some drained lowland forests are generally net CH_4 sinks (Dutaur and Verchot, 2007; Feng et al., 2020). This was also the case in our riparian forest, which was a minor net ecosystem-level sink of CH_4 (annual average − 0.24 kg CH_4-C ha^{-1} y^{-1}). Like our study, most of investigations highlighted soil water content as the leading determinant for all CH_4 fluxes from forest ecosystems (Covey and Megonigal, 2019; Feng et al., 2020). Riparian forests such as our study area are in the transitional zone between upland and wetland forests where environmental conditions typical for both forest types are combined (Flanagan et al., 2020). In our riparian forest soil CH_4 flux varied from net consumption to net emission (from −61 to 210 µg CH_4-C

m^{-2} h^{-1}; Table 1; Fig. 5; Supplementary Fig. 2) and followed the temporal dynamics of SWC (Figs. 2 & 5).

However, relatively recent findings on CH_4 exchange between the trees and the atmosphere demonstrate that CH_4 emission from tree stems and other biotic surfaces in forest ecosystems might decrease their sink strength, even becoming ecosystem-scale net CH_4 sources during certain periods (Pitz and Megonigal, 2017; Covey and Megonigal, 2019; Feng et al., 2020). In contrast to some investigations, which emphasize the CH_4 production directly within stems (Barba et al., 2019; Yip et al., 2019; Barba et al., 2021), our results show that methane has been formed within the soil and transported by trees to the atmosphere. This assumption is supported by the fact that the lowest parts of stems emit significantly more methane than the higher sections and CH_4 stem flux is negatively correlated with the dissolved oxygen concentration in groundwater (Fig. 7).

In our study the ecosystem was a net CH_4 source only during the wet conditions with high SWC and groundwater table when the stems emitted more than the soil, and the stem fluxes constituted 81% of the ecosystem-level fluxes (Figs. 2 and 3). For the entire 2.5-year study period ecosystem flux was still slightly negative indicating that this riparian alder forest was a net sink of CH_4. In a similar riparian ecosystem, a cottonwood forest in Alberta, Canada, the stem CH_4 emissions offset 86% of the soil uptake (Flanagan et al., 2020).

Shoemaker et al. (2014) demonstrates that due to the changes in late summer water balance, a temperate coniferous forest in Maine, USA changed from an annual CH_4 source to sink. These changes are typical for temperate forest ecosystems where weather conditions change seasonally (Dutaur and Verchot, 2007; Covey and Megonigal, 2019; Knox et al., 2019) and in the tropics at constantly high air and soil temperature where the seasonality occurs mostly on the basis of precipitation regime (Sakabe et al., 2018; Dalmagro et al., 2019; Griffis et al., 2020).

The temporal variations of CH_4 fluxes in forests can be characterised as short-term (diurnal), synoptic (depending on weather conditions), and seasonal (long-term) changes (Vargas and Barba, 2019). In our study, some diurnal pattern was observed only for ecosystem-level CH_4 fluxes and only during the wet period growing season (September 2017, May–July 2018, and May–September 2019) when the daytime EC fluxes exceeded the nighttime fluxes, whereas in the dormant season, the difference was not significant (Supplementary Fig. 6). Likewise, Dalmagro et al. (2019) found, that in a tropical forested wetland in Pantanal, Brazil during periods of higher water table depth (anaerobic soil), daytime fluxes were clearly higher than nighttime. In contrast, Sakabe et al. (2018) found significantly higher nighttime CH_4 from the EC measurements in a tropical peatland forest in Indonesia.

Regarding the soil and stem CH_4 fluxes, we could not find any clear diurnal pattern. In contrast some other studies have shown that daytime CH_4 fluxes from tree stems exceed the nighttime fluxes (Pangala et al., 2014; Megonigal et al., 2019).

There is evidence that cryptogamic cover (lichens, mosses, algae) on tree stems can emit methane (Lenhart et al., 2015). However, our initial comparison of stem chambers with cryptogams and those without could not find any remarkable differences in CH_4 flux. Nevertheless, the role of microorganisms on the bark and within the stems remains unclear and only a few recent studies shed light on it (Yip et al., 2019; Jeffrey et al., 2021; Putkinen et al., 2021).

Our study showed a clear dependence of CH_4 soil fluxes on soil water content,(Fig. 6). Methanogenesis in soil requires anaerobic conditions which are supported by high water table (Le Mer and Roger, 2001). Soil and air temperature also emerged as significant factors controlling methane fluxes (Figs. 6 and 9). However, the role of freezing-thawing effect on CH_4 soil fluxes was not obvious. We could see some increase in CH_4 fluxes at around-zero soil temperature in February 2019. It could be related to the impact of snowmelt water, which filled the soil pores and created short-term peaks in CH_4 fluxes, still being insignificant for the annual CH_4 budget of this forest (Fig. 6). Likewise, Pihlatie et al. (2010) did not find any freeze-thaw effect in CH_4 fluxes from a peatland forest soil. Under analogous conditions in drained peatland forests high N_2O but no CH_4 fluxes were measured (Viru et al., 2020). In February–March 2018, snow cover of 15–25 cm likely decreased the CH_4 soil flux (Fig. 2) as observed by Borken et al. (2006) observed a similar effect of snow cover on CH_4 fluxes.

We were able to demonstrate a clear effect of soil water content (SWC) on both CH_4 fluxes from the tree stem and ecosystem levels. We found a significant positive correlation (Spearman's $\rho = 0.74$) between the soil and tree stem CH_4 fluxes (Fig. 4). There was an optimal SWC range at 0.6–0.7 m^3 m^{-3} at which the CH_4 stem fluxes were the highest whereas the optimum for soil CH_4 fluxes occurs at a SWC range of 0.4–0.5 m^3 m^{-3} (Supplementary Fig. 4). This refers to a likely reciprocal alteration of the role of the soil and tree stems, which depends on the soil water conditions. It can be that the stem flux is more sensitive to SWC changes whereas soil emissions peak at a relatively high SWC values, especially during the rapid decrease of SWC during the onset of dry period in May 2018 (Fig. 2). Likewise, SWC range from 0.45 to 0.65 m^3 m^{-3} appears to be optimal for ecosystem-level CH_4 fluxes (Supplementary Fig. 5).

Soil temperature showed a negative Spearman's ρ correlation with both soil and stem CH_4 fluxes, most likely due to the negative correlation between the soil water content and temperature (Fig. 4).

Regarding the budget of CH_4 in riparian forests we were able to demonstrate the role of the canopy in situ. During the dry period the canopy is a net CH_4 source, emitted about 20% of the CH_4 from all sources during this time periods (Figs. 2 & 3b; without accounting for the gap-filled CH_4 fluxes; Fig. 8). The dry period coincided with a heat wave in June–July 2018 Krasnova et al., 2022 and potentially high fluxes of UV-B radiation (unpublished data from the nearby SMEAR Estonia station, see also Noe et al., 2015) that can be interpreted as evidence of the abiotic aerobic production of CH_4 from leaves (Keppler et al., 2006;

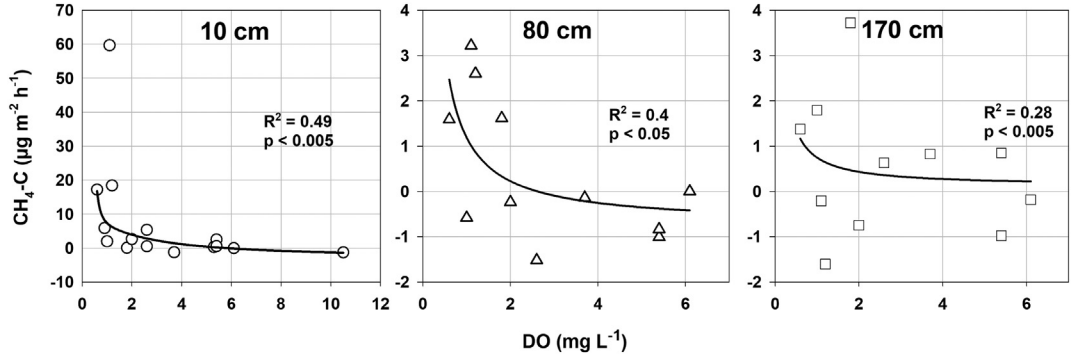

Fig. 7. Relationships between the groundwater dissolved oxygen (DO) concentration and stem CH_4 flux at the heights of 10 ($n = 15$), 80 ($n = 11$) and 170 cm (n = 11). The curves show non-linear regression line based on third order polynomial equations.

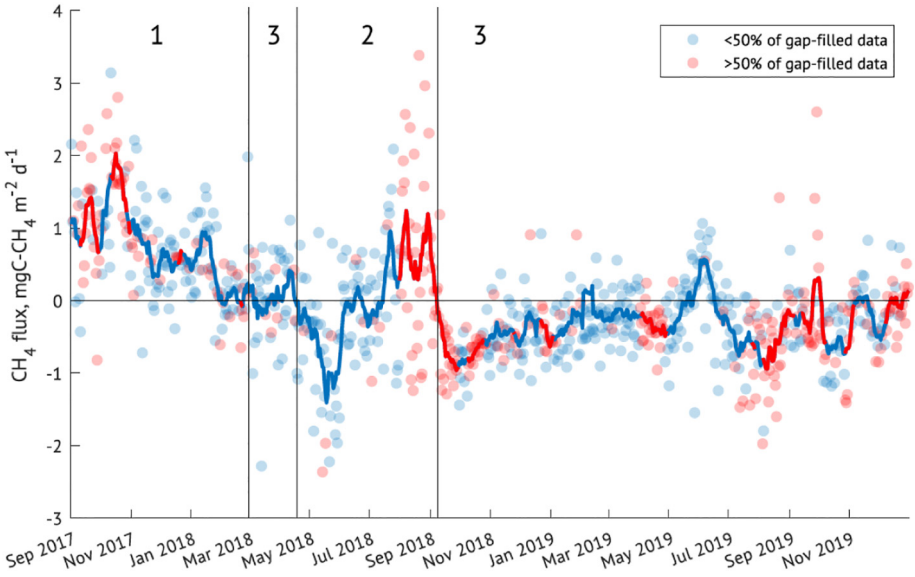

Fig. 8. Seasonal cycle of ecosystem CH_4 flux measured with QCLAS in eddy tower. Flux values above zero indicate emission while below the zero mean consumption of CH_4. The markers denote daily total values, the fitted line is a seven-day running mean. The periods marked with red colour represent time intervals with gap-filled data (MDS-method) exceeding 50%. Periods of interest: 1 -wet (2017-09-01 … 2018-03-01), 2 - dry (2018-04-15… 2018-09-10). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Vigano et al., 2008; Covey and Megonigal, 2019). Likewise, Mikkelsen et al. (2012) have demonstrated the CH_4 release from forest canopy using profile measurements at different heights. During the rest of our study (outside of wet and dry periods), the influence of the canopy on the forest CH_4 budget was large, but in the opposite direction as a net CH_4 sink. This can be related to microbial CH_4 consumption within the canopy as proposed by Putkinen et al. (2021), or to several meteorological and microclimatological conditions within the canopy (see Mikkelsen et al., 2012). In addition, advective transport and storage fluxes of methane may play a role in this process, which emphasizes the need for further profile measurements within the canopy (Rebmann et al., 2018).

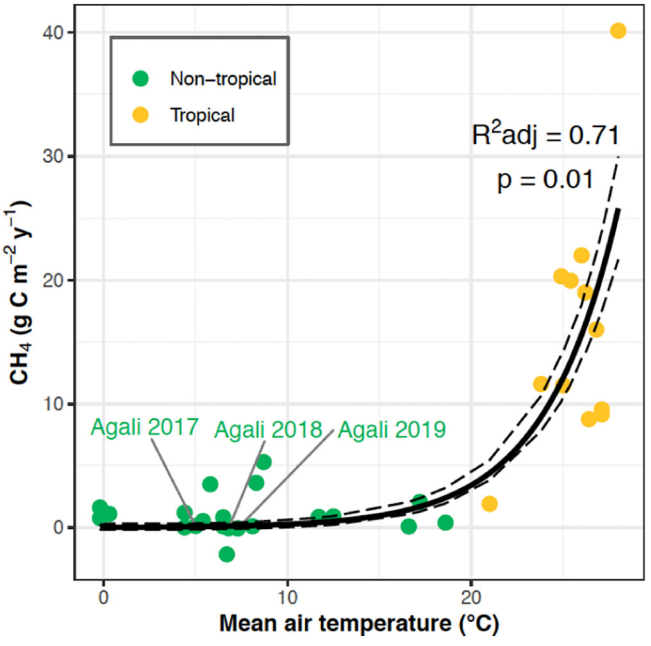

Fig. 9. Relationship between mean annual air temperature and the EC-measured mean annual CH_4 emission in forest ecosystems across the climate zones. Dashed line shows 95% confidence limits. Values for the Agali study site in our research for 2017 (Sept-Dec), 2018 and 2019 are indicated by green symbols. See Supplementary Table 2 for details. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The results of our long-term study show that the role of riparian alder forests as net CH_4 sinks accrues from a complex array of soil and plant processes that both produce and consume this powerful greenhouse gas. These processes respond to environmental variation somewhat independently such that the both the source and sink strength significantly vary over time, including occasionally switching the forest from a net CH_4 sink to a net source. Thus, the buffering capacity of this riparian alder forest (and certainly other riparian forests) on the atmospheric CH_4 budget is high and responds to perturbations such as global climate change. This complexity makes it challenging to forecast without building a deeper understanding of CH_4 cycling processes in forests generally.

For better understanding of carbon budgets of riparian forests, we need long-term, high-frequency measurements of fluxes from the soil and tree stems in combination with ecosystem-level EC measurements. Likewise, the role of canopy in forest ecosystem CH_4 budgets needs to be better understood and therefore, canopy flux measurements with shoot chambers and gradient analysis of CH_4 concentration within the canopy are strongly recommended for further studies. The identification of microorganisms and biogeochemical pathways associated with CH_4 production and consumption is another future challenge.

5. Conclusions

Our study showed that riparian deciduous forests growing on gleysols in a transitional zone from mineral to organic soils with relatively high groundwater table is a weak long-term CH_4 sink. Thus, the first hypothesis that this riparian forest ecosystem is a net CH_4 sink was supported. However, there was a significant difference in CH_4 fluxes between the wet and dry periods, showing differences in the contributions of soils, stems, and canopy processes to ecosystem-level (EC) fluxes. During the wet period in autumn and early winter 2017/2018, 81% of ecosystem CH_4 emissions was emitted by tree stems and the sum of soil and stem fluxes was similar to the ecosystem (EC) fluxes indicating the canopy was neither a net CH_4 source nor sink. In the dry period (late spring and summer 2018), CH_4 was consumed at the soil surface and emitted, most likely, from the canopy, while the stem emissions were very low. Soil water content was the most

important environmental factor controlling both soil and stem fluxes. Likewise, there was a significant positive correlation between soil moisture and EC CH_4 fluxes. Accordingly, a positive correlation between soil and stem fluxes was observed that supports our third and fourth hypotheses. Soil temperature showed a negative correlation with both soil and stem CH_4 fluxes, most likely due to the negative correlation between the soil water content and temperature. Quite surprisingly, we found an optimum SWC value that differed for soil fluxes versus stem CH_4 fluxes.

CRediT authorship contribution statement

Ülo Mander, Kaido Soosaar, Katerina Machacova and Ülo Niinemets designed this study; Ülo Mander, Kaido Soosaar, Alisa Krasnova, Jaan Pärn, Mikk Espenberg, Jordi Escuer-Gatius, Thomas Schindler, J. Patrick Megonigal and Mari Pihlatie wrote the paper; Thomas Schindler, Martin Maddison, Kaido Soosaar and Ülo Mander conducted the field work, Ülo Mander, Kaido Soosaar Alisa Krasnova, Mikk Espenberg, Jordi Escuer-Gatius, Kuno Kasak, Reti R.anniku and Katerina Machacova carried out data checks and analysis, and all authors commented on the paper.

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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.

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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.2021.151723.

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