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Soil greenhouse gas fluxes in floodplain forests of the Danube National Park: effects of flooding and soil microclimate

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Abstract The relevance of soil greenhouse gas (GHG) fluxes from temperate floodplain forests has yet remained elusive. We studied the soil methane (CH₄), nitrous oxide (N₂O) and carbon dioxide (CO₂) dynamics at three forest sites along a flooding gradient in the Danube National Park (Austria) to estimate annual GHG budgets and to assess if and how seasonal flooding affects individual GHG fluxes. Soil surface GHG fluxes were determined along with GHG concentrations in soil air and pore-water at a non-flooded (NF), an infrequently-flooded (IF), and a frequently-flooded (FF) site. Both study years were characterized by dry summers, and only the FF site was flooded during the study period. Soils at all sites were annual CH₄ sinks (NF: -4.50 ± 0.85 ,

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Division of Terrestrial Ecosystem Research, Department of Microbiology and Ecosystem Science, Center of Microbiology and Environmental Systems Science, Djerassiplatz 1, 1030 Vienna, Austria IF: -2.54 ± 0.57 , FF: -0.67 ± 1.06 kg CH₄-C ha⁻¹ year⁻¹) and the sink strength correlated positively with soil moisture. Pulse-like CH₄ emissions were not observed during or after flooding. Soil N₂O fluxes showed large temporal and spatial variations, without any significant differences between sites (average NF: 6.5 ± 7.1 , IF: 10.4 ± 14.3 , FF: $9.4 \pm 10.5 \text{ } \mu\text{g} \text{ } \text{N}_2\text{O-N} \text{ } \text{m}^{-2} \text{ } \text{h}^{-1}$). Pulse N₂O emissions (up to ~80 μ g N₂O-N m⁻² h⁻¹) occurred during freeze/thaw events, but not during or after flooding. Mean annual soil CO₂ effluxes at NF and IF were 9.4 ± 1.1 and 9.4 ± 2.1 t C ha⁻¹ year⁻¹, respectively. Soil CO₂ efflux was significantly higher at the FF site $(18.54 \pm 6.21 \text{ t C ha}^{-1} \text{ year}^{-1})$. High soil air CO₂ concentrations (> 10%) in aerated deeper soil layers indicated a substantial contribution of the usually waterlogged sub-soils to the summertime soil CO₂ efflux at the FF site. Overall, our results suggest that the studied temperate floodplain forest soils do not absorb/ emit substantially more CH₄ and N₂O than soils of comparable upland forests, whereas low groundwater level can lead to periodically enhanced CO₂ emissions from normally waterlogged soil layers.

Keywords Temperate floodplain forest \cdot Flooding \cdot N₂O \cdot CH₄ \cdot Soil CO₂ efflux \cdot Soil carbon \cdot Nitrate \cdot ¹³C \cdot Freeze–thaw

Introduction

Floodplain forests comprise~5% of the European forest area (Barbati et al. 2011) and there is a trend towards further areal expansion due to on-going ecological revitalization and the re-connection of floodplains to the main river bodies (Schiemer et al. 1999; Hein et al. 2016). Periodic flooding is the main feature that distinguishes floodplain forests from their upland counterparts. The unique and dynamic connection between terrestrial and aquatic ecosystems accelerates biogeochemical processes, such as carbon (C) and nitrogen (N) cycling (McClain et al. 2003; Krause et al. 2017), thereby potentially triggering the production and release of greenhouse gases (GHGs) from the forest soils. In contrast to upland forests, soil GHG fluxes in temperate floodplain forests, such as those along the Danube River, are yet poorly studied and quantified.

Floodplain forest soils have been suggested to sequester C globally (Dybala et al. 2019), and along the Danube river in particular (Zehetner et al. 2009). The production and efflux of CO_2 from temperate floodplain forests should therefore not exceed the C input in form of plant litter and the sedimentation of organic matter. The few studies that reported soil CO_2 fluxes along individual Danube tributaries found that CO_2 fluxes from the floodplain soils were comparable to those from surrounding temperate upland forests (Batlle-Aguilar et al. 2012; Acosta et al. 2017). While there is accordingly less evidence that soil CO₂ fluxes of temperate floodplain forests differ much from those of upland forest, the tight connection to the river and to the groundwater system could promote the production of methane (CH₄) and nitrous oxide (N₂O). For instance, the floodplain forests in the Amazon basin have been identified as significant natural CH₄ and N_2O sources to the atmosphere (Pangala et al. 2015; Figueiredo et al. 2019). However, even in large-scale European research projects of the last 20 years (CarboEurope IP, Carbomont, Nitroeurope etc.) soil CH₄ and N₂O fluxes of temperate floodplain forests were mostly overlooked.

Soil CH₄ fluxes might particularly be affected by the duration and frequency of flooding. Expansion of anaerobic microsites (e.g. during flooding or with changes in the groundwater table) can shift the balance from microbial CH₄ consumption towards net CH₄ production, and thereby turn the soil from a CH_4 sink into a source of CH_4 (Soosaar et al. 2011; Pugh et al. 2018). Temporary CH_4 pulse-emissions could further be triggered by physical force, such as pressure driven gas flow or ebullition; e.g. if CH_4 captured in the pore space of deeper soil layers is replaced by flood- or groundwater (Bartlett et al. 1990; Männistö et al. 2019). The magnitude of the CH_4 flux could as well be influenced by physical soil characteristics, which determine the ability to drain the access water past surface flooding.

Previous research in riparian wetlands and forests has demonstrated the effects of flooding, groundwater table fluctuations and soil oxygen availability on nitrification and especially denitrification processes (Pinay et al. 2000; Hefting et al. 2004, 2006; Forshay and Stanley 2005; Burgin and Groffman 2012; Welti et al. 2012; Shrestha et al. 2014). However, soil N₂O emissions were rarely measured in temperate floodplain forests, and the effects of flooding on actual N₂O fluxes has remained unclear. Furthermore, existing field studies often lack the high temporal measurement frequency that could eventually identify hot moments of N₂O release from the soil (Burgin and Groffman 2012; Batlle-Aguilar et al. 2012; Batson et al. 2015; Petrakis et al. 2017; Machado dos Santos Pinto et al. 2020).

Based on that, we designed a case study encompassing three sites along a flooding gradient in the floodplain forests of the Danube River, to quantify soil CO₂, CH₄ and N₂O fluxes and to assess the influence of the local environment and of flooding on GHG fluxes. We hypothesized that (I) flooding causes soil CH₄ pulse emissions (short-term increases by an order of magnitude or more) and that (II) the soil N_2O efflux significantly increases during post-flooding periods, with high soil moisture contents. Under non-flooding conditions, floodplain forest soils are expected to act as CH₄ sinks and as N₂O sources. We further hypothesized that (III) the soil CO₂ efflux is reduced during waterlogging periods, but is promoted during inter-flood periods, due to the then favourable soil moisture conditions. Overall, we hypothesized that flooding significantly increases the annual site-specific soil GHG global warming potential (particularly due to elevated CH₄ and N₂O emissions), when compared to those of non-flooded sites and other upland forest.

Materials and methods

Site description

The study was conducted in the Danube National Park in Austria, a semi-natural temperate floodplain area, which covers approximately 10.000 hectares along the Danube River, south of the city of Vienna. The national park's land-cover consists of 65% forests, 15% meadows and 20% water bodies, and has a long history of land use, including water regulation, logging, and agriculture (https://www. donauauen.at/der-nationalpark/zahlen-daten-fakten). Along the national park, the Danube River has the character of an alpine stream. River discharge ranges from 600 to 900 m³ sec⁻¹ at low flow conditions and up to 8500-11,000 m³ sec⁻¹ in the event of a 100-year flood, causing large fluctuations of the water table with up to seven meters in height. A dam (the "Marchfeld dike", completed in 1905) prevents flooding of the most northerly park areas and their surroundings.

Mean annual temperature (between 1981 and 2010), measured at the close by meteorological station of Groß-Enzersdorf, is 10.3 °C. Mean annual precipitation during the same period was 567 mm, with peaks during spring and summertime (data from the Zentralanstalt für Meteorologie und Geodynamik 2020).

Three forest sites were selected in a sector of the national park near the village of Stopfenreuth (48° 08' 39.7" N 16° 53' 03.7" E). Sites were selected along a~1 km transect, consisting of a non-flooded site (NF) outside the Marchfeld dike (146.8 m a.s.l.), an infrequently flooded site (IF), which is flooded approximately every 5-10 years (143.7 m a.s.l.), and a lower lying (139.7 m a.s.l.), frequentlyflooded site (FF, several inundations per year) near a detached Danube side arm. Mature stands of predominately silver poplar (Populus alba L.) comprised the vegetation at the FF and IF sites, while mature common ash (Fraxinus excelsior L.) dominated the forest stand at NF. The parent material of the soils is a carbonate-rich gravel layer, several meters in thickness. Soils at NF and IF were classified as Calcaric Fluvisols and those at FF as Calcaric Gleysols (FAO 1998).

Soil parameters

Three randomly distributed soil pits were excavated at each site. In each soil pit, a single soil sample was taken at 5, 15, 25, 40 and 75 cm depth (sample cylinder centre) and considered as being representative for the 0-10, 10-20, 20-30, 30-50, and 50-100 cm soil layers. Stainless-steel cylinders (7.4 cm diameter, 5 cm height) were inserted laterally into the profile wall to obtain the soil samples. Soil bulk density was determined by dividing the oven dry soil mass by the cylinder volume. No coarse fragments (stones, roots) were present. Soil texture was determined on a single soil profile at each site. All other soil parameters were determined for all three soil profiles. Soil physicochemical analyses were carried out following international guidelines for forest soil monitoring (Cools and De Vos 2016). Briefly, air dried soil was sieved to 2 mm, and soil texture and particle-size distribution were determined using the pipette method. Soil pH was potentiometrically measured in a 0.01 M $CaCl_2$ slurry, using a soil-to-solution ratio of 1:5 (v/v) (Metrohm pH Meter 713, Metrohm, Herisau, Switzerland). A Scheibler calcimeter was used to measure the soil CaCO₃ content using the classic gas-volumetric technique. Total soil C (Ctot) and total soil N (Ntot) were determined by dry combustion using a LECO C/N TruMAC Analyzer (LECO, Saint Joseph, MI, USA). Soil organic C (Corg) contents were calculated as the difference between \tilde{C}_{tot} and soil CaCO₃ content.

Environmental parameters

Soil temperature and soil moisture were continuously measured in one profile at 5, 15, 30, 50, 100 cm soil depth of each site using GS3 probes (Decagon, Pullman, WA, USA). The sensors were inserted laterally into the wall of a single soil pit at each site (pits were refilled thereafter). Temporal resolution was 30 min and data were stored on EM 50 dataloggers (Decagon, Pullman, WA, USA). In addition, soil temperature (5 cm depth) and soil moisture (0–20 cm depth) were measured manually during all GHG measurement campaigns adjacent to each soil GHG chamber, using a portable thermometer and a Field Scout TDR Moisture Meter (Spectrum Technologies Inc., Aurora, IL, USA). The GS3 sensors, as well as the Field Scout moisture sensors were calibrated for site specific soil pre-conditions by installing them in an excavated undisturbed soil block $(30 \times 30 \text{ cm vol-} \text{ume})$ in the laboratory at various levels of soil water content (actual soil moisture was determined from actual fresh weights and the bulk densities of the soil blocks). Precipitation and air temperature were obtained from the close-by ZAMG weather station in Groß-Enzersdorf. Hourly resolved Danube water levels were obtained from the freely accessible database "https://www.noel.gv.at/wasserstand" (location "Wildungsmauer").

Soil solution and surface water chemistry

At each site, one soil pit was equipped with ceramic suction cups at 15, 30, 50, and 100 cm soil depth for soil solution sampling. The suction cups were connected to water storage bottles and a pump which induced a constant under-pressure of 0.30 bar. The pump was activated every 2 h for a period of 30 min. The storage bottles were emptied every 10-20 days. Dissolved organic carbon (DOC) and total dissolved N (TDN) in the soil solution were measured after filtration (cellulose acetate filters, 0.45 µm) using a Total Organic Carbon Analyser (TOC-L CSH/CSN, Shimadzu, Kyoto, Japan) including a Total Nitrogen Unit (TNM-L, Shimadzu, Kyoto, Japan). Ammonium (NH_4^+) and nitrate (NO_3^-) concentrations in the soil water were determined using ion chromatography (Dionex ICS-1000, Thermo Fisher, Waltham, MA, USA).

While suction cups at the FF site yielded sufficient amounts of soil solution during most of the sampling dates and across all soil depths, the soil solution yield at the NF and the IF site were limited due to technical problems and due to the dry summer conditions. All suction cups at the NF and IF sites lost their ceramic tips and needed replacement, which took place in spring 2018. At the NF site the soil solution yield was further limited by periodic pump failures, leaving only two sampling occasions with sufficient soil solution yield for analyses.

Monthly average Danube surface water NH_4^+ and nitrate NO_3^- concentrations were derived from the freely available water quality database: Wasserinformationssystem Austria—WISA; H2O Fachdatenbank (https://wasser.umweltbundesamt.at/h2odb/index. xhtml). At the FF site, surface (flood) water was sampled (3 times) during an intensive flood-measurement campaign in March 2019. In addition, soil solution (at 30, 50 and 100 cm depth) was sampled during the flood event in parallel with surface GHG measurements (5 times) by directly withdrawing soil solution from the installed gas capillary tubes (see below). All samples were filtered and analysed as described above.

Soil greenhouse gas measurements

Soil air CO₂, CH₄, and N₂O concentrations, and soil surface GHG fluxes were measured manually every 3 weeks from April 2017 until April 2019. Measurements took place between 9 am and 2 pm in random order, to avoid confounding effects due to potential diurnal variations in soil GHG production/consumption. To gain a higher temporal resolution, an automated GHG sampling system was installed at each site to capture soil surface fluxes in daily resolution throughout the study period. We further performed an intensive manual measurement campaign during a flood-event in March 2019, to investigate GHG fluxes during an and across an inundation event. Ground vegetation (primarily Galanthus nivalis and Allium ursinum L. during springtime) was left in place in chambers during manual CH₄/N₂O measurements and in the auto-chamber, but was removed from the separate collars installed for soil CO2 efflux measurements.

To determine GHG concentrations in soil air at different depth levels, soil air was sampled across one single soil profile at each site. An excavated soil pit was equipped with stainless steel capillaries. The steel capillaries ended in~5 cm long perforated Teflon tubings, which were horizontally inserted 30 cm into the pit-wall (at soil depths of 5, 15, 30, 50, 100 cm), to avoid any disturbance due to the soil mixing during pit re-filling. The capillary end reaching out of the soil was connected to a three-way Luer lock for gas sampling with a syringe. After flushing the Luer lock and the needle, aliquots of 15 ml gas were drawn from each capillary and injected into preevacuated 12 ml glass vials. Soil air CO₂, CH₄, and N₂O concentrations were measured using gas chromatography as described further below. During pore water sampling, we also determined dissolved GHG concentrations. In the field, we collected a 5 ml water sample into a 20 ml syringe drawing in additional 15 ml of synthetic air, closing the stopcock, and shaking the syringe for 3 min to equilibrate the air and water sample. We then transferred 12 ml of the gas to 10 ml pre-evacuated glass vials for gas chromatographic measurements of GHGs. Pore-water GHG concentrations were calculated as described in Ding et al. (2004). We simultaneously used the capillaries as a mean to roughly estimate the groundwater level, depending on if we sampled air or water from a corresponding soil depth-layer.

Six 1×1 m plots (n=6) were established at each site for manual soil surface GHG flux measurements. The plots were randomly distributed within an area of 25×25 m. Each plot was equipped with one opaque static chamber (diameter 30 cm, height 15 cm) for soil CH₄ and N₂O flux measurements and one basecollar (diameter 10 cm, height 4 cm) for soil CO₂ flux measurements. All chambers and collars were inserted 3 cm into the mineral soil to generate a sufficient sealing. One plot at each site was arranged in a way that the measurement chambers were located directly above the steel capillaries for soil air GHG concentration sampling (as described above). Soil surface CH₄ and N₂O fluxes were manually measured by closing the static chambers with sealed lids. The chambers were closed for 20 min and 25 ml air samples were drawn at time 0, 5, 10 and 20 min by inserting a syringe (glass, 50 ml) needle through a rubber septum. Gas samples were immediately injected into pre-evacuated 20 ml glass vials and stored until analysis. For the intensive flood-measurement campaign, we constructed floating chambers (static, same size, same closure times as described above) to measure GHG fluxes from the water surface.

Soil CO₂ efflux was measured manually with a portable EGM4 infrared gas analyser (PPSystems, USA) attached to a SRC1 soil respiration chamber (PPSystems, USA). For measurements, the SRC1 chamber was placed on the pre-installed collars. Closing time was 90 s and the CO₂ flux was calculated from the linear increase in headspace CO₂ concentration.

For the determination of daily variations (1/day), GHG fluxes were measured using an automated gas sampling system (AGPS—patent DE 198 52 859). The system has been described in detail in (Kitzler et al. 2006). Gas samples (0, 45, 90 min) were taken automatically between 9 and 11 am. The sampled soil area was $(0.7 \times 0.7 \text{ m})$. The headspace volume of the chamber was 49 l. The fraction collector had a capacity of 40 headspace vials (20 ml), and power was supplied by 2×12 V/DC batteries. Gas samples were collected from this device every 13 days and stored in the laboratory at 4 °C until analysis. During flooding (at FF), the chamber lid of the automated system was removed and temporarily stored at the installed towers, to prevent damage from floodwater. Chambers were immediately re-installed after floodwaters receded.

All collected gas samples were analysed with a gas chromatograph (AGILENT 6890 N, Palo Alto, CA, USA) equipped with a ⁶³Ni-electron-capture detector (ECD) for N₂O and a flame ionization detector (FID) for CH₄. An Argon-methane mixture was used as carrier gas for ECD, with a flow rate of 9 ml min⁻¹, while helium served as the carrier gas for the FID (flow rate: 15 ml min⁻¹). Calibration was performed using gas standards with 1.11, 2.11 and 3.98 ppm CH₄ and 1.02, 1.95 and 4.05 ppm N₂O. Methane and N₂O fluxes were calculated as described in Metcalfe et al. (2007):

$$GHG \ flux = \Delta C / \Delta t * 273.15 / (T_{air} + 273.15) * p / 1000 * M / 22.41 * V / A,$$

where GHG flux is the hourly flux of the respective GHG, $\Delta C/\Delta t$ is the concentration change (ppb) over time (h), T_{air} is the air temperature (°C), p is the atmospheric pressure (Pa), M the molecular weight $(g \text{ mol}^{-1})$, 22.41 is the molar volume of an ideal gas at standard temperature and pressure (1 mol^{-1}) , V is the chamber volume (m^3) , and A is the chamber area (m²). The term (T_{air} +273.15) is used for the conversion of air temperature from degree Celsius to degree Kelvin. For calculation of CH4 fluxes, M is 12.01 g mol⁻¹ and flux units are μ g CH₄-C h⁻¹ m⁻², respectively. For calculation of N2O flux, M is 28.02 g mol⁻¹ and flux units are μ g N₂O-N h⁻¹ m⁻². The criteria for a valid single flux measurement being distinguished from zero was an $R^2 > 0.7$ (Welch et al. 2019) and a value above the limit of detection limit (LOD) of the gas chromatography system of $\pm 2.52 \,\mu g$ CH_4 -C m⁻² h⁻¹ (4 data points), and $\pm 0.53 \mu g N_2$ O-N m^{-2} h⁻¹, respectively (Parkin et al. 2012). Changes in GHG concentrations with $R^2 < 0.7$ and smaller values than the LOD were visually checked and zero flux was assigned to those if the regression line was horizontal.

The global warming potential (GWP) was calculated based on annual (2018) sums for all three GHG fluxes investigated. The net GWP was calculated based on the 100-year climate warming factor, with GWPs 27.2-times and 273-times (IPCC, 2021) higher for CH_4 and N_2O than for CO_2 , respectively. To account for warming potentials on a shorter timeframe we alternatively calculated the 20-year GWPs using conversion factors of 80.8 and 273 for CH₄ and N₂O, respectively (IPCC 2021). GWPs are expressed in CO₂ equivalents (CO₂eq) in t ha⁻¹ year⁻¹. To estimate if C from inorganic sources (e.g. degassing of the carbonate system of the groundwater or Danube water) significantly contributed to the soil CO₂ fluxes, the C isotope ratios of soil air and surface CO₂ fluxes were assessed during three sampling dates (May 18, August 07, November 23 in 2018). Additionally, the C isotope ratios of C_{org} were assessed once from a single soil pit per site (same depths as for other soil parameters). The C isotope ratios of CO₂ and of Corg were analyzed by continuous-flow isotope-ratio mass spectrometry (IRMS) on a Delta V Advantage Isotope Ratio Mass Spectrometer coupled to a Gas-Bench system or an elemental analyser (Thermo Fisher Scientific, Bremen, Germany) at the University of Vienna. To assess the isotopic signature of soil respired CO₂, the Keeling plot approach was used (Keeling 1958). The intercept of a linear regression of δ^{13} C of sampled CO₂ versus 1/[CO₂] provides an estimate of δ^{13} C of soil-respired CO₂ (where [CO₂] was the CO₂ concentration in %). Before C_{org} measurements carbonates were removed from ground soil aliquots (~50 mg) by reaction with 0.5 mL 2 M HCl, followed by drying and mixing.

Data analyses

Manual soil GHG flux measurements were up-scaled to annual cumulative fluxes by means of linear interpolation between consecutive measurement dates for each individual plot during 2018, the study year with a full annual record. Site differences between soil GHG fluxes were tested by one-way repeated measures ANOVA, followed by Tukey post-hoc tests, with p values being adjusting using the Bonferroni method. Data were square root transformed if normality assumptions tested via Shapiro–Wilk-Test were not met. Sphericity was accounted for using the Greenhouse–Geisser correction. To test for differences in soil physio-chemical parameters (C_{org} content, C_{org} stock, N_{tot} content, N_{tot} stock, C/N, bulk density, soil

pH, carbonate content) across sites and soil depth layers, we applied two-way ANOVA and Tukey post-hoc tests. Correlation coefficients between environmental parameters (soil moisture and temperature) and GHG fluxes, as well as correlation coefficients between soil GHG fluxes and soil air GHG concentrations at each individual site, were calculated using Pearson correlations. Additionally, to evaluate relations between GHG fluxes, GHG concentrations in soil and topsoil physico-chemical properties (C-, N-, carbonatecontents, bulk density, soil-texture, -temperature and -moisture) across sites, we performed principal component analysis (PCA). All statistical analyses were performed with R Version 3.5.1, using the packages "rstatix" (Kassambara 2021) for ANOVA and "Ggally" (Schloerke et al. 2018) for correlation analyses. The relative biotic (SOM decomposition, microbial respiration) and abiotic source contributions to the soil CO₂ efflux (bedrock weathering and/ or degassing of abiotic CO₂ from groundwater) were estimated following a two pool mixing model with the isotope signatures of soil organic matter (C_{org}) as proxy for $\leq \delta^{13} \text{CO}_2$ of microbial respiration and a δ^{13} C signature of 0% for the abiotic (carbonate) source (Schindlbacher et al. 2015).

Results

Soil physico-chemical parameters

Carbonate contents of the mineral soils were high (>20%) at all three sites (Fig. S1). Average carbonate contents were significantly higher at the FF site, when compared to the NF and FF sites (p < 0.05). Soil pH values ranged between 7.2 and 7.8 and were highest at the FF site (Fig. S1). Soil texture was dominated by silt (>60%) at all three sites. Sand contents increased with soil depth and dominated (50-60%) in the deepest soil layer at the NF and IF sites (Fig. S2). Clay contents gradually decreased with soil depth at the NF and IF sites, but were generally higher at the IF than at the NF site (Fig. S2). At FF, sand contents showed irregular depth patterns, with highest sand contents at 20-30 cm depth and the lowest (~10%) sand content in the deepest soil layer (Fig. S2). Soil organic C contents were highest in the topsoil layer (0-10 cm) at all three sites (Fig. 1). They decreased gradually with soil depth at the NF and IF sites, but Fig. 1 Organic carbon (C_{org}) contents (a), soil C_{org} stocks (b), total soil nitrogen (N_{tot}) contents (c), and soil N_{tot} stocks (d) at different mineral soil layer depths (Means \pm SD). FF frequently-flooded site, IF infrequently-flooded site, NF: Non-flooded site. Different letters indicate statistically significant differences (p < 0.05)



remained constant between 10 and 100 cm at the FF site. Due to the higher $C_{\rm org}$ contents in the deeper soil, soil C_{org} stocks were significantly higher at the FF site compared to the NF and IF sites (Fig. 1). Soil total N contents showed similar soil depth related patterns as C_{org} (Fig. 1). Total C_{org} stocks (0-100 cm soil depth) were 136 ± 9 , 125 ± 14 , and 169 ± 9 t C ha⁻¹, at the NF, IF, and the FF site, respectively. Total C_{org} stocks at the FF site were significantly higher than those at the NF and the IF sites (p < 0.01). Total N stocks were 9.5 ± 1.0 , 8.5 ± 1.2 , and 8.8 ± 0.6 t N ha⁻¹ and did not differ significantly among the three study sites. Organic layers at the NF and the IF sites comprised only of the most recent leaf litter (0-1 cm), whereas flooding at FF caused periodic lateral litter input, which deposited up to 5 cm thick layers. The PCA also revealed that the three sites were markedly

different, since they were clearly separated along the first two principal components (PC) which explained 44.6 and 16.8% of the total variation in the data (Fig. S3). Sand and C_{org} content were most important for the separation along PC1. Silt, carbonate and N_{tot} contents also contributed to the separation along PC1. The separation along PC2 was mainly due to bulk density and—to a minor degree—to clay content and the C/N ratio.

Climate, flooding, and the soil environment

Both study years (2017 and 2018) were characterized by low summer precipitation (Figs. 2, 3 and 4). Air temperatures were within the long-term averages, following the typical seasonal course and ranged between + 32.7 °C (Aug 2017) and - 9.6 °C (Feb



Fig. 2 Soil environment and GHG fluxes at the non-flooded (NF) site. Panels A and B show soil temperature and soil moisture at different soil depths, respectively. Black bars in panel B show daily precipitation inputs. Panels C, D, and E show the soil surface fluxes and below the soil air concentrations

of CO₂, CH₄, and N₂O at different soil depths (contour-plots), respectively. Open symbols represent manually measured surface fluxes (mean \pm SE, n=6) and grey bars show daily measured auto-chamber (n=1) fluxes

2018). Danube water levels ranged between 103 and 595 cm during the study period. The "infrequently-flooded" site IF was not flooded during the study period. Only the site closest to the river (FF) experienced periodic surface flooding (Fig. 4a). While the

FF site was regularly inundated, flood water retreat was delayed by up to 2 weeks. The reason for this was the slower infiltration of the inland (flood) water bodies, which became disconnected from the stream during the flood retreat. Groundwater levels were



Infrequently-flooded (IF)

Fig. 3 Soil environment and GHG fluxes at the infrequentlyflooded (IF) site. Panels **A** and **B** show soil temperature and soil moisture at different soil depths, respectively. Black bars in panel **B** show daily precipitation inputs. Panels **C**, **D**, and **E** show the soil surface fluxes and below the soil air concentra-

Soil temperatures followed the seasonal course of the air temperatures, with the typical delayed and flattened response curve with increasing soil depth (Figs. 2, 3 and

measured auto-chamber (n = 1) fluxes

tions of CO2, CH4, and N2O at different soil depths (contour-

plots), respectively. Open symbols represent manually meas-

ured surface fluxes (mean \pm SE, n=6) and grey bars show daily

always lower than 100 cm soil depth at the NF and the IF sites. At the FF site, groundwater levels persistently reached beyond 100 cm soil depth, and with exception of both summers, groundwater levels were always close to the soil surface (Fig. 4).

4). There was no significant difference in soil temperatures between the NF, IF, and FF sites. Average top-soil



Fig. 4 Danube water level, soil environment and GHG fluxes at the frequently-flooded (FF) site. Panel **A** shows the Danube river water level at the closeby station "Wildungsmauer". Lines in Panel **A** show the corresponding site altitudes (NF, IF, FF). In the case the water level crossed the full line (FF), the site was flooded. Panels **B** and **C** show soil temperature and soil moisture at different soil depths, respectively. Black bars in panel **C** show daily precipitation inputs. Panels **D**, **E**, and **F**

show the soil surface fluxes and below the soil air concentrations of CO₂, CH₄, and N₂O at different soil depths (contourplots), respectively. Open symbols represent manually measured surface fluxes (mean \pm SE, n=6) and grey bars show daily measured auto-chamber (n=1) fluxes. The white lines in the contour-plots indicate an approximation of the groundwater table position within the soil profile

moisture levels during the study period (0–20 cm, manually measured) were highest at the FF site (57.8 ± 8.0 Vol%), followed by the IF (39.1 ± 4.4 Vol%) and the NF site (24.7 ± 7.9 Vol%); the differences between the sites were highly significant (p<0.001). Soil moisture showed a similar temporal course at the NF and the IF sites, with depressions during both summers, and highest moisture levels during the dormant seasons (as a result of this soil temperature and soil moisture were negatively correlated; Fig. 5). During the frost period in March 2018, liquid top-soil moisture levels sharply decreased at the NF site, and particularly so at the IF site (Figs. 2 and 3), but not at the FF site. The course of soil moisture at the flooded site (FF) differed substantially from the other sites, due to groundwater influx and periodic flooding. Sub-soils (50+cm depth) at the FF site were waterlogged throughout the whole study period due to groundwater influx (Fig. 4). The dry summer 2017 caused top-soil moisture to decrease at the FF site, until rewetting occurred in late September 2017 due



Fig. 5 Correlation matrix of soil surface GHG fluxes and soil environmental parameters (at 5 cm soil depth) at the three study sites (green, *NF* non-flooded; orange, *IF* infrequently-flooded; purple, *FF* frequently-flooded). Grey values repre-

sent correlation coefficients for all site types. P-values indicate significant correlation with ***=p<0.001, **=p<0.01, *=p<0.05 calculated with Spearman correlation coefficients

to rainfall (Fig. 4). During July and August 2018, FF soil moisture decreased significantly down to a minimum depth of 50 cm, shortly increased again during rewetting (in early September), and thereafter remained at low levels, until soil water saturation occurred in late autumn (Fig. 4).

Soil solution and surface water chemistry

Soil solution DOC concentrations varied between 7 and 70 mg l^{-1} (Fig. S4). Average DOC concentrations were 39 ± 20 , 35 ± 16 , 23 ± 12 , and 23 ± 14 mg l⁻¹ at 15, 30, 50, and 100 cm soil depth at the FF site across all sampling dates. Average DOC concentrations at the IF site were 17 ± 6 , 16 ± 10 , 11 ± 6 , and 25 ± 17 mg l⁻¹ at 15, 30, 50, and 100 cm soil depth. DOC concentrations at the NF site ranged between 11 and 21 mg l^{-1} . Ammonium concentrations were below the detection limit of 0.4 mg N l⁻¹ at all sites during all sampling dates. Nitrate concentrations in soil solution at the FF site were always below the detection limit of 2.0 mg 1^{-1} . At the IF site, NO_3^- concentrations averaged 135 mg l⁻¹ and occasionally reached values of up to 250 mg l^{-1} (Fig. S5). Nitrate concentrations at the NF site ranged between 33 and 120 mg l^{-1} . The temporal trends in soil solution DOC and nitrate concentrations are shown in figures S2 and S3. Nitrate concentrations in the main channel of the river Danube ranged between 1.2 and 2.9 mg l^{-1} during the study period (NH₄⁺ was undetectable < 0.05 mg l⁻¹). During the intensive measurement campaign in March 2019 NO₃⁻ concentrations in surface flood-water ranged between 3.0 and 7.8 mg l^{-1} . Concentrations of NO₃⁻ as well as NH₄⁺ concentrations in soil solution all remained below detection limit during this flooding period.

Soil greenhouse gas fluxes and concentrations

Carbon dioxide

Mean soil CO₂ effluxes at the FF site (194 \pm 167 mg CO_2 -C m⁻² h⁻¹) were significantly (p < 0.001) higher than at the NF $(111 \pm 79 \text{ mg CO}_2\text{-C m}^{-2} \text{ h}^{-1})$ and the IF sites $(110 \pm 74 \text{ mg CO}_2\text{-C m}^{-2} \text{ h}^{-1})$, the latter sites showing reduced fluxes during both summers (Figs. 2c and 3c). At the FF site such a reduction in soil CO₂ efflux during the dry summers was not observed, and fluxes periodically declined only for short periods after the flood events (e.g. August and September 2017). Accordingly, soils at the FF site emitted almost twice as much CO₂-C as soils at the NF and IF sites (Table 1). Consistent with soil CO_2 efflux patterns during other flood events, soil CO2 efflux ceased during the intensively studied March 2019 surface-flooding period and recovered shortly (3 days) after surface water retreatment (Fig. 6).

Manually measured soil CO_2 effluxes showed the typical seasonal patterns and were closely correlated to soil temperatures at all three sites (Fig. 5). Soil CO_2 efflux was weakly and negatively correlated to soil moisture at the NF and IF sites (Fig. 5), but this was rather caused by the generally higher soil moisture during the dormant seasons (reflected in negative correlation between soil temperature

Site	NF	IF	FF		NF	IF	FF	
Element fl	uxes			CO_2 equivalents (t ha ⁻¹)				
$\frac{\text{CO}_2\text{-C}}{(\text{t ha}^{-1})}$	9.35±1.06a	9.44±2.11a	18.54 ± 6.21 b	GWP-CO ₂	34.32 ± 3.90	34.64±7.74	68.05±27.77	
CH ₄ -C (kg ha ⁻¹)	$-4.50 \pm 0.85a$	-2.54 ± 0.57 b	$-0.67 \pm 1.06c$	GWP-CH ₄ 100 year GWP-CH ₄ 20 year	-0.16 ± 0.03 -0.48 ± 0.08	-0.09 ± 0.02 -0.27 ± 0.06	-0.02 ± 0.04 -0.07 ± 0.11	
N_2O-N (kg ha ⁻¹)	$0.51 \pm 0.09a$	$0.94 \pm 0.17b$	0.74 ± 0.32 ab	GWP-N ₂ O	0.44 ± 0.08	0.81 ± 0.14	0.63 ± 0.27	
				Total GWP 100 year	34.6±3.9a	$35.4 \pm 7.8a$	$68.7 \pm 22.8b$	
				Total GWP 20 year	34.3±3.8a	$35.2 \pm 7.8a$	$68.6 \pm 22.8b$	

Table 1 Annual cumulative soil greenhouse gas fluxes and corresponding global warming potentials (GWP; reported as CO_2 equivalents) from the three study sites during the study year 2018

Means \pm SD. Different letters indicate statistically significant differences (p<0.05) between sites Conversion factors were 80.8 (20 year GWP) and 27.2 (100 year GWP) for CH₄ and 273 (20 and 100 year GWP) times for N₂O, respectively (IPCC 2021)

NF non-flooded, IF infrequently-flooded, FF frequently-flooded



Fig. 6 Surface greenhouse gas (GHG) fluxes (open square: CH_4 , open triangle: N_2O , open circle: CO_2) at the frequently-flooded site during and shortly after flooding in March 2019.

and soil moisture, Fig. 5). Due to the long (90 min) auto-chamber closure times, the computed soil CO_2 effluxes from the auto-chambers were an order of magnitude lower than those from the IRGA measurements (Figs. 2, 3, and 4). Overall, the auto-chamber CO_2 fluxes correlated well with the corresponding manually measured fluxes (NF: r=0.73, p<0.001; IF: r=0.76, p<0.0001; FF: r=0.88, p<0.0001) and auto-chamber fluxes showed a correspondingly similar relationship with soil temperature and soil moisture (data not shown).

Soil air CO_2 concentrations resembled the seasonal course of the soil CO_2 efflux at all sites and showed the typical CO_2 concentration gradients within the soil profiles (highest concentrations in deeper soil layers and decreasing concentrations towards the soil surface; Figs. 2c, 3c, and 4d). Soil air CO_2 concentrations were lowest at the NF site, followed by the IF site, but were exceptionally high at the FF site (up to~100.000 ppm in the deeper soil). Soil CO_2 effluxes were positively correlated with soil air CO_2

The blue shaded area indicates the period of surface flooding. During surface flooding, GHG fluxes were measured at the water surface by means of floating chambers

concentrations at all soil depths at the NF and IF sites, and with soil air CO_2 concentrations at a soil depth of 30 cm and deeper at the FF site (Table 2).

Soil C_{org} exhibited $\delta^{13}C$ values of $-25.4\pm0.8\%$ (NF), $-25.7\pm1.2\%$ (IF) and $-26.7\pm0.4\%$ (FF), the decreasing standard deviation showing lower increases in $\delta^{13}C$ signatures with soil depth at the FF compared to the NF and IF sites (Table S1). Soil emitted CO₂ exhibited $\delta^{13}C$ values of -25.4 ± 0.5 to $-21.5\pm0.2\%$ (NF), $-26.9\pm0.4\%$ to $-23.8\pm0.4\%$ (IF) and -25.6 ± 0.4 to $-22.4\pm0.4\%$ at the FF site during the three sampling campaigns (Table S1).

Methane

Overall, soils at all three sites were net CH_4 sinks (Table 1). During the two study years, manually measured CH_4 fluxes ranged on average between $-50.5\pm24.5 \ \mu\text{g} \ CH_4-C \ m^{-2} \ h^{-1}$ at the NF, $-33.7\pm25.8 \ \mu\text{g} \ CH_4-C \ m^{-2} \ h^{-1}$ at the IF, and $-10.8\pm21.4 \ \mu\text{g} \ CH_4-C \ m^{-2} \ h^{-1}$ at the FF sites, with

Table 2 Pearson correlation coefficients between soil air greenhouse gas (GHG) concentrations at different soil depths and the corresponding soil surface GHG fluxes

Site	Non-flooded (NF)			Infrequently-flooded (IF)			Frequentl	Frequently-flooded (FF)		
GHG	CO ₂	CH_4	N ₂ O	CO ₂	CH ₄	N ₂ O	CO ₂	CH ₄	N ₂ O	
Soil depth 10 cm	0.78**	0.13	- 0.01	0.41**	- 0.22	0.30*	0.16	0.24	0.36**	
20 cm	0.82**	0.31	0.17	0.40**	- 0.23	0.38**	0.27	0.14	0.31*	
30 cm	0.81**	0.21	0.16	0.61**	- 0.23	0.34*	0.57**	0.02	0.31*	
50 cm	0.90**	0.17	0.16	0.58**	- 0.11	0.44**	0.85**	0.02	0.36*	
100 cm	0.88**	0.17	0.16	0.65**	- 0.24	0.36**	0.84**	- 0.09	0.35*	

Surface fluxes were obtained from the chamber directly above the soil air sampling capillaries

*p<0.10

**p<0.05

fluxes differing significantly between individual sites (p < 0.001). Manually measured CH₄ fluxes were positively correlated with soil temperature at the NF and IF sites, and positively correlated with soil moisture at all three sites (Fig. 5). Methane fluxes derived from auto-chamber measurements overall fluctuated in the range of those from manual chamber measurements (Figs. 2, 3 and 4), but there was no significant correlation between auto-chamber and manually measured fluxes at either site. At the NF and IF sites, manually measured CH₄ fluxes were positive (emission) during a thaw period in March 2018 and during a re-wetting period in May 2018, whereas CH_4 uptake was measured during all the remaining times. Auto-chamber measurements also suggested CH₄ emissions during these periods, as well as during January 2019 at the NF site. At the FF site, CH_4 fluxes were continuously negative (uptake) during summer 2018. During the remaining time, fluxes oscillated around the zeroline (Fig. 4e). Manually measured CH_4 fluxes at the FF site became positive shortly after a flood-event in July 2017, but emissions remained below 30 µg C m^{-2} h⁻¹, and turned into CH₄ uptake shortly thereafter. Overall, the manual as well as auto-chamber measurements did not indicate any significant CH_4 emission pulses during and after flooding (Fig. 4e). Our intensive measurements during the flood-event in March 2019 did not show any pulse CH₄ emissions either. CH_4 emissions (from the flood-water surface) increased shortly after inundation, but the increase was of minor magnitude, and fluxes rapidly declined and turned into CH_4 uptake once the water had retreated (Fig. 6).

Soil air CH₄ concentrations showed distinctive patterns at the different sites. All sites had in common that close to the soil surface (5 cm depth), soil air CH₄ concentrations were close to zero. In deeper soil layers, CH₄ concentrations reached a maximum of around ~ 5 ppm at the NF and IF sites (Figs. 2d and 3d), while deeper-soil CH_4 concentrations reached up to > 300 ppm at the FF site (Fig. 4d). At the NF site, soil air CH₄ concentrations peaked during summer 2017 at 30–50 cm soil depth, while top-soil CH_4 concentrations remained below atmospheric CH₄ concentrations at the same time. Close to the surface soil air CH₄ concentrations increased only once, to about 3 ppm, after a rewetting event in May 2018, which was accompanied by CH₄ emission from the soil surface (Fig. 2d). During October 2018 we observed a second peak in deep-soil CH_4 concentrations at the NF site (after soil rewetting in mid-September). Topsoil CH₄ concentrations nonetheless remained close to zero and soils showed pronounced CH₄ uptake during this period. At the IF site, we observed a similar increase in deep soil CH₄ concentrations during summer 2017, and an increase in topsoil CH₄ concentration during May 2018, which was as well accompanied by slight CH₄ emissions from the soil surface (Fig. 3d). At the FF site, deep-soil pore-water CH_4 concentrations were>300 ppm during June 2017, but sharply decreased after ground water drawdown during July-August and remained at low levels during winter time and during spring 2018 (Fig. 4e). Deep-soil pore-water CH₄ concentrations once again peaked in June 2018 (accompanied with low soil surface CH_4 emissions), but concentrations sharply decreased during the dry summer months and the following winter/spring period (Fig. 4e). There was no correlation between soil CH4 fluxes and the corresponding soil air or pore water CH₄ concentrations at any soil depth (Table 2).

Nitrous oxide

Soils at all three sites acted as net N₂O sources (Table 1). Manually measured N₂O effluxes during the 2 years of study ranged on average between 6.5 ± 7.1 µg N₂O–N m⁻² h⁻¹ at the NF site, $10.4 \pm 14.3 \ \mu g \ N_2 O-N \ m^{-2} \ h^{-1}$ at the IF site, and $9.4 \pm 10.5 \ \mu\text{g} \ \text{N}_2\text{O}-\text{N} \ \text{m}^{-2} \ \text{h}^{-1}$ at the FF site. There was no significant difference between the N₂O fluxes of any of the three sites. Nitrous oxide efflux was generally higher during 2017 than during 2018 at all sites (Figs. 2e, 3e and 4f). Fluxes were not correlated with soil temperature, but they were weakly positively correlated with soil moisture at the NF and the FF sites (Fig. 5). During the freeze-thaw event in March 2018, manually as well as automatically measured N₂O fluxes showed pulse emissions at the IF site (most severely frozen soil, Fig. 3e). At the NF site (only shallow soil frost), N₂O efflux increased as well, but to a lower extent (Fig. 2e). At the FF site (only frozen litter layer) the N₂O fluxes slightly increased, but remained far below the summer 2017 fluxes at this site (Fig. 4f). Auto-chamber measurements generally were in the range of manual N₂O measurements, and resembled the fluxes during the freeze/thaw periods at all sites. Auto-chamber fluxes were only significantly

correlated with the manual chamber fluxes at the IF (F=0.505, p=0.009) and the FF sites (F=0.619, p=0.0004). During the intensive measurement campaign during the March 2019 flood, N₂O fluxes from the water surface, as well as soil surface fluxes after water retreat were close to zero (Fig. 6).

Soil air N₂O concentrations peaked at all sites at all soil depths during autumn 2017, but this was not reflected in accelerated soil N₂O fluxes (Fig. 2e, 3e and 4f). A second, less pronounced increase in soil air N₂O concentrations occurred after soil rewetting in summer 2018, which was (at least at the IF site) accompanied by a simultaneous increase in soil surface N₂O emissions (Fig. 3e). During the freeze/thaw event in March 2018, soil air N₂O concentrations were exceptionally low at all three sites and at all soil depths. Soil air N₂O fluxes at the NF site, but were positively correlated at the IF and the FF sites at certain soil depths (Table 2).

Discussion

Carbon dioxide fluxes

When compared to the fluxes of CH_4 and N_2O , soil CO_2 efflux contributed overwhelmingly to the GWP of the soil GHG fluxes in the floodplain forest (>97% CO_2 eq at all three sites). Annual soil CO_2 effluxes at the NF and the IF sites were in the range of those from comparable deciduous upland forests (e.g. Epron et al. 1999; Ruehr and Buchmann 2010; Oishi et al. 2013; Warner et al. 2019). However, with more than 18 t C ha⁻¹, the soil respiratory loss at FF was about twice as high as the efflux of typical deciduous broadleaf upland forests (Warner et al. 2019), and far beyond previously reported fluxes in floodplain forests along the Danube and its tributaries (Acosta et al. 2017; Machado dos Santos Pinto et al. 2020). There are several different processes, which could have added to the high soil CO₂ efflux at our FF site. First, periodic flooding causes lateral inputs and accumulation of leaf litter at the FF site. The FF site is situated in a depression and leaf litter from surrounding areas have moved into the site with the retreating flood water. The actual rates of litter C input and loss were not quantified in our study, but we visually observed the build-up of 2–5 cm thick layers of fresh and partly decomposed leaf litter after floodwater retreat during September and October 2017. Such an input of easily decomposable C typically increases subsequent soil respiration. The litter input and accumulation could have been the cause of particularly high CO_2 fluxes (auto-chambers, Fig. 4) following the two 2017 flood events at the FF site. Another cause of high soil CO₂ efflux at the FF site could be related to the dry summer and low Danube water level (and subsequently groundwater tables). Soils at the FF site contained higher SOC stocks in the subsoil than the soils at the NF and IF sites, likely due to previous sedimentation processes and the preservation of C_{ore}, due to unfavourable anoxic conditions under constant waterlogging. During the dry summer in 2018, groundwater levels, however, fell to approximately one meter depth for almost three consecutive months. During this time, soil air CO_2 concentrations in the subsoil increased to extremely high levels. This indicates that Corg in the aerated subsoil became accessible for heterotrophic decomposers, which in turn could have significantly contributed to the soil surface CO_2 efflux. A network of cracks (clearly visible at the soil surface) could have promoted the transport of CO_2 from the deeper soil to the soil surface. As hypothesized, soil CO₂ efflux was supressed during periods of soil water-logging during and after flood events. However, such periods lasted only for a couple of days and CO₂ emissions recovered quickly thereafter.

However, how forest ecosystem C dynamics are affected by flooding and drought also depends on their effects on plant CO₂ fixation and plant C allocation. We did not assess tree biomass growth and plant C uptake in this study, but we retrieved radial wood increment cores from those trees, which were studied for stem GHG efflux in 2019, to assess if tree growth was severely negatively affected by the two dry summers. The tree ring widths from poplar (at the FF and IF sites) could not be clearly differentiated, due to the diffuse wood properties of this softwood species, but tree rings from ash did not indicate any negative effect of summer drought on wood increment growth (data not shown). This suggests that annual growth of ash tress was not affected by the dry summer conditions and further suggests that the growth of poplar was likely not affected either, especially as poplar trees develop deeper rooting systems and should have always been connected to the groundwater (Singer et al. 2013). We further did not observe any visual drought stress signs in the tree canopy at any site. If tree growth can be considered to be largely unaffected, then the dry summers had positively affected the ecosystem CO_2 balance (unchanged biomass uptake, less soil C loss) at the NF and IF sites, but negatively affected the CO_2 balance (unchanged biomass uptake, much higher soil C loss) at the FF site. It is likely that the FF site served as a net CO_2 source during 2018. The high soil respiratory loss is hardly compensable by plant biomass C uptake (Gower et al. 1996; Megonigal et al. 1997; Rieger et al. 2015) or the observed sedimentation of leaf litter.

Significant parts of the Danube watershed are calcareous, causing high limestone contents of the floodplain bedrock-gravel and high carbonate contents of the soils in the Danube National Park. Therefore, streamwater and groundwater contain high concentrations of dissolved inorganic C (DIC, HCO₃⁻ and CO_3^{2-}), which can degas and thereby contribute to the soil CO2 efflux. Accordingly, an ignorance of potential inorganic CO₂ sources could lead to an overestimation of biotic fluxes. The isotopic composition of soil CO₂ emissions (-24 to -27%) relative to soil C_{org} (-25 to -27%) clearly indicates a primary biotic source of the CO₂ emitted from the floodplain soils. Similar slight ¹³C enrichments in soil CO₂ compared to Corg was as well documented for non-calcareous forest soils (Formánek and Ambus 2004; Werth and Kuzyakov 2010). Carbon isotope fractionation during CO₂ diffusion (efflux) processes can cause a ¹³C enrichment of topsoil CO_2 by up to 4%. Therefore, our two-pool mixing model output (~6% inorganic contribution, Table S1), which neglects such isotope fractionation, marks the upper limit, and it is likely that the real inorganic contribution to the soil CO_2 efflux was even lower or negligible at all.

Methane fluxes

Contradicting our hypothesis (I) we did not observe any significant CH_4 pulse emissions during or after flooding. Even the forest soil at the FF site was a minor (- 0.7 kg CH_4 -C ha⁻¹ year⁻¹) annual atmospheric CH_4 sink. As expected, CH_4 was emitted from soil during and after flooding, but emissions were of minor magnitude, short-lived and returned to neutral fluxes or CH_4 uptake within days after flood-water retreat. This is in contrast to observations from temperate forest-wetlands, which were identified as significant regional CH₄ sources (Itoh et al. 2007; Christiansen et al. 2012; Pangala et al. 2015; Pitz et al. 2018). However, in such forests, flooding or rainwater accumulation typically leads to extended periods of water-logging due to stagnant conditions and slow drainage. The floodplains along the upper Danube typically drain well, and, depending on the severity of the flood event and the position in the floodplain landscape, surface floods typically retreat within hours to days. The low CH₄ emissions during and after flooding in our study likely were a matter of a combination of short inundation, well-draining soils and a high CH_4 oxidation capacity of the topsoils. Though we temporarily measured deep soil air or pore water CH_4 concentrations of > 100 ppm, at the same time soil CH_4 emissions from the soil surface were low or even negative. Accordingly, upward diffusing CH_4 must have been oxidized once it reached the aerated topsoil layer. This also likely was the reason for the non-correlation between any soil air CH₄ concentrations beneath 5 cm depth and the concurrent soil surface CH_4 fluxes (Table 2). The important role of aerated topsoil layers in CH₄ uptake has been documented in previous studies on peat (Macdonald et al. 1998) and floodplain forest soils (Boon et al. 1997; Samaritani et al. 2011; Jacinthe 2015), where topsoil aeration had led to a substantial reduction of the soil CH_4 efflux. Bodelier et al. (2011) reported high abundances of methanotrophic microorganisms in floodplain forest soils, and suggested that particularly active methanotrophs occur in the topsoil of frequently flooded floodplain forests. It has been suggested that tree roots can serve as conduits for CH₄ from deeper anoxic soil layers towards the atmosphere – and that the resulting stem surface emissions add significantly to the forest ecosystem CH₄ flux (Pangala et al. 2013, 2015; Schindler et al. 2020). An accompanying study quantified the CH₄ stem surface emissions at the three study sites. Stems emitted CH₄ at all three sites, but stem emissions only compensated for a minor proportion of soil CH₄ uptake (Moldaschl et al. 2021).

In the present study we were able to constrain the duration of flux events to a relatively narrow time window (some hourly during the intensive campaign during March 2019 flood+daily measurements with auto-chambers), thereby reducing the risk of overestimating single flux events, or missing them on the

other hand. Though we did not observe any pulse fluxes, the clear positive correlation of CH₄ fluxes and topsoil moisture indicates that soil CH₄ fluxes were overall driven by precipitation and flooding, while soil temperatures had less influence (Fig. 5). The non-flooded soils (at the NF and IF sites), both, were atmospheric CH₄ sinks, showing sink-strengths of -2.5 to -4.5 kg CH₄-C ha⁻¹ year⁻¹. Such atmospheric sink strengths are comparable with those of similar upland deciduous forest soils (Born et al. 1990; Bowden et al. 2000; Fender et al. 2013; Gatica et al. 2020) and a non-flooded floodplain forest along a close by Danube tributary (Traisen River, Lower Austria) (Machado dos Santos Pinto et al. 2020). The periodically flooded soils at the FF site served as weak annual net CH_4 sink, which confirms findings of Batson et al. (2015), who as well reported overall soil CH₄ uptake in regularly flooded temperate forest stands along a side river of the Potomac River (Northern Virginia, USA), and Silverthorn and Richardson (2021) who observed only slightly weaker CH₄ uptake of riparian forest soil with groundwater discharge, than without. Jacinthe (2015) also reported overall soil CH₄ uptake (-3.9 kg CH_4 –C ha⁻¹ year⁻¹) from occasionally flooded forest soils along the White River (Indiana, USA), whereas frequently flooded soils in this study were suggested as moderate CH₄ source (2.6 kg CH_4 –C ha⁻¹ year⁻¹).

Nitrous oxide fluxes

Contrary to our hypothesis, N₂O emissions did not peak after flooding or after surface- and/or ground water retreat. All three sites were annual net N₂O sources to the atmosphere, and average fluxes did not differ between sites. Higher annual cumulative N₂O fluxes during the dry year 2018 at the IF than at the NF site (Table 1) suggest that higher soil moisture positively affected the site specific N₂O production at the IF site. Soils at the IF site had higher topsoil clay contents and therefore a higher water storage capacity than soils at the NF site. The N₂O source strengths of the three sites (0.5–0.9 kg N ha^{-1} year⁻¹) were in the mid- to upper range of those of comparable temperate upland deciduous forests (Bowden et al. 2000; Kesik et al. 2005; Fan and Yoh 2020). Machado dos Santos Pinto et al. (2020) measured N_2O emissions in a similar range compared to our study in non-flooded floodplain forests along a Danube tributary. Similar N₂O fluxes as in our study were also reported by De Carlo et al. (2019). Site specific N_2O emissions did also not vary with the distance to the river body in their study. Batson et al. (2015) also measured close to zero soil N₂O emissions at all their floodplain forests, from close to the water body towards upland positions. The comparably high temporal measurement resolution in our study setup enabled us to assess the imminent effects of surface flooding on the soil N₂O fluxes. We did not observe any pulse N₂O emissions after water retreat, such as were suggested in a recent mesocosm study (Ley et al. 2018) with soils from a temperate floodplain of the Thur river (Switzerland). In our study, N₂O emissions frequently increased after surface flood events-eventually the reason for the stronger correlation between soil moisture and N₂O fluxes at the FF site (Fig. 5)—but similarly high N₂O emissions were also measured during intermediate periods, without any flooding (Fig. 4).

Clear pulse N₂O emissions were only observed during a freeze-thaw event in late winter (March 2018 at the NF and particularly at the IF site) and were not related to flooding. Nitrous oxide pulse emissions during freeze-thaw events have been observed in various ecosystems and were found to contribute significantly to the annual GHG budgets of forest soils (Kim et al. 2012; Medinets et al. 2016). The exact origin of the emitted N₂O in our study remains open, since we were not able to distinguish between specific N_2O formation processes. Nonetheless we made two interesting observations; (i) emissions already increased during the period of frost-extension into the soil, and (ii) soil air N₂O concentrations were near zero during the surface emission pulse. The early rise in N₂O emissions implies that the accelerated N₂O emissions did not result from accelerated N cycling during thaw, but rather arose from biological or physical processes which occurred already in the frozen/freezing soil. Low soil air N₂O concentrations during the simultaneously high soil surface N₂O emissions indicated that the pulse N₂O emissions during freeze/thaw originated from the very topsoil (from above the shallowest soil air sampling depth at 5 cm) or/and from the litter layer. In the frost-free study period, the positive correlations between soil air concentrations at all depths and surface N₂O fluxes (Table 2) suggest both, topsoil and deeper soil as N₂O sources.

We further hypothesized that lateral dissolved N input via surface flooding and/or moving groundwater

increases N transformation rates and consequently the soil N₂O efflux. Our observations did not confirm this hypothesis. Groundwater and Danube surface water NO_3^- concentrations were low (<2 mg l⁻) and rather caused a dilution of the soil solution N pool than adding to it (FF site). In contrast, we observed surprisingly high soil solution NO₃⁻ concentration at the sites which were not flooded during the study period (the NF and IF sites). Soil solution NO₃⁻ concentrations between 50 and 250 mg l⁻¹ as measured at the NF and IF sites are extremely high for temperate forests (Gundersen et al. 2006), and were only observed after e.g. intensive fertilization (Mortensen et al. 1998). Interestingly, the only related study we found as well reported unexpectedly high soil solution NO_3^- concentrations (>100 mg l⁻¹) at a forest site along the Thur river, and in accordance to our observations, the soil NO₃⁻ concentrations dropped to those of the river/groundwater system during and after inundation (Huber et al. 2012). The reasons for the high NO₃⁻concentrations have remained open in the study by Huber et al. (2012) as well as in our study. Our observations nonetheless suggest that NO₃-concentrations in the soil water did not promote soil N₂O efflux (N₂O fluxes were generally low despite the high NO_3^{-} concentrations in the soil solution). Soil water NO_3^- accumulation indicates rapid soil nitrification, but a low sink strength for NO_3^{-} , i.e. low soil denitrification activity, at the NF and IF sites. This further indicates that nitrifiers contribute to a greater extent to soil N₂O efflux than denitrifiers. Another explanation might be the high soil pH (7.5–7.7) at our floodplain sites. Such high soil pH values typically shift the denitrification end productratio towards N_2 instead of N_2O (Simek et al. 2002) and also lowers N2O formation during nitrification (Mørkved et al. 2007).

Conclusions

Two years of detailed soil GHG surveys at three floodplain forest sites within the Danube National Park did not reveal any evidence that the studied temperate floodplain soils emitted significantly more CH_4 and/or N_2O than soils of comparable upland forests. Surface flooding did not cause any of the expected pulse emissions of CH₄ and N₂O, and even the frequently flooded site served overall as an annual CH₄ sink. At all three sites, the GWP of the soil GHG fluxes was predominately (>97%) determined by the soil CO₂ efflux. During a year with exceptionally low summer precipitation, the annual soil CO_2 efflux was roughly twice as high at the frequently-flooded site-likely a matter of soil aeration and enhanced decomposition of SOM during the dry summer in subsoils. Hence, summer drought could result in loss of stored deep soil C to the atmosphere at frequently-flooded sites, or at sites adjacent the water bodies or with high standing groundwater tables. Carbon isotope analyses confirmed that the measured soil CO₂ fluxes were overwhelmingly related to biological activity, and that degassing of inorganic C from the calcareous soils and/or the groundwater played a minor role, if any. The spatial up-scaling was impeded by the limited site replication in this case study. Nonetheless, the extensive GHG measurements at the three sites indicate that temperate floodplain forests, such as the ones studied, unlikely represent significant regional soil GHG sources, and that the return frequency of flooding only has limited effects on annual soil GHG budgets of floodplain forests.

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Data availability Data and other relevant materials are readily available on request.

Code availability R programming code used for statistical analysis is available on request.

Declarations

Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

Consent for publication All authors consent to the submission and publication of this manuscript.

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