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Biogeochemical response to drying-rewetting in riparian soils influences carbon mobilization

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ABSTRACT

Organic-rich riparian soils in northern boreal landscapes are often the primary source of organic and inorganic carbon (C) to headwater streams. During extreme hydro-climatic events, such as droughts, the production and mobilization of C in these soils may be sensitive to changes in groundwater levels. Yet, the biogeochemical effects of drying and rewetting have been under-investigated in boreal riparian zones, particularly when compared to peat soils in discrete landscape components (i.e., mires). Here, we experimentally assess the response of riparian soil cores to simulated drought and rewetting and test whether mobilization of dissolved organic matter (DOM), carbon dioxide (CO_2), and methane (CH_4) are altered by geochemical and biological drivers over a two-month rewetting period. Drought oxidized the soil profile, upregulated activities of oxidative enzymes, and replenished terminal electron acceptors (TEAs), most notably sulfate (SO_4^{2-}), which likely suppressed DOM concentrations over the short term. However, over the longer term, soil DOM mobilization increased in response to rewetting, unrelated to the intensity of experimental drought. Enzyme activity during the rewetting phase indicates that the persistent increases in DOM may be linked to microbially-mediated decomposition of organic matter following drought. By contrast, CO_2 production was sensitive to drought intensity, with concentrations suppressed in soils subjected to the most extreme drying treatment. Elevated SO_4^{2-} concentrations also delayed the recovery of CH_4 production in soils by creating a pool of more favorable TEAs. Our results collectively show that mobilization of different C forms in riparian soils is influenced by drying-rewetting events through multiple biogeochemical mechanisms operating at different time scales. These findings have broader implications for the lateral transfer of organic and inorganic C from riparian zones to streams in response to predicted increases in climate variability.

1. Introduction

Peat soils are characterized by their high organic matter (OM) content and receive much attention due to their potential as carbon (C) sinks (Loisel et al., 2021). The formation of peat is largely caused by persistently elevated water tables, which limit oxygen availability and slow microbial degradation, leading to OM accumulation (Beer and Blodau, 2007). Such conditions are common across northern boreal landscapes, where peatlands store vast amounts of C in open mires (wetlands) and wet forests (Gorham, 1991), but also in riparian soils along headwater streams (Ledesma et al., 2018). These OM pools are vulnerable to ongoing changes in climate and hydrology (Loisel et al., 2021; Swindles et al., 2019), and are particularly sensitive to oxygenation caused by fluctuations in groundwater levels. Yet, while the effects of drought and drying-rewetting events on C cycling in discrete wetlands are well studied (Clark et al., 2012; Knorr and Blodau, 2009), how these events influence biogeochemical processes in OM-rich riparian soils has received less attention. Due to their proximity to streams, riparian zones are critical in regulating solute transport across land-water boundaries (Krause et al., 2024). Thus, how riparian soils respond to drying-rewetting events could greatly affect water quality in boreal landscapes.

OM accumulated in riparian soils along boreal streams acts as both a barrier and a source for solutes transported across the land-water interface (Lidman et al., 2017). In the case of C, boreal riparian soils often serve as the primary source of the dissolved organic matter (DOM)

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(Ledesma et al., 2018) dissolved inorganic carbon (DIC), mostly as carbon dioxide (CO_2) (Öquist et al., 2009), and methane (CH_4) (Campeau et al., 2018) supplied to streams. Overall, this lateral mobilization has consequences for the broader landscape C balance (Öquist et al., 2014), as well as implications for the co-transport of organophilic elements (e.g., Škerlep et al. (2023)), and the supply of organic energy to aquatic food webs (Berggren et al., 2010; Lupon et al., 2023). Thus, the factors that influence C mobilization in riparian soils have far-reaching effects on aquatic ecosystems and elemental cycling at landscape scales. While there has been much focus on how high flow conditions mobilize different forms of C from boreal riparian zones (e.g., Laudon et al. (2011)), these interface soils are also subject to strong fluctuations in groundwater levels in response to hydrological events (e.g., floods or drought; Baker et al. (2000)) and seasonal changes in catchment water balance (Burt et al., 2002). Such dynamics make it highly likely that drying-rewetting events are a common occurrence for organic soils along these streams.

Transitions between high and low groundwater levels can initiate a series of chemical and biological responses that influence C mobilization in riparian soils. When groundwater levels drop during periods of low flow or drought, soils become oxygenated. This replenishes the pool of available terminal electron acceptors (TEAs), upregulates aerobic microbial activity, and facilitates OM decomposition (Estop-Aragonés et al., 2012). An increase in redox potential also decreases pH and changes the solubility of OM and several other elements (Knorr, 2013; Szkokan-Emilson et al., 2013). Finally, depending on the intensity of the drought, rewetting of dry soils may also trigger pulses of microbial activity as labile OM forms become rapidly accessible (Meisner et al., 2015). Yet, the diversity and duration of different metabolic pathways in the post-wetting phase are likely constrained by the availability of TEAs generated during the dry phase (Burgin and Loecke, 2023). Additionally, microbial enzyme activity that is upregulated during dry periods may persist after soils are rewetted, continuing to influence C cycling after droughts end (Fenner and Freeman, 2011). In this way, a single drying-rewetting cycle in riparian soils could induce short-term changes in C production, but also longer-term responses that, in part, hinge on the biological and chemical responses to drying.

In addition to this mechanistic understanding, there is increasing evidence that the outcome of drying-rewetting dynamics in catchments is biogeochemically propagated through river systems. Indeed, several studies have documented an increase in the mobilization of inorganic nutrients (e.g., Loecke et al. (2017)) and DOM (e.g., Romaní et al. (2006)) when extended drought periods are followed by floods. Further, for boreal landscapes, data from riparian soils (Škerlep et al., 2023), small streams (Laudon et al., 2021b), and larger rivers (Lucas et al., 2013) all suggest that drought events can significantly increase the production of sulfate (SO_4^{2-}), which is widely known to reduce the solubility and lateral transfer of DOM (Clark et al., 2006). More recently, Tiwari et al. (2022) used long-term data to show that summer drought in boreal streams suppressed DOM concentrations, but that drier summers also led to greater DOM concentrations and altered DOM properties in ensuing autumn rainfall (see also Rulli et al. (2022)). Collectively, these observations indicate an important role for drying-rewetting cycles; however, our understanding of how physical, chemical, and biological responses to such events influence the production and fate of different C forms in riparian soils remains limited.

Here, we used a lab experiment with intact cores to ask how riparian soils along boreal headwater streams biogeochemically respond to drying-rewetting events. Our experiment simulated two levels of drought, after which we followed the production of DOM, dissolved CO_2, and dissolved CH_4 over a two-month rewetting phase. Simultaneously, we analyzed a series of biological and chemical variables that may drive or constrain the production of different C forms during drought and rewetting. We used these data to test predictions from four non-mutually exclusive hypotheses regarding the controls over C mobilization. First, given the hypothesis that SO_4^{2-} constrains DOM solubility in soils (Clark et al., 2006), we predicted that DOM and SO_4^{2-} concentrations would be inversely related during the rewetting phase. Second, we tested the hypothesis that enhanced oxidative enzymatic activity during drought can promote DOM production and that this effect can persist upon rewetting (Fenner and Freeman, 2011). This hypothesis leads to the prediction that DOM concentrations would increase due to elevated exoenzyme activity throughout the rewetting phase. Third, we tested the hypothesis that microbial CO_2 production is ultimately constrained by the availability of organic substrate in solution, and thus predicted that, during the rewetting phase, dissolved CO_2 would increase as DOM increases. Finally, we tested the hypothesis that the production of more favorable TEAs during drought would limit methanogenesis during the rewetting phase (Burgin and Loecke, 2023) and thus predicted that CH_4 production would be suppressed until other, more favorable TEAs were exhausted from the cores.

2. Methods

2.1. Site description and sampling

Soil cores for the experiment were collected from a riparian area within the Krycklan Catchment Study (KCS), in northern boreal Sweden (64°14'N, 19°46'E). The local climate is humid and subarctic, with annual mean temperatures of 1.8 °C (40 years). Approximately 30 % of annual precipitation (623 mm) is snow, with an average of 167 days of snow coverage annually (Laudon et al., 2021a). We collected cores from a riparian zone adjacent to a headwater stream (C10; Stormyrbäcken) where soils were water saturated but not flooded at the time of sampling (November 2022). Vegetation at the site was dominated by Norway spruce (*Picea Abies* (L.) H. Kartst.) and occasional birch trees (*Betula* sp.), with a layer of sphagnum moss (*Sphagnum* sp.) covering the soil. All cores were collected from a 3 × 3 m area within the riparian zone, approximately 5 m from a second-order stream. The soil profile consisted of a 35–40 cm thick peat soil layer (O horizon) underlaid by an organic-rich mineral layer (A horizon). The soils are classified as Histosols (FAO classification) and are saturated during most of the year. The moss layer and the Oi layer were removed for the core sampling to expose the soil underneath and avoid effects from fresh vegetation decomposition. Cores were collected using a custom-designed soil corer with a removable inner tube that served as the casing for the cores in the lab. The corer was made using a PVC pipe, to which a saw blade was attached at the bottom to help cut smoothly through the soil profile. The inner tube was made of 3 mm thick PC plastic that snugly fit into the soil corer. The soil cores measured 15 cm in diameter and were between 23 and 26 cm deep. Once removed from the soil corer, a water-tight lid was fitted to the bottom of cores to prevent leaking.

In total, 33 cores were collected by avoiding areas with too many roots and undecomposed wood, with a distance of at least 30 cm from each other. Soils in the cores were dominated by the Oa soil horizon, which consists of well-decomposed organic material with some fiber and a dark color. The surface (3–6 cm) Oe horizon contained mostly poorly decomposed mosses and some spruce needles. A distinct sulfidic smell was present during the soil collection, which suggests the presence of reduced sulfur (S) in the deeper soil profiles. Upon collection, the cores were brought to a dedicated climate-controlled experimental room, and the bottom lids were further sealed with aquarium-grade silicone. Once sealed, all cores were weighed to determine their initial water content and track their individual water loss through the experiment.

Using the same sampling technique as described above, we also collected five extra soil cores to characterize the site. From these, we determined the average soil water content (air-drying at 60 °C for 48 h) and soil organic matter content as loss on ignition (% LOI) over 5 h at 550 °C. Mass fractions of soil C and N were measured using an elemental analyzer (Flash EA, 2000; Thermo Fisher Scientific, Bremen, Germany).

2.2. Experimental design

The experiment was conducted in a closed climate-controlled room, where temperature/airflow could be controlled, and no other experiments were ongoing. To avoid effects from fresh decomposition or other disturbances caused by sample collection, all cores were first incubated in the dark at 7 °C for 4 months. During this time, the cores were weighed weekly any evaporated water was replaced by deionized water to maintain cores at field moisture and avoid exposure to oxygen. Two weeks prior to the start of the drought phase, the temperature in the experimental room was raised to 20 °C, to simulate summer temperatures. For soil-water sampling, a MacroRhizon sampler (length 10 cm; diameter 4.5 mm; pore size 0.15 μm; Rhizosphere Research Products, Netherlands) was inserted from the side at 5 cm above the bottom of each core (18–21 cm below the soil surface).

15 cores were randomly selected and divided into 3 equally sized drought treatment groups: Dry (75 ± 3 % water decrease from initial water weight), Semi-dry (36 ± 1 % water decrease), and Control (kept at field wetness). The two drought treatments were selected to represent an extreme scenario where pore water is largely gone (Dry), and a scenario where pore water was still present, but the water levels were decreased, and the deeper soil layers were exposed to oxygen (Semi-dry). Prior to the onset of drought, soil solution from all cores was sampled to establish pre-treatment conditions. Following the pre-drought sampling, the Dry treatments were left to dry, while any evaporated water from the Semi-dry and Control treatments was replaced by deionized water to maintain weight. During the experimental period, cores were weighed every 2–4 days to monitor the rates of drying and replenish water in cores that were not undergoing drying. To further mimic drought conditions, air circulation was increased, and a dehumidifier was installed in the experiment room after 2 weeks. Once Dry cores lost approximately 35 % of their water, we started drying the Semi-dry cores. The total drought duration was 43 days for the Dry cores and 14 days for the Semi-dry cores, at which point the Dry and Semi-dry cores lost 75 ± 3 % and 36 ± 1 % of their pre-drought water content.

After the drought, each core was rewetted to its pre-drought condition by placing the core on a scale and slowly adding deionized water until the pre-drought weight was reached. Soil solution from each core was then sampled eight times over 57 days, during which time any water lost through evaporation or sampling was restored to weight.

2.3. Soil water sampling and analysis

Soil water was sampled with MacroRhizon samplers, using 50 mL syringes to apply under-pressure over 7–8 h. As soon as the syringe was removed from the sampler 5 mL of soil water was subsampled for dissolved inorganic carbon (DIC) analysis. Samples were then taken and analyzed for enzyme activity assays. Between each subsampling, the syringes were capped to prevent oxygenation of the remaining soil water sample. The remaining soil water was filtered (0.45 μm), measured for pH (Mettler Toledo), and subsampled for DOC, Fe determination, ion chromatography (IC), and nutrient analysis. Following each sampling, the cores were weighed and refilled with deionized water to their pre-drought weight.

Samples for DIC and DOC were stored cold (4 °C), while the samples for inorganic nutrients and anions (SO_4^{2-} & Cl^-) were stored frozen (−18 °C) until analysis. Subsamples for DOC analysis were acidified (200 μL of 2 M HCl to 20 mL sample). DOC was measured by combustion (870 °C) of acidified water samples (bubbled with O_2) and then analyzed with an infrared gas analyzer (Formacs HT-I from Skalar). Dissolved nutrients were analyzed on a segmented flow analyzer (QuAAtro 39, SEAL analytical). Nitrate-N (as nitrate + nitrite; NO_3^-) was measured after reagents and samples passed a copperized cadmium reduction coil to form an azo dye [method: MT3B Q-126-12 Rev 1]. Ammonium-N (NH_4^+) was measured with the salicylate method [method: Q-033-04 Rev. 8] and phosphate-P (PO_4^-) with the molybdenum blue method [method: MT3A Q-125-12 Rev 1]. Fe^{2+} and total Fe were determined using a colorimetric Ferrozine method adopted from Huang and Hall (2017). Briefly, 100 μL of sample was mixed with 2 mL of color reagent (1 g L−1 Ferrozine in 0.5 M HEPES buffer adjusted to pH 8 with NaOH) and 100 μL MQ water to determine Fe^{2+}. For total Fe, 100 μL of sample was first mixed 10 % hydroxylamine hydrochloride to reduce all Fe, and then the color reagent was added. The mixtures were then incubated for 30 min and Fe concentrations determined on a HORIBA Aqualog spectrophotometer at 562 nm. Standards for Fe^{2+} ($(NH_4)_2Fe\ (SO_4)_2{\bullet}6H_2O$) and Fe^{3+} ($FeCl_3$) dissolved in 0.5 M HCl were used for every sampling occasion.

2.4. DIC and CH_4 analysis

DIC concentrations and speciation were determined using a headspace method where 5 mL of soil solution was injected into a 22.5 mL glass vial with N_2 headspace. The vials were preinjected with 0.1 mL 85 % H_3PO_4 to acidify the sample and release any DIC into the headspace of the vial. The concentrations of CO_2 and CH_4 in the headspace gas samples were then determined using a GC-FID (PerkinElmer Clarus 500; Waltham, MA, USA) equipped with a methanizer operating at 250 °C and connected to an autosampler (PerkinElmer Turbo Matrix 110; Waltham, MA, USA). Other DIC species (i.e., HCO_3^- and CO_3^{2-}) were calculated using equations for carbonate equilibrium and accounting for differences in pH. Due to the low pH in our soil water, HCO_3^- and CO_3^{2-} represented an insignificant proportion of the total DIC and were therefore omitted from the analysis. Thus, hereafter, we only refer to concentrations of CO_2.

2.5. Enzyme assays and Attenuated Total Reflectance Fourier Transform Infrared Spectroscopy

We used colorimetric assays to measure rates of phenol oxidase and peroxidase enzyme activities. Phenol oxidase and peroxidase activities were measured simultaneously using modified methods from Saiya-Cork et al. (2002) and Prosser et al. (2011). Briefly, 100 μL of sample was mixed with 100 μL of 50 mM sodium acetate buffer (pH 5) and 25 μL of 10 mM L-3,4-dihydroxyphenylalanine (L-DOPA) in 96 well plates, with 5 μL of 0.3 % peroxide (H_2O_2) solution added to the peroxidase assay. Plates were incubated at room temperature for 24 h and then analyzed for absorbance at 450 nm. Peroxidase activity is determined by subtracting phenol oxidase activity. All absorbance was measured with a BioTek Epoch Microplate Spectrophotometer (Agilent Technologies, Santa Clara, CA). All enzyme activities were assayed in triplicate with controls and concentrations were corrected for incubation length after analysis.

Attenuated Total Reflectance Fourier Transform Infrared Spectroscopy (ATR-FTIR) allows for analysis of liquid samples without requiring extensive sample preparation (Fomina et al., 2023). This allowed us to obtain information on the DOM functional group composition directly from the filtered soil water samples. Measurements were recorded in the mid-infrared (MIR) region 4000–400 cm^{-1}, with a resolution of 2 cm^{-1} on a Bruker Vertex 80v FT-IR spectrometer (vacuum bench) with DTGS and MCT detector. For each sample, 100 scans were averaged and corrected against ambient air (H_2O and CO_2) as background. All samples were baseline corrected and normalized by total area to allow for better comparison of samples regardless of signal intensity. MRC-ALS was performed to resolve a component with water vapor peaks, and the data were recombined by removing the component. Interpreting FTIR spectra of soil water is challenging due to their complex composition, which includes an undefined mixture of various organic and inorganic components. A definite assignment, feasible for defined organic substances, is impossible for soil water samples since overlapping absorption bands from various components create a summed FTIR spectrum. Therefore, rather than determining specific compounds, we evaluated the relative absorption bands that are specific for functional groups (summarized in

Table 1
Assignment of FTIR peaks to specific OM functional groups.

Peaks	Assignment	References
950 cm^{-1}	C–O–C and C–O stretching vibrations in polysaccharides	Tandy et al. (2010)
1075 cm^{-1}	Ester, phenol C–O–C, C–OH stretch, attributed to polysaccharides or polysaccharide-like compounds	Chapman et al. (2001) Artz et al. (2008)
1415 cm^{-1}	Aliphatic C–H bend or Phenolic C–O stretch, OH deformation	Biester et al. (2014) Artz et al. (2008)
1612 cm^{-1}	Aromatic C=C stretch and/or carboxylate C–O asymmetric stretch and/or conjugated ketone C=O stretch	He et al. (2011) Chapman et al. (2001)
1712 cm^{-1}	Free organic acid carboxylic C=O	Chapman et al. (2001) Artz et al. (2008)
1735 cm^{-1}	Carbonyl C=O stretch	Artz et al. (2008)

Table 1) within the DOM pool. The change in functional groups was done by calculating the proportion of different groups relative to the amount of polysaccharides.

2.6. *Statistical analysis*

Repeated-measures ANOVAs were used to assess the effects of drought treatment, time, and any interactions between the two. Tukey HSD post-hoc tests were then used to test the effects of the treatments at each sampling occasion and the effect of time on each level of drought treatment. Finally, t-tests were used for pairwise comparisons of drought treatments at each time point. Bonferroni corrections were done to avoid type I errors and adjusted p-values (p_{adj}) are reported. Spearman's rank correlation was used to test the strength and direction of association between variables. Linear regressions were performed to determine the slope (β) and relationships between variables. In text, significant relationships ($p < 0.05$) are referred to as weak (r value 0–0.39), moderate (0.4–0.59), and strong (0.6–1), where specific r values are not presented. Statistical analysis and figure production were done in R Studio (version 4.2.2; R Core Team, 2024).

3. Results

Soil properties and solute concentrations were similar across the 15 cores at the outset of the experimental drought, with no significant differences between cores assigned to different treatments (Table 2).

3.1. *DOM dynamics*

In the Control treatments, DOC concentrations increased slightly following the drought period, after which they remained constant for the 57 days following rewetting (Fig. 1). Immediately following rewetting DOC concentrations in the Semi-dry (47 mg L^{-1}) and Dry (44 mg L^{-1}) treatments decreased in comparison to Controls (Day 1; $p_{adj} < 0.05$). By Day 9, DOC concentrations in both dried treatments (Dry and Semi-dry combined) recovered to levels comparable to Control treatments (78 mg L^{-1}). After 21 days, DOC concentrations were higher in the dried treatments than in the Controls (significant treatment effect from Day 34; $p_{adj} < 0.01$). Thereafter, the Semi-dry and Dry treatments exhibited increases in DOC concentrations by an average of 96 % and 98 %, respectively, over the length of the experiment ($p_{adj} < 0.001$), while there was no significant effect of time on Control treatments. The intensity of drying (i.e., Dry vs. Semi-dry), however, did not affect DOC concentrations at any point in the experiment.

3.2. *Inorganic solutes*

In response to drying, average soil solution pH initially decreased from 4.5 to 3.8 (SD 0.24) in the dried cores on the first day of the rewetting phase, and then slowly recovered to pre-drought conditions by day 14 (data not shown). Dissolved inorganic N following rewetting was mainly present as NH_4^+ (average 3.5 mg L^{-1}, SD 1.8) with negligible amounts of NO_3 (average 17 μg L^{-1}, SD 17) throughout the experiment (data not shown). NH_4^+ concentrations gradually increased throughout the experiment in all treatments, but there was no significant treatment effect at any time point. By comparison, concentrations of SO_4^{2-} were low (<1.2 mg L^{-1}) in all treatments during the pre-drought period but increased significantly in response to drying and rewetting ($p_{adj} < 0.001$; Fig. 2). Three days after rewetting, average SO_4^{2-} concentrations increased to 21 mg L^{-1} in Dry treatments and 17 mg L^{-1} in Semi-dry treatments. Concentrations in dried treatments remained elevated ($p_{adj} < 0.001$) relative to Controls during the first 9 days after rewetting but decreased drastically by day 14 and returned to pre-drought values by day 21 ($p_{adj} > 0.05$). In Control treatments, SO_4^{2-} concentrations remained low throughout the experiment (Fig. 2). SO_4^{2-} concentrations in Control treatments were not correlated with DOC concentrations; however, SO_4^{2-} was strongly negatively correlated with DOC in Dry ($\beta = -1.7$, $r = -0.67$, $p < 0.001$) and Semi-dry treatments ($\beta = -3.0$, $r = -0.70$, $p < 0.001$). Chloride concentrations showed no significant change in any of the treatments over time (Supp. Fig. 1). Finally, Fe^{2+} concentrations decreased in dried treatments on day 1 but recovered quickly and showed no significant differences with Controls on any other days ($p > 0.05$, Supp. Fig. 2). In general. both Fe^{2+} and total Fe concentrations varied unpredictably during the experiment in all treatments and showed no clear trends.

3.3. *Enzymatic activity*

Average rates of enzyme activity increased in both Dry and Semi-dry treatments following rewetting, although rates between Control and dried treatments were not statistically different except on day 1 (Fig. 3). Phenol oxidase activity was generally low throughout the experiment but was elevated in dried treatments between days 3–9 (average; Dry = 0.27, Semi-dry = 0.26, Control = 0.12 nmol L-DOPA h^{-1}). After 14 days, phenol oxidase activity in dried treatments decreased and remained similar to Control treatments. Overall, peroxidase activity was higher than phenol oxidase activity and progressively increased over time in both dried treatments. From day 6, both Dry and Semi-dry treatments had higher rates of peroxidase activity than the Control treatment (average from day 6; 4.8 and 5.1 compared to 4.0 nmol L-DOPA h^{-1}), although these relationships were never significant ($p_{adj} > 0.05$) due to

Table 2
Soil properties, including organic matter content (OM%), C:N ratio, and percent water content, and average pre-drought solute concentrations in the soil cores.

	Soil properties (n = 5)			Pre-drought soil solution (n = 15)							
	OM %	C:N	Water	pH	DOC	CO_2	CH_4	SO_4	NO_3	NH_4	PO_4
	LOI		%		mg C L^{-1}			mg L^{-1}			
Mean	94	25	87	4.5	66	33	3.1	0.3	0.013	1.1	1.7
SD	0.5	1.4	1.6	2.9	17	6.0	1.1	0.3	0.002	0.47	2.3

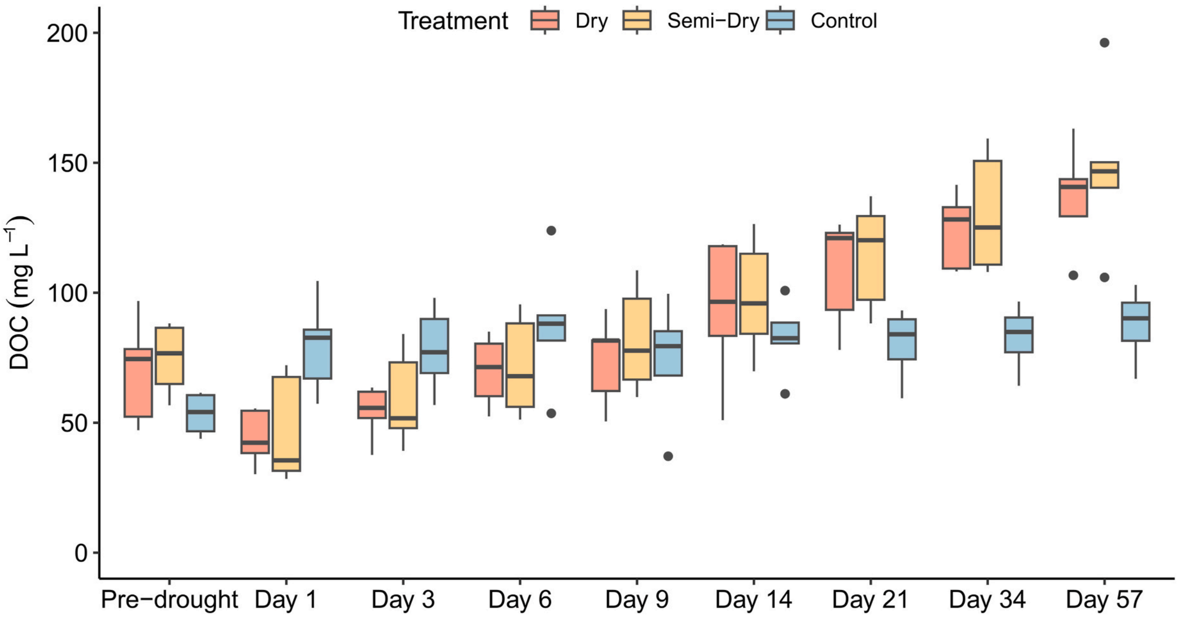

Fig. 1. Changes in soil solution DOC concentrations under different drought treatments over time in a laboratory experiment on boreal riparian soil. Box plots show the median (n = 5) with whiskers to the 1st or 3rd quartiles, and black dots represent outliers.

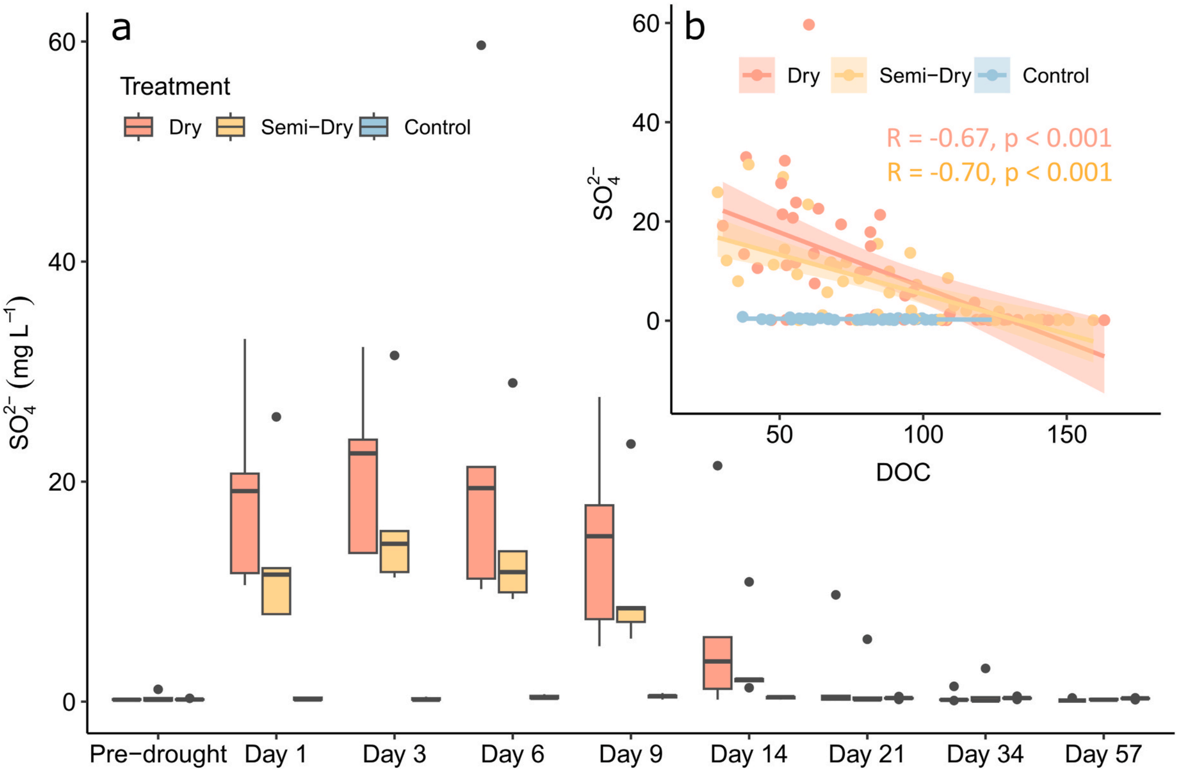

Fig. 2. (a) Changes in soil solution sulfate (SO_4^{2-}) concentrations under different drought treatments over time in a laboratory experiment on boreal riparian soil. Box plots show the median (n = 5) with whiskers to the 1st or 3rd quartiles, and black dots represent outliers. (b) Linear relationships (solid lines) between SO_4^{2-} and DOC in the different treatments throughout the experiment. Solid lines and confidence intervals (95 %) represent significant relationships, while the dashed (blue) line indicates a non-significant relationship. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

the high variance within treatments. Nonetheless, considering all sample dates, peroxidase activity was strongly positively correlated with DOC concentrations in Semi-dry ($\beta = 19$, r = 0.78, $p < 0.001$) and Dry treatments ($\beta = 17$, r = 0.72, $p < 0.001$), while there was no significant correlation between these variables in Control treatments (Fig. 4).

3.4. *Organic matter composition*

The FTIR spectra collected from our soil solutions were typical of peat material, with high absorption in the regions 3400 - 3200, 3000 - 2800, and 1800 - 800 cm^{-1} (Artz et al., 2008). Peaks in the 1800 - 800 cm^{-1} region showed a mixture of OM functional groups including

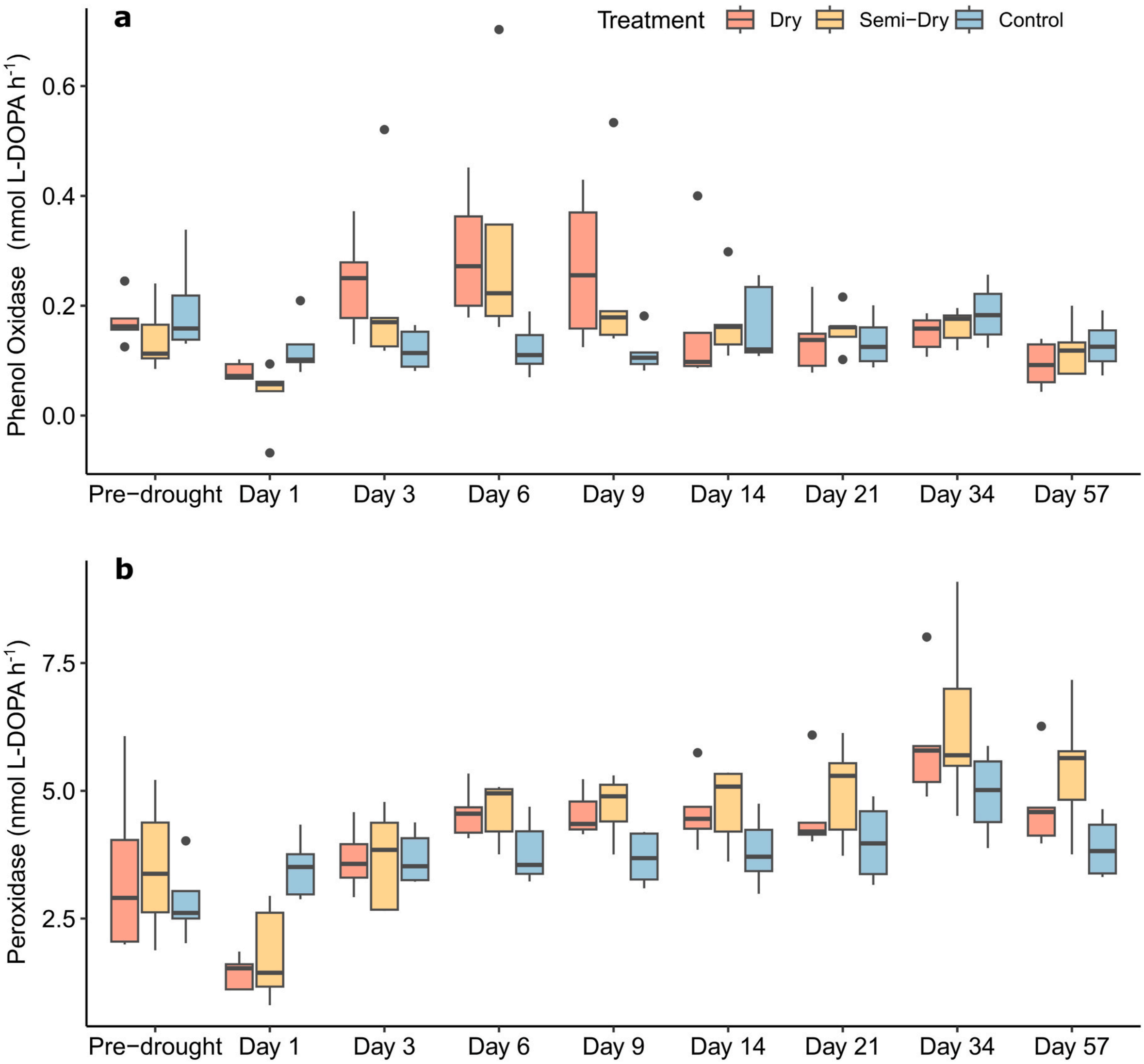

Fig. 3. Changes in soil solution (a) phenol oxidase and (b) peroxidase activity under different drought treatments over time in a laboratory experiment on boreal riparian soil. Box plots show the median (n = 5) with whiskers to the 1st or 3rd quartiles, and black dots represent outliers.

polysaccharides (950 cm^{-1} and 1075 cm^{-1}), phenolic and aliphatic structures (1370-1470 cm^{-1}), aromatic and/or aliphatic carboxylates (1612 cm^{-1}), and C═O bonds in esters and free organic acids (1735 cm^{-1} & 1712 cm^{-1}). A strong inorganic SO_4^{2-} peak at ~1120 cm^{-1} (S═O stretching), overlapped with the peak at ~1075 cm^{-1}, therefore we used the 950 cm^{-1} peak as further confirmation of the polysaccharide indicator (Supp. Fig. 3). Directly post-drought, there was a decrease in the 1712/1735 ratio, which suggests a relative increase in non-conjugated esters and a decrease in carboxylic acids, which could reflect reduced organic acid mobility due to protonation under lower pH (Hruška et al., 2003). Some changes in DOM functional groups persisted even on days 34 and 57, when dried cores exhibited higher 1612/1075, 1712/1075, and 1415/1075 ratios, indicating a relative increase in aromatic, carboxylic, and aliphatic moieties, and a relative decrease in polysaccharides (Supp. Fig. 3). These ratios have previously been used as a humification index and suggest that once anoxic conditions reestablish, the DOM contains a higher humic content (Broder et al., 2012). In addition, this indicates that the DOM was more oxidized (higher 1712/1075) and with a higher recalcitrance (1612/1075) in the treatments exposed to drought. Drought did, however, not affect the proportion of aromatic to aliphatic moieties (1612/1415).

3.5. CO_2 and CH_4 dynamics

Average pre-drought CO_2 concentrations across all soil cores were 33 mg C L^{-1}. After rewetting, concentrations of both CO_2 and CH_4 decreased drastically in Dry and Semi-dry treatments (Fig. 5a). CO_2 concentrations in dried treatments remained significantly lower than in Controls for the first 3 days ($p_{adj} < 0.01$), after which there were no significant differences between the Control treatment and either of the dried treatments. Interestingly, however, beginning on day 6, there was a notable difference between Semi-dry and Dry treatments, with higher concentrations in Semi-dry treatments (significant only for days 6, 9 & 21). In Dry treatments, average CO_2 concentrations were highest on day 14 (25 mg C L^{-1}), while in Semi-dry treatments, concentrations continued to increase until day 34 (38 mg C L^{-1}). For both the Semi-dry ($\beta = -1.7$, r = 0.73, $p < 0.001$) and Dry ($\beta = -1.9$, r = 0.61, $p < 0.001$) treatments, there was a strong significant relationship between CO_2 and DOC, while this was not the case for Control treatments (Fig. 6a).

CH_4 concentrations decreased to near zero after the drought and remained low for 14 days following rewetting (Fig. 5b). From day 21, concentrations in both dried treatments gradually increased and matched pre-drought concentrations by day 57. The increase coincided with the loss of SO_4^{2-} and produced the excluding relationship between CH_4 and SO_4^{2-} (Fig. 6b). There were no significant differences between

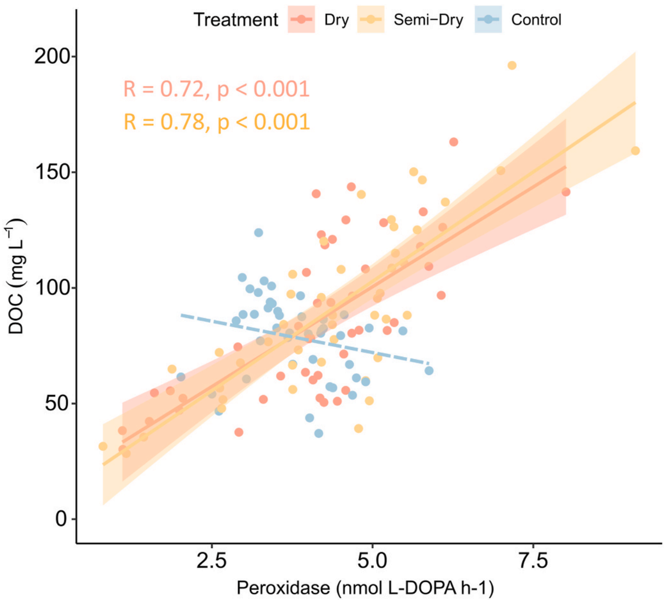

Fig. 4. Linear relationships between soil solution peroxidase activity and DOC concentrations in a laboratory experiment on boreal riparian soil. Solid lines and confidence intervals (95 %) represent significant relationships, while the dashed line indicates a non-significant relationship.

Dry and Semi-dry treatments, although CH_4 concentrations were slightly higher in Semi-dry treatments during the last two sampling occasions. In Control treatments, CH_4 concentrations showed a slight, albeit insignificant, decrease over time ($p_{adj} = 0.85$).

4. Discussion

Organic-rich riparian soils line boreal headwater streams and are an important source of C to surface waters (Ledesma et al., 2018). The biogeochemical conditions created by interactions with groundwater make these soils sensitive to fluctuations in water tables, including prolonged periods of drought (Knorr et al., 2009). Our experimental drought clearly altered soil redox conditions, oxidized reduced elements, and led to an initial decrease in DOM concentrations upon rewetting. After this initial response, soils returned to pre-drought redox conditions; however, DOM concentrations continued to increase throughout the experiment. Although drought intensity did not influence DOM concentrations, extreme drought suppressed dissolved CO_2 production throughout the rewetting phase. CH_4 production, on the other hand, was suppressed until other favorable TEAs were exhausted. Our findings highlight the need to understand both the immediate and longer-lasting effects of drought on the biogeochemistry of organic riparian soils. Given expected increases in the occurrence of extreme hydro-climatic events in high-latitude systems (Balting et al., 2021; Bevacqua et al., 2024), these longer-term drought effects in particular could play an important role in shaping the biogeochemical conditions of boreal headwater streams.

4.1. Short-term effects on redox condition and DOM dynamics

Initial biogeochemical responses following rewetting were indicative of changes in redox chemistry caused by the oxygenation of normally anoxic, organic rich soils (Weyer et al., 2018). In low relief boreal landscapes, riparian zones are characterized by high water tables and high organic matter content, which together promote anoxic conditions (Ledesma et al., 2018). As expected, our experimental drought oxidized these soils, which was most evident from the high SO_4^{2-} and low CH_4 concentrations observed upon rewetting. Iron, another indicator of changing redox conditions, behaved unpredictably in this study, potentially owing to complicated interactions with DOM in peat soils, which could also have caused problems with the ferrozine method used (Bhattacharyya et al., 2018). Organic-rich soils can contain considerable amounts of sulfides (Skyllberg et al., 2003), which are oxidized to SO_4^{2-} in the presence of oxygen. Consistent with our first hypothesis, this change in redox chemistry and increase in SO_4^{2-} led to a decrease in DOM concentrations immediately after rewetting. Concurrently, we observed a relative decrease in FTIR peaks related to free organic acids, which are protonated under lower pH and therefore less soluble in water (Evans et al., 2012). The increase in SO_4^{2-} concentrations is accompanied by an increase in H^+, which protonates DOM molecules, thereby making them less soluble in water (Tipping and Woof, 1990). In the present study, the change in pH after drought corresponds to a ~6x increase in H^+ concentrations. This strong negative relationship between SO_4^{2-} and DOM (Fig. 2b) has often been observed in both soil and freshwater environments, with established links to surface water browning (Clark et al., 2006, 2012). Despite this evidence that the lower DOM concentrations were caused by an increase in SO_4^{2-}, we cannot completely exclude that some DOM was broken down during the drought phase and that there was less soluble OM available for dissolution upon rewetting. During drought, water was only lost from the cores through evaporation, meaning that most ions stayed in the cores, and there should not be any major changes in ionic strength upon rewetting. This notion is supported by the fact that chloride concentrations remained consistent throughout. Nevertheless, we cannot exclude that some of the changes on day 1 were related to slow dissolution rates and changes in the soil solution matrix.

It is generally held that high SO_4^{2-} concentrations during periods of peak atmospheric deposition led to a suppression of DOM, with subsequent recovery leading to the widely observed trends in surface water browning (Monteith et al., 2007). While sulfur deposition levels in the Krycklan Catchment have largely receded to preindustrial levels (Laudon et al., 2021a), the legacy of these inputs can still be found in organic soils that contain large amounts of sulfides (Skyllberg et al., 2003; Szkokan-Emilson et al., 2013). As evident from this and other studies, extreme drought and subsequent rewetting create pulses of SO_4^{2-}, which temporarily lower DOM concentrations in both soils and associated freshwaters (Clark et al., 2005; Ledesma et al., 2016; Škerlep et al., 2023). Such patterns have also been observed on larger scales and are suggested to temporarily control DOM dynamics (Szkokan-Emilson et al., 2013). Although dramatic, this immediate change to redox chemistry was rather short-lived in our experiment. Indeed, after approximately 9 days, SO_4^{2-} concentrations rapidly decreased, suggesting that other, preferred TEAs had been consumed, and the reduction of SO_4^{2-} to sulfides became the most efficient pathway for microbial metabolism. The speed of this transition reflects the modest pools of SO_4^{2-} generated during experimental drought, but also the notably low concentrations of NO_3, a more favorable TEA, which showed no response to soil oxidation, potentially because net nitrification is constrained under such acidic conditions (Ste-Marie and Paré, 1999). In a similar experiment on an ombrotrophic peat in the UK, SO_4^{2-} concentrations decreased about two weeks after rewetting and returned to pre-drought levels by week four (Clark et al., 2006). This difference in recovery rate likely reflects the much higher sulfur deposition rates in the UK than in northern Sweden, resulting in considerably higher SO_4^{2-} concentrations after drought (>60 mg L^{-1}; Clark et al. (2006)).

4.2. Long-term changes to DOM dynamics

While the short-term effects of drought on DOM dynamics in organic soils are reasonably well understood, the long-term effects remain less clear. In our experiment, DOM concentrations recovered to pre-drought conditions within 9 days but then continued increasing to almost double pre-drought levels over two months. This longer-term change could reflect a legacy effect of drought on microbial metabolism and/or changes to OM properties that increase its mobility in soils. Accordingly,

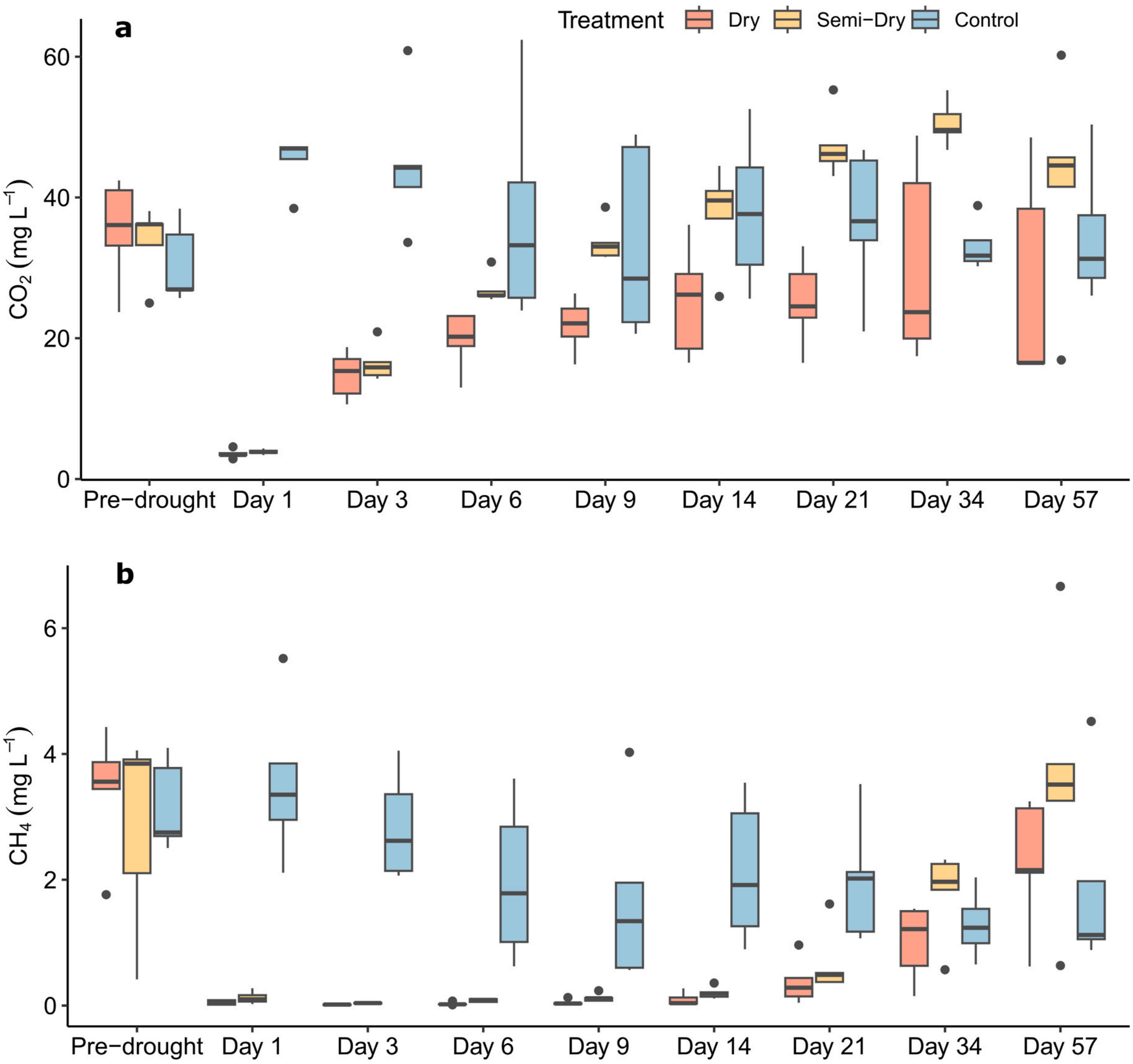

Fig. 5. Changes in soil solution dissolved CO_2 (a) and CH_4 (b) concentrations under different drought treatments over time in a laboratory experiment on boreal riparian soil. Box plots show the median (n = 5) with whiskers to the 1st or 3rd quartiles, and black dots represent outliers.

drought-induced increases in oxygen and other TEAs allow for higher rates of microbial decomposition and thereby higher production of DOM and CO_2 (Bragazza et al., 2016; Sutton-Grier et al., 2011). However, once more favorable TEAs are consumed, one would assume that decomposition rates should regress to pre-drought levels, and DOM would not increase further. Despite this expectation, DOM concentrations continued to increase long after SO_4^{2-} was consumed.

Another potentially important post-drought TEA in organic soils is dissolved OM itself, which can act as both an electron donor and acceptor, depending on redox conditions (Klüpfel et al., 2014; Yu et al., 2016). In the context of our study, this would suggest that OM oxidized during the drought could sustain increased levels of microbial respiration by acting as a TEA. While our FTIR results show that the DOM pool was more oxidized following drought (ratio between carboxylic groups and polysaccharides; 1712/1075), CO_2 concentrations did not exceed pre-drought levels, making this mechanism unlikely. The onset of methanogenesis by day 21 further suggests that redox conditions returned to pre-drought levels by the time we started to observe elevated DOM concentrations. Thus, while we see a strong correlation between DOM and CO_2 in dried treatments (both Dry and Semi-dry), it would appear that the continued increase in DOC is not directly linked to post-drought changes in microbial respiration.

Consistent with our second hypothesis, our results instead suggest that observed increases in DOM during rewetting were linked to a persistent, drought-induced change in the enzymatic breakdown of complex organic molecules. Microbes generate extracellular enzymes to help degrade and transform OM, both possible pathways that lead to increased DOM in the post-drought period (Sinsabaugh, 2010). Although there was no significant treatment effect overall, both enzymes were elevated at timepoints following drought: phenol oxidase was notably high during the early stage of rewetting, whereas peroxidase showed a slower progression of change. Phenol oxidase and peroxidase are produced for a variety of reasons (Sinsabaugh, 2010), but both enzymes are involved in breaking down complex organic molecules (e.g. lignin) and can be expressed for microbial C and N acquisition. In peat soils, high quantities of phenolic compounds inhibit hydrolytic enzyme activity, which slows down OM decomposition (Verhoeven and Liefveld, 1997; Wetzel, 1992). Microorganisms can excrete phenol oxidase to break down recalcitrant phenolic molecules, but this enzyme requires oxygen, limiting its function in anoxic environments. Such inhibition of OM decomposition has been dubbed the enzymic “latch”, and is suggested to be in part responsible for the high OM accumulation in anoxic environments (Freeman et al., 2001). Episodic oxygenation of riparian soils during drought should therefore promote phenol oxidase activity,

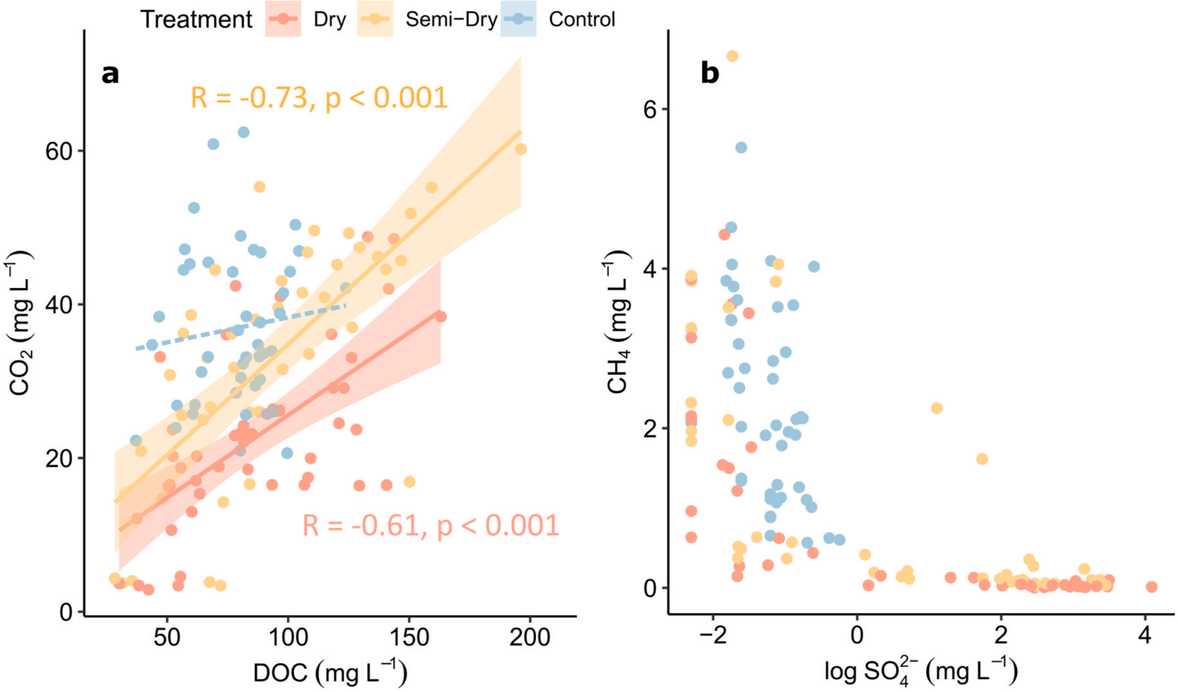

Fig. 6. Linear relationships between soil solution (a) DOC and CO_2 concentrations, and (b) log(SO_4^{2-}) and CH_4 concentrations in a laboratory experiment on boreal riparian soil. Solid lines and confidence intervals (95 %) represent significant relationships, while dashed or no lines indicate a non-significant relationship.

thereby removing phenolic compounds, and increasing OM breakdown by hydrolytic enzymes after rewetting (Worrall et al., 2005). Over the years, the effects of the enzymic "latch" have been heavily debated, with support both for (Pinsonneault et al., 2016) and against (Hall et al., 2014; Urbanová and Hájek, 2021) its relevance to C cycling in peat soils. However, while our results are consistent with increases in phenol oxidase post-drought, the FTIR results did not indicate a decline in phenolic compounds (1415/1075). Assessing the influence of phenol oxidase on DOM may require additional measurements of soil phenolic contents and post-drought activity of hydrolytic enzymes.

Peroxidase activity is also linked to OM decomposition (e.g. Tian and Shi, 2014), and for this enzyme we observed a strong correlation with DOM concentrations in dried treatments (Fig. 4), suggesting that its activity may be responsible for the increases in DOM during the rewetting phase. Contrary to phenol oxidase, peroxidase has been shown to be active even under anoxic conditions (Merino et al., 2020). This would allow for continued elevated rates of OM breakdown even after the onset of anoxia. By oxidizing phenolic compounds, peroxidase releases carbohydrates and proteins (Tian and Shi, 2014), which directly increases DOM concentrations and can also act as a substrate for microbes to further break down OM. Indeed, the FTIR spectra showed an increase in oxidized (carboxyl groups) and more recalcitrant functional groups (aromatics, aliphatic), likely produced during the breakdown of polysaccharides (Biester et al., 2014). Small organic acids and other polar organic molecules are considerably more water soluble than long polysaccharide chains such as cellulose. A higher proportion of these more water-soluble organic compounds, such as organic acids, could potentially explain why DOM concentrations increase in drought-exposed treatments. Overall, we cannot resolve the precise mechanisms behind the observed longer-term increases in DOM following drought. However, our results suggest that post-wetting DOM mobilization results not only from changes in redox but also from either increased microbial excretion of enzymes or a renewed capacity of existing enzymes to form complexes with OM (Sinsabaugh, 2010).

4.3. CO_2 and CH_4 dynamics

Headwater streams are often important sources of CO_2 to the atmosphere, and a large fraction of this gas is imported from near-stream soils (Campeau et al., 2018; Hope et al., 2001; Hotchkiss et al., 2015). In this sense, our experiment provides direct insight into how the potential for riparian soils to contribute CO_2 to streams may be altered by drying-rewetting dynamics. During drought, the lack of hydrological connectivity and exposure of soil pores to the atmosphere decreases lateral export and increases direct vertical losses of soil gas (Hope et al., 2001; Smith et al., 2017), which were not captured in our study. Following rewetting, CO_2 concentrations were initially low and increased toward pre-drought levels over several weeks. These initially low concentrations likely reflect the rapid flushing of aerated soils with water, which diluted an already weak dissolved CO_2 signal. The recovery of CO_2 during the rewetting phase was likely aided by the increased availability of O_2 and other TEAs to soil microbes, but also by parallel increases in DOM. Indeed, consistent with our third hypothesis, the change in CO_2 in the post-drought phase was strongly correlated with DOM concentrations (Fig. 6), suggesting that increased organic energy supply augmented microbial respiration during drought recovery. If this correlation is causal, it would suggest that, while microbial metabolism is not important for driving DOM mobilization following drought, the increases in DOM may nonetheless be influencing microbial metabolism and CO_2 production.

Somewhat surprisingly, CO_2 increased more rapidly in Semi-dry than in Dry treatments, suggesting that drought intensity affected microbial respiration. This is especially interesting since drought intensity did not affect either DOM or SO_4^{2-}, suggesting the effect on CO_2 did not result from a change in substrate availability or redox conditions. Rather, it is likely that extreme drought slowed down the post-drought recovery of the microbial community, which led to lowered microbial respiration (Meisner et al., 2015; Stirling et al., 2020). In addition, extreme drought could have affected soil OM properties. For example, the lack of porewater during extreme drought could make OM more hydrophobic and therefore less accessible for microbial decomposition during the rewetting phase (Goebel et al., 2011). However, our results did not indicate any changes to DOM composition that would suggest differences in OM hydrophobicity between drought treatments. Regardless of the mechanism, our findings indicate that extreme droughts may lead to lower lateral exports of CO_2 to streams in post-wetting time. On the other hand, intermediate drought intensity (i.e., Semi-Dry treatment) may slightly increase riparian CO_2 concentrations after rewetting and sustain elevated loading to streams over several months. The increase in DOM exports could also lead to higher stream CO_2 production and emissions within the aquatic network during post-rewetting periods (Lupon et al., 2019).

Small boreal streams can support globally high rates of CH_4 evasion (Campeau and Del Giorgio, 2014; Rocher-Ros et al., 2023), and a large fraction of this gas is produced in near-stream soils (Lupon et al., 2019). Our results show that periods of drought aerate soils, downregulate the net production of CH_4, and increase production of more favorable TEAs, which then suppress methanogenesis after rewetting (Knorr and Blodau, 2009; Yu et al., 2016). Thus, consistent with our hypothesis, only once concentrations of SO_4^{2-} decreased (~21 days) did we observe the slow onset of CH_4 accumulation in riparian soils (Fig. 6b). By comparison, the observed CH_4 decrease in Controls over the course of the experiment likely reflects the gradual consumption of labile substances that can be fermented to acetate, which is the main organic precursor for methanogenesis in peat soils (Bonaiuti et al., 2020). Our findings suggest that drying-rewetting events that mobilize SO_4^{2-} in riparian soils may have particularly important consequences for methanogenesis. Such events are well-documented in northern landscapes, including Krycklan, and while their implications for riparian DOC mobilization have received attention (e.g., Ledesma et al. (2016); Škerlep et al. (2023)), their effects on CH_4 dynamics have been largely ignored. In this context, more work is needed to evaluate whether the signals from this mechanism can be observed in stream CH_4 records.

4.4. Implications for lateral C transport and conclusions

Across boreal headwaters, riparian soils act as important sources of C to streams (Ledesma et al., 2018; Lupon et al., 2019), with the forms and amounts depending on the biogeochemical and hydrological conditions of riparian soils (Grabs et al., 2012). Our results show that, while droughts surely alter the hydrological pathways in the catchment, they also change the capacity of riparian soils to act as sources for dominant forms of organic and inorganic C supplied to boreal streams. Such changes would likely come during the rewetting period in autumn, and it is unclear from our experiment how long these effects might last. Additionally, contrary to previous research (Tiwari et al., 2022), we found that the intensity of drought did not affect post-drought DOM concentrations. This difference suggests that post-drought recovery observed in the field may reflect both the local effect of drying studied here but also the broader-scale patterns of rewetting and hydrological reconnection. For example, following prolonged droughts, slow recovery of groundwater tables likely delays reconnection between surface soils and streams, thereby creating a lag effect on stream water DOM recovery. Furthermore, while our experiment addressed drought responses in soils collected from a relatively wet riparian area, there is considerable heterogeneity in water table height and dynamics amongst riparian locations (Grabs et al., 2012; Reidy et al., 2025). This hydrogeomorphic variability is likely to alter the response to drying-rewetting events locally. For instance, interface zones fed by strong hydrological connections support water tables at or very near the soil surface throughout the summer (Reidy et al., 2025) and may only experience drying events during the most extreme droughts. By comparison, other hydrogeomorphic settings, with more dynamic water tables, likely experience some form of drying-rewetting event during most years. Regardless, our experiment provides new insights into how predicted increases in the frequency of extreme hydrological events in northern landscapes may influence C production and mobilization across land-water boundaries.

CRediT authorship contribution statement

Martin Škerlep: Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Melissa Reidy:** Writing – review & editing, Methodology, Conceptualization. **Hjalmar Laudon:** Writing – review & editing, Resources, Project administration, Funding acquisition. **Ryan A. Sponseller:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2025.110012.

References

Artz, R.R., Chapman, S.J., Robertson, A.J., Potts, J.M., Laggoun-Défarge, F., Gogo, S., Comont, L., Disnar, J.-R., Francez, A.-J., 2008. FTIR spectroscopy can be used as a screening tool for organic matter quality in regenerating cutover peatlands. Soil Biology and Biochemistry 40 (2), 515–527.

Baker, M.A., Valett, H.M., Dahm, C.N., 2000. Organic carbon supply and metabolism in a shallow groundwater ecosystem. Ecology 81 (11), 3133–3148.

Balting, D.F., AghaKouchak, A., Lohmann, G., Ionita, M., 2021. Northern hemisphere drought risk in a warming climate. NPJ Climate and Atmospheric Science 4 (1), 61.

Beer, J., Blodau, C., 2007. Transport and thermodynamics constrain belowground carbon turnover in a northern peatland. Geochimica et Cosmochimica Acta 71 (12), 2989–3002.

Berggren, M., Ström, L., Laudon, H., Karlsson, J., Jonsson, A., Giesler, R., Bergström, A. K., Jansson, M., 2010. Lake secondary production fueled by rapid transfer of low molecular weight organic carbon from terrestrial sources to aquatic consumers. Ecology Letters 13 (7), 870–880.

Bevacqua, E., Rakovec, O., Schumacher, D.L., Kumar, R., Thober, S., Samaniego, L., Seneviratne, S.I., Zscheischler, J., 2024. Direct and lagged climate change effects intensified the 2022 European drought. Nature Geoscience 1–8.

Bhattacharyya, A., Schmidt, M.P., Stavitski, E., Martínez, C.E., 2018. Iron speciation in peats: chemical and spectroscopic evidence for the co-occurrence of ferric and ferrous iron in organic complexes and mineral precipitates. Organic Geochemistry 115, 124–137.

Biester, H., Knorr, K.-H., Schellekens, J., Basler, A., Hermanns, Y.-M., 2014. Comparison of different methods to determine the degree of peat decomposition in peat bogs. Biogeosciences 11 (10), 2691–2707.

Bonaiuti, S., Blodau, C., Knorr, K.-H., 2020. Evaluating biogeochemical indicators of methanogenic conditions and thermodynamic constraints in peat. Applied Geochemistry 114, 104471.

Bragazza, L., Buttler, A., Robroek, B.J., Albrecht, R., Zaccone, C., Jassey, V.E., Signarbieux, C., 2016. Persistent high temperature and low precipitation reduce peat carbon accumulation. Global Change Biology 22 (12), 4114–4123.

Broder, T., Blodau, C., Biester, H., Knorr, K.-H., 2012. Peat decomposition records in three pristine ombrotrophic bogs in southern patagonia. Biogeosciences 9 (4), 1479–1491.

Burgin, A., Loecke, T., 2023. The biogeochemical redox paradox: how can we make a foundational concept more predictive of biogeochemical state changes? Biogeochemistry 164 (2), 349–370.

Burt, T., Pinay, G., Matheson, F., Haycock, N., Butturini, A., Clement, J., Danielescu, S., Dowrick, D., Hefting, M., Hillbricht-Ilkowska, A., 2002. Water table fluctuations in the riparian zone: comparative results from a Pan-European experiment. Journal of Hydrology 265 (1–4), 129–148.

Campeau, A., Del Giorgio, P.A., 2014. Patterns in CH4 and CO2 concentrations across boreal Rivers: major drivers and implications for fluvial greenhouse emissions under climate change scenarios. Global Change Biology 20 (4), 1075–1088.

Campeau, A., Bishop, K., Nilsson, M., Klemedtsson, L., Laudon, H., Leith, F., Öquist, M., Wallin, M., 2018. Stable carbon isotopes reveal soil-stream DIC linkages in contrasting headwater catchments. Journal of Geophysical Research: Biogeosciences 123 (1), 149–167.

Chapman, S., Campbell, C., Fraser, A., Puri, G., 2001. FTIR spectroscopy of peat in and bordering Scots pine woodland: relationship with chemical and biological properties. Soil Biology and Biochemistry 33 (9), 1193–1200.

Clark, J.M., Chapman, P.J., Adamson, J.K., Lane, S.N., 2005. Influence of drought-induced acidification on the mobility of dissolved organic carbon in peat soils. Global Change Biology 11 (5), 791–809.

Clark, J.M., Chapman, P.J., Heathwaite, A.L., Adamson, J.K., 2006. Suppression of dissolved organic carbon by sulfate induced acidification during simulated droughts. Environmental Science & Technology 40 (6), 1776–1783.

Clark, J., Heinemeyer, A., Martin, P., Bottrell, S., 2012. Processes controlling DOC in pore water during simulated drought cycles in six different UK peats. Biogeochemistry 109 (1), 253–270.

Estop-Aragonés, C., Knorr, K.H., Blodau, C., 2012. Controls on in situ oxygen and dissolved inorganic carbon dynamics in peats of a temperate fen. Journal of Geophysical Research: Biogeosciences 117 (G2).

Evans, C.D., Jones, T.G., Burden, A., Ostle, N., Zieliński, P., Cooper, M.D., Peacock, M., Clark, J.M., Oulehle, F., Cooper, D., 2012. Acidity controls on dissolved organic carbon mobility in organic soils. Global Change Biology 18 (11), 3317–3331.

Fenner, N., Freeman, C., 2011. Drought-induced carbon loss in peatlands. Nature Geoscience 4 (12), 895–900. https://doi.org/10.1038/ngeo1323.

Fomina, P.S., Proskurnin, M.A., Mizaikoff, B., Volkov, D.S., 2023. Infrared spectroscopy in aqueous solutions: capabilities and challenges. Critical Reviews in Analytical Chemistry 53 (8), 1748–1765.

Freeman, C., Ostle, N., Kang, H., 2001. An enzymic'latch'on a global carbon Store. Nature 409 (6817), 149-149.

Goebel, M.O., Bachmann, J., Reichstein, M., Janssens, I.A., Guggenberger, G., 2011. Soil water repellency and its implications for organic matter Decomposition–Is there a link to extreme climatic events? Global Change Biology 17 (8), 2640–2656.

Grabs, T., Bishop, K., Laudon, H., Lyon, S.W., Seibert, J., 2012. Riparian zone hydrology and soil water total organic carbon (TOC): implications for spatial variability and upscaling of lateral riparian TOC exports. Biogeosciences 9 (10), 3901–3916.

Hall, S.J., Treffkorn, J., Silver, W.L., 2014. Breaking the enzymatic latch: impacts of reducing conditions on hydrolytic enzyme activity in tropical forest soils. Ecology 95 (10), 2964–2973.

He, Z., Honeycutt, C.W., Zhang, H., 2011. Elemental and fourier transform-infrared spectroscopic analysis of water-and pyrophosphate-extracted soil organic matter. Soil Science 176 (4), 183–189.

Hope, D., Palmer, S.M., Billett, M.F., Dawson, J.J., 2001. Carbon dioxide and methane evasion from a temperate peatland stream. Limnology & Oceanography 46 (4), 847–857.

Hotchkiss, E., Hall Jr, R., Sponseller, R., Butman, D., Klaminder, J., Laudon, H., Rosvall, M., Karlsson, J., 2015. Sources of and processes controlling CO 2 emissions change with the size of streams and Rivers. Nature Geoscience 8 (9), 696–699.

Hruška, J., Köhler, S., Laudon, H., Bishop, K., 2003. Is a universal model of organic acidity possible: comparison of the acid/base properties of dissolved organic carbon in the boreal and temperate zones. Environmental Science & Technology 37 (9), 1726–1730.

Huang, W., Hall, S.J., 2017. Optimized high-throughput methods for quantifying iron biogeochemical dynamics in soil. Geoderma 306, 67–72.

Klüpfel, L., Piepenbrock, A., Kappler, A., Sander, M., 2014. Humic substances as fully regenerable electron acceptors in recurrently anoxic environments. Nature Geoscience 7 (3), 195–200.

Knorr, K.H., 2013. DOC-Dynamics in a small headwater catchment as driven by redox fluctuations and hydrological flow paths – are DOC exports mediated by iron reduction/oxidation cycles? Biogeosciences 10 (2), 891–904. https://doi.org/10.5194/bg-10-891-2013.

Knorr, K.-H., Blodau, C., 2009. Impact of experimental drought and rewetting on redox transformations and methanogenesis in mesocosms of a northern fen soil. Soil Biology and Biochemistry 41 (6), 1187–1198. https://doi.org/10.1016/j.soilbio.2009.02.030.

Knorr, K.-H., Lischeid, G., Blodau, C., 2009. Dynamics of redox processes in a minerotrophic fen exposed to a water table manipulation. Geoderma 153 (3–4), 379–392. https://doi.org/10.1016/j.geoderma.2009.08.023.

Krause, S., Lewandowski, J., Grimm, N.B., Hannah, D.M., Pinay, G., McDonald, K., Martí, E., Argerich, A., Pfister, L., Klaus, J., 2024. Ecohydrological interfaces as hotspots of ecosystem processes. Ecohydrological Interfaces 1–28.

Laudon, H., Berggren, M., Ågren, A., Buffam, I., Bishop, K., Grabs, T., Jansson, M., Köhler, S., 2011. Patterns and dynamics of dissolved organic carbon (DOC) in boreal streams: the role of processes, connectivity, and scaling. Ecosystems 14 (6), 880–893. https://doi.org/10.1007/s10021-011-9452-8.

Laudon, H., Hasselquist, E.M., Peichl, M., Lindgren, K., Sponseller, R., Lidman, F., Kuglerova, L., Hasselquist, N.J., Bishop, K., Nilsson, M.B., 2021a. Northern landscapes in transition: evidence, approach and ways forward using the krycklan Catchment study. Hydrological Processes 35 (4), e14170.

Laudon, H., Sponseller, R.A., Bishop, K., 2021b. From legacy effects of acid deposition in boreal streams to future environmental threats. Environmental Research Letters 16 (1), 015007.

Ledesma, J.L., Futter, M.N., Laudon, H., Evans, C.D., Kohler, S.J., 2016. Boreal forest riparian zones regulate stream sulfate and dissolved organic carbon. Science of the Total Environment 560–561, 110–122. https://doi.org/10.1016/j.scitotenv.2016.03.230.

Ledesma, J.L., Futter, M.N., Blackburn, M., Lidman, F., Grabs, T., Sponseller, R.A., Laudon, H., Bishop, K.H., Köhler, S.J., 2018. Towards an improved conceptualization of riparian zones in boreal forest headwaters. Ecosystems 21, 297–315.

Lidman, F., Boily, Å., Laudon, H., Köhler, S.J., 2017. From soil water to surface water – how the riparian zone controls element transport from a boreal forest to a stream. Biogeosciences 14 (12), 3001–3014. https://doi.org/10.5194/bg-14-3001-2017.

Loecke, T.D., Burgin, A.J., Riveros-Iregui, D.A., Ward, A.S., Thomas, S.A., Davis, C.A., Clair, M.A.S., 2017. Weather whiplash in agricultural regions drives deterioration of water quality. Biogeochemistry 133 (1), 7–15.

Loisel, J., Gallego-Sala, A.V., Amesbury, M., Magnan, G., Anshari, G., Beilman, D., Benavides, J., Blewett, J., Camill, P., Charman, D., 2021. Expert assessment of future vulnerability of the global peatland carbon sink. Nature Climate Change 11 (1), 70–77.

Lucas, R.W., Sponseller, R.A., Laudon, H., 2013. Controls over base cation concentrations in stream and river waters: a long-term analysis on the role of deposition and climate. Ecosystems 16, 707–721.

Lupon, A., Denfeld, B.A., Laudon, H., Leach, J., Karlsson, J., Sponseller, R.A., 2019. Groundwater inflows control patterns and sources of greenhouse gas emissions from streams. Limnology & Oceanography 64 (4), 1545–1557.

Lupon, A., Ploum, S.W., Leach, J.A., Kuglerová, L., Laudon, H., 2023. Groundwater flow paths drive longitudinal patterns of stream dissolved organic carbon (DOC) concentrations in boreal landscapes. Hydrology and Earth System Sciences 27 (2), 613–625.

Meisner, A., Rousk, J., Bååth, E., 2015. Prolonged drought changes the bacterial growth response to rewetting. Soil Biology and Biochemistry 88, 314–322.

Merino, C., Kuzyakov, Y., Godoy, K., Cornejo, P., Matus, F., 2020. Synergy effect of peroxidase enzymes and fenton reactions greatly increase the anaerobic oxidation of soil organic matter. Scientific Reports 10 (1), 11289.

Monteith, D.T., Stoddard, J.L., Evans, C.D., de Wit, H.A., Forsius, M., Hogasen, T., Wilander, A., Skjelkvale, B.L., Jeffries, D.S., Vuorenmaa, J., Keller, B., Kopacek, J., Vesely, J., 2007. Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. Nature 450 (7169), 537–540. https://doi.org/10.1038/nature06316.

Öquist, M.G., Wallin, M., Seibert, J., Bishop, K., Laudon, H., 2009. Dissolved inorganic carbon export across the soil/stream interface and its fate in a boreal headwater stream. Environmental Science & Technology 43 (19), 7364–7369.

Öquist, M., Bishop, K., Grelle, A., Klemedtsson, L., Kohler, S., Laudon, H., Lindroth, A., Ottosson Löfvenius, M., Wallin, M.B., Nilsson, Mö B., 2014. The full annual carbon balance of boreal forests is highly sensitive to precipitation. Environmental Science and Technology Letters 1 (7), 315–319.

Pinsonneault, A.J., Moore, T.R., Roulet, N.T., 2016. Temperature the dominant control on the enzyme-latch across a range of temperate peatland types. Soil Biology and Biochemistry 97, 121–130.

Reidy, M., Berggren, M., Lupon, A., Laudon, H., Sponseller, R.A., 2025. Riparian zone heterogeneity influences the amount and fate of biodegradable dissolved organic carbon at the land-water interface. Journal of Geophysical Research: Biogeosciences 130 (5), e2024JG008471.

Rocher-Ros, G., Stanley, E.H., Loken, L.C., Casson, N.J., Raymond, P.A., Liu, S., Amatulli, G., Sponseller, R.A., 2023. Global methane emissions from Rivers and streams. Nature 621 (7979), 530–535.

Romaní, A.M., Vázquez, E., Butturini, A., 2006. Microbial availability and size fractionation of dissolved organic carbon after drought in an intermittent stream: biogeochemical link across the stream–riparian interface. Microbial Ecology 52, 501–512.

Rulli, M.P., Bergström, A.K., Sponseller, R.A., Berggren, M., 2022. Seasonal patterns in nutrient bioavailability in boreal headwater streams. Limnology & Oceanography 67 (5), 1169–1183.

Sinsabaugh, R.L., 2010. Phenol oxidase, peroxidase and organic matter dynamics of soil. Soil Biology and Biochemistry 42 (3), 391–404.

Škerlep, M., Nehzati, S., Sponseller, R.A., Persson, P., Laudon, H., Kritzberg, E., 2023. Differential trends in iron concentrations of boreal streams linked to catchment characteristics. Global Biogeochemical Cycles 37 (3), e2022GB007484.

Skyllberg, U., Qian, J., Frech, W., Xia, K., Bleam, W.F., 2003. Distribution of Mercury, methyl Mercury and organic sulphur species in soil, soil solution and stream of a boreal forest catchment. Biogeochemistry 64, 53–76.

Smith, A.P., Bond-Lamberty, B., Benscoter, B.W., Tfaily, M.M., Hinkle, C.R., Liu, C., Bailey, V.L., 2017. Shifts in pore connectivity from precipitation versus groundwater rewetting increases soil carbon loss after drought. Nature Communications 8 (1), 1335.

Ste-Marie, C., Paré, D., 1999. Soil, pH and N availability effects on net nitrification in the forest floors of a range of boreal forest stands. Soil Biology and Biochemistry 31 (11), 1579–1589.

Stirling, E., Fitzpatrick, R., Mosley, L., 2020. Drought effects on wet soils in inland wetlands and peatlands. Earth-Science Reviews 210, 103387.

Sutton-Grier, A.E., Keller, J.K., Koch, R., Gilmour, C., Megonigal, J.P., 2011. Electron donors and acceptors influence anaerobic soil organic matter mineralization in tidal marshes. Soil Biology and Biochemistry 43 (7), 1576–1583.

Swindles, G.T., Morris, P.J., Mullan, D.J., Payne, R.J., Roland, T.P., Amesbury, M.J., Lamentowicz, M., Turner, T.E., Gallego-Sala, A., Sim, T., 2019. Widespread drying of European peatlands in recent centuries. Nature Geoscience 12 (11), 922–928.

Szkokan-Emilson, E., Kielstra, B., Watmough, S., Gunn, J., 2013. Drought-induced release of metals from peatlands in watersheds recovering from historical metal and sulphur deposition. Biogeochemistry 116, 131–145.

Tandy, S., Healey, J.R., Nason, M.A., Williamson, J.C., Jones, D.L., Thain, S.C., 2010. FT-IR as an alternative method for measuring chemical properties during composting. Bioresource Technology 101 (14), 5431–5436.

Tian, L., Shi, W., 2014. Soil peroxidase regulates organic matter decomposition through improving the accessibility of reducing sugars and amino acids. Biology and Fertility of Soils 50, 785–794.

Tipping, E., Woof, C., 1990. Humic substances in acid organic soils: modelling their release to the soil solution in terms of humic charge. Journal of Soil Science 41 (4), 573–586.

Tiwari, T., Sponseller, R.A., Laudon, H., 2022. The emerging role of drought as a regulator of dissolved organic carbon in boreal landscapes. Nature Communications 13 (1), 1–11.

Urbanová, Z., Hájek, T., 2021. Revisiting the concept of 'Enzymic latch'on carbon in peatlands. Science of the Total Environment 779, 146384.

Verhoeven, J., Liefveld, W., 1997. The ecological significance of organochemical compounds in Sphagnum. Acta Botanica Neerlandica 46 (2), 117–130.

Wetzel, R.G., 1992. Gradient-dominated ecosystems: sources and regulatory functions of dissolved organic matter in freshwater ecosystems. Hydrobiologia 229, 181–198.

Weyer, C., Peiffer, S., Lischeid, G., 2018. Stream water quality affected by interacting hydrological and biogeochemical processes in a riparian wetland. Journal of Hydrology 563, 260–272.

Worrall, F., Burt, T., Adamson, J., 2005. Fluxes of dissolved carbon dioxide and inorganic carbon from an upland peat catchment: implications for soil respiration. Biogeochemistry 73, 515–539.

Yu, Z.-G., Göttlicher, J., Steininger, R., Knorr, K.-H., 2016. Organic sulfur and organic matter redox processes contribute to electron flow in anoxic incubations of peat. Environmental Chemistry 13 (5), 816–825.