



# Aerobic and anaerobic decomposition rates in drained peatlands: Impact of botanical composition

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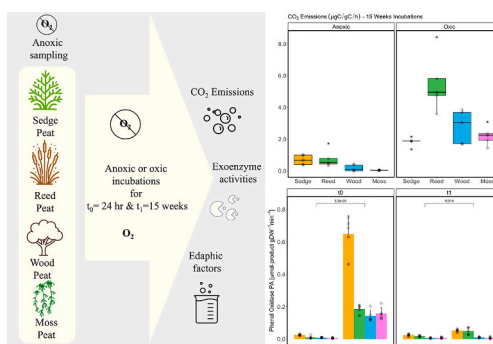
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## HIGHLIGHTS

- Peat decomposition plays a major role in human-induced land subsidence rates.
- Categorising peatlands by botanical composition offers insights into peat vulnerability and management strategies.
- Anaerobic peat decomposition rates are slower than aerobic ones, but still impact land subsidence rates.

## GRAPHICAL ABSTRACT



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## ABSTRACT

Drained peatlands in temperate climates are under threat from climate change and human activities. The resulting decomposition of organic matter plays a major role in regulating the associated land subsidence rates, yet the determinants of aerobic and anaerobic peat decomposition rates are not fully understood. In this study, we sought to gain insight into the drivers of decomposition rates in botanically diverse peatlands (sedge, reed, wood, and moss dominant) under oxic and anoxic conditions. Peat samples were collected from the anoxic zone and incubated for 24 h (short) and 15 weeks (long) under either oxic or anoxic conditions. CO<sub>2</sub> emissions, hydrolytic and oxidative exoenzyme potential activities, phenolic compound concentrations, and several edaphic factors were measured at the end of each incubation period.

We found that 15 weeks of oxygen exposure of anoxic peat samples accelerated the average CO<sub>2</sub> emissions by 3.9-fold. Reed and sedge peat respired more than wood and moss peat under anoxic conditions. Interestingly, CO<sub>2</sub> emissions from anoxic peat layers under permanently anoxic conditions were substantial and given the thickness of peat deposits in the field, such activities may play an important role in long-term land subsidence rates and total CO<sub>2</sub> emissions from drained peatlands. The results from the long-term incubations showed that decomposition rates appear to be also controlled by factors other than oxygen intrusion such as substrate availability. In summary, the botanical composition of the peat matrix, incubation conditions and time of

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incubation are all important factors that need to be considered when predicting peat decomposition and subsequent land subsidence rates.

## 1. Introduction

Peat is formed from the accumulation of organic components derived from plant and animal detritus under water-saturated conditions, where organic matter (OM) decomposition is slowed down due to acidity, anoxic conditions, and nutrients limitations (Rydin and Jeglum, 2013). Consequently, undisturbed peatlands function as carbon reservoirs, housing an estimated 30–44 % of the global soil organic carbon (Joosten et al., 2016; Parish et al., 2008).

Frequent and prolonged droughts due to climate change and intense human activities, such as drainage, expose water-saturated peat layers to free oxygen ( $O_2$ ), accelerating decomposition of OM, resulting in increased carbon dioxide ( $CO_2$ ) emissions (Fenner and Freeman, 2011; Höper et al., 2008). The consequences of this process are substantial, particularly in drained peatlands in Europe, estimated to emit approximately 600 Mt. of carbon dioxide ( $CO_2$ ) annually (UNEP, 2022). Accelerated decomposition, coupled with various processes such as shrinkage, consolidation, and creep, contributes to land subsidence rates of 0.8 to 5 cm/year (Galloway et al., 2016; Leifeld et al., 2011). The Netherlands, being one of the most densely populated delta plains worldwide, is a prime example of the impact of peatland management practices (Gerding et al., 2015). Over the last 1000 years, the Dutch coastal plain has experienced an estimated peat volume loss of 19.8 km<sup>3</sup>, with approximately 16.2 km<sup>3</sup> attributed to human-induced aerobic peat decomposition (Erkens et al., 2016).

Peat decomposition is primarily a microbial induced process that involves the conversion of complex organic molecules into simpler substrates such as sugars, amino acids, and ultimately, inorganic forms such as ammonium and carbon dioxide (Findlay, 2013). During the decay of OM, the intermediate products are used by microorganisms to survive, grow, and reproduce. Several groups of microorganisms have developed extracellular enzymes (exoenzymes) to degrade complex organic molecules. These exoenzymes can be divided into two major groups, namely hydrolytic and oxidative exoenzymes, which respectively require water and oxygen to function (Sinsabaugh et al., 2008).

One of the hypotheses explaining slow decomposition rates that lead to peat formation is referred to as the *Enzymic Latch* hypothesis (Freeman et al., 2001). This hypothesis proposes that under anoxic conditions oxidative exoenzymes do not function, and hydrolytic exoenzymes are inhibited by phenolic compounds (Dunn and Freeman, 2018). Phenolic compounds (PCs) are plant secondary metabolites present in peat at higher concentrations (Březinová and Vymazal, 2018). This hypothesis also explains the increase in decomposition rates when peatlands are drained. Oxygen intrusion into peat activates oxidative exoenzymes that can degrade PCs in the peat matrix. This releases the latch, allowing hydrolytic exoenzymes to function without inhibition by PCs, thus facilitating more rapid peat degradation (Brouns et al., 2014a, 2014b). Once the latch is released, decomposition rates will remain high, even if water-logged conditions are restored.

Although it is generally accepted that oxygen intrusion stimulates peat decomposition, other factors such as pH, temperature, moisture content and iron availability in the system can also regulate aerobic decomposition rates (Hall et al., 2014; T. Li et al., 2019; McGivern et al., 2021; Urbanová and Hájek, 2021). In contrast to the Enzymic Latch hypothesis, the *Iron-Gate* hypothesis suggests that the presence of iron in the system can inhibit peat decomposition during the decline of the water-table by lowering the pH, thereby leading to increased sorption of lignin compounds and inhibition of oxidative exoenzyme potential activity (Wang et al., 2017). Studies to date have reported a range of exoenzyme potential activities under oxic and anoxic conditions in peatland systems, making it difficult to disentangle the ultimate drivers

of peat formation and decomposition (Brouns et al., 2016; Huang et al., 2021; Wen et al., 2019).

The quality of the substrate, determined by the botanical composition of peatlands, also influences exoenzyme potential activities, and subsequently, decomposition rates (Bridgman and Richardson, 1992). *Carex* spp. (sedge), *Phragmites* spp. (reed), *Alnus* spp., *Betula* spp. (wood) and *Sphagnum* spp. (moss) are among the most common plants in temperate peatlands, such as those found in drained Dutch peatlands. These plant groups exhibit different chemical compositions, including diverse phenolic compounds which contribute to the formation of various quality recalcitrant materials in the peat matrix (Hájek et al., 2011; Verhoeven and Liefveld, 1997; Verhoeven and Toth, 1995). (Bambalov, 2007) found that OM loss over the course of 12 months from *Carex* spp., *Phragmites* spp. and *Alnus* spp. were 41 %, 37 % and 20.7 %, respectively. Other research has shown that fresh *Sphagnum* spp. is degraded slower than *Carex* spp. peat due to its sphagnum acid content, and the addition of *Sphagnum* spp. to *Carex* spp. also reduces decomposition rates (Naumova et al., 2013; van Breemen, 1995; Verhoeven and Toth, 1995). These authors concluded that peat characteristics, based on major plant material, were one of the major drivers of decomposition rates, providing important information to guide local peatland management practices.

In land subsidence studies, the role of peat decomposition has traditionally centred around aerobic peat oxidation, primarily driven by the high reduction potential of oxygen ( $O_2$ ). Oxygen serves as a terminal electron acceptor (TEA), promoting enzymatic activities with a high energy yield. However, in oxygen-depleted conditions, alternative terminal electron acceptors (ATEAs) come into play, contingent on their respective reduction potentials. Following oxygen, ATEAs such as  $NO_3^-$ ,  $SO_4^{2-}$ ,  $Mn^{4+}$  and/or  $Fe^{+3}$  ions exhibit the highest reduction potentials (Gao et al., 2019; Merino et al., 2020; Wang et al., 2017). These diverse ATEAs can be transported through water mass flow, including seepage, infiltration, reversed drainage, and pressure drains, facilitating anaerobic metabolic activities among microorganisms. The presence of these ATEAs may lead to peat degradation and associated production of  $CO_2$  in anoxic peat layers, depending on the microbial composition and physico-chemical properties of the peat matrix (de Jong et al., 2020; Fan et al., 2021; Sutton-Grier et al., 2011; Walpen et al., 2018). Li et al. (2021) has demonstrated that iron reduction regulates a substantial portion of  $CO_2$  emissions in oxygen-depleted paddy soils. Another study found that members of the phylum *Acidobacteriota* can degrade *Sphagnum* originated peat through anaerobic reduction of humic substances as terminal electron acceptor in acidic bogs, producing  $CO_2$  as an end product (James et al., 2021). A recent study showed that anaerobic processes determine the decomposition rates and  $CO_2$  emissions during water table decline in peatlands (Fairbairn et al., 2023). These findings underscore the importance of recognizing that anaerobic decomposition can occur in water-saturated peat layers and subsequently stimulate aerobic decomposition rates after drainage, a factor often overlooked in previous land subsidence studies.

Given the urgency of effective  $CO_2$ -mitigation measures and adaptive management practices in drained peatlands, as well as the existing blind spots in the field of land subsidence concerning the influence of anaerobic and aerobic decomposition and their drivers, this study aims to understand aerobic and anaerobic peat decomposition rates as being one of the mechanisms of land subsidence. Our study sought to investigate (1) aerobic decomposition rates in comparison to anaerobic decomposition rates and to (2) examine the role of botanical composition in determining decomposition rates in Dutch peatlands.

We hypothesized that (1) anaerobic decomposition rates would be slower than the aerobic decomposition rates but would still significantly

contribute (half of the average aerobic respiration rates) to potential human-induced land subsidence rates in the long term. The botanical composition of peat matrix is expected to be one of the major drivers of decomposition rates both under oxic and anoxic conditions. Thus, (2) sedge- and reed-dominated peat sites are hypothesized to show faster decomposition rates as compared to wood- and moss-dominated peatlands due to difference in the levels of the recalcitrance of the substrates.

The outcomes of this research will form the basis for the future development of deterministic land subsidence- and CO<sub>2</sub> emission-models for drained peatlands in the Netherlands, thereby contributing to the search for feasible and sustainable peatland management strategies.

## 2. Materials and methods

### 2.1. Field sampling

Four peat sites in the Netherlands were chosen based on the predominant plant residues found in the peat matrix at depths between 100 and 205 cm below the surface (Table 1). As a result of the land subsidence (due to compaction and decomposition) and land management of the past, the peat at these depths is approximately 2500–4000 years old. The sample location with *Alnus* and *Salix* spp. (wood) peat at Zegveld, is a dairy farm where average groundwater level at 70 cm below surface and the porewater is rich in sulphate (Total S > 500 mmol/kgDW, SO<sub>4</sub><sup>2-</sup> > 10,000 µmol/L). *Carex* spp. (sedge) peat was collected from the Rouveen sample location. The field is also used for dairy farming, and fed by seepage water that has low ion concentrations (EC = 68.3 ± 2.9 µS/cm). *Sphagnum* spp. (moss) peat was sampled at Bunschoten, a location situated in a village park grassland. In this area, moss peat has been preserved below an artificial fill, and groundwater level fluctuates between 80 and 110 cm below the surface. Lastly, the De Onlanden sample location is a protected wetland which was used for agricultural purposes in the past. In this sample location, *Phragmites* spp. (reed) dominates both the aboveground vegetation and the peat matrix. All sites have been exposed in various degrees to human disturbance such as drainage, fertilisation, and grazing, over the last centuries. To overcome these differences in disturbances, sampling depths were selected based on the level of decomposition as classified in the field following the adapted humification scale for drained Dutch peatlands (Erkens et al., 2013). Further details regarding the history and additional characteristics of the field sites can be found in Supplementary Data, Table S.1, Table S.2 & Table S.3).

In each sample locations, five field replicates were collected from the permanently anoxic zone (depth > 100 cm) with a six cm wide soil gouge auger (Eijkelkamp, Breda, The Netherlands). Soil samples were wrapped with stretch film immediately to limit contact with air. Then, samples were quickly placed in O<sub>2</sub>-proof bags (Anaerocult, Merck, Germany) together with an anoxic patch (Thermo Fisher Scientific, Oxoid, AnaeroGen™) to remove any available O<sub>2</sub> in the bag. Sealed samples were transferred to the laboratory in a cooling box at approximately four degrees Celsius.

### 2.2. Sample treatment and incubations

Samples were homogenized and sorted in an anoxic chamber (Vinyl Anaerobic Chamber, Coy Laboratory Products, The U.S.A.). Two set of subsamples were prepared for oxic and anoxic incubations in 50 mL

plastic tubes. These samples were then transferred to larger glass bottles (500 mL), where high humidity was maintained in the headspace by using wet perlite to reduce evaporation loss. The lids of the bottles were placed on top without being tightly closed, allowing for regular refreshment of the headspace. Samples were then incubated at 22 °C for 24 h and 15 weeks, either inside the anoxic chamber (for anoxic incubations) or in a temperature-controlled incubator (for oxic incubations). Each 500 mL glass bottle contained four 50 mL plastic tubes with peat samples. One tube was harvested after 24 h and another after 15 weeks of incubation for respiration measurements. Other parameters for both 24-h and 15-week of incubations were taken from the third and the fourth plastic tubes (Fig. 1).

### 2.3. Measured Parameters

#### 2.3.1. Microbial basal respiration rates

Aerobic and anaerobic microbial basal respiration rates (BRR) were measured by monitoring the accumulation of CO<sub>2</sub> in the head space with the respirometer (Biometric Systems, Germany, and Biont Research, The Netherlands) for short-term (t<sub>0</sub> = 24 h) and long-term (t<sub>1</sub> = 15 weeks) incubations. 50 ± 1.5 g of peat was collected from incubated samples and placed in a new glass bottle (500 mL). The bottles were attached to the respirometer and CO<sub>2</sub> emissions were measured with the interval of 120 min. The system automatically flushed the headspace with either nitrogen for anoxic measurements or air for oxic measurements when the CO<sub>2</sub> levels reached 0.4 ppm. After the measurements, samples were oven-dried for 72 h at 70 °C to determine their dry weight. Observed fluxes in BRR were corrected for shifts in pH by using CO<sub>2</sub> and pH relations derived from Henry's law (Henry, 1803) and expressed as "µgC/gC/h" by using C/N ratio data.

#### 2.3.2. Exoenzyme potential activities

Phenol oxidase (POX) potential activity was determined using the L-DOPA (l-3,4-dihydroxyphenylalanine) assay (adapted from Dunn et al., 2014). Samples were incubated with 10 mL of 10 mM L-DOPA substrate in Turaxx tubes (IKA®-Werke GmbH & Co. KG), and potential activity was measured using transparent 96-well plates with light spectrophotometry at 475 nm.

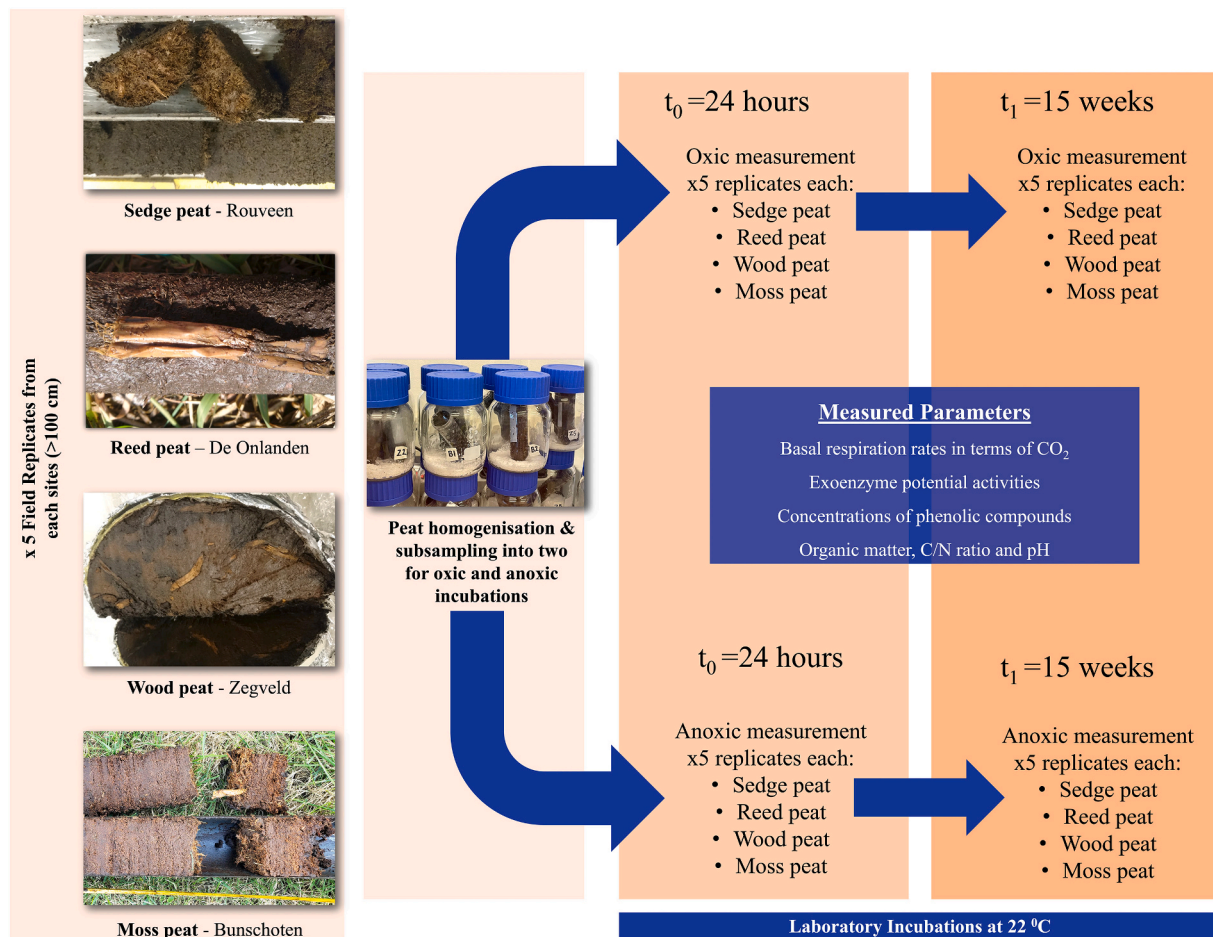
The peat samples were analysed for five hydrolytic exoenzymes (β-D-glucosidase, Arylsulfatase, β-D-xylosidase, N-acetyl-β-D-glucosaminidase, Phosphatase) using the fluorogenic 4-methylumbelliferone (MUF) assay (adapted from Dunn et al., 2014). Stirring Turaxx tubes (IKA®-Werke GmbH & Co. KG) were used to blend and incubate the samples with the 1 mM relevant substrate (Sigma-Aldrich®, the U.S.) (Supplementary Table S.4). The slurry was then transferred to two mL Eppendorf tubes and centrifuged at 14,000 rpm for 5 min. The supernatant was measured using black bottom 96-well plates (Thermo Fisher Scientific Inc.®) with fluorescence spectroscopy (Excitation: 360/40, Emission: 460/40).

Oxic samples were measured under laboratory conditions with 20 % oxygen present, while measurements on anoxic samples were all performed at <0.3 % oxygen within the anoxic chamber (Vinyl Anaerobic Chamber, Type A, Coy Laboratory Products Inc., the U.S.A.). Samples were measured at the beginning of the experiment (t<sub>0</sub>, Fig. 1) and after the 15-week incubation period (t<sub>1</sub>, Fig. 1).

**Table 1**

Selected field sites in the Netherlands based on the predominant plant residues (LOI\* = Loss on ignition).

Sites	Coordinates	Peat type	LOI (%)	pH	Bulk density g/cm <sup>3</sup>
Zegveld	52°08'14.9"N 4°50'23.7"E	Wood	78.3 ± 2.2	5.8 ± 0.10	0.17 ± 0.02
Rouveen	52°38'04.6"N 6°05'21.9"E	Sedge	92.2 ± 0.6	6.0 ± 0.02	0.11 ± 0.02
Bunschoten	52°14'54.1"N 5°21'49.8"E	Moss	88.5 ± 1.3	6.0 ± 0.10	0.30 ± 0.05
De Onlanden	53°10'33.9"N 6°31'28.4"E	Reed	84.4 ± 0.6	5.8 ± 0.10	0.53 ± 0.03



**Fig. 1.** Experimental flow and monitoring scheme of the parameters during incubations ( $t_0$ : 24 h short-term incubations, the initial conditions of anoxic peat samples and the first response to oxygen exposure.  $t_1$ : 15 weeks long-term anoxic and oxic incubations under laboratory conditions).

### 2.3.3. Concentration of phenolic compounds

Methanol soluble (MSPCs) and water soluble (WSPCs) phenolic compounds were measured using the Folin-Ciocalteu assay (Kähkönen et al., 1999). MSPCs were extracted from 1 g of peat by shaking the samples with 15 mL of 100 % methanol on a temperature-controlled rotary shaker at 150 rpm for 60 min at 40 °C, while WSPCs were extracted using MilliQ water. The samples were then centrifuged at 4000 rpm for 10 min, and 10  $\mu\text{L}$  of the supernatant was mixed with 30  $\mu\text{L}$  of Folin-Ciocalteu reagent and incubated in the dark for 8 min. Subsequently, 100  $\mu\text{L}$  of  $\text{Na}_2\text{CO}_3$  was added, and the samples were incubated in the dark for an additional 40 min before being measured in transparent 96 flat-bottom plates at 760 nm. The concentrations were expressed as equivalent amounts of gallic acid.

The concentration of total flavonoids (TFs) was determined using the aluminium chloride colorimetric method and expressed in terms of quercetin equivalence (Chang et al., 2002). The extraction protocol for TFs was the same as that for MSPCs, using 100 % methanol as the extraction solvent. After centrifugation, 100  $\mu\text{L}$  of 10 % aluminium chloride was added, and the samples were incubated in the dark for 30 min. Then, 300  $\mu\text{L}$  of the sample was transferred to transparent 96-well plates, and the absorbance was measured at 435 nm with light spectrophotometry.

### 2.3.4. Organic matter content, C/N ratio, pH and gravimetric moisture content

Organic matter content was determined by loss on ignition (5 h, 550 °C). pH changes were measured in a demi water extract by using a Sentix 41 pH electrode (WTW GmbH, Weilheim, Germany) before and

after the long-term incubations. Thirty millilitres of MilliQ water were added to 5 g of peat and shaken for 2 h at 22 °C. The samples were then centrifuged at 4000 rpm for 10 min, and the supernatant was used to measure pH. Gravimetric moisture content was determined using sub-samples of 50 g of peat before and after oven-drying for 72 h at 70 °C. Oven-dried samples were subsequently used to determine the C/N ratio in the 15-week incubation series using an elemental analyzer. (FlashS-mart™ Elemental Analyzer, Thermo Fisher Scientific Inc., the US).

### 2.4. Data analysis

All statistical analyses were conducted using the computing environment R (R Core Team, 2022). Tailored codes for basal respiration were developed by Biont Research, The Netherlands.

Linear mixed effect models followed by ANOVA (Type II) were conducted to analyse basal respiration rates. Botanical types (reed, sedge, wood and moss), treatment conditions (oxic and anoxic), and time points ( $t_0$  and  $t_1$ ) were included as explanatory variables in the model. Additionally, interaction effects among these variables were considered within the model. Furthermore, each field replicate was treated as a random factor.

The effects of short-term oxygen intrusion, long-term anoxic, and oxic incubations on various peat types with distinct botanical compositions were assessed through linear modelling. The response variable in these models was the absolute difference between the two tested groups. Following each linear model, a *t*-test was performed to investigate whether sedge and reed peat exhibited higher respiration rates compared to wood and moss peat. Outlier determination was done with



Grubb's test. The potential activity of exoenzymes was individually assessed under varied conditions and time intervals using *t*-tests and compared across four peat types using ANOVA (Type II). Relationship between measured variables were checked with Pearson correlation.

### 3. Results

#### 3.1. Microbial basal respiration rates

Throughout the incubation period, anaerobic respiration rates remained slower than aerobic respiration rates. Short-term oxygen intrusion ( $t_0 = 24$  h) accelerated the average  $\text{CO}_2$  emissions by 1.4-fold compared to the short-term anoxic samples. Long-term oxygen availability ( $t_1 = 15$  weeks) increased the average  $\text{CO}_2$  emissions by 3.9-fold, compared to the initial anoxic conditions. Anaerobic respiration rates, on the other hand, decreased by 1.9-fold in long-term anoxic samples (Table 2). The greatest difference between botanical peat types was observed in long-term oxic incubations (Fig. 2 A).  $\text{CO}_2$  emission rates of reed peat samples were the fastest ( $5.51 \pm 1.82 \mu\text{gC/gC/h}$ ), while sedge peat yielded the slowest rates ( $1.83 \pm 0.29 \mu\text{gC/gC/h}$ ).

Based on the outlier-adjusted models, we found that botanical type, treatment (oxic or anoxic conditions), and time (short- and long-term incubations) all significantly influenced basal respiration rates, with observable interaction effects among these variables (ANOVA, Type II,  $p < 0.001$ ).

Short-term oxygen intrusion ( $t_0 = 24$  h) significantly accelerated the respiration rates for all peat types (ANOVA, Type II,  $p < 0.001$ ). However, reed and sedge samples did not respire faster than wood and moss samples. The fastest respiration response to short-term oxygenation was observed in sedge peat, followed by moss, wood, and reed (Fig. 2B).

Long-term anoxic incubations ( $t_1 = 15$  weeks) resulted in a reduction in respiration rates for reed, moss, and wood peat, while sedge peat's respiration rates showed a slight acceleration (Fig. 2C). Reed and sedge peat respired faster than wood and moss peat under anoxic conditions (*t*-test,  $p < 0.01$ ). Aerobic respiration rates from long-term incubations did not follow the same order of respiration rates (*t*-test,  $p > 0.1$ ).

#### 3.2. Exoenzyme potential activities

##### 3.2.1. Phenol oxidase potential activity

We observed higher average phenol oxidase (POX) potential activities under oxic conditions as compared to those observed in samples kept under anoxic conditions (Fig. 3 A). Upon initial exposure to oxygen ( $t_0 = 24$  h), there was a sharp increase in POX potential activity observed in sedge peat, which mirrors the pattern observed for basal respiration rates. After long-term oxic incubation ( $t_1 = 15$  weeks), there was a substantial decrease in POX potential activity across all sites, with potential activity levels dropping by a factor of ten (Fig. 3B). Relative POX potential activities were higher in sedge and reed peat compared to wood and moss peat under both oxic and anoxic conditions in long-term incubations (*t*-test,  $p < 0.01$ ,  $n = 10$ ).

##### 3.2.2. Hydrolytic exoenzyme potential activities

The relative potential activity of hydrolytic exoenzymes in botanically diverse peatlands varied significantly depending on both

incubation conditions and durations (ANOVA (Type II),  $p < 0.01$ , Fig. 4). Short-term oxygenation did not alter exoenzyme potential activities significantly, except for  $\beta$ -D-xylosidase and Arylsulfatase. Their potential activity increased significantly in short-term oxidised samples in all peat types except sedge peat (*t*-test,  $p < 0.01$ ,  $p < 0.05$  for  $\beta$ -D-xylosidase and Arylsulfatase, respectively). During the short-term incubations, the  $\beta$ -D-glucosidase and Phosphatase exoenzyme potential activities in anoxic reed peat exhibited higher rates than in the corresponding oxygenated reed peat. Arylsulfatase potential activities significantly increased in moss peat but decreased for sedge peat after short-term oxic incubations (ANOVA (Type II) followed by Tukey's HSD Test  $p < 0.001$ ).

In long-term incubations ( $t_1 = 15$  weeks), hydrolytic exoenzyme potential activities displayed a shift, resulting in reduced potential activity levels under oxic conditions compared to anoxic conditions, with the exception of Phosphatase (*t*-test,  $p < 0.001$ ). Phosphatase potential activity in long-term oxic samples increased significantly for all sites except reed peat (ANOVA,  $p < 0.001$ ). The largest decreases for all hydrolytic exoenzyme potential activities were observed in reed peat, with Arylsulfatase potential activities falling below the detection limit. N-acetyl- $\beta$ -D-glucosaminidase activities were not significantly affected by either incubation condition or the length of incubation.

Maintaining anoxic conditions for 15 weeks resulted in significant rises of enzyme potential activities compared to initial anoxic samples ( $t_0 = 24$  h) (Supplementary Data, Fig.S.1) Although the average hydrolytic exoenzyme potential activity increased under long-term oxic conditions compared to the initial short-term anoxic incubations ( $t_0 = 24$  h), there was high variability within peat types and among different hydrolytic exoenzymes. Phosphatase, Arylsulfatase and  $\beta$ -D-xylosidase potential activities were significantly higher in sedge and moss peat under long-term oxic conditions compared to initial anoxic conditions. Long-term oxic wood and sedge peat samples showed higher potential activities for  $\beta$ -D-glucosidase compared to the corresponding initial anoxic samples. In contrast, both  $\beta$ -D-xylosidase and  $\beta$ -D-glucosidase potential activities were significantly lower for oxic reed peat.

#### 3.3. Concentration of phenolic compounds

The different samples displayed a high level of variation with respect to the concentrations of phenolic compounds. Water-soluble phenolics (WSPCs) did not differ in oxic versus and anoxic samples, but sedge peat under long-term oxic conditions displayed the lowest concentrations (Fig. 5).

The most prominent effects were observed for the concentrations of methanol-soluble phenolics (MSPCs). Oxygenated peat samples showed significantly lower concentrations in MSPCs in comparison to the peat samples which were kept under anoxic conditions (*t*-test,  $p < 0.001$ ).

After the removal of outliers, total flavonoids (TFs) concentrations were similar among long-term incubated anoxic samples for each botanical peat type. Comparatively, TFs concentrations were relatively higher in the long-term incubated oxic samples as compared to the anoxic ones.

#### 3.4. Edaphic factors and microbial activity

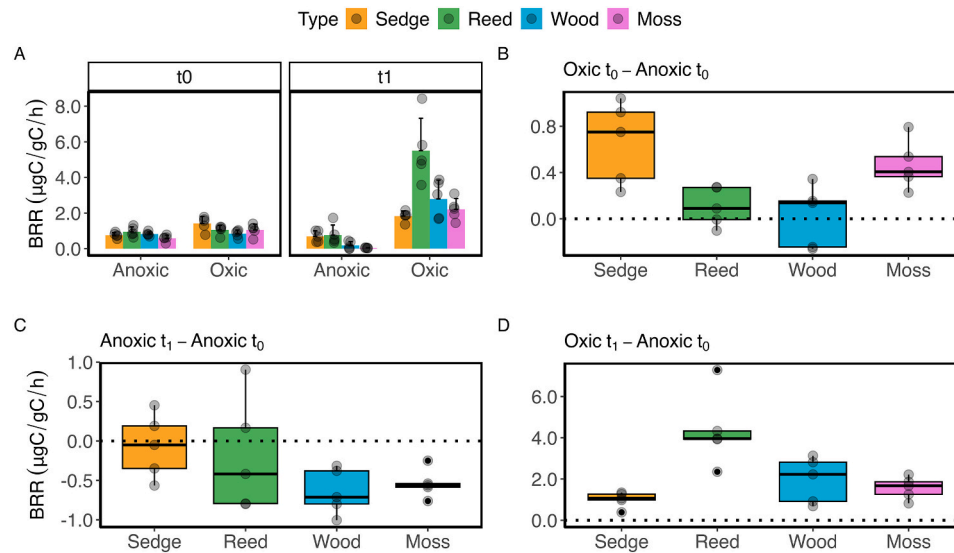
With the exception of Phosphatase, all exoenzymes potential activities exhibited positive correlations with each other ( $CI = 0.95$ , Pearson Correlation, Fig. 6A). Phosphatase potential activity was higher in samples characterised by higher organic matter content and lower methanol-soluble phenolics. Only N-acetyl- $\beta$ -D-glucosaminidase and  $\beta$ -D-glucosidase displayed significant negative correlations with microbial basal respiration rates. Additionally, pH was negatively correlated with exoenzyme potential activities. Basal respiration rates were negatively correlated with water content, and methanol-soluble phenolics.

Organic matter (%) and water content (%) remained relatively constant over the incubation experiment. During the 15-week incubation period, the pH of anoxic samples showed a slight increase, whereas

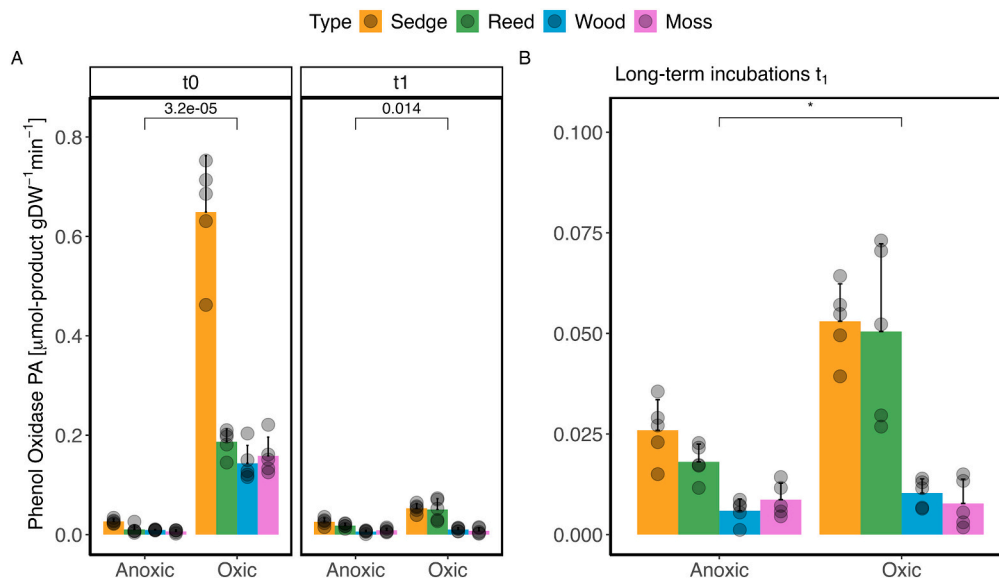
**Table 2**

Average  $\text{CO}_2$  emissions from oxic and anoxic samples at  $t_0$  (24h) and  $t_1$  (15 weeks) incubations ( $n = 20$ , with five samples per field sites for each condition and time).

Condition	Time	Mean [ $\mu\text{gC/gC/h}$ ]	Standard deviation ( $\pm$ sd)
Anoxic	$t_0$	0.78	0.22
Anoxic	$t_1$	0.42	0.45
Oxic	$t_0$	1.09	0.35
Oxic	$t_1$	3.09	1.79



**Fig. 2.** A. Microbial basal respiration rates (BRR,  $\mu\text{gC/gC/h}$ ) from botanically different peatlands after short- ( $t_0 = 24$  h) and long-term ( $t_1 = 15$  weeks) oxic and anoxic incubations B. Relative response in short-term oxic incubations [ $\text{Oxic } (t_0) - \text{Anoxic } (t_0)$ ] C. Relative response in long-term anoxic incubations [ $\text{Anoxic } (t_1) - \text{Anoxic } (t_0)$ ] D. Relative response in long-term oxic incubations [ $\text{Oxic } (t_1) - \text{Anoxic } (t_0)$ ]



**Fig. 3.** Average Phenol oxidase potential activities from botanically different peatlands at A. same scale for short- ( $t_0 = 24$  h) and long-term incubations B. smaller scale for long-term incubations ( $t_1 = 15$  weeks) ( $t$ -test,  $n = 20$ , \*\*\* $p < 0.001$ , \* $p < 0.01$ ).

the pH of oxic samples decreased. Notably, the pH measurement of oxic reed samples from long-term incubations was the lowest among the different botanical peat types (Supplementary Table S.5).

pH and  $\text{CO}_2$  emission rates showed a strong negative correlation (Fig. 6B). In long-term oxic samples, acidity increased, with the highest  $\text{CO}_2$  emissions observed in reed with the lowest pH  $\sim 2$ , followed by moss, wood and sedge.

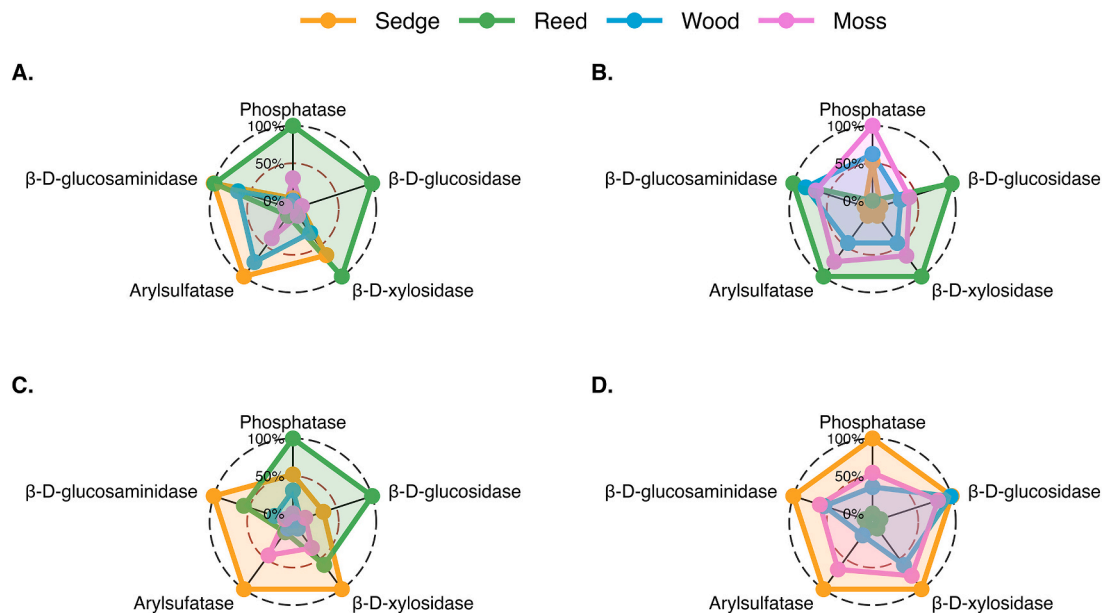
#### 4. Discussions

In this study, we aimed to explore aerobic and anaerobic peat decomposition rates and to examine botanical composition as a potential determinant of decomposition in drained peatlands. We found that, although anaerobic decomposition rates were lower than observed under oxic condition, they were still significant and potentially important contributors to total peat decomposition. We also observed that the

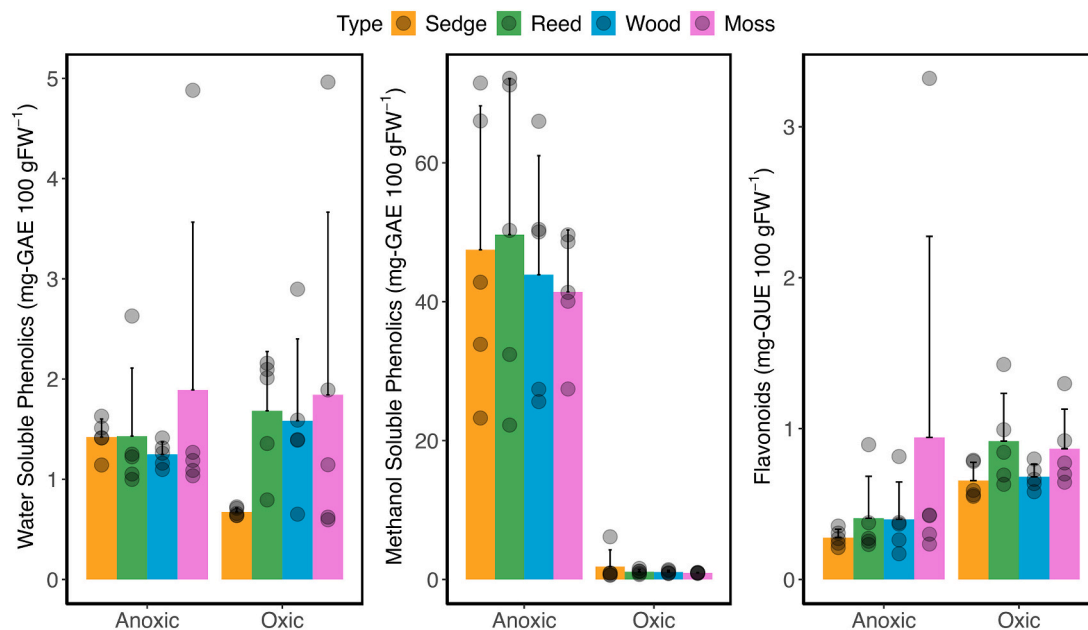
botanical composition of peat had a major impact on exoenzyme potential activities and decomposition rates in drained peatlands.

##### 4.1. Microbial basal respiration rates

We found that aerobic respiration rates were faster than anaerobic rates in both short- and long-term incubations, which aligns well with previous findings (Mettrop et al., 2014; Moore and Dalva, 1997; Urbanová and Hájek, 2021). In short-term incubations, anaerobic respiration rates exceeded half of the rates observed under oxic conditions. Despite a clear increase in microbial activity in peat samples under oxic conditions within the first 24 h, the high moisture content in the peat likely hampered oxygen diffusion, thereby allowing for the retention of a high proportion of anoxic pores within the substrate matrix (Fairbairn et al., 2023; Keiluweit et al., 2016; Lacroix et al., 2021). As a consequence, the microbial community transitioned gradually from



**Fig. 4.** Relative differences of average potential hydrolytic exoenzyme activities among A. short-term anoxic incubations ( $t_0 = 24$  h), B. short-term oxic incubations ( $t_0 = 24$  h), C. long-term anoxic incubations ( $t_1 = 15$  weeks), D. long-term oxic incubations ( $t_1 = 15$  weeks).

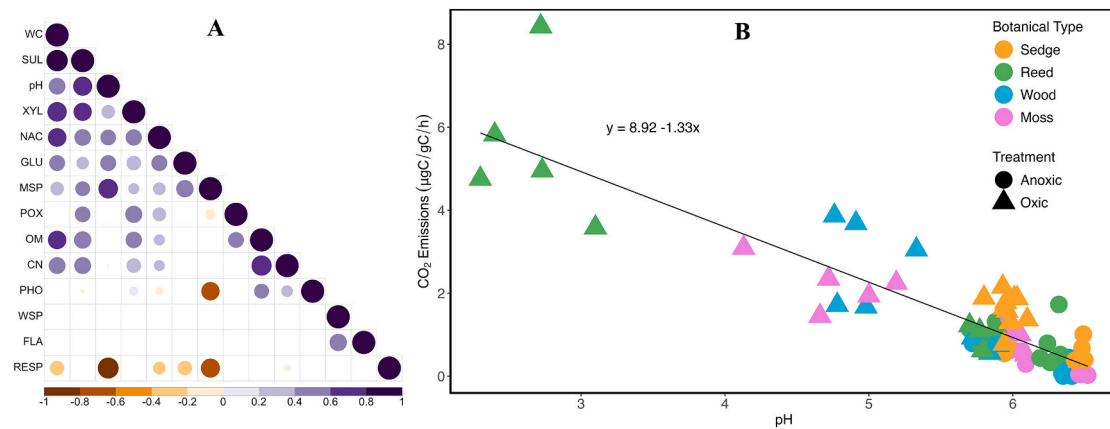


**Fig. 5.** Concentration of phenolic compounds of long-term incubations ( $t_1 = 15$  weeks) (Gallic acid (GAE) was used to express the concentrations of Water – and Methanol – soluble phenolics, Quercetin (QUE) was used for flavonoids).

anaerobic to aerobic metabolism. This gradual shift led to minimal differences in terms of microbial basal respiration rates between short-term oxic and short-term anoxic incubations. In long-term incubations, on the other hand, the disparity between the two treatments was more pronounced. Average respiration rates from anoxic samples decreased, suggesting potential limitations in electron donors or acceptors in the system (Sutton-Grier et al., 2011). Notably, carbon loss in terms of  $\text{CO}_2$  emissions in long-term oxic incubations was 3.9 times higher, highlighting the importance of maintaining a high-water table in peatlands (Evans et al., 2021; Glatzel et al., 2006; Stuart et al., 2022).

We expected the botanical composition of peat to be an important factor in determining respiration rates, but short-term incubations were primarily influenced by oxygen availability rather than the peat matrix.

However, in long-term anoxic incubations, sedge and reed exhibited higher respiration rates as compared to wood and moss peat. This suggests that sedge and reed might provide electron donors for a more extended period due to the availability of less recalcitrant substrates (Gao et al., 2019; Reiche et al., 2010; Szajdak et al., 2019). The data shows that botanical peat composition may play a more substantial role under anoxic conditions, particularly if the inflow water has low concentrations of alternative electron donors (Bauer et al., 2007; Rush et al., 2021). Short-term oxygen exposure triggered higher respiration rates in sedge peat. This may be attributed to the abundance of easily degradable organic material in the sedge matrix (Kane et al., 2019). In the long term, sedge peat showed lower, but stable,  $\text{CO}_2$  emission rates, indicating that factors other than oxygen might have driven decomposition



**Fig. 6.** A. Pearson correlation between variables (CI = 0.95, insignificant results were left blank, ordered based on first principal component). WC: water content, SUL: arylsulfatase, XYL:  $\beta$ -D xylosidase, NAC: N-Acetyl- $\beta$ -D glucosaminidase, GLU:  $\beta$ -D glucosidase, MSP: methanol soluble phenolics, POX: phenol oxidase, OM: organic matter, CN: C/N ratio, PHO: phosphatase, WSP: water soluble phenolics, FLA: flavonoids, RESP: basal respiration rates B. Relationship between CO<sub>2</sub> emissions and pH after long-term oxic and anoxic incubations ( $t_1 = 15$  weeks).

rates. Such factors might include substrate availability, pore size distribution and connectivity or microbial community composition (de Jong et al., 2020; Kitson and Bell, 2020; McCarter et al., 2020).

Reed peat exhibited the highest CO<sub>2</sub> emission rates under long-term oxic incubations, possibly due to pyrite oxidation rather than microbial-driven reactions, as suggested by lower pH values and low exoenzyme potential activities (Brouns et al., 2014b; Rydin and Jeglum, 2013). Pyrite oxidation can release sulphate ions and protons, as well as cause the formation of iron oxides. Sulphate ions can react with water to form sulphuric acid. The formed sulphuric acid can then facilitate the dissolution of iron compounds present in the peat, leading to the release of iron ions (Fe<sup>2+</sup>). These iron ions can subsequently react with oxygen and water to form iron oxides such as hematite (Fe<sub>2</sub>O<sub>3</sub>) or goethite (FeOOH), resulting in the formation of yellowish or reddish spots known as yellow mottle or iron pads. Monitoring yellow spots in the long-term oxic reed samples provides strong evidence of this chemical process (Dent, 1986; Vermaat et al., 2016). This emphasizes the importance of including examinations of chemical characteristics of peat sites for a more complete understanding of CO<sub>2</sub> dynamics in peatlands (Bourbonniere, 2009; Sjögersten et al., 2016).

This study primarily focussed on CO<sub>2</sub> emissions resulting from microbial decomposition. However, methane (CH<sub>4</sub>) can also be generated via microbial metabolism, especially under anoxic conditions (Boonman et al., 2024). While CH<sub>4</sub> emissions make up to 7 % of the total CO<sub>2</sub> and CH<sub>4</sub> emissions from Rouveen anoxic zone, this number drops to 0.3 % in Zegveld (Erkens et al., 2021). This indicates carbon loss via methanogenesis may also contribute to total carbon loss in peatland systems. Thus, CH<sub>4</sub> and CO<sub>2</sub> emissions from both oxic and anoxic layers should be considered when estimating total carbon loss as input for future land subsidence models. Although nitrous oxide is also an important greenhouse gas emitted from degraded peatlands in Europe (Liu et al., 2020; Velthof et al., 2022), nitrogen cycling activities and related emissions fell outside the scope of our study.

It should be noted that our study conducted controlled laboratory incubations to focus solely on how botanical composition impacts peat decomposition. However, it is important to also consider varying moisture and temperature conditions to accurately reflect in situ decomposition rates. While laboratory experiments help understand interactions and mechanisms, combining them with field observations is essential for assessing peatland carbon balance.

#### 4.2. Exoenzyme measurements, phenolic compounds, and edaphic factors

Exoenzyme potential activities have been used as major explanatory variables of both microbial respiration rates and peat decomposition

rates (Sinsabaugh et al., 2012; Sinsabaugh and Follstad Shah, 2011). The two hypotheses mostly discussed regarding the role of exoenzyme potential activity in peat decomposition are the *Enzymic Latch* and *Iron-Gate* (Freeman et al., 2001; Wang et al., 2017). While the Enzymic Latch emphasizes oxygen availability as the primary driver of exoenzyme potential activity and consequently, peat decomposition, the Iron-Gate hypothesis posits that iron can regulate peat decomposition regardless of oxygen diffusion. Our data provide evidence that peat decomposition can be controlled by factors other than purely enzymatic mechanisms.

The results of Phenol oxidase (POX) from our short-term incubations are in line with the Enzymic Latch hypothesis, which states oxygen intrusion releases the latch effect with high POX potential activity and increased respiration rates (Freeman et al., 2004; Pind et al., 1994). However, this latch effect is less visible among hydrolytic exoenzyme potential activities, even though the average potential activity increased (Brouns et al., 2014a). This might suggest that hydrolytic exoenzyme potential activities are decoupled by POX potential activities, which is contrary to the Enzymic Latch hypothesis (Wang et al., 2022). Peat decomposition rates with short-term disturbance might mainly depend on the available substrates under anoxic conditions rather than hydrolytic exoenzyme potential activities. For instance, sedge peat showed a rapid response in terms of CO<sub>2</sub> production after oxygenation, accompanied by high POX potential activity. However, hydrolytic exoenzyme potential activities were not significantly different from those at other peat sites. This suggests that POX can either provide substrate for microbial metabolism or degraded and available substrates under anoxic conditions are directly utilised by microorganisms (Walpen et al., 2018). The latter indicates the importance of electron donors and acceptors (i.e. iron, sulphate, dissolved organic matter, phenolics and such) carried via inflow and the role of anaerobic decomposition in drained peatlands (Kane et al., 2013; Sutton-Grier et al., 2011).

POX potential activities decreased sharply in long-term incubated samples and were comparable between oxic and anoxic conditions, contrary to the Enzymic Latch, as also observed in other long-term monitoring studies (Li et al., 2020; Toberman et al., 2010). The Iron-Gate hypothesis proposes that the oxidation of ferrous iron reduces hydroxyl radicals, leading to a lowered pH in the peat matrix and consequently reducing POX potential activity. In addition, iron and aromatics form a complex that reduces the available substrates for POX (Wang et al., 2017). Since the pH of our peat matrix did not change significantly, except in the case of reed peat, the Iron Gate hypothesis seems to be less applicable to explaining potential activity in the long term for the Rouveen, Zegveld and Bunschoten sites. Although the De Onlanden site may be influenced by iron oxidation, the significant CO<sub>2</sub> emissions observed here speak against the Iron-Gate hypothesis.



Reduced POX potential activities in long-term oxic incubations could be explained by substrate limitation for POX (Li et al., 2020). The result of lower methanol-soluble phenolics in long-term oxic incubations compared to anoxic samples also supports this mechanism. It is worth noting that phenolics can also serve as carbon sources for microorganisms, providing an alternative explanation for the lower concentrations of methanol-soluble phenolics (MSPCs) (Walpen et al., 2018). To further evaluate the applicability of the iron gate hypothesis, it is necessary to monitor iron species and complexations, along with POX redox mediators.

The potential activity of POX also differed between botanical peat types. The POX potential activity in sedge and reed peat was significantly higher compared to wood and moss between oxic and anoxic long-term incubations. This may be due to differences in composition of phenolics between botanical types (Dungait et al., 2012; Min et al., 2015). Sedge and reed peat might have more soluble phenolics and easily accessed sorbed phenolics as a substrate for POX, as opposed to wood and moss peat. This may increase not only the available POX potential activity, but also its production by microorganisms (Allison and Vitousek, 2004; Appel, 1993). However, our soluble phenolics data do not support this mechanism. Future studies should therefore consider identifying different forms of phenolic compounds between botanical peat types to better predict the fate of phenolics and their effects on peat decomposition.

Another explanation in variety in POX potential activities across botanical peatlands might be differences in the microbial community composition, which determine the POX pool in the peat matrix (Freeman et al., 2012). Molecular examinations of POX gene diversity and gene expression may provide valuable insight into POX genes distributions and potential activity, although limitations related to for instance primer design and gene annotation must also be kept in mind.

Short-term oxygenation only significantly altered  $\beta$ -D-xylosidase and Arylsulfatase potential activities, with an increase observed across all sites except for a decrease in sedge. This finding suggests that not all exoenzymes are affected to the same degree by oxygen intrusion, with affects being impacted by peat type and available substrates in its matrix. In the future, investigating the chemical properties of various botanical compositions can aid in determining which specific hydrolytic exoenzymes to monitor for insights into peat decomposition at different sites.

Long-term oxic and anoxic incubations also revealed diverse hydrolytic exoenzyme potential activities across different peat types, which is not in support of either the Iron Gate or Enzymic Latch hypotheses. While increased average hydrolytic exoenzyme potential activities in long-term oxic incubations were observed, our results also indicated higher hydrolytic exoenzyme potential activity with long-term anoxic incubations compared to long-term oxic samples and short-term anoxic samples. This discrepancy may be attributed to a limitation of carbon sources (Hall et al., 2014). In long-term incubations, easily available carbon and nutrient sources may become depleted under anoxic conditions. For survival, microorganisms have to invest in exoenzymes, allowing them to extract essential resources from peat (Schimmel and Weintraub, 2003).

A clear increase in Arylsulfatase exoenzyme potential activity was observed for both sedge and moss peat during longer anoxic incubations. Elevated Arylsulfatase potential activity in anoxic peatlands may be linked to the microbial process of sulphate reduction. In oxygen-depleted environments like waterlogged peatlands, sulphate-reducing bacteria can thrive, using sulphate as an electron acceptor for anaerobic respiration. As a result, sulphide ions are released, and organic matter, often containing sulphate ester bonds, is consumed. Arylsulfatase may be produced or upregulated by microorganisms in response to the increased availability of sulphate esters due to sulphate reduction (Giannini et al., 2020; Kunito et al., 2018; Lu et al., 2018).

Significant differences among hydrolytic exoenzyme potential activities were observed in long-term oxic and anoxic incubations,

particularly for Phosphatase potential activities (Wang et al., 2022; Xu et al., 2021). The increase in Phosphatase potential activity under long-term oxic incubations in peat samples may be attributed to either enhanced nitrogen availability, creating a phosphorus limitation, or shifts in microbial community structure (Romanowicz et al., 2015; Xu et al., 2021). In addition, oxic conditions in peatlands might decrease the availability of phosphorus due to co-precipitation with iron, which needs to be hydrolysed for microbial uptake (Qin et al., 2021).

$\beta$ -D-xylosidase and Arylsulfatase exoenzyme potential activities were higher in sedge samples during long-term oxic and anoxic incubations, but N-acetyl- $\beta$ -D-glucosaminidase and  $\beta$ -D-glucosidase exoenzymes potential activities were similar across different peat types. However, we generally observed relatively low emission rates in sedge peat, demonstrating that elevated exoenzyme potential activity does not necessarily translate to higher emission rates. Consequently, such increased enzyme potential activity may not always correlate with carbon loss from the ecosystem, and final carbon losses may ultimately be determined by other activities related to differences in microbial community composition (Moorhead et al., 2013). Long-term oxic reed samples showed the lowest hydrolytic exoenzyme potential activities due to acidification of the samples by pyrite oxidation. Lower pH inhibited their potential activity, which resulted in the oxidation of pyrite and increased production of CO<sub>2</sub> (Brouns et al., 2014b; Vermaat et al., 2016).

In this experiment, edaphic factors, excluding pH, did not offer clear insights into the determinant of variability in peat decomposition rates across various peatlands. The loss on ignition methodology is a coarse but robust method to get an idea about the carbon content of ecosystems. To analyse carbon content extensively, different carbon substrates can be analysed by using the Soxhlet method or Fourier Transform Infrared Spectroscopy (FTIR) in the future (Fan and Brown, 2001; Heiri et al., 2001).

In summary, although respiration rates increased with short- and long-term oxygenation, oxidative and hydrolytic exoenzyme activities do not align with the responses proposed by the Enzymic Latch and Iron-Gate Hypotheses. The high variability among peat types in hydrolytic exoenzyme activities suggests that the decomposition of organic matter can be regulated by additional factors such as peat botanical composition and availability of alternative substrates. Exoenzymes can serve as valuable indicators of organic matter decay, although caution should be exercised when relating such measurements to carbon loss and ultimately soil subsidence.

## 5. Conclusions

Due to their potential roles in land subsidence in drained peatlands, we investigated aerobic and anaerobic peat decomposition rates across a range of botanical peat compositions. Our findings demonstrate that anaerobic decomposition, as indicated by CO<sub>2</sub> emissions, can be significant and can affect aerobic decomposition rates during declines in the water table. Therefore, deterministic land subsidence models should consider incorporating these deeper peat layers for more accurate forecasting.

Exoenzyme activities varied under different incubation times and conditions, exhibiting substantial variability across peat types and between the different enzymes examined. Our data revealed interactions between peat type and different exoenzyme activities, suggesting that peat botanical composition serves to regulate these enzymes in a content-specific manner, challenging both the Enzymic Latch and Iron-Gate Hypotheses.

## CRediT authorship contribution statement

**Duygu Tolunay:** Writing – original draft, Visualization, Methodology, Formal analysis, Conceptualization. **George A. Kowalchuk:** Writing – review & editing, Supervision. **Gilles Erkens:** Writing – review & editing, Supervision. **Mariet M. Hefting:** Writing – review &

editing, Supervision, Methodology, Conceptualization.

## Declaration of competing interest

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

## Data availability

Data will be made available on request.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.172639>.

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