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Research article

Altered litter quality drives changes in litter decomposition following implementation of a regenerative measure in Dutch peat meadows

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ABSTRACT

The majority of NW European peatlands are degraded due to conventional grassland-based livestock farming (i.e. lowered groundwater levels, high nutrient inputs and high mowing frequencies) leading to increased CO_2 emissions and soil nutrient levels, and reduced biodiversity. Creating regenerative ditch borders along drainage ditches that surround agricultural fields could ameliorate some of these negative effects. We investigated the effects of ditch border type (conventional vs. regenerative) on litter decomposition (standardized litter using Tea Bag Index, and locally collected leaf and root litter), vegetation composition, litter quality, and soil characteristics along transects that extended from the water's edge into the adjoining field (40 cm, 80 cm, 360 cm and 640 cm) in a peat polder in North Holland, the Netherlands. The decomposition rate of standardized litter was unaffected by ditch border type, however the stabilization factor was 43% and 35% lower in regenerative ditch borders at 40 cm and 80 cm from the water's edge, respectively. Leaf litter collected from regenerative borders decomposed 75% slower than leaf litter from conventional borders. Regenerative soils were higher in organic matter content, carbon and nitrogen content, and soil moisture content, and lower in bulk density and soil compaction. This pattern was related with a lower decomposition rate and stabilization of standardized litter. Changes in litter decomposition are predominantly driven by a lower leaf litter quality produced at regenerative borders. Efforts to reduce carbon emissions should therefore focus on reducing decomposition rates by creating conditions that stimulate plant species producing litter of a lower quality.

1. Introduction

Peatlands provide important ecosystem services such as carbon storage, water regulation, and the conservation of biodiversity (Joosten et al., 2017; Minayeva et al., 2017; Gorham et al., 2012; Verhoeven and Setter, 2010). They store vast amounts of carbon (±547 Gt of C) due to waterlogged conditions resulting in low oxygen availability which favors the accumulation of organic matter (Leifeld and Menichetti, 2018; Yu et al., 2010; Gorham, 1991). Peatlands cover 10% of the European land surface of which approximately half is used for agriculture (Tanneberger et al., 2021; Schrier-Uijl et al., 2014). In the Netherlands, peat meadows have been drained since the 1100s for conversion to agriculture, a practice which has intensified in the last five decades (Verhoeven and Setter, 2010; Van de Ven, 1993). Today, 82% of Dutch peat meadows are used for grassland-based livestock farming where drainage (lowering of ground water level to between −30 cm and −70 cm) is a common practice to ensure high grass production and to allow heavy machinery to work the land in spring, and where the production system is highly dependent on external inputs (manure and artificial fertilizer) (Deru et al., 2018; van Bruchem et al., 1999). Drainage enhances oxygen diffusion into the topsoil layer which stimulates heterotrophic respiration (i.e. peat oxidation) (Brouns et al., 2014). Consequently, drainage contributes to land subsidence, results in higher CO_2 emissions (shifting peat systems from carbon sinks into carbon sources) and increases nutrient releases (Leifeld et al., 2019; Erkens et al., 2016; Joosten, 2009; van den Akker et al., 2008). As a result, 75–95% of the Dutch peatlands are now degraded with large implications for the soil carbon cycle and national carbon emissions through

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atmospheric and surface water CO_2 exchanges (Tanneberger et al., 2021).

Several restoration measures have been proposed and researched to mitigate degradation of peatland agroecosystems with the focus on raising groundwater levels to reduce peat mineralization and stimulate carbon storage. Examples of these measures are rewetting, active and passive subsurface water infiltration and raising of ditchwater levels, all of which are mostly mechanical measures (Boonman et al., 2022; Hoekstra et al., 2020; van de Riet et al., 2013). There is an emerging emphasis in Dutch peat restoration programs to transition towards an agroecosystem where nature restoration is combined with the production of food, also defined as “regenerative agriculture” (Schreefel et al., 2020). Here, the objective is to stimulate ecosystem services, and promote climate adaptation, biodiversity and human well-being by implementing various measures that create a more heterogenous agroecosystem (Schreefel et al., 2020; Erisman et al., 2017). One type of measure that is particularly relevant for agricultural peatlands is converting ditch borders, a 1.5–5 m strip of land between surface waters and an adjoining field. By creating a dynamic transition between water and land where natural conditions are stimulated, a “regenerative” ditch border can be constructed that functions as a biodiverse corridor along the agricultural field (van Vossen and Verhagen, 2009). These borders can also contribute to nutrient removal and thereby improve water quality (Hefting et al., 2013; Mayer et al., 2007; Hefting and De Klein, 1998). Despite their implementation on a relatively large scale, their potential role in modifying soil carbon storage, and therefore contributing to climate adaptation, has until now received no systematic research attention.

During the construction of regenerative ditch borders, the nutrient rich topsoil layer (including the vegetation) is removed to create a gentle slope ($\leq$5 m, ±20%) from the field towards the waterside. Topsoil removal in fen ecosystems often reduces nutrient availability and creates wetter conditions (Klimkowska et al., 2015). Moreover, long-term effects of topsoil removal in fen meadows include lower soil bulk density, higher soil organic matter (SOM) content, and higher soil C/N ratio (Emsens et al., 2015). Wetter conditions, induced by rewetting of agricultural fens, are already known to have the ability to (partially) induce carbon storage and shift the ecosystem towards a carbon sink by reducing respiration (CO_2 emissions) from decomposition of organic matter (Evans et al., 2021; Günther et al., 2020; Peacock et al., 2019; van de Riet et al., 2013). A decreased bulk density and increased SOM content, induced by topsoil removal, is beneficial for restoring the carbon balance when rewetting (Harpenslager et al., 2015). Changing soil characteristics due to changes in management can also alter the vegetation composition. Wetter and nutrient poor conditions are less suitable for pasture grasses such as *Lolium perenne* which are inundation sensitive, and favor fen plant species which are inundation tolerant (Klimkowska et al., 2015). This vegetation shift could be accompanied by a shift in litter quality, consisting of a combination of structural (e.g. lignin content) and chemical traits (e.g. nitrogen content), which could affect litter decomposition rates through plant ‘afterlife’ effects determined by their set of traits (Freschet et al., 2012; Cornelissen et al., 2003). Thus, either directly through altering soil characteristics or indirectly through altering litter quality by a shift in the vegetation composition, the implementation of regenerative ditch borders could lead to changed local conditions, reduced litter degradation, and consequently increased soil carbon storage.

Carbon storage in peatlands results from the sum of processes that determine SOM stabilization. SOM stabilization is primarily regulated by above- and below-ground litter inputs, litter decomposition, and soil microbial community structure and metabolic activity which are formed by environmental conditions (Cotrufo et al., 2015; Schmidt et al., 2011). Litter decomposition is therefore a key process for assessing the effect of restoration efforts on the soil carbon cycle. Litter decomposition is generally considered to be controlled by climate (e.g. temperature and moisture availability), litter quality and decomposer organism activity (Bradford et al., 2016; Aerts, 1997). Climatic conditions affect litter decomposition rates directly through their effect on reaction kinetics, oxygen availability, and microbial physiology and indirectly through altering the chemical composition of litter, litter quality determines nutrient release rates directly and indirectly through affecting microbial growth and turnover, and decomposer organism activity regulates enzymatic hydrolysis of litter (Suseela and Tharayil, 2017; Bradford et al., 2016; Prescott, 2010; Aerts, 1997). However, small-scale differences in microenvironmental soil parameters are found to explain more variation in decomposition than macroclimatic conditions (Joly et al., 2017). Standardized decomposition assays using a common litter type are useful for quantifying such microenvironmental effects. The Tea Bag Index (TBI), which uses a standardized litter of tea leaves to estimate the ability of microorganisms to break down organic matter has been widely applied in this context (Keuskamp et al., 2013). Within an ecosystem, TBI is responsive to changes in abiotic soil parameters, such as soil moisture, which makes it a good indicator for assessing management-induced changes in peat meadows. This method enables us to estimate the environmental effects on litter decomposition independent from litter quality effects of local litter. Thus, combining TBI with measures of the decomposition rate of local litter allows us to quantify the effects of regenerative ditch borders on litter decomposition and consequently soil carbon storage through this key process.

In this study we answer the following questions: (1) do ditch border type and distance to the water’s edge (i.e. soil water content) affect litter decomposition conditions (quantified using standardized litter)?; (2) do ditch border type-induced changes in vegetation composition affect litter quality and litter decomposition rates?; and (3) to what extent are soil characteristics affected by ditch border type and can this explain variation in litter decomposition of standardized litter. We hypothesized that regenerative ditch borders alter microenvironmental soil characteristics, such as an increased soil moisture content, which will lead to reduced TBI litter decomposition rates. This effect will be strongest near the waterside where the soil moisture content is the highest. Furthermore, changes in vegetation composition (i.e. shift from an inundation intolerant *Lolium perenne* L. dominated ecosystem to an inundation tolerant *Phragmites australis* (Cav.) Trin. ex Steud. dominated ecosystem) will lead to reduced local litter decomposition rates due to a decrease in litter quality (e.g. higher lignin content). To test these hypotheses, we performed a one-year field study in a Dutch fen peat meadow. We measured litter decomposition over four seasonal incubation periods (using the Tea Bag Index and local root and leaf litter bags), soil parameters and vegetation composition over a transect from the waterside extending into the adjacent agricultural field at 20 different ditch borders subject to either a conventional or a regenerative type of management.

2. Materials and methods

2.1. Site description

This study was carried out in the Vereenigde Binnenpolder located near Spaarnwoude, province of North Holland, the Netherlands (52°40′34.1’’N, 4°69′55.4’’E). This area is situated ±14 km NW of Amsterdam on Holocene coastal deposits, and classified as a minerotrophic (fen) peat (sedge-peat with traces of reed) polder (van ’t Veer, 2022; Vos, 2015). The polder is divided into a series of fields separated by water-filled drainage ditches (Fig. 1A). All of these fields are currently being used for livestock farming and have been subject to water level management (i.e. drainage) since the 12th century (van der Aar, 1984). We use the term “agricultural field” to refer to the part of each field where agricultural activity (mowing, fertilizing and livestock grazing) is conducted, and “ditch border (DB)” (Fig. 1B) to refer to the strip of land surrounding each field adjacent to the water-filled drainage ditch. It’s considered a relatively extensively managed polder due to the relatively higher water tables, the primary use of raw straw manure and

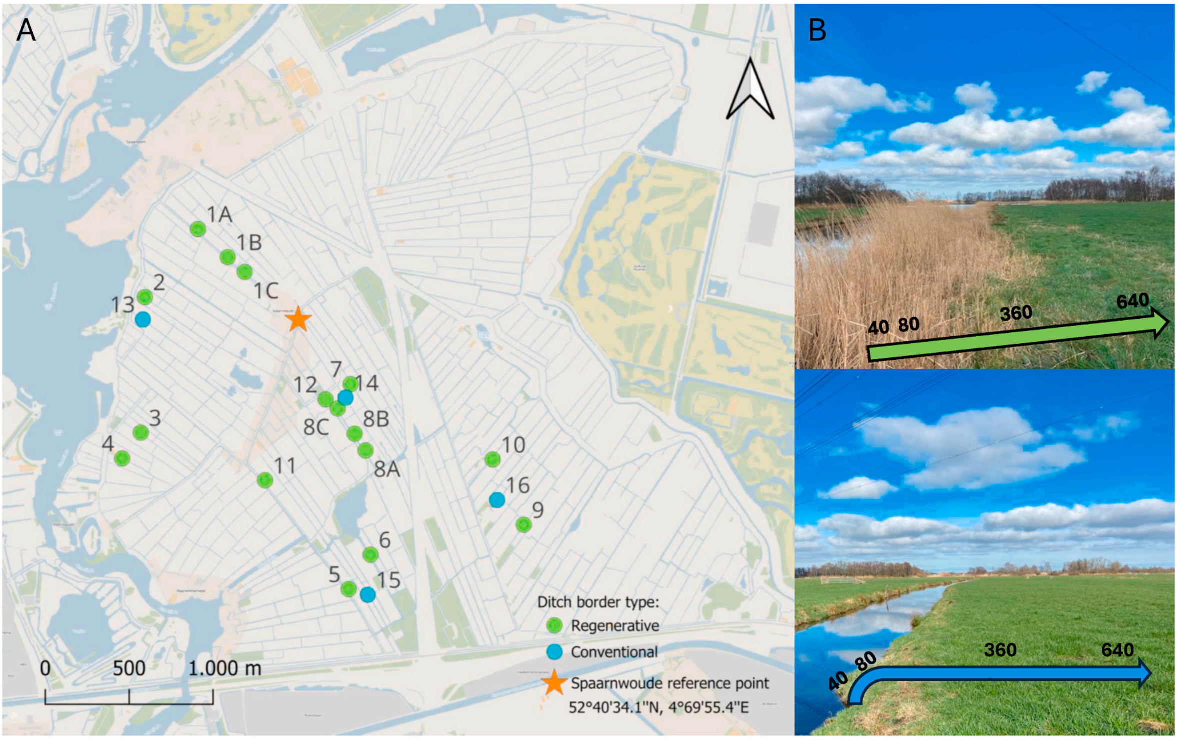

Fig. 1. Locations of sampling transects in the study area (Vereenigde Binnenpolder, Spaarnwoude, province of North Holland) (A) and transect set-up (B). A: Coloured points indicate the ditch border type at each ditch border (green: regenerative; and blue: conventional) and the numbers indicate the ditch border numbers. The orange star represents a reference point with given latitude and longitude. Blue lines and areas are the water-filled drainage ditches and open water and light green areas, surrounded by light blue lines, are peat agricultural fields. B: Transects in a conventional DB (blue arrow; bottom) and in a regenerative DB (green arrow; top). Numbers indicate the distance from the edge of the water-filled drainage ditch (cm). Due to topsoil removal and the establishment of a gentle slope between field and water's edge the 40 cm and 80 cm transect points in regenerative DBs are typically at lower elevation than the corresponding points in conventional DBs.

the attention paid to conservation of breeding habitat for meadow birds in comparison to other fen polders in the region. One pumping station controls the inlet water levels and therefore we assume that ditch water levels were similar across the polder (pumping station the Vereenigde Binnenpolder, winter level −2.12 m NAP [Amsterdam Ordnance Datum] and summer level −2.02 m NAP).

Regenerative ditch borders (RDBs) were established in this polder (±4 ha in total) by excavating the topsoil layer and creating a gentle slope starting at a distance of 5 m into the agricultural field towards the waterside in 1997. Additional regenerative management at these borders entails no application of manure or pesticides, exclusion from grass production and no or delayed mowing. Despite these criteria, there is variation in the presence of cows (i.e. grazing intensity), in mowing and in the vegetation composition creating a range in RDBs. Conventional management entails mandatory buffer zones starting at a distance of one and a half meters into the agricultural field towards the waterside, where no manure or pesticides are allowed to be applied and where organic material harvested from the ditch is deposited in fall (Rijksdienst voor Ondernemend Nederland, 2024). Conventional ditch borders (CDBs) are included in grass production and are typically on the same mowing schedule as the adjoining agricultural field (1–3 mowing rounds per year).

2.2. Experimental set-up

Throughout the polder, 20 DBs were selected, of which 16 DBs were subject to the regenerative DB type and four to the conventional DB type (Fig. 1A). With this set-up we covered a broad range in management choices (see Appendix A.1), vegetation composition and hydrological properties of regenerative DBs.

At each ditch border a transect from the ditch into the agricultural field was set up with measuring points established at 40 cm, 80 cm, 360 cm and 640 cm distance from the water's edge, in March 2023. The first two measuring points were located on the slope, the third point was located close to the transition between the excavated zone and the agricultural field, and the fourth point was located in the agricultural field (Fig. 1B). Dataloggers (TOMST TMS-4) were deployed at each of the 20 DBs, which logged soil moisture (to a depth of −14 cm) (Time-Domain transmission method, using 2.5 GHz electromagnetic pulses) and soil and air temperature (at depths of −6 cm, +2 cm and +15 cm) (MAXIM/DALLAS Semiconductor DS7505U+), measuring every 15 min (Wild et al., 2019). The loggers were placed at transect point 360 cm and shielded with stainless steel bars. Lolly software (version 1.51) was used to extract the data in the field and daily averages were calculated. The soil moisture loggers were calibrated by taking a soil sample at 360 cm from a conventional and regenerative DB and watering these samples to their water holding capacity. The samples were subsequently oven dried (30 °C) over a period of two weeks and regularly weighed after which we could establish a correlation between the datalogger values and the gravimetric soil moisture content of the samples ($R^2 > 0.8$).

2.3. Litter decomposition

Litter decomposition was measured over a one-year period (March 2023 to March 2024) divided over four separate sampling rounds (Table 1). The Tea Bag Index (TBI) using standardized litter (Keuskamp et al., 2013) and litter bags containing locally collected leaves and roots were used as indices to quantify litter decomposition rates. For the TBI, Lipton rooibos (EAN 87 22700 18843 8) and Lipton green tea (EAN 87 10908 90359 5) were used as litter. The first round of sampling included both woven (i.e. nylon) and non-woven (i.e. polylactic acid (PLA); biodegradable) tea bags; in the following three rounds only non-woven tea bags were incubated. There was no effect of tea bag material on the DB type based on data from the first round. Before incubation, the tea

Table 1
Division of the tea bag and litter bag experiments over the four seasonal incubation periods (spring, summer, autumn and winter). Plastic tea bags were referred to as 'woven' and biodegradable tea bags as 'non-woven'; root litter bags were referred to as 'root litter' and leaf litter bags as 'leaf litter'. In each incubation period, soil samples were taken for each transect point in each DB which was referred to as 'Date soil sampling'.

Season – incubation period	Tea Bag Index	Litterbags	Date soil sampling
Spring 27/03/2023–30/06/2023	Non-woven and woven	–	June 14/06/2023–20/06/2023
Summer 26/06/2023–29/09/2023	Non-woven	–	August 22/08/2023–30/08/2023
Autumn 26/09/2023–20/12/2023	Non-woven	Root litter	October 17/10/2023–31/10/2023
Winter 18/12/2023–19/03/2024	Non-woven	Root and leaf litter	January 9/01/2024–18/01/2024

bags were weighed, and the non-woven bags were wrapped in a coarse mesh (8 mm mesh size) to prevent damage to the fragile bag material during deployment and retrieval. The tea bags were buried at a depth of −8 cm at the four transect points in all DBs, and were retrieved after an incubation period of 88–94 days with the exception of 81–85 days in the autumn incubation period.

For preparation of local root litter bags, soil cores (10 cm x ⌀ 4.8 cm) were collected (n = 3) at all transect points in all DBs in August (n = 80 in total; Table 1) to extract roots by washing soil samples through a sieve (mesh size 1.2 mm). The washed roots were then dried at 30 °C for 72 h. No distinction between dead and live roots was made. Two root mixes were made: one from all root material collected from transect points in RDBs and one from all root material from transect points in CDBs. For the leaf litter bags, we decided to only collect the leaves of the dominant plant species of each of the two DB types. Therefore, leaf litter of two grass species, *Lolium perenne* (dominant in CDBs; mean coverage CDB: 38% & RDB: 20% at 40 and 80 cm) and *Phragmites australis* (dominant in RDBs; mean coverage CDB: 0% & RDB: 43% at 40 and 80 cm), were collected in autumn (start of November) after senescence. The collected leaves were dried at 30 °C for 72 h. Leaf and root material of regenerative and conventional borders was separately cut into small fragments (0.5–1 cm) and thoroughly mixed. Next, non-woven tea bags (the same material as used for TBI incubations, see above) were cut open and emptied, filled with 1 g of dried litter material, sewed back up and wrapped in the coarse mesh. The litter bags were buried at a depth of −8 cm alongside the tea bags at all four transect points. We set-up a reciprocal transplant design to disentangle litter quality and microenvironmental effects. In this design, the conventional leaf and root litter bags were incubated in all CDBs and in a selection of RDBs (DB numbers 5, 6, 9 and 10) and the regenerative leaf and root litter bags were incubated in all CDBs and all RDBs. All litter bags were retrieved together with the tea bags after a period of 81–85 days in the autumn incubation period and 88–91 days in the winter incubation period.

After retrieval, all bags were dried at 70 °C for 72 h and dried soil particles were removed from the outside of the bag. The bags were cut open and the remaining tea or local litter was collected and weighed. The start weight of the tea bags was calculated by subtracting the bag weight determined by Keuskamp et al. (2013) from the initial measured weight. All root litter after incubation, as well as the two root mixes before incubation, was additionally burned at 550 °C for 4 h (muffle furnace) to determine mineral content. The start and end weight were corrected with the remaining ash fraction of the two root mixes and root litter after incubation, respectively. We calculated mass loss of green tea and rooibos by:

$$Mass\ loss = \frac{(mass_{start} - mass_{end})}{mass_{start}} \times 100\% \qquad \text{(eq. 1)}$$

where, $mass_{start}$ is the start weight of the tea or litter (g), $mass_{end}$ is the end weight of the tea or litter (g) after incubation both excluding bag weight.

We used the tea bag data to estimate the decomposition rate (TBI-k) and the stabilization factor (TBI-S) of standardized litter using the TBI formulas (Keuskamp et al., 2013) and the tea bag and litter bag data to estimate the decomposition rate of green tea, rooibos and litter (k) with the first-order exponential decay function (Olson, 1963):

$$X_{(t)} = X_0 * \exp\left(-kt\right) \qquad \text{(eq. 2)}$$

where, k is the decomposition rate, t the time period of decomposition (years), X_0 the initial mass (g) and $X_{(t)}$ the mass (g) after t years of decomposition.

2.4. Soil characteristics

During all four litter decomposition incubation periods, one series of soil samples was collected to determine the gravimetric soil moisture content (SMC), soil pH, bulk density (BD), total carbon (C) and nitrogen (N) content, C/N ratio and soil organic matter content (SOM) (Table 1). Triplicate soil cores (10 cm x ⌀ 4.8 cm) were collected (Table 1) from each transect point in all DBs (i.e. 240 cores from 80 transect points) using a stainless-steel core and were stored in a cold room at 4 °C until processing in the laboratory (±1–2 weeks). Soil resistance (N/m^2) was measured as an indicator of soil compaction (SC) and bearing capacity using a penetrometer (06.01.SA, Eijkelkamp, Giesbeek, the Netherlands). Measurements were performed directly in the field (to a depth of −10 cm) with three measuring points per transect point, to correct for soil heterogeneity.

The triplicate soil cores were thoroughly mixed after which soil and roots were separated. We determined pH of the soil by adding 25 ml KCL solution (0.1 M) to 10 g of fresh weight soil (WTW INOLAB Level 2); SMC by weighing 20 g of fresh weight soil before and after drying at 70 °C for 48 h; total C and N content through flash combustion of the dried ground soil using an elemental analyzer (FLASH EA 1112 elemental analyzer; Thermo Fisher Scientific, Rodana, Italy), SOM content by loss on ignition (LOI) of dried (550 °C for 4 h, muffle furnace) ground soil, and BD by using the SMC, the combined fresh weight and volume of the three soil cores.

2.5. Vegetation cover

Vegetation cover and composition was characterized using the Braun-Blanquet method in May 2023 (Braun-Blanquet, 1925). Plant species cover was measured in a rectangular shaped plot (200 × 50cm) placed parallel to the water's edge for all transect points. There was no overlap in plots between transect points 40 cm and 80 cm.

2.6. Litter mix characteristics

The total C and N content, C/N ratio, ash fraction (LOI) and lignin content of a subset of the litter mixes were measured to explain any possible differences in litter decomposition. Lignin content was quantified by using the extraction (using water, methanol, and chloroform) and hydrolysis method by Poorter and Villar (1997). The residue should consist of cellulose and lignin only (hemi cellulose, proteins and silicates could still be present) and was then analyzed for its total C and N content and ash fraction (LOI) content. Residue weight was corrected for ash fraction (i.e. sand correction). Finally, total N content was used to correct for left-over proteins in the residue and lignin content was then quantified based on the known difference in total C content between lignin and cellulose (Poorter and Villar, 1997).

2.7. Data analysis

We tested the response variables TBI-k, TBI-S, green tea k and mass loss and rooibos k and mass loss with linear mixed-effects (lme) models, using DB type (categorical) and distance to water's edge (categorical) as fixed effects and DB number (1A-16, see Fig. 1A) and season as random effects (Bates et al., 2015). We also tested the response variables decomposition rate of root and leaf litter with lme models using DB type, distance to the water's edge and species origin (leaf litter) or litter mix origin (root litter) as fixed effects and DB number and season (only for root litter) as random effects (= full reciprocal transplant design). There were no effects of the microenvironment within species or litter mix (see Appendix A.2 & A.3), thus, the analyses were repeated without the reciprocal part of the transplant design (i.e. DB type removed from analysis). We tested mean daily soil moisture and soil temperature as response variables using DB type as fixed effect and DB number and season as random effects with lme models. Gravimetric soil moisture content was also tested as response variable using DB type and season as fixed effects and DB number as random effect with an lme model. Model assumptions were tested by visual inspection. Normality of the residuals was inspected through Q-Q plots and homogeneity of the variance through residual vs. fitted plots. When necessary (log) transformations of the response variables were performed. All models included both main effects and two-way interactions. ANOVA tests were performed for the models (Kuznetsova et al., 2017) and planned contrast analyses were carried out to test for differences between the two DB types/species origin/litter mix origin within each distance to the water's edge or seasons when the interaction term was significant ($\alpha = 0.05$) (Searle et al., 2012). When the interaction was not significant, planned contrast analyses with distance to the water's edge or seasons (differences between distances to the water's edge) and DB type (difference between conventional and regenerative type) alone were performed. We repeated all the above statistical analyses with a subset of the data that excluded all observations from the measuring point 640 cm from the water's edge. As these points were located outside the ditch border and therefore where no direct difference between DB type would be expected, we wanted to see if our conclusions were robust to the inclusion of these datapoints.

A Principal Component Analysis (PCA) was performed with all soil parameters with all four soil sampling rounds (n = 320) (SMC, soil pH, total C and N content, C/N ratio, SOM, soil compaction and bulk density) (Kassambara and Mundt, 2020). We used a Pearson Correlation Matrix to determine the correlation coefficients between the soil parameters and the scores of Principal Components 1 (PC1) and 2 (PC2) and we tested the scores of PC1 as response variables using DB type as fixed effect and DB number and season as random effects with linear mixed effects models. Linear relations with TBI-k, TBI-S, mass loss of green tea and mass loss of rooibos as response variables, with PC1 scores as fixed effect and DB number and season as random effects was tested using linear mixed effects models. ANOVA tests were retrieved for these

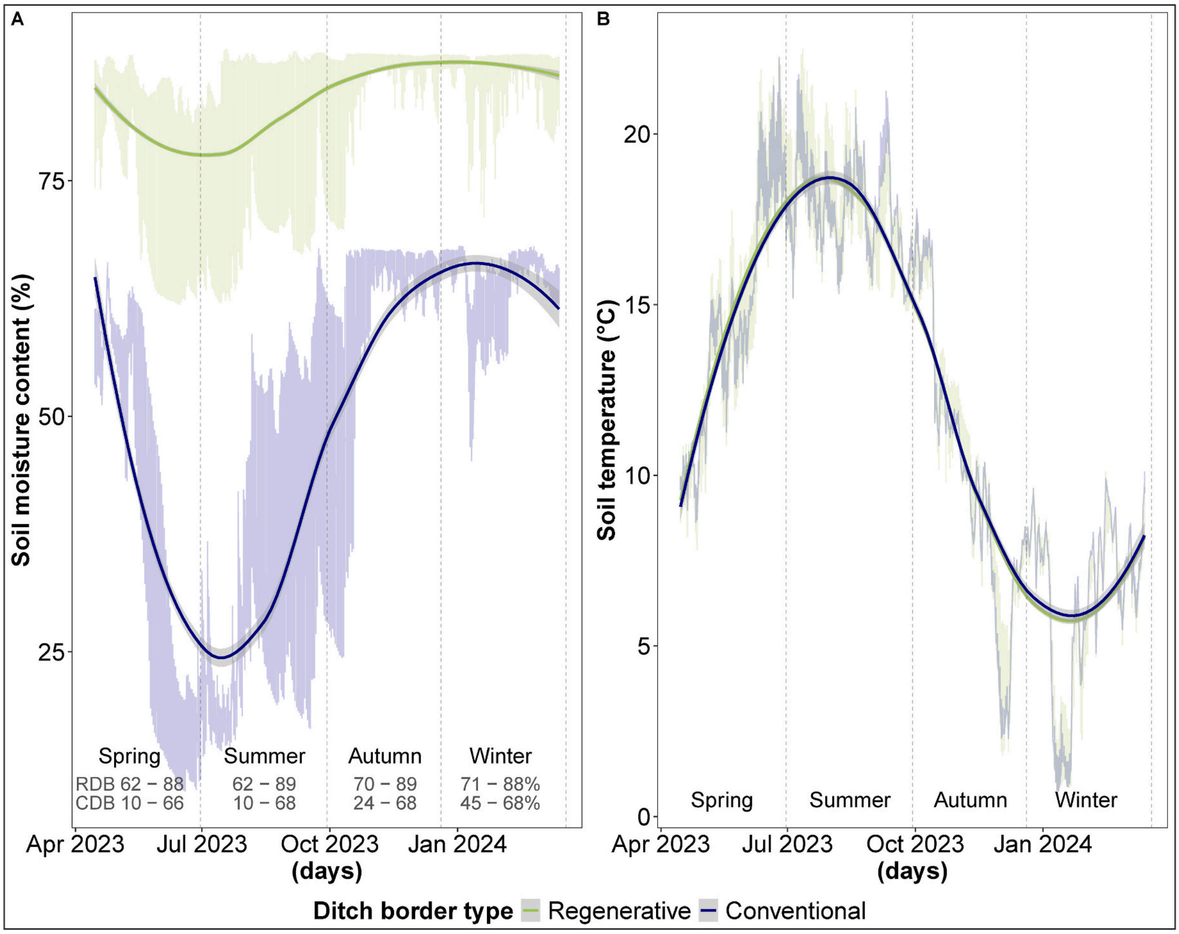

Fig. 2. Mean daily soil moisture content (A) and mean daily soil temperature (B) in the DBs throughout the year measured with the TOMST sensors at transect point 360 cm (t0 at 15-04-2023 and tend at 14-03-2024). The percentages in 3A represent the min-max mean daily soil moisture ranges of both DB types in each incubation period. Dashed lines indicate the boundaries between the four incubation periods (spring, summer, autumn and winter). The fitted lines represent the overall soil moisture and temperature for each ditch border type (smooth conditional means, method = "loess", span = "0.75"); the grey area around the dark lines represents the confidence interval around the smooth (0.95, SE); and the faded blue and green areas represent the actual soil temperature and soil moisture range of the ditch border types.

models (Kuznetsova et al., 2017) and the r-squared (including fixed and random effects) of the correlations were determined (Bartoń, 2024).

All statistical analyses were carried out in R (version 4.4.1, R Core Team, 2024).

3. Results

3.1. Abiotic conditions

Overall, the conventional ditch borders (CDBs) were relatively drier throughout the entire year (see Appendix A.4; Fig. 2A). This observation matched the gravimetric soil moisture content from the soil samples taken throughout the year where on average RDBs had a soil moisture content of 72 ± 1.06% (SE) and CDBs of 56 ± 2.04% (see Appendix A.4). The spring incubation period was characterized by a wet start in 2023, yet it experienced a drier end. For the summer incubation period this trend was reversed. The autumn and winter incubation periods were both characterized by continued wet soil conditions. Additionally, there was a period of frost during the winter incubation period in January, although mean daily soil temperatures remained above 0 °C (Fig. 2B). Mean daily soil temperature was uniform among DBs and no relevant fluctuations between DB types were observed, at least at 360 cm, yet patterns might change closer to the water's edge (see Appendix A.4).

3.2. Standardized litter decomposition not affected by ditch border type

There was no effect of DB type on the TBI-k of standardized litter. The mean TBI-k was 0.011 ± 2.16e-4 day^{-1} for the regenerative DB type and 0.012 ± 4.54e-4 for the conventional DB type. The distance to the water's edge had a significant effect on TBI-k (Table 2). TBI-k increased with increasing distance to the water's edge from 0.0102 ± 2.66e-4 up to 0.0119 ± 4.12e-4 which was equal to a 17% increase overall (Fig. 3A).

DB type significantly affected the TBI-S (stabilization factor) of standardized litter, however this effect was dependent on the distance to the water's edge (Table 2). TBI-S was lower at 40 cm and 80 cm in the regenerative DB type: from 0.188 ± 0.03 down to 0.108 ± 0.01 (43% lower) and from 0.232 ± 0.02 down to 0.152 ± 0.01 (35% lower), respectively. TBI-S was not significantly different between the two DB types at 360 cm and 640 cm (Fig. 3B). When the analyses were repeated without data taken at 640 cm from water's edge, DB type now had a significant effect on TBI-k (see Appendix A.5). However, no significant effects were found between DB types within each distance to the water's edge in the planned contrast analysis.

Table 2
ANOVA table of the Linear Mixed-Effects models with the decomposition rate (TBI-k), stabilization factor (TBI-S), mass loss green tea, mass loss rooibos, root litter k and leaf litter k as response variables; ditch border type (conventional and regenerative) and distance to water's edge (40 cm, 80 cm, 360 cm and 640 cm) as fixed effects; and ditch border number (1A-16) and season (June, August, October and January) as random effects. Conventional DBs were replicated 4 times and regenerative DBs 16 times. The significant p values are highlighted in bold.

	Ditch border type		Distance to water's edge		Ditch border type x Distance to water's edge	
	F_1	*P*	F_3	*P*	F_3	*P*
TBI-k	3.1	0.096	3	**0.032**	0.9	0.443
TBI-S	6.3	**0.022**	20	**<0.001**	4.2	**0.006**
Green tea k	5.7	**0.027**	18.9	**<0.001**	3.4	**0.019**
Rooibos k	0.08	0.232	1.4	0.779	4.5	**0.004**
Mass loss green tea	5.8	**0.026**	7.7	**0.004**	4.5	**0.004**
Mass loss rooibos	0.003	0.96	1.9	0.127	4.7	**0.003**
Root litter k	0.1	0.766	0.9	0.441	1.8	0.148
Leaf litter k	362.8	**<0.001**	3.7	**0.018**	0.5	0.68

3.3. Changes in local litter quality strongly affected litter decomposition rates

Plant species and ditch border type significantly affected the decomposition rate of leaf litter, however root litter remained unaffected by litter origin and ditch border type (Table 2). Leaf litter of *Phragmites australis*, incubated and originating from RDBs, showed 75% lower decomposition rates in comparison to leaf litter of *Lolium perenne*, incubated and originating from CDBs, from 2.653 ± 0.12 (*L. perenne*) down to 0.652 ± 0.02 (*P. australis*) (Fig. 4). *Lolium perenne* leaf litter was approximately twice as high in total N content resulting in a twice as low C/N ratio in comparison to *P. australis* leaf litter (see Appendix A.6). The lignin content was higher for *P. australis* leaf litter (see Appendix A.6). Although differences in root litter traits were found between litter origins, they were substantially smaller in magnitude (see Appendix A.6).

3.4. Effects of ditch border type on the decomposition environment

Principal Component 1 (PC1) explained 65.1% of the variance in soil chemical and physical characteristics across the dataset and was strongly correlated with total C and N content, SOM content, SMC, BD and SC. Principal component 2 (PC2) explained 12.6% of the variance and was strongly correlated with soil pH (Table 3; Fig. 5). SMC, SOM, C and N content were all strongly positively correlated with each other. SMC was strongly negatively correlated with BD reflecting the difference between loose peat soils high in SMC content and C content from compact and drier peat soils with a high BD. The RDBs resulted mostly in soils characterized as the former and the CDBs as the latter (See Appendix A.4), however there was substantial variation in soils in RDBs and overlap with CDBs. Increasing distance to the water's edge resulted in a higher BD and SC and in an lower SMC, SOM content and total C and N content overall.

3.5. Decomposition environment explained patterns in litter decomposition better than ditch border type

PC1 values were positively correlated with higher BD and SC (associated with the CDBs), whereas negative PC1 values were correlated with higher SMC, total C and N content, C/N ratio and SOM content (associated with RDBs).

The TBI-k was positively correlated with PC1, although the correlation was not strong ($R^2 = 0.14$; Fig. 6A). Moreover, the TBI-S was positively correlated to PC1 (Fig. 6B). TBI-k and TBI-S were both decreasing with soils characterized by a higher SOM content, SMC and total C and N content and by a lower BD and SC, which included mostly soils from RDBs. The mass loss of green tea – of rooibos were negatively correlated with PC1 (Fig. 6C & D), thus increasing in soils mostly in RDBs.

4. Discussion

Our results show that litter decomposition was predominantly controlled by changes in litter quality and microenvironmental conditions played a subordinate role when changing from conventional to regenerative DBs in agricultural fen ecosystems. Ditch border type did not affect litter decomposition of standardized litter, however regenerative DBs lowered litter quality through changes in vegetation composition which greatly reduced local litter decomposition rates. Local soil characteristics were altered by ditch border type and soils in regenerative DBs were associated with higher values of soil moisture content, soil organic matter content and carbon/to nitrogen ratio and with lower bulk density and soil compaction. Soil characteristics were better predictors of standardized litter decomposition dynamics than ditch border type and soils from regenerative ditch borders showed a reduced decomposition rate and stabilization of standardized litter, although their predictive power remained low. The distance to the water's edge did affect

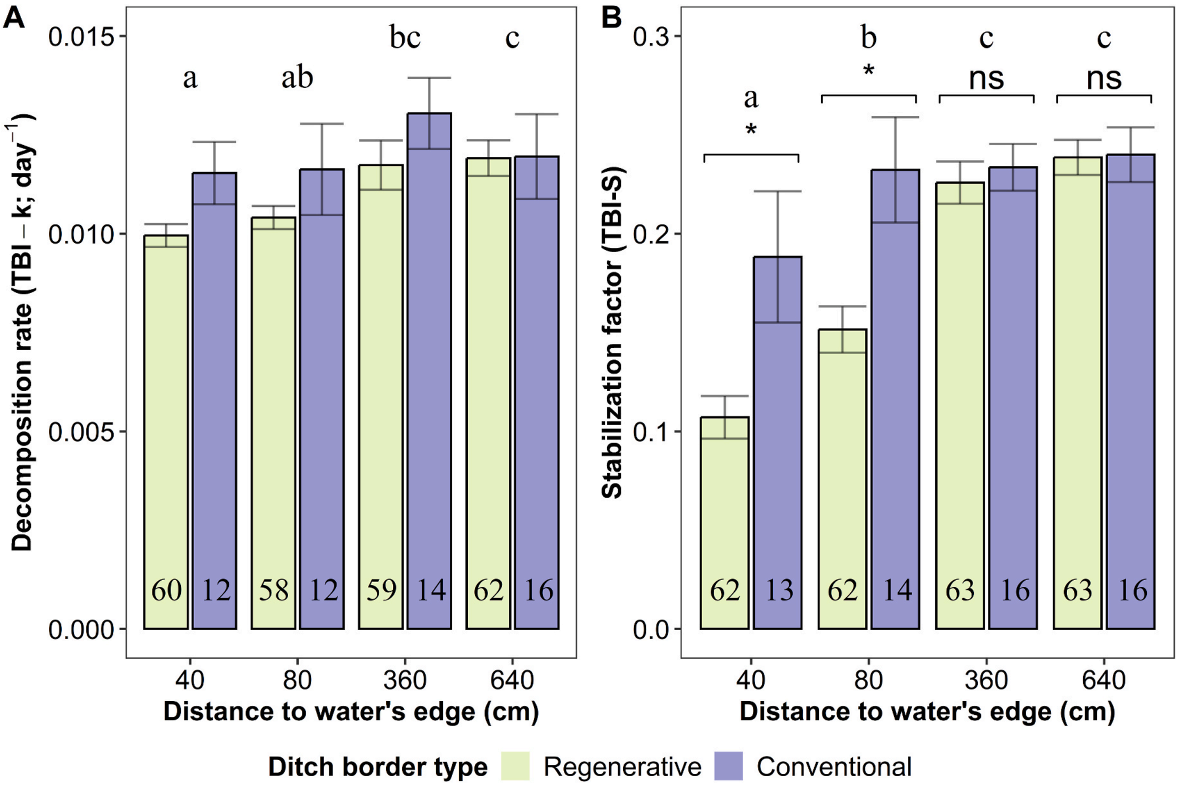

Fig. 3. TBI decomposition rate (TBI-k; day^{-1}) (A) and TBI stabilization factor (TBI-S) (B) at the four distances to the water's edge (cm) in conventional and regenerative DBs. Each bar is the mean decomposition rate (no. replicates in bars) of the sampling seasons with SE as error bars. Different letters indicate solely the significant differences between the four distances to the water's edge, averaged over the two DB types (Tukey $p < 0.05$), while asterisk indicate significant effects of DB type within each distance to the water's edge.

decomposition rates, implying that microenvironmental conditions do matter, although this effect is equal for the two ditch border types.

4.1. Litter decomposition of standardized litter unaffected by implementation of regenerative ditch borders

Ditch border type did not affect the decomposition rate of standardized litter. This result compared well to TBI values reported for k and S by Keuskamp et al. (2013) where both disturbed (k: 9.4e-3 ± 0.9e-3 and S: 0.23 ± 0.05) and undisturbed (k: 10.2e-3 ± 0.7e-3 and S: 0.2 ± 0.01) peatlands are included. This agreement provides support for our study and highlights the comparability of TBI between comparable ecosystems. Other studies have also found that restoration measures in peatlands did not lead to differences in decomposition rate (Keuskamp et al., 2013; MacDonald et al., 2018). Our results also showed a lower stabilization factor of standardized litter at 40 cm and 80 cm, distances closest to the waterside, in regenerative DBs. Similar declining patterns are found for the stabilization factor under peat restoration (MacDonald et al., 2018; Keuskamp et al., 2013). The stabilization factor is strongly determined by environmental factors, such as soil moisture content and soil temperature (Fanin et al., 2020). Increased soil moisture levels are found to increase the mass loss of green tea and therefore decrease the stabilization factor (Petraglia et al., 2019). At transect points 40 cm and 80 cm from the water's edge in regenerative DBs the soil moisture content difference in comparison with conventional DBs was largest and this could explain the decrease in stabilization factor here, but not at greater distances from the water's edge.

Litter decomposition is the combined product of multiple processes, such as leaching, enzymatic hydrolysis and fragmentation which result in the breakdown of organic material. The TBI provides a proxy for decomposition including all these processes and not only for decomposition through microbial decomposition. When leaf litter enters the soil and wet conditions prevail, water soluble substances, such as dissolved organic carbon, leach out of the litter (Seelen et al., 2019). Soils with a high soil moisture content (≥90%) can have similar (litter) leaching rates as aquatic environments (Lind et al., 2022). As regenerative DBs had consistently higher soil moisture content (annual mean of 72%) it is possible that more soluble material was leached from the tea bags in comparison to drier conventional DBs (52%). Thus, no effect of ditch border type on the decomposition rate does not necessarily mean all decomposition processes were equal between ditch border types. In regenerative borders leaching likely contributed more to decomposition whereas microbial hydrolysis played a larger role in the drier conventional borders. If this is the case, this difference could in turn lead to underestimation of the effect of ditch border type due to masking of decreased microbial decomposition rates in regenerative DBs. Attempts to correct for leaching haven been made in some studies (Lind et al., 2022), however corrections are challenging and possibly erroneous as leaching is a continuous process that can occur in stochastic pulses (Sarneel et al., 2023). Disentangling carbon losses through microbial activity (CO_2) and leaching (dissolved organic carbon) is therefore key in further improving our understanding of litter decomposition in fen ecosystems and especially for evaluating the effect of fen restoration measures as this often involves raised water levels.

Higher soil moisture levels, through changes in water levels, are known to affect microbial community composition (van Dijk et al., 2009). Wetter conditions in regenerative borders could therefore induce shifts in the microbial community. Vegetation composition also affects the microbial community through litter quality and root exudates of the specific plant species present (Eisenhauer et al., 2010). We did not measure changes in microbial communities, but data on this could provide further understanding of litter decomposition patterns under peat restoration measures. The small mesh size of the tea and litter bags excluded decomposition by soil macrofauna. Soil macrofauna is also

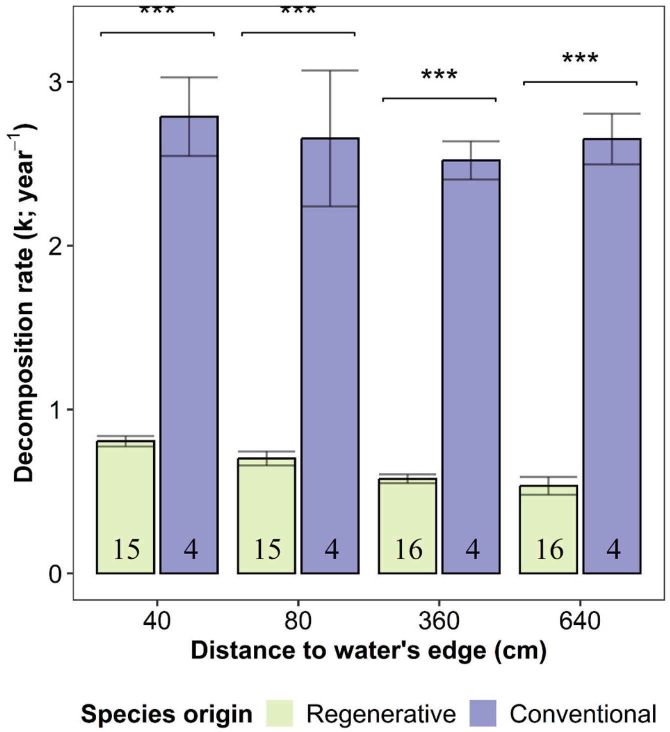

Fig. 4. First order decomposition rate (k; year^{-1}) of leaf litter at the four distances to the water's edge (cm) with leaf litter of *Lolium perenne* (= conventional species origin) and *Phragmites australis* (= regenerative species origin). Each bar is the mean decomposition rate over the year (no. replicates in bars) with SE as error bars. Asterisk indicates significant effects of litter origin within each distance to the water's edge with ns $>$ 0.05, * $<$0.05, ** $<$0.01 and *** $<$0.001.

known to promote litter decomposition in a broad range of ecosystems (García-Palacios et al., 2013). Water level changes in drained peatlands can affect soil fauna communities and the direction of change can vary between species groups (Laiho et al., 2001). By restricting litter decomposition, in our current study, to microbial decomposition we could therefore have potentially underestimated or overestimated the effect of ditch border type on litter decomposition.

4.2. Changes in litter quality exerted strong control on litter decomposition rates

In regenerative DBs the helophyte *Phragmites australis* was often present (mean cover at 40 cm and 80 cm 43%), but was absent in all conventional DBs. It is known that *P. australis* can benefit from fen restoration efforts (Zerbe et al., 2013). Small-scale heterogeneity in environmental conditions is known to affect the plant community structure and consequently the combination of plant species traits which can in turn impact ecosystem functioning (Suding et al., 2008; Lavorel and Garnier, 2002). In our study, *P. australis* leaf litter showed much lower decomposition rates in comparison to *Lolium perenne* leaf litter. *Phragmites australis* leaf litter had roughly half the total nitrogen content and was higher in lignin content than *L. perenne* leaf litter. A high lignin content and low nitrogen content are both associated with slower litter decomposition rates (Cornwell et al., 2008). As decomposition rates of standardized litter were unaffected by ditch border type, it is very likely that leaf litter traits exerted a stronger control on leaf litter decomposition than differences in soil characteristics and associated decomposer communities due to ditch border type. Plant litter quality and not changes in water level (moisture effects) is previously shown to be the main driver of litter decomposition changes and thus soil carbon storage in forests, boreal peatlands, grasslands and shrublands (Fanin et al., 2020; Petraglia et al., 2019; Straková et al., 2011, 2012). Ditch border type does not change microenvironmental controls on litter

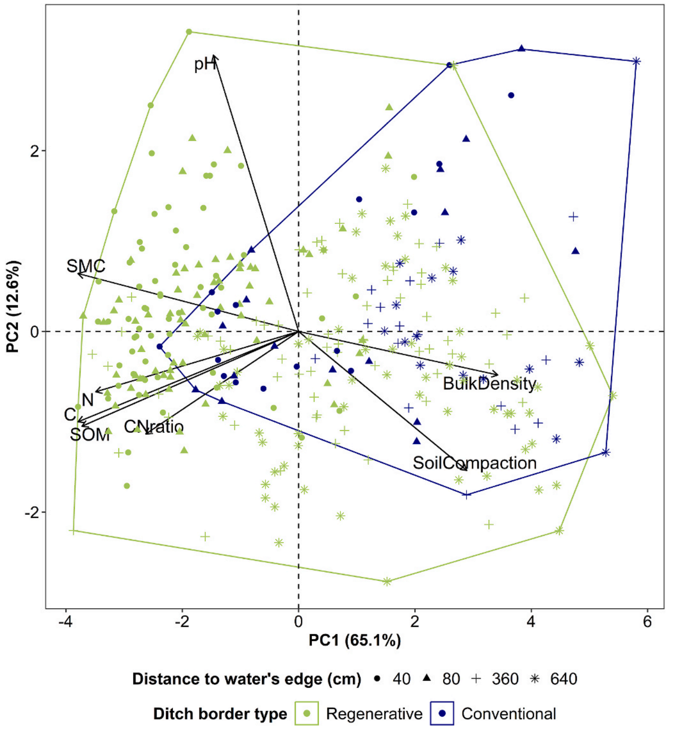

Fig. 5. PCA of the soil parameters (soil pH (pH), bulk density (BD), soil compaction (SC), soil moisture content (SMC), total carbon (C) and nitrogen content (N), C/N ratio, soil organic matter content (SOM)) in all seasons (spring, summer, autumn and winter). Symbols depict distances to the water's edge with regenerative (green) and conventional (blue) DB types.

Table 3
Pearson correlation matrix of soil parameters (soil pH (pH), N content (N), C content, CN ratio, soil moisture content (SMC), soil compaction (SC), soil organic matter content (SOM) and bulk density (BD)) and the principal components 1 and 2 (PC1 and PC2) accompanying the PCA analysis (Fig. 5). All Pearson correlation coefficients ≥0.75 are highlighted in bold.

	pH	N	C	CN ratio	SMC	SC	SOM	BD	PC1	PC2
pH	–	–	–	–	–	–	–	–	–	–
N	0.24	–	–	–	–	–	–	–	–	–
C	0.25	**0.91**	–	–	–	–	–	–	–	–
CN ratio	0.15	0.35	0.69	–	–	–	–	–	–	–
SMC	0.39	**0.77**	**0.82**	0.53	–	–	–	–	–	–
SC	−0.31	−0.45	−0.52	−0.40	**−0.76**	–	–	–	–	–
SOM	0.23	**0.90**	**0.97**	0.65	**0.80**	−0.49	–	–	–	–
BD	−0.22	−0.69	−0.70	−0.40	**−0.88**	0.72	−0.69	–	–	–
PC1	−0.36	**−0.87**	**−0.94**	−0.65	**−0.94**	0.72	**−0.93**	**0.85**	–	–
PC2	**0.76**	−0.17	−0.25	−0.28	0.16	−0.38	−0.26	−0.12	0	–

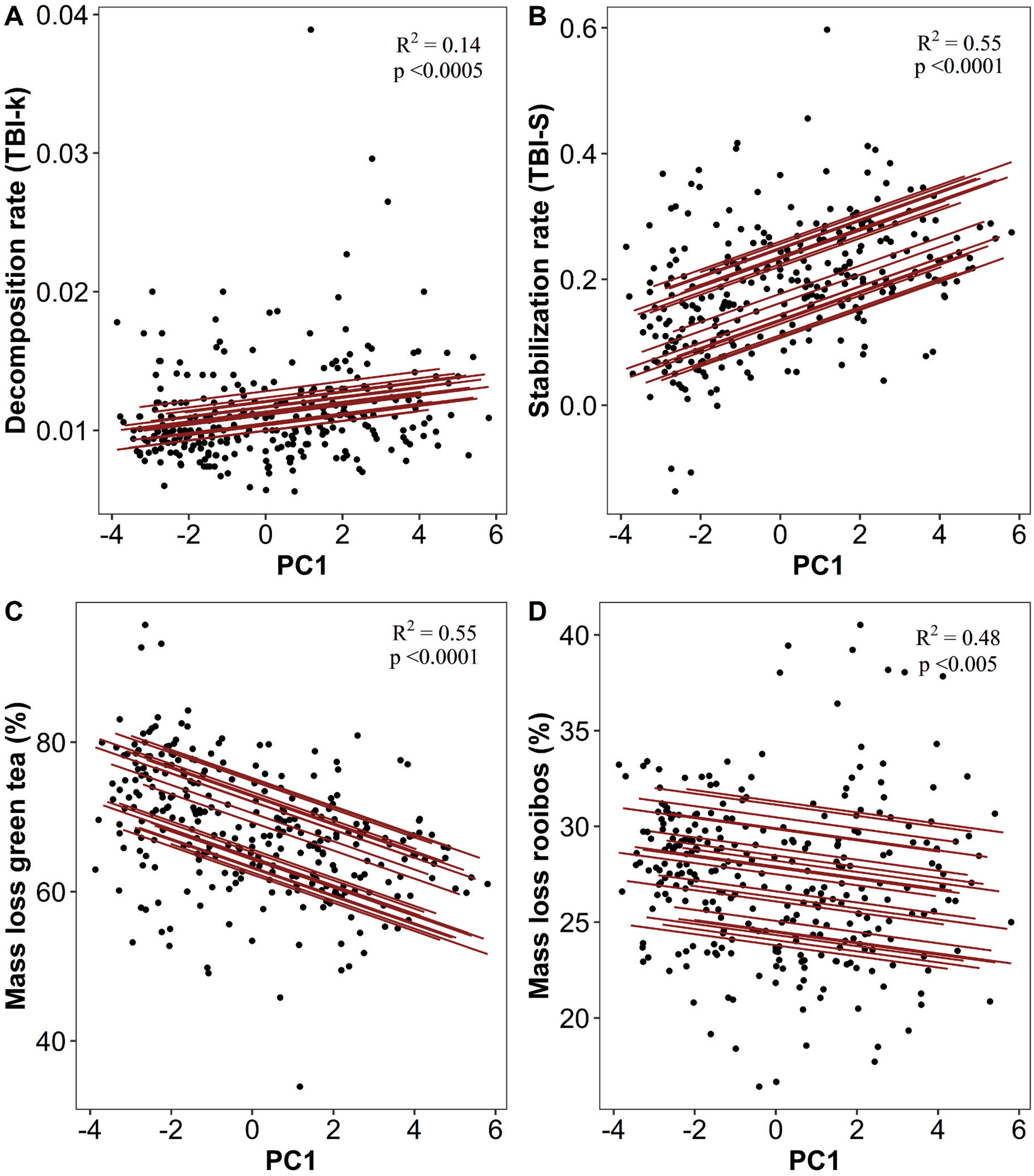

Fig. 6. Predicted relationships for each ditch border (red lines) between the TBI decomposition rate (A), TBI stabilization factor (B), mass loss green tea (C) and mass loss rooibos (D) and the PC1 values (extrapolated from Fig. 5). The black points represent all transect points (40 cm, 80 cm, 360 cm and 640 cm) from the two ditch border types (Conventional and Regenerative) across all four seasons (Spring, Summer, Autumn and Winter). The R-squared (R^2) and p-values (p) of the linear-mixed effect models with TBI decomposition rate, TBI stabilization factor, mass loss green tea and mass loss rooibos as response variables, with PC1 values as fixed effect and with ditch border number (1A-16) and season (June, August, October and January) as random effects are given for each linear relationship.

decomposition in a way we can detect with standardized litter bags, yet it does change the type of litter produced which has a large effect on litter decomposition rates. Shifts in vegetation composition due to regenerative ditch borders therefore seem to be the predominant control on litter decomposition and are inhibiting litter decomposition rates by producing litter of lower quality (after life effect, Freschet et al., 2012). This inhibited litter decomposition rate mediated through changes in litter quality can subsequently contribute to the accumulation of soil organic matter in these areas (Cornwell et al., 2008).

In contrast to leaf litter incubations, decomposition of root litter showed no effect of litter origin even though differences in root traits were found between litter origins. Root litter from regenerative DBs was higher in lignin content and lower in total nitrogen content in comparison to root litter from conventional DBs which could be an indicator for lower decomposition rates. Nevertheless, root litter decomposition rates do not always correspond to leaf litter decomposition rates (Hobbie et al., 2010; Sun et al., 2018). The control of lignin and nitrogen content observed on decomposition rates of leaf litter is absent in (first-order) root decomposition. While other root traits such as root diameter, initial nonstructural carbohydrates, total phenolics, bound phenolics and condensed tannins are more suitable to understand root litter decomposition patterns (Sun et al., 2018). Root litter decomposition rates were slower by a factor of 10 in comparison to leaf litter decomposition rates in our study which is also highlighted in other studies comparing leaf and root decomposition (Pang et al., 2022; Sun et al., 2018; Freschet et al., 2013; Cusack et al., 2009). The 90 day litter incubation period may therefore have been too short to pick up any root decomposition patterns, given their slow decomposition rate. This could explain why there was no effect of root litter quality, and hence litter origin, on root litter decomposition rates in contrast to the faster decomposing leaf litter.

4.3. Soil characteristics explained patterns in litter decomposition better than ditch border type

Regenerative DBs, as expected, were generally lower in bulk density and compaction and higher in soil moisture content and soil organic matter content, most likely as a result of topsoil removal. Nevertheless, there was still considerable overlap in soil characteristics between the two ditch border types. Changing from conventional to regenerative management of ditch borders does therefore not always lead to consistent and durable differentiation in soil characteristics. This variation in soil characteristics after restoration is also found in a study of rewetting of drained fens across fen regions in Europe, as well as for other landscape parameters. Pre-drainage conditions are often not reached after rewetting and differences with near-natural fens persisted over the long term (Kreyling et al., 2021).

The substantial variation in soil characteristics among different regenerative DBs could account for the non-effect of ditch border type on decomposition of standardized litter. Our analysis of decomposition dynamics in relation to soil characteristics indicated that soils with a higher soil organic matter content, soil moisture content, total carbon and nitrogen content and with a lower bulk density and soil compaction showed reduced decomposition rates and lower stabilization factor of standardized litter. MacDonald et al. (2018) and (Elumeeva et al., 2018) show a decrease in the stabilization factor when soil moisture levels increase, which is also apparent from the results of our study. Soil characteristics better explained the variation in stabilization than the variation in decomposition rate. A large range of soil characteristics in different studies (i.e. moisture, soil pH, temperature, electrical conductivity and bulk density) have been found to be better predictors of the stabilization factor than the decomposition rate and at times no relationships with the decomposition rate are found at all (Daebeler et al., 2022; Fu et al., 2022; Elumeeva et al., 2018; MacDonald et al., 2018). MacDonald et al. (2018) found no correlations between soil characteristics, such as soil pH, temperature and water table depth, and decomposition rate after peatland restoration and argued that peat quality may be of greater importance in determining decomposition rates. The botanical composition of peat itself can influence decomposition rates (Tolunay et al., 2024). In this way, differences in intrinsic decomposability could possibly override local changes in microenvironmental soil parameters. There might be small-scale intrinsic differences between the peat soils due to differences in peat origin or historic use in our study that were not captured which might better explain variation in decomposition rates. In conclusion, changes in microenvironmental soil characteristics induced by changing ditch border type can affect litter decomposition, mostly litter stabilization, yet due to their large variation they are not the main factor controlling litter decomposition rates. The lack of effect of soil characteristics on litter decomposition could arise when changes in litter quality directly affects the microbial community and changes in litter decomposition are thus not mediated through changes in the soil (Joly et al., 2017).

4.4. Broader implications

It is important to put these results into the context of soil carbon stocks, to get a better insight what scaling-up the implementation of regenerative ditch borders would mean for carbon storage. Under the simplifying assumption of an equal litter input among the ditch border types, the change in stock is determined by differences in litter decomposition rates (carbon stock = input/k). With an average carbon content (10.8 kg C m^{-2} in the top 0.1 m) this would mean a carbon stock increase of 10.4 ton C ha^{-1} in the top 0.1 m in regenerative ditch borders based on microenvironmental changes only (TBI). In combination with the lowered litter quality which strongly reduced decomposition rates, regenerative DBs could be responsible for a substantial reduction in decomposition on the long term. If reed biomass exceeds grass biomass inputs and if reed litter is not removed after mowing they can especially be effective for organic matter accumulation and, thus, soil carbon storage. When litter transformation yields more complexly structured and recalcitrant particles it will favor soil carbon storage, as these particles are less susceptible to decomposition and will therefore persist in soils (Prescott, 2010). Reed litter, which is of lower quality, hence more complex and recalcitrant, could therefore promote soil carbon storage in ditch borders. We expect that these decomposition patterns are sustained in other agricultural peat meadows, as litter quality showed such a strong effect on decomposition which predominated direct soil microenvironmental effects. In the context of peatland soils, this result implies that creating the right soil conditions for plant species which produce litter of lower qualities is key when designing management practices for enhancing soil carbon storage. Consequently, the implementation of regenerative DBs on a large scale in agricultural peat meadows could promote soil organic matter accumulation by generating more complex and recalcitrant litter which could enhance soil carbon storage in these areas.

5. Conclusions

Ditch border type affected the stabilization factor, but not the decomposition rates of standardized litter. Soils of regenerative ditch borders were higher in carbon and moisture content and were less compact and dense in comparison to soils of conventional borders, although there was substantial overlap in these soil characteristics between the two ditch border types. These soil characteristics were related to a lower stabilization factor and to some extent a lower decomposition rate, yet their control on litter decomposition is minimal. Shifts in vegetation composition in regenerative ditch borders, especially the increasing dominance of *Phragmites australis*, were found to reduce leaf litter decomposition rates and could thereby promote organic matter accumulation. Consequently, consistent with previous studies, changes in leaf litter quality are the predominant controls of management effects on litter decomposition, and changes in microenvironmental conditions play a negligible role at small spatial scales (Bradford et al., 2016; Saint-Laurent and Arsenault-Boucher, 2020). The effect of management on decomposition is primarily mediated by changes in vegetation composition. It is important to focus on creating soil conditions for plant species that produce litter of a lower quality, through implementing regenerative ditch borders, and in this way contribute to reduced litter decomposition rates and enhanced carbon storage.

CRediT authorship contribution statement

Sanne E. Bethe: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **James T. Weedon:** Writing – review & editing, Validation, Supervision, Methodology, Conceptualization. **Julia Marinissen:** Writing – review & editing, Methodology, Investigation. **Matty P. Berg:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2025.124725.

Data availability

Data will be made available on request.

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