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Soil depth and nutrient status are stronger drivers for short-term production and decomposition in temperate fens than water regime in a climatically dry year

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Abstract

This study investigated whether rewetting of drained temperate, groundwater-fed fens results in consistent shifts of above- and belowground production and litter mass loss of vascular plants, as compared to undrained fens, and how these processes relate to abiotic and biotic factors. We tested the hypotheses that (1) due to higher availability nutrient rewetted and drained fens exhibit higher production, (2) due to higher decomposability of plant biomass rewetted fens show higher plant biomass decomposition than undrained, and (3) in rewetted fens, less peat is potentially formed than in undrained fens. We analysed the effects of hydrological status (undrained, drained, rewetted) on plant production and litter mass loss during one year in 39 peatland sites across temperate Europe. Above- and belowground productivity, as well as mass loss of autochthonous vascular plant litter and Rooibos tea were measured above- and belowground.

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Aboveground vascular plant production was higher in rewetted fens than in undrained fens, in line with our first hypothesis. This difference was linked to the proportional graminoid cover and N content in aboveground biomass. In contrast to our first hypothesis, belowground production did not differ between fens of different hydrological status. It was highest in the 0-5 cm horizon, where soil temperature, and microbial biomass were also highest. Likewise, and in contrast to our second hypothesis, decomposition of above- and belowground vascular plant biomass was not affected by hydrological status. Only Rooibos tea mass loss showed small, ecologically irrelevant differences between differing hydrological statuses. Decomposition of aboveground biomass at soil surface was higher with higher nitrogen and phosphor content of the biomass, higher soil temperature, and higher cover proportion of herbs in the vegetation. Belowground biomass loss was positively correlated with phosphor content in soil porewater and aboveground biomass. One-third of the overall belowground biomass production took place in the 0-5 cm horizon, while decomposition in this horizon was lower than in the subsoil, irrespective of hydrological status. Our third hypothesis was also not confirmed because belowground production, decomposition and peat formation potential did not differ between the hydrological status. Although aboveground vascular plant production was higher in rewetted fens higher than in undrained, this difference will not result in a higher peat formation potential in rewetted fens due to the strong decomposition in of the easily degradable aboveground vascular plant biomass on a long time. Rather than hydrological status, soil depth, and nitrogen and phosphor availability had stronger impact on short-term vascular plant production and mass loss in the temperate fens studied. All these results were obtained during an extremely dry and warm growing season throughout Europe and causing deep drop downs of the water level at most sites. These meteorological conditions may have impacted the observed pattern of productivity and decomposition in unknown way.

1 Introduction

Peatlands are terrestrial wetlands in which waterlogging has led to accumulation of dead plant material in the soil, i.e., peat formation. The worldwide ~5 million km^2 of peatlands (3-4% of the land area) contain about one third of the world's soil carbon (Unep, 2022). Despite their crucial role in the global carbon cycle, ~500,000 ha of intact peatlands is drained annually (Unep, 2022). Drained peatlands lose their carbon sink function and their typical biodiversity (Van Diggelen et al., 2006; Klimkowska et al., 2010). Rewetting of drained fens leads to reduced greenhouse gas emissions (Couwenberg et al., 2011; Wilson, 2016). It remains open whether rewetting also leads to renewed peat formation, i.e., carbon sequestration, and to increased nutrient retention.

Peat formation results from the imbalance between plant biomass production and decomposition. Both processes are affected by rewetting of drained peatlands. An elevated water level may decrease plant biomass production (Zak et al., 2014), or increase production (Schwieger et al., 2021), or may result in ongoing high biomass production rates of easily decomposable fresh biomass. Rewetting lowers peat decomposition (Mrotzek et al., 2020), may lower aboveground litter decomposition and does probably not affect belowground decomposition (Schwieger et al., 2021). Whether rewetting of formerly drained peatlands results in renewed peat formation is therefore unclear. Peat formation models have been developed for bogs (e.g. (Clymo et al., 1998; Frolking et al., 2010), and do not fully apply to fens, because in bogs peat mosses (*Sphagnum* spec.) drive peat formation by input of biomass at the soil surface. In fens, the input of belowground vascular plant biomass, e.g. from sedges (*Carex spec.*), is important for peat accumulation and can dominate. Vascular plant roots grow into the older peat, decompose partly, and by this contribute to peat accumulation ("displacement peat", Weber, 1930 according to Joosten, 2016). Effects of nutrient status and litter quality of sedge species on decomposition in fens have been mainly studied in mesocosm experiments (Emsens et al., 2016a; Hinzke et al., 2021). Studies on in situ effects of rewetting fens on production and decomposition are rare (Schwieger et al., 2021) reported belowground plant biomass production to increase more than decomposition of fresh belowground litter with rewetting due to changes in plant species composition. In situ observations of belowground biomass production patterns, as well as data on root responses to changing environmental conditions, are generally rare (Norby and Jackson, 2000). In case of fen peatlands, even less empirical work has been conducted on productivity and decomposition at the ecosystem level, neither in their undrained state (Berube and Rochefort, 2018), nor after rewetting. Depending on the type of fen also brown mosses (*Amblystegiaceae*) can contribute significantly to peat formation by input at soil surface. The relative contribution of both can differ strongly with more litter input by sedges under nutrient rich conditions and a dynamic water level, in contrast to more input by brown mosses under nutrient poor conditions with a stable water level (Jaszczuk et al., 2024).

In this study, we investigated whether rewetting of formerly drained temperate fens changes the pattern of production and decomposition of vascular plants compared to undrained fens. We also analysed how both processes are affected by abiotic and biotic factors. We conducted a field study covering undrained, drained, and rewetted fens across temperate Europe. All field sites are currently or were historically groundwater-fed, base-rich, nutrient-poor percolation mires, with the vegetation dominated by small sedges. We hypothesize that (1) rewetted and drained fens produce more vascular plant biomass than undrained fens due to a higher availability of nutrients, (2) rewetted fens show higher plant biomass mass loss than undrained fens because higher decomposability of plant biomass, and (3) in rewetted fens, less displacement peat is formed than in undrained fens. We tested these hypotheses by accessing the differences in production and decomposition between undrained, drained, and rewetted fens, and analysing the effect of a wide range of abiotic and biotic factors on production and decomposition. Because the input of root and rhizome litter leads to peat formation not only at the surface but also in deeper layers, we analysed patterns of production and decomposition in the top, as well in the subsoil. Our results allow us to (i) assess the peat formation potential of rewetted fens compared to that of undrained and drained fens, and (ii) identify key factors linked to peat formation potential.

2 Methods

2.1 Site selection

We selected 39 fen sites (minimum peat thickness 0.5 m) in 13 regions of temperate lowland Europe, covering a wide longitudinal (1,800 km) and climatological (oceanic to continental) gradient. Originally, these fens were supplied by groundwater with mostly calcium as dominant cation and bicarbonate as dominant anion, and experienced no or limited flooding by water from rivers or brooks. As a study region, we delineated a (part of) a fen-containing catchment area of a small river or brook with a homogeneous pattern of sedimentary layers and similar hydrogeology. Within each region, three fen sites differing in "hydrological status" were selected: undrained, drained, and rewetted. Classification into the three hydrological states was primarily based on our expertise in combination with knowledge on fen history and water level dynamics from local researchers and managers. For undrained (i.e., near-natural) fen sites, we selected sites that did not have a known history of drainage/drainage ditches, exhibited groundwater levels near the peat surface for most of the year, and showed a substantial cover of sedges (*Carex* spp.) and brown mosses, i.e., typical fen vegetation. For drained fens, we selected sites with drainage ditches, low water tables (often > 0.5 m below the surface, typically in summer), and plant species typical for moist or wet grasslands. For rewetted fens, we selected sites which had been drained previously, in which groundwater levels had been restored to peat surface level, and where plant species of fens had reappeared, indicating that wetter conditions were already present few years to several decades prior to our sampling campaign. The drainage duration prior to rewetting is in the range of many decades to centuries for all sites. We ascertained that water levels of rewetted sites were similar to those of undrained sites, and that drained sites had lower water levels by testing several water level variables measured in this study. We found no significant differences for median, highest (0.95 percentile), and lowest (0.05 percentile) water levels calculated for the period 15 September 2017 to 15 September 2018 between undrained and rewetted sites, while drained sites had significantly lower values for these variables than undrained and rewetted sites (median and highest water level tested by one-way ANOVA and post hoc Tukey's HSD; lowest water level tested with Kruskal-Wallis & Wilcoxon rank sum). Each site contained a homogeneous and representative plot of 4 m x 8 m where all measurements were conducted. All sites were mown, except for one drained site, which was grazed by cattle. More details about the site selection and features are listed in Emsens et al. (2020).

2.2 Plant production and plant biomass decomposition correlations with other variables

We measured or calculated several dependent variables for productivity and decomposition, and a large set of independent variables related to water level, soil pore water chemistry, soil temperature, soil bulk properties, cover of functional plant groups, nutrients in aboveground vascular plant biomass, and soil microbial biomass (Fig. 1, Table S2).

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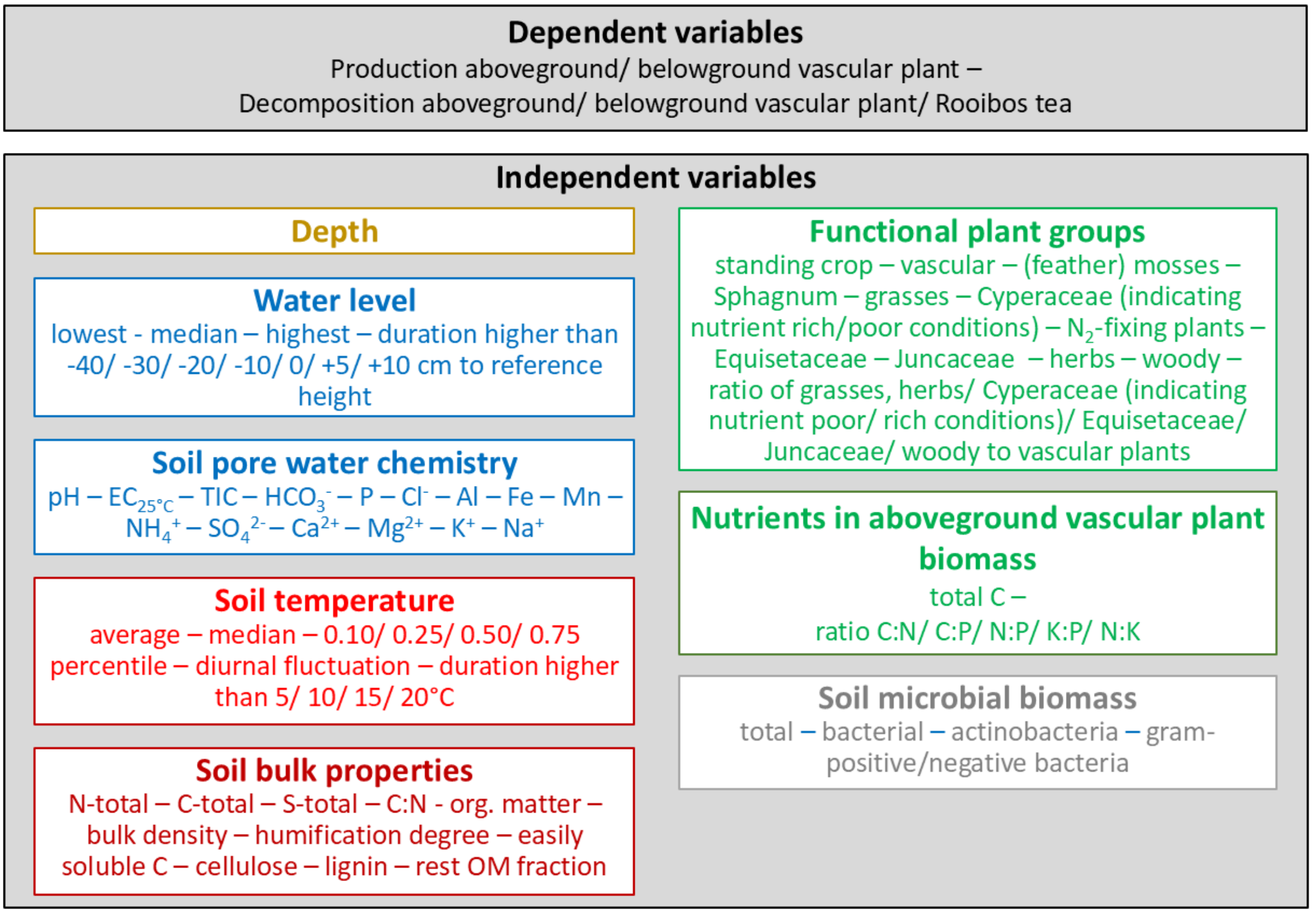

Fig. 1: Graphical overview of the study's dependent and independent variables, the latter grouped into those related to water level, soil pore water chemistry, soil temperature, soil bulk properties, plant aboveground biomass, functional plant groups, and soil microbial biomass.

2.3 Measurement of plant production

We measured above- and belowground vascular plant production at each site in three replicates. Aboveground production was measured in 0.38 m x 0.38 m subplots which were pre-clipped in 2017 (8 September 2017 to 13 October 2017) and harvested in 2018 (26 August 2018 to 19 October 2018; resulting in 350 to 375 d; average 365.5 d). At five sites (3 drained, 1 rewetted, 1 undrained), measurements of aboveground production had to be omitted due to disturbance by cattle grazing or accidental early mowing.

Belowground vascular plant production by roots and rhizomes was measured with vertically installed ingrowth cores (0-50 cm depth, diameter 5 cm). Ingrowth cores consisted of a plastic mesh with a mesh size of 2 mm (Mesh Plastic Canvas Artist Sheet from Darice Inc., Strongsville, OH, USA), which were shaped into tubes (length 55 cm, diameter 5 cm), closed at the lower end with plastic plugs, and filled with sand and nylon grains. The mixture of sand and nylon grains resembled the average peat dry bulk density of all sites (0.21 kg L^{-1}). For installation into the respective peatland plot, a vertical hole with a 5.5 cm diameter peat gouge was made into the peat. After re-collection in 2018, each ingrowth core was divided in 0-5, 15-20, and 45-50 cm depth sections. The 5-15 and 20-45 cm sections were pooled and summed with all depth sections to cumulative root biomass 0-50 cm. Within one to three days after collection of the ingrowth cores, the belowground biomass was carefully washed out from the cores in water and removing remaining substrate grains with forceps. Some 33 replicate samples (out of total of 468) from a total of 14 sites were lost. Above- and belowground biomass samples were dried at 70°C until constant weight within two days after isolation of the biomass and weighed. For each site, we calculated average values of aboveground vascular plant production (g m^2; 34 sites), belowground production at 0-5, 15-20 and 45-50 cm depths (g m^2; 39 sites), total belowground biomass production for the 0-50 cm depth (g m^2; 39 sites), and the ratio of total belowground to aboveground biomass production (g g^{-1})

2.4 Measurement of plant biomass decomposition

We measured plant biomass decomposition by incubating two types of material: standardised plant litter material to assess the effect of site conditions on decomposition, and local above- and belowground vascular plant biomass in fine mesh bags (0.14 mm) to quantify the combined effect of site conditions and local litter quality on decomposition. As standardised plant litter material, Rooibos tea was selected, which is commercially available in tetrahedron-shaped synthetic tea bags containing about 1.85 g DW of tea (Lipton, Unilever), and widely used in decomposition studies (Keuskamp et al., 2013). The fine mesh of litter and Rooibos tea bags prevented meso- and macrofauna to enter the tea and litter bags, and therefore the measured decomposition could largely be attributed to microbial and microfauna activity. In addition, the ratio of mass loss of local plant biomass to mass loss of Rooibos tea was used to evaluate the impact of type of plant material on decomposition. During the same period as for the production measurements (ca. 365 d), local aboveground vascular plant biomass and Rooibos tea were incubated at soil surface; and local (site specific) belowground plant biomass and Rooibos tea at 0-5, 15-20 and 45-50 cm soil depth.

Above- and belowground biomass used in the decomposition study was sampled locally from each site prior to incubation. At each site, a mixed sample of aboveground vascular plant material was obtained from the three biomass production plots (see above; 0.38 m x 0.38 m). For that, a representative sample of plant material was harvested from the end of May through June 2017, dried for 48 h at 60°C, clipped in 1-2 cm pieces, and mixed. For each site, five incubation bags were made with on average 3.09 g DW biomass. Fresh local belowground vascular plant biomass (further indicated in this paper as "belowground biomass") was collected at each site in peat cores of 0-30 cm depth and 30x30 cm surface from five locations per site. Peat cores were stored cooled (4 °C) until further processing. Within 30 d, ca. 20 g DW of roots and rhizomes were isolated from each core by washing with water. For each site, the isolated biomass was clipped in ca. 1-2 cm pieces, mixed, and dried at 30°C to a constant weight. Per site, 11 bags with on average 0.37 g DW belowground biomass per bag were made. Above- and belowground biomass was placed in separate nylon mesh bags (size 5.5 cm x 5.5 cm for roots and 12 cm x4 cm for aboveground material, mesh size 0.14 mm) for incubation. The mesh of these bags was washed 2 times in demineralized water for 1 h and then dried in order to wash off non-polymerized substance prior to use. The litter bags and the Rooibos tea bags were placed in washed frames consisting of an inner nylon mesh (tulle with a mesh size of 3 mm, 20 g m^{-2}) and outer sheets of a high-density polyethylene woven mesh (TopZeven, The Netherlands, mesh size 10 mm x 10 mm, 420 g m^{-2}, final frame size 55 cm x 24 cm). At each site at soil surface, five bags with Rooibos tea and five bags with local shoot biomass were incubated, and belowground five bags each at 0-5 cm soil depth, and three bags each at 15-20 and 45-50 cm of tea and belowground biomass. Litter and tea bags were stored cool and processed within three days after collection, carefully cleaned with water to remove external litter and peat and dried at 60°C until constant weight, and then weighed. Bags were discarded in case of damage or ingrowth of roots. Decomposition was calculated as the ratio of mass loss to the initial dry weight. For each site we calculated average values for the replicates which were used for statistical analyses. The majority of litter and tea bags could be retrieved and used for data analyses (for aboveground biomass at soil surface 168 bags out of a total of 195, for belowground biomass incubated in the peat soil 402 bags out of a total of 429, for Rooibos tea bags 573 out of a total of 624), resulting in averaged weight values for all sites and depths except for decomposition at soil surface of one drained site.

Not all frames with the belowground incubation bags stayed completely below the soil surface at all sites. The relative position of the frame top shifted above the soil surface for 73 % of all frames, because of peat shrinkage due to a strong water table dropdown during the extremely dry and hot summer in 2018. At the end of the incubation period, the frames shifted upward by, on average, 2.6 cm (maximum 6.4 cm). This vertical shift might have affected the mass loss by exposing the incubation bags at 0-5 cm depth to the atmosphere, and also decomposition bags installed at 15-20 and 45-50 cm depth were moved to higher locations thereby. Therefore, the site averaged change in relative soil depth position (“frame shift”) was included in the analyses of the influence of environmental factors on decomposition.

2.5 Calculation of peat formation potential

The peat formation potential (PFP) of vascular plant biomass was calculated, i.e., the biomass added during ca. 365 days was by subtracting the biomass lost by decomposition from the production. For each site, PFP of aboveground biomass, and of belowground biomass (g m^2) at 0-5, 15-20, 45-50 and 5-10 + 20-45 cm depth, were calculated. For calculation at 0-5, 15-20, 45-50 cm depth we used the corresponding mass loss measurements. For the 5-10 and 20-45 cm depth, where mass loss was not measured, we used the averaged value of the measurements at 0-5, 15-20, 45-50 cm depth. Finally, the PFT of belowground biomass was summed for 0 to 50 cm depth, and the ratio of total belowground PFT to aboveground PFT were calculated (g $g\text{-}^{1}$).

2.6 Measurement of environmental conditions

Water levels relative to soil surface were measured with pressure loggers at hourly intervals in shallow piezometers (bottom of filter ranged from 50 cm below soil surface at undrained and rewetted sites to 140 cm at drained sites), which were anchored to the topsoil. Water levels relative to soil surface were calculated from the pressure measurements of the loggers, local barometric pressure measured at nearby meteorological stations or local barometric loggers, and were corrected for the average difference between the occasional manual water level measurements and concurrent water levels based on pressure measurement. Due to extremely low rainfall and high evapotranspiration and thus groundwater levels falling below the pressure sensors in the summer of 2018, logger failure and damage to piezometers affected 17 out of the total of 39 sites, leading to gaps in water level measurements during more than 15 % of the incubation period (7 undrained, 4 drained, 6 rewetted sites). At the other 22 sites, gaps were less than 0.05 % of the measurement period for production and decomposition. In order to make use of the water level data, gaps were linearly interpolated. Therefore, calculated variables related to low water levels were estimated to be likely less deep than in reality for a considerable part of the sites. Water levels were calculated relative to the depth where the production and decomposition variables were measured by applying a correction of 0, 2.5, 17.5 and 47.5 cm to water levels relative to soil surface at respectively soil surface and 0-5, 15-20 and 45-50 cm. For the ca. 365 days period of the measurements of decomposition and production, we calculated summary statistics of water level variables reflecting the seasonal dynamics: median level, highest water level (0.95 percentile), lowest water level (0.05 percentile), and durations of exceedance of water levels +10, +5, 0, -10, -20, -30, -40 cm relative to a reference level (a positive value is above the reference level).

Soil temperature was measured at 4-hour intervals with loggers (IButtons, types DS1921G-F5 and DS1922L). At each site, loggers were installed in one of the litter bag incubation frames at 2.5, 17.5, and 47.5 cm depths. Data were retrieved from 63 loggers (27 at 0-5 cm, 27 at 15-20 cm and 9 at 45-50 cm depth). The high failure rate of loggers (46 %) was caused by empty batteries and malfunctions. For each operating logger, the median, the 0.10, 0.25, 0.75, 0.90 percentiles, the average of the diurnal fluctuation, and the duration of exceeding 5, 10, 15 and 20 °C, respectively, were calculated for describing the seasonal and diurnal dynamics during the incubation period.

Peat samples were collected at three depths (0-5, 15-20, and 45-50 cm) using a saw, a Russian peat corer or a profile sampler (Eijkelkamp Soil and Water, Giesbeek, NL) from the end of May through June 2017 (for a total of 117 soil samples). The humification degree of the peat was quantified with the Von Post scale (Post, 1922). Two sample sets (separately for soil bulk variables and PLFA) were always produced from two sets of five well-mixed subsamples per depth. Sampling equipment was thoroughly washed with demineralized water between each use. A third set of volumetric samples was taken at the same depths (at depths 0-5 and 15-20 cm, and 45-50 cm) for measurements of dry bulk density. All samples were individually packed in PE bags and aluminium foil, and cooled immediately after collection in cooling boxes with melting ice packs. Samples for analysing soil chemistry, PLFA, and bulk density were frozen (-18 °C) at the end of each day. Dry soil bulk density (kg L^{-1}) was determined by weighing oven-dried (70 °C) soil samples with known sampling volumes. Total organic matter content was determined by loss on ignition (450 °C, 4 h). Total C, N and S was measured using dry combustion (Thermo Scientific Flash2000 CHNS/O Analyzer, USA). The fraction of alpha-cellulose ("cellulose"), ADF-lignin, and easily soluble matter was determined using the sequential acid detergent fibre method (Rowland et al. 1994). From these three fractions, the mineral fraction was calculated. Phospholipid fatty acids (PLFAs) were quantified according to standard methods (Frostegård and Bååth, 1996; Oravecz et al., 2004; Šnajdr et al., 2008) for details see (Emsens et al., 2020). From these analyses, total microbial, as well as bacterial, actinobacterial, Gram-positive and Gram-negative bacterial biomass (in mg L^{-1} soil) was calculated.

Pore water samples were collected with macrorhizons (pore size 0.22 µm; Rhizosphere, Wageningen, NL) at 0-5, 15-20, and 45-50 cm depth. Prior to subsampling, the rhizons were flushed with pore water. Electrical conductivity (EC; converted to 25°C), pH, and alkalinity were measured at the day of sampling: EC and pH with portable equipment (WTW Multi 3430 set F, WTW TetraCon 925 IDS, SenTix 940) and alkalinity by titration to pH 4.2 with 0.01 M HCl. Subsamples for analysis of metal concentration were acidified by adding 0.7 ml 65% ultrapure HNO_3^- per 100 mL. To subsamples for Cl^-, NH_4^+, NO_3^- and SO_4^{2-} analysis, Thymol (200 mg L^{-1}) was added to conserve NH_4^+. All samples were stored at 4°C before transportation to the laboratory. Ca^{2+} was analysed with Flame Photometry (Jenway PFP7). K^+, Mg^{2+} and Fe were analysed using Flame Atomic Absorption Spectroscopy (FAAS; contrAA 700, Analytik Jena); whereas Na^+, Al, Mn and P were analysed with ICP-MS (NexION 300D, Perkin Elmer), and Cl^-, NH_4^+, NO_3^- and SO_4^{2-} with a Continuous Flow Analyser (CFA; San++ Skalar).

2.7 Vegetation recording and chemical measurements in aboveground plant biomass.

At each site, vegetation was recorded in one 2 m x 2 m plot. Cover (%) of vascular plants, mosses, and litter was recorded, together with the cover of each species. Taxonomic classification of species followed the European species list of TURBOVEG. The cover of the following functional groups was calculated by summing up cover of their species: grasses (Gramineae), herbs (not woody, not Gramineae or Cyperaceae), Cyperaceae, Equisetaceae, Juncaceae, woody plants, Cyperaceae of nutrient rich conditions (*Carex acuta, C. acutiformis, C. disticha, C. elata, C. x elytroides, C. paniculata, C. pseudocyperus, C. rostrata, Eleocharis palustris, Scirpus lacustris, S. tabernaemontani, S. sylvaticus*), Cyperaceae indicative for nutrient poor conditions (*Carex appropinquata, C. cespitosa, C. curta, C. diandra, C. dioica, C. echinata, C. lasiocarpa, C. lepidocarpa, C. limosa, C. nigra, C. panicea, Eriophorum angustifolium, E. gracile*), feather mosses (*Brachythecium spec., Calliergon spec., Calliergonella cuspidata, Climacium dendroides, Drepanocladus spec., Philonotis spec., Hamatocaulis vernicosus, Tomentypnum nitens*), and peat mosses (*Sphagnum spec*). For the functional groups for vascular plants, also the ratio of their cover with total vascular plant cover was calculated (see for the complete list Table S3).

Based on a mixed sample of the vascular plant production subplots, total C and N were measured using dry combustion method (Thermo Scientific Flash2000 CHNS/O Analyzer, USA), and total P with CFA (San++ Skalar) and K with FAAS (contrAA 700, Analytik Jena) after microwave assisted acid digestion (SpeedWave Four, Berghof, Germany). The ratios of C:N, C:P, N:P, K:P and N:K (in g g^{-1}) were calculated as variables for nutrient stoichiometry.

2.8 Analyses of the effect of hydrological status and soil depth

The effects of hydrological status (undrained, rewetted, drained) and depth (soil surface; 0-5, 15-20, 45-50 cm) were tested for all independent variables as applicable (e.g., only including hydrological status for aboveground vascular plant production and total belowground biomass production). If normality of the model residuals was met, we used linear mixed effects models for the two-factor models and one-way ANOVA for the models with only hydrological status as an independent factor. Plot location was included in the two-factor models as a random effect because of within-plot dependence for measurements at the different depth levels. If the interaction term in the models was nonsignificant, we re-ran the tests including main effects only. If normality of the model residuals was not met, we performed non-parametric testing of the effects of factors with the Kruskal-Wallis test and in case of a significant effects pairwise testing for differences with the Wilcox signed rank test. All analyses were performed in R 4.2 (R Core Team, 2021) and significance for statistical tests was accepted at $p < 0.05$.

2.9 Impact of environmental factors on plant production and plant biomass decomposition

Random forest (RF) analysis (Breiman, 2001) was used to explore the influence of abiotic and biotic factors on production and decomposition. Random forests are a supervised machine learning technique, where the variables which are most important to explain the observations of a study can be delineated. Variables are decorrelated during the analysis by using variable subsets, meaning that also less impactful, but still relevant variables have a chance to be detected. We used as explanatory variables several measured or calculated variables describing water level, soil temperature, soil bulk properties, pore water chemistry, soil microbial biomass (via PLFA), plant functional groups, aboveground vascular plant standing crop biomass and nutrient stoichiometry (Fig. 2 and Table S2). We also included in each RF analysis three random variables (i.e., randomly generated numbers). In the case of a RF model would select one or more of these random variables we would regard its variable selection unreliable. Analyses for belowground production and plant biomass (litter and Rooibos tea) decomposition were carried out (i) for all three soil depths (0-5, 15-20 and 45-50 cm) combined, and (ii) separately per depth. For analysis of total aboveground and belowground biomass production, data measured at all depths were included in the analyses. As soil temperature data were not available at all sites, these analyses were conducted (i) excluding soil temperature data, on a dataset of all sites and (ii) including soil temperature data, on the respective subset of sites for which these data were available. Results of the respective model with higher explanatory power are shown here, the results for the other models are shown in the Supplement. The selection of explanatory variable groups differed for the different dependent variables analysed (Table S2). For belowground production and decomposition, also the shift of the relative vertical position of the incubation frames (frame shift) was included, to explicitly address whether changes in relative depth of incubation bags affected decomposition.

For variable importance and p value calculation, we used the permutation-based Altmann approach (Altmann 2010). We grew 100 forests with 10,000 trees per forest, a minimum node size of 1, and selected explanatory variables which had a p value < 0.05 in 90% of the forests. To measure to what extend the explanatory variables account for variation of the dependent variables, we calculated the mean, root mean squared error (RMSE), and mean absolute error (MAE) of the cross validated r^2 based on 10 times repeated 5-fold cross validation of random forests. Random forests were implemented in R 4.3.1 (R Core Team, 2023) with ranger v. 0.16.0 (Wright and Ziegler, 2017). Cross-validation was done using the package caret v. 6.0.94 (Kuhn, 2008). Additionally, we used the packages doParallel v. 1.0.17 (Microsoft Corporation and Weston, 2022), dplyr v. 1.1.4 (Wickham et al., 2023), fastDummies v. 1.7.4 (Kaplan, 2024), ggplot2 v. 3.5.1 (Wickham, 2016), pdp v. 0.8.1 (Greenwell, 2017), svglite v. 2.1.3 (Wickham et al., 2023), and tidyr v. 1.3.1 (Wickham et al., 2024).

For interpretation of the influence of explanatory variables, we took highly correlated variable groups into account. Such clusters of correlated variables were identified by hierarchical clustering with the package stats 4.2.1, cut tree level 8.5 (Table S3).

3 Results

3.1 Effect of hydrological status and soil depth

The effect of hydrological status and soil depth was analysed for above- and belowground vascular plant production, decomposition, and peat formation potential (PFP) of local plant litter, and above- and belowground decomposition of standard material (Rooibos tea). The hydrological status, i.e., undrained, drained, or rewetted, had a significant effect for three of the eight response variables analysed, i.e., for aboveground production, aboveground PFP, and belowground decomposition of standard material, while soil depth affected all response variables significantly. No significant interaction effects between hydrological status and soil depth on any of the belowground response variables were detected (belowground plant production, belowground PFP, mass loss of Rooibos tea, mass loss of belowground biomass and the ratio of root biomass:Rooibos tea mass loss with ANOVA p-values of 0.621, 0.346, 0.832, 0.782 and 0.951, respectively).

Aboveground vascular plant production was significantly lower in undrained than in rewetted and drained fens (mean values 274, 484, 486 g $m^{2,}$ respectively; ANOVA: F=4.4, p=0.021; Fig. 2a). Aboveground PFP in undrained fens was significantly lower than in rewetted fens, but did not differ from drained fens (mean values 93, 194, 156 g $m^{2,}$ respectively; Kruskal-Wallis test χ^2=7.2, p=0.027; Fig. 2c). Cumulated belowground plant production in the 0-50 cm soil layer (ANOVA: F=0.5, p=0.614; Fig. 2b) and in the three separate soil depths was not significantly affected by hydrological status (Kruskal-Wallis test χ^2=1.2, p=0.554; results not shown). Also, belowground PFP did not differ between hydrological statuses (ANOVA F=0.5, p=0.621; Fig. 2d). These patterns resulted in a higher belowground:aboveground ratio for production in undrained than rewetted or drained fens (mean values 1.38, 0.70, 0.50 g $g^{-1,}$ respectively; Kruskal-Wallis test χ^2= 10.5, p=0.005), and also a higher belowground:aboveground ratio for PFP (mean values 1.00, 0.50, 0.37 g $g^{-1,}$ respectively; Kruskal-Wallis test χ^2= 7.9, p=0.019).

Concerning belowground decomposition, only Rooibos tea was significantly affected by hydrological status (Kruskal-Wallis test χ^2=15.7, p<0.001; Fig. 3b) with slightly higher belowground decomposition in undrained than in drained and rewetted fens (mean values 0.41, 0.38 and 0.38 g g^{-1}, respectively). Rooibos tea mass loss did, however, not differ significantly between hydrological status at soil surface (ANOVA: F=1.4, p=0.253; Fig. 3a). Mass loss of belowground plant biomass was not affected by hydrological status (ANOVA: F=0.5, p=0.622; Fig. 3d). Likewise, mass loss of aboveground vascular biomass at the soil surface was unaffected by the hydrological status (ANOVA: F=2.3, p=0.112; Fig. 3c).

Belowground plant production decreased significantly with soil depth (mean values for 0-5, 20-25 and 45-50 cm depth 77.8, 28.5 and 5.6 g m^2, respectively; Kruskal-Wallis test χ^2=77.5, p<0.001; Fig. 2e). The same applied for PFP (mean values 52.9, 17.2 and 3.1 g m^2 respectively; Kruskal-Wallis test χ^2=78.0, p<0.001; Fig. 2f). The 0-5 cm layer contributed with a mean average percentage of 33.5 to the total root production of the upper 50 cm of soil. Rooibos tea mass loss decreased significantly with soil depth (Kruskal-Wallis test χ^2=16.0, p=0.001; Fig. 3e). Soil depth also had a significant effect on mass loss of belowground plant biomass (ANOVA: F=18.6, p<0.001, Fig. 3f), with higher values in the 15-20 and 45-50 cm layer than in the 0-5 cm layer, and higher values at soil surface than inside soil. At soil surface, mass loss of aboveground vascular plant biomass was significantly higher than that of Rooibos tea (mean values 0.65 and 0.39 g g^{-1}, respectively; t-test p<0.001), while at 0-5 cm depth, belowground litter mass loss was lower than that of Rooibos tea (mean values 0.33 and 0.41 g g^{-1}, respectively; t-test p=0.005). At 15-20 and 45-50 cm depth, there was no difference between mass loss of belowground litter and that of Rooibos tea (t-test p 0.454 and 0.098, respectively). In contrast to Rooibos tea, belowground plant litter showed more variation in mass loss at all soil depths (SD for 0-5 cm depth 0.054 and 0.143 g g^{-1}, for 15-20 cm depth 0.036 and 0.159 g g^{-1}, for 45-50 cm depth 0.030 and 0.152 g g^{-1}, respectively).

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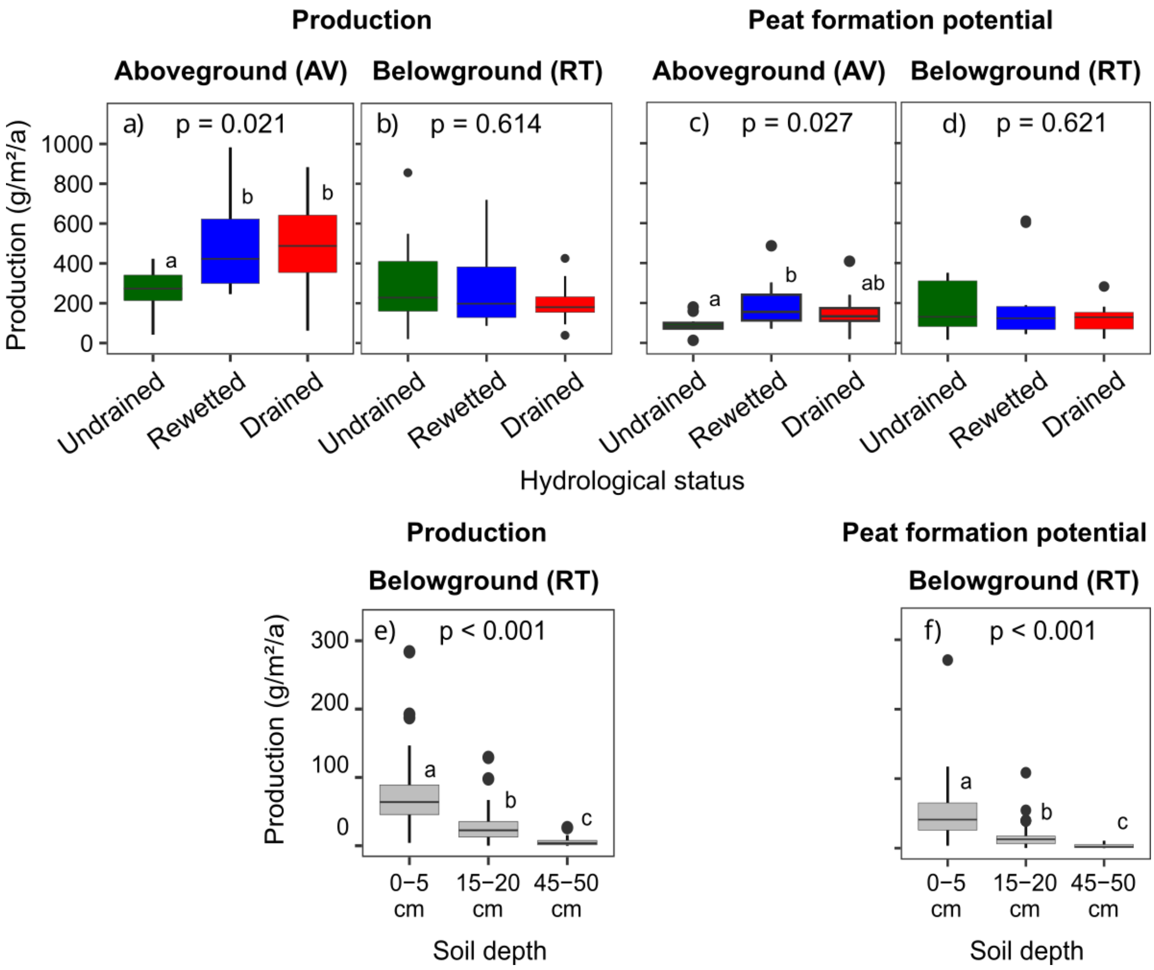

360 **Fig. 2: a) Aboveground vascular plant biomass production after ca. 365 days at soil surface and b) of belowground vascular plant biomass at 0-50 cm depth, c) aboveground peat formation potential, d) belowground peat formation potential at 0-50 cm depth in relation to hydrological status, and e) production and f) peat formation potential of belowground biomass for separate soil depths. Biomass types: AV = aboveground vascular plant biomass, RT = belowground vascular plant biomass. In each graph, p-values and significant differences (lowercase letters) are indicated. The interaction between hydrological status and soil depth was not**
365 **significant for any dependent variable.**

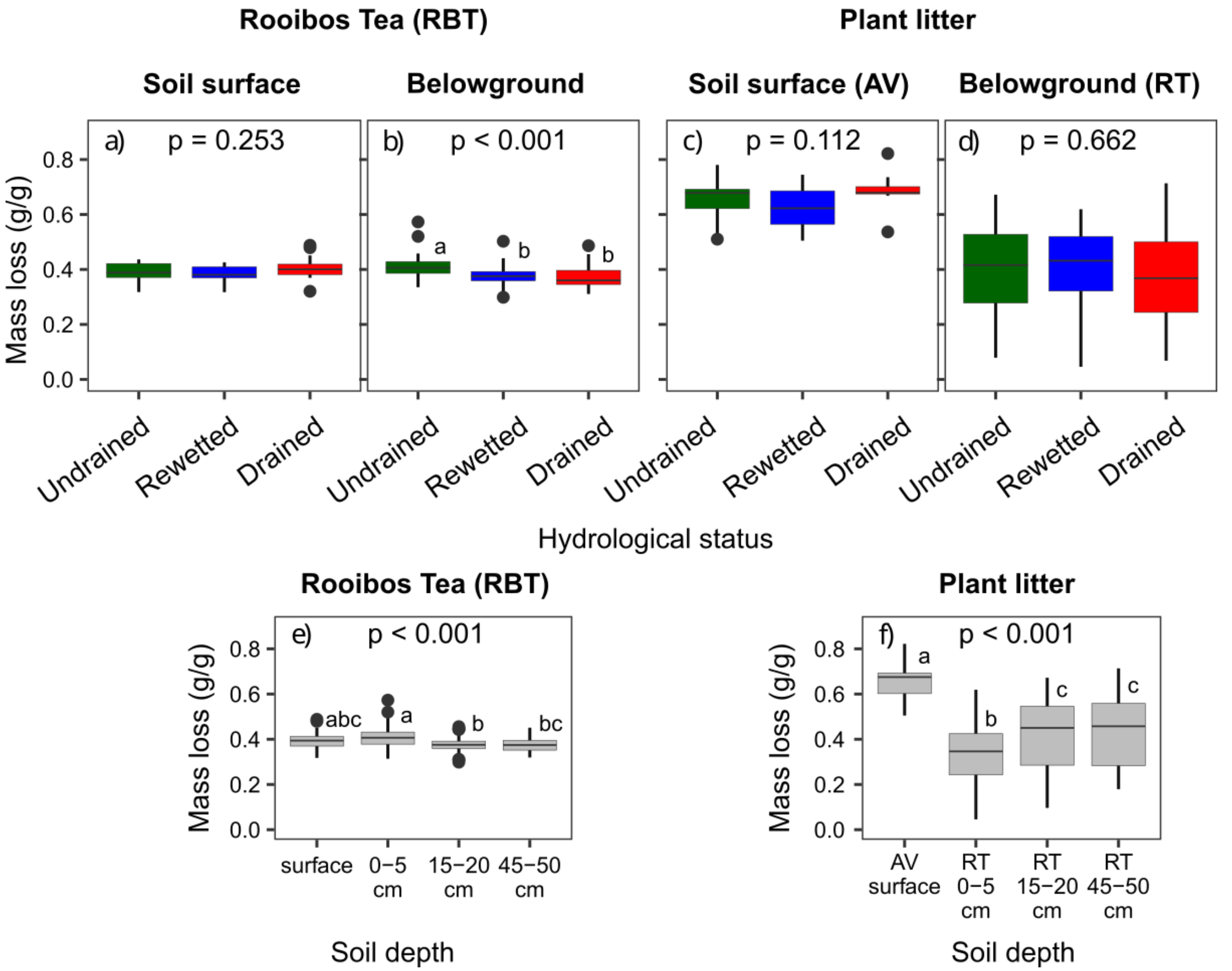

Fig. 3: Mass loss by decomposition of standard material (Rooibos tea) and local plant litter after ca. 365 days in relation to hydrological status and soil depth. Biomass types: RBT = Rooibos tea, AV = aboveground vascular plant biomass, RT = belowground vascular plant biomass. In each graph, p-values and significant differences (lowercase letters) are indicated. The interaction between hydrological status and soil depth was not significant for any dependent variable.

3.2 Effect of abiotic and biotic variables on production and decomposition

All Random forest (RF) analyses for above- and belowground production and decomposition resulted in low to moderate mean cross-validated r^2 values (CVr^2 0.12 to 0.66), with highest values for aboveground vascular plant production, belowground production, and plant litter decomposition analysed across the depth levels, respectively (Table S4-6). The low to moderate explanatory power of the RF analyses indicates that, despite the breadth of explanatory variables included here, other drivers not accounted for are of importance, and/or a very large variability of these biological measurements and underlying processes.

Aboveground vascular plant production increased with standing aboveground biomass, low herb cover in the plant communities, low moss cover, and high humification degree of the uppermost peat layer (Fig. 4a). The mean CVr^2 of 0.44 indicated a relatively high explanatory power of the model. Taken together, stands dominated by tall graminoids on degraded peat showed the highest aboveground production. Belowground vascular plant production decreased strongly with soil depth (Fig. 2), which also was the most strongly correlated variable in the RF analysis across all depth layers (mean CVr^2 of 0.58; Fig. 4b). Belowground plant production was positively linked to soil depth (higher in topsoil than subsoil), total microbial biomass, decreased when water levels exceeded 10 cm above surface, and decreased with bulk density exceeding 10 % (Fig. 4b). For the subset with existing soil temperature data, a similar pattern was found, while soil temperature had almost as much explanatory power as soil depth. Belowground production increased with higher diurnal fluctuations in soil temperature, and a longer duration of high soil temperature. This influence of soil temperature was strongly related to soil depth, with the topsoil having a more dynamic and periodically higher temperature than the subsoil (Fig. S7).

Aboveground litter decomposition was better explained by the RF model of the subset including soil temperature (mean CVr^2 = 0.42; Fig. 4c) than by the model without soil temperature (mean CVr^2 = 0.32; Fig S11). More important than the positive effect of soil temperature, however, was biomass C:N ratio with sharply decreasing decomposition above a C:N of 25, and a high cover of Juncaceae. Belowground plant litter decomposition differed between soil depth layers (Fig 4f). Correspondingly, the RF model across all depth layers reached a mean CVr^2 of 0.66 with depth and frame shift (coding if the frame moved upwards out of the substrate) being the strongest descriptors (Fig. S10), while RF models for each depth layer separately had low explanatory power of the models (mean CVr^2 between 0.20 and 0.39). The strong effect of frameshift was due to the samples at surface layer having a frame shift of 0 (i.e., this indicated an effect of surface vs. subsurface rather than of the frameshift itself). Restricted to the samples incubated in the soil with upward frame shift values between 0.6 to 7.4 cm, an effect of frame shift was negligible (Fig. S10). Interestingly, belowground plant litter decomposition at 0-5 cm soil depth was most strongly and negatively linked to several variables related to microbial biomass (Fig. 4d, S12). No such link between decomposition and microbial biomass was found at deeper layers (Fig. 4e&f). At all levels, though, porewater P concentrations were positively linked to decomposition. Fitting to this, quality of aboveground biomass with ratios of different elements (K, C, N, respectively) to P content showed also a trend towards more decomposition with more P.

Decomposition of standard material (Rooibos tea) was not well explained by our environmental data across all depth layers, reaching only a mean CVr^2 of 0.12 (Fig. 4g). There was a trend of reduced standard material decomposition with lower pore water ammonium concentrations, lower bulk density, lower vascular plant cover and standing biomass, and depth closer to soil surface. Note that the latter fits well to the results shown in Fig. 3c. The RF analysis of decomposition at 0-5 cm depth with soil temperature variables yielded a higher CVr^2 (0.28) than the analysis without these variables (0.21) indicating higher temperature stimulates decomposition. The analyses for the 45-50 cm depth had a medium high CVr^2 (0.53) with the strongest explanatory factor low water level having a positive effect on mass loss (i.e., wetter = higher mass loss, Fig. S23). However, overall the Rooibos tea decomposition range was narrow, concomitant with a low explanatory power of the models (Fig. 3c).

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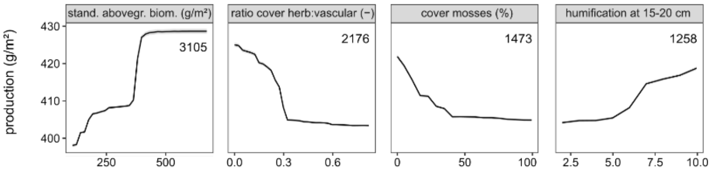
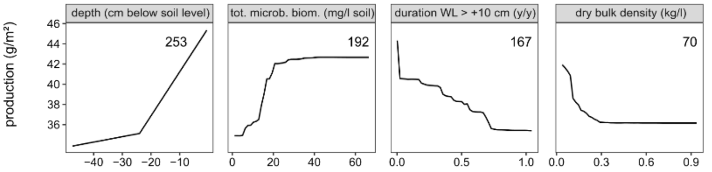
Preprint. Discussion started: 2 December 2025

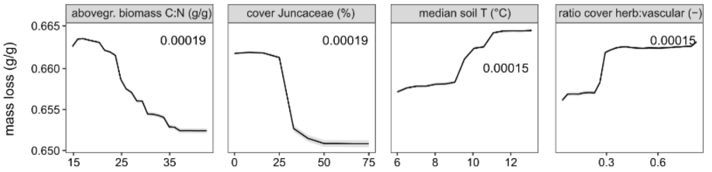
a) Production aboveground biomass
cross validated r^2: mean=0.437; RMSE=179.3; MAE=138.3



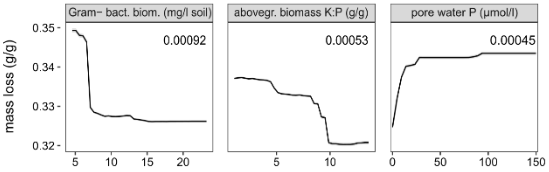
b) Production belowground biomass, in 0−5, 15−20, and 45−50 cm horizons, without soil T
cross validated r^2: mean=0.581; RSME=30.9; MAE=20.1



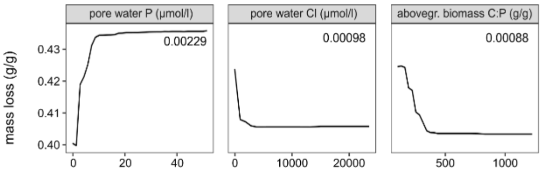
c) Mass loss aboveground biomass, at soil surface, with soil T
cross validated r^2: mean=0.416; RMSE=0.06; MAE=0.05



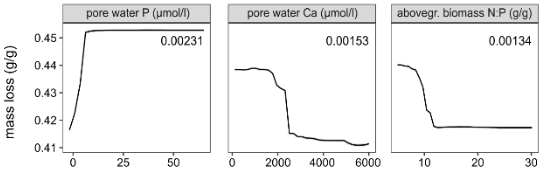
d) Mass loss belowground biomass, in 0−5 cm horizon, without soil T
cross validated r^2: mean=0.203; RMSE=0.14; MAE=0.12



e) Mass loss belowground biomass, in 15−20 cm horizon, without soil T
cross validated r^2: mean=0.253; RMSE=0.15; MAE=0.13



f) Mass losss belowground biomass, in 45−50 cm horizon, without soil T
cross validated r^2: mean=0.392; RMSE=0.13; MAE=0.12



g) Mass loss Rooibos tea, at soil surface, and in 0−5, 15−20, and 45−50 cm horizons
without soil T; cross validated r^2: mean=0.123; RMSE=0.04; MAE=0.03

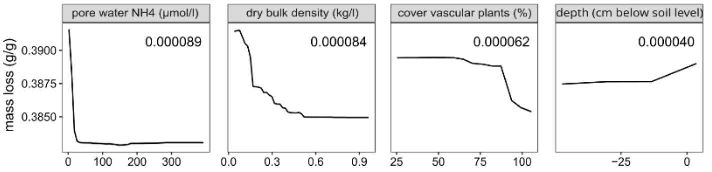


Fig. 4: Partial plots of the effects of abiotic and biotic explanatory variables on above- and belowground plant production, plant litter decomposition, and Rooibos tea decomposition. The variable and unit of the x-axis are indicated in the header of each panel. For each repeated Random forest analyses the mean, RMSE and MAE of the cross-validated r^2 provide measures of explanatory power. Shown are up to four of the most important explanatory variables, with always only one variable per explanatory cluster of highly correlated variables (see Tab. S3-5 for details) being shown. The number in each partial plot indicates the Altmann variable importance (comparable only within the same analysis, not between analyses). For belowground dependent variables distinction is made in analyses with soil temperature variables being excluded or included as independent variables (respectively "without soil T" and "with soil T"). In the Supplement, partial plots of all selected variables for all analyses conducted are shown (Fig. S1-S27). Meaning of shortened headers: stand. = standing crop, abovegr. biom. = aboveground vascular biomass, herb = herbaceous, humification = humification degree at given soil depth according to Von Post, soil T = soil temperature, WL = water level.

4 Discussion

4.1 Drivers of plant production

Our first hypothesis that rewetted fens have a higher vascular plant production than undrained fens due to a higher nutrient availability for plants in the former was confirmed for aboveground vascular plant production. We cannot, however, confirm that nutrient availability is strongly driving this pattern: nutrient-related chemistry variables for bulk soil, pore water and aboveground vascular plant biomass had no or only a weak effect on aboveground vascular plant production. Our analyses found properties of the aboveground vegetation itself like standing vascular plant biomass and the ratio of herbaceous plant cover to summed vascular plant cover as the most influencing factors. The lack of explanatory power of nutrient-related variables is in contrast with findings of other studies, where higher production or peak standing crop of vascular plants is related to nutrient status (Wassen, 1995; Kotowski and Van Diggelen, 2004). Emsens et al. (2017) found a higher peak standing crop with lower N:P ratios in aboveground biomass, implying higher production in fens with relatively high P availability. While higher production of aboveground vascular plant biomass in rewetted fens compared to undrained fens may suppress production by mosses (Jaszczuk et al., 2024), this was not corroborated by our data: Although there was a weak inverse relationship between aboveground vascular plant production and cover of mosses in our data set (Pearson r = -0.60; Fig. S28), both undrained and rewetted sites showed a broad range of aboveground vascular plant production and moss cover. Moreover, there was no significant difference in aboveground vascular plant production between rewetted and drained fens, implying that rewetting of drained fens did not impact aboveground vascular plant production. The RF analyses also showed not any correlation between water level variables and vascular plant production, although median, highest and lowest water level were lower at drained sites than at undrained and rewetted sites.

For belowground vascular plant production, our first hypothesis must be rejected, because the three hydrological states did not differ in the combined belowground production at 0-50 cm soil depth, or in belowground production for the separate soil depths. All the variables with equally moderate explanatory power in the analyses of separate depths are interrelated: with increasing soil depth, high and median water levels are higher, the 0.75 and 0.90 percentile of soil temperature are lower, and microbial biomass decreases (Table S7). Belowground plant production analysed for cumulated 0-50 cm depth and for separate soil depths was apparently also not affected by water level nor by hydrological status. Belowground production appears to be

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Preprint. Discussion started: 2 December 2025

mainly governed by soil depth, and most production of roots and rhizomes takes place in the topsoil where soil temperatures during the growing season are highest and most microbial biomass is located. The positive correlation between belowground plant production and bacterial biomass might at least in part be due to direct mutual benefits: the microbial community provides nutrients for plants by mineralization, and roots and rhizomes provide fresh litter and organic exudates, which stimulate bacterial growth (Rupp et al., 2021; Moore et al., 2020).

4.2 Drivers of decomposition

Our results contradict our second hypothesis, i.e., that rewetted fens have a higher mass loss of fresh biomass than undrained fens, because of higher microbial activity and higher decomposability of plant biomass. The mass loss of Rooibos tea and local aboveground vascular plant biomass incubated at soil surface for one year did not differ between the hydrological statuses. Strikingly, mass loss of local belowground vascular plant biomass did also not differ between the hydrological states. The relatively high variation in mass loss of belowground plant litter within each hydrological status suggests that variation in belowground litter quality or local microbial decomposition activity is an important factor governing mass loss rate, potentially overruling the effects of the hydrological status, also found by (Schwieger et al., 2021). At the same time, some factors had a considerable effect on belowground biomass loss. Decomposition of local aboveground biomass was higher with a higher nitrogen content of the biomass, a higher cover proportion of herbs in the vegetation (both indicators for biomass quality), and a higher soil temperature (enhancing microbial activity). Additionally, phosphor-related variables (P) were positively correlated to belowground biomass loss. Total pore water P concentration was one of the important variables positively affecting belowground biomass loss in all analyses for combined and separate soil depths. A positive effect of P on mass loss of above- and below ground biomass is also reflected in nutrient stoichiometry variables in aboveground biomass (C:P, N:P, K:P) being linked to belowground decomposition, and points to the importance of P availability on mass loss. These effects could suggest that a high nutrient availability, in particular P, might affect decomposition by microorganisms, and litter quality and thereby decomposability. These P related effects occurred in a broad gradient of low to high soil total P content (see (Aggenbach et al., 2013; Emsens et al., 2017) for comparison with overlapping fen sites). An eutrophication experiment with fen *Carex* species and high NPK addition resulted a higher mass loss of the aboveground biomass of each species, and overall increased litter decomposability, because the eutrophic *Carex* species were more abundant and produced more easily degradable biomass than mesotrophic species under eutrophic conditions (Emsens et al., 2016b). Aerts et al. (1992) found for leaf litter of several fen *Carex* species, that short-term (three months) litter decay was affected strongly by P-related litter quality variables, while long-term (> 1 year) most strongly by the ratios of phenolics:N, phenolics:P, lignin:N, and C:N. Likewise, the pattern of mass loss rate of roots of *C. diandra*, and roots and rhizomes of *C. lasiocarpa* is positively related with litter P content (Scheffer and Aerts, 2000). All these findings support the trend found in our study: the decomposition of vascular plant litter is higher for higher P availability. Because we did not find an effect of hydrological status on decomposition of above- and belowground biomass, the effects of soil nutrient status seem to overrule the biochemical effects of water level. However, the explanatory power of analyses for separate depths was low, implying that other factors beyond those covered in

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Preprint. Discussion started: 2 December 2025

this study are involved in decomposition of local litter, and/or there might be a natural, high variability of decomposability of fresh litter.

In contrast to belowground biomass, subsurface mass loss of Rooibos tea was, surprisingly, highest in undrained fens. However, the difference of Rooibos tea mass loss between sites was small compared to the variation of autochthonous belowground biomass loss, and therefore, the pattern of Rooibos tea mass loss has likely minor ecological relevance. Moreover, likely most easily degradable and leachable material had already been lost in the 365 days of incubation in all sites, (compare (Keuskamp et al., 2013; Blume-Werry et al., 2021), leaving only recalcitrant material decomposing very slowly and thereby biomass losses converging to similar numbers across sites.

In contrast to hydrological status having no effect on belowground litter mass loss, soil depth had a strong effect, with lower mass loss rates in the topsoil than in the subsoil. A parallel study conducted at the same sites as our study, which focused on the microbial diversity by PCR-analyses of the 16S rRNA, found also dominant effect of soil depth on prokaryote community composition and predicted functional genes. Hydrological status had in this study a minor effect (Emsens et al., 2020). The pattern of mass loss rate of autochthonous plant litter, prokaryote community composition, and functional genes correlate with higher microbial biomass in the topsoil compared to the subsoil. Mass loss of belowground biomass in the analyses for 0-5 cm depth had also a strong negative correlation with bacterial biomass (Table S7).

4.3 Influence of hydrological status on peat formation

The input of root and rhizome litter is considered an important process in the formation of "displacement peat" in fens. Based on our measurements at several soil depths, most of the peat formation potential is taking place in the upper 45 cm of the peat profile (average 98 % of the 0-50 cm layer) and a considerable part (average 36 %) at the 0-5 cm soil depth. We hypothesized that rewetted fens show less displacement peat formation than undrained fens. However, the vertical patterns for belowground biomass production and decomposition were similar among undrained, rewetted and even drained fens, as we found no effect of the hydrological status and no interaction effects between hydrological status and soil depth. The same applies for the calculated peat formation potential of belowground vascular plant biomass (litter input minus its decomposition), implying there was no effect of hydrological status on belowground litter accumulation. Net production of aboveground vascular plant biomass was higher in rewetted fens than in undrained fens, while its mass loss was similar for both hydrological statuses. Therefore, rewetted fens might have a higher peat formation potential as compared to undrained fens. However, mass loss of aboveground vascular plant biomass is high, especially on longer time scales, and higher than the moss loss measured during one year in our study (Graf and Rochefort, 2009). Therefore, aboveground plant litter does not contribute strongly to peat formation (Michaelis et al., 2020). The lower mass loss of belowground litter compared to aboveground vascular plant litter we found in our study is in line with a metastudy of Freschet et al. (2013) who found that roots generally decompose slower than leaves within the same plant species. The strong contribution of roots and rhizomes to peat formation in fens is in line with a detailed palaeontological analysis of the peat profile at two German sites, which are also part of our study. Here, Michaelis et al. (2020) showed that the old, less decomposed peat consists mainly of radicel fragments of several *Carex* species which grow under relatively nutrient poor conditions. Important to note that in our study undrained fens, the ratio of belowground to aboveground vascular plant peat formation potential is ca. 2 times higher than in rewetted fens. Therefore, in rewetted fens a smaller proportion of the vascular litter input contributes to displacement peat formation.

Therefore, we cannot confirm our third hypothesis. The high variation of belowground biomass production and decomposition within each hydrological status indicates that other environmental factors (as indicated above) than hydrological status are important, at least on the comparatively short time scale (one year) of this study. This outcome was surprising, because most water level variables used for this study and indicator values for water level derived from the plant species composition indicated wetter conditions in undrained and rewetted fens than in drained fens, and no distinction between undrained and rewetted fens (see Methods). This might imply that the hydrological status is not the dominating factor for the balance between production and decomposition of fresh litter of belowground biomass in the short term (one year), in contrast to long-term effects of water table on the net carbon balance of peat soils. A metastudy of Couwenberg et al. (2011) found net carbon loss with low water levels in drained peatlands (implying decomposition of old peat is higher than net plant production) and net carbon accumulation with water levels close to soil surface in undrained and rewetted peatlands (implying net plant production is higher than the decomposition of old peat). These contrasting results of the effect of hydrological status could imply that the relatively short-term mass loss of fresh litter is to a much lesser extend affected by hydrological regime than the (long-term) decomposition of old peat. Our study did not include measurements of peat decomposition, and in situ studies of peat decomposition are very rare. Despite such studies being very challenging, investigating the effects of rewetting and other environmental conditions like nutrient status on peat decomposition in situ needs more attention.

Moreover, the outcome of our study was likely influenced by the extremely dry and hot summer of 2018, which coincided with the measurements of production and decomposition in our study. The drought resulted in extreme water table dropdowns, even in several undrained fens. Unknown is how the pattern of production and decomposition measured deviated from pattern during average and wetter meteorological conditions. The extreme low water level during the summer and autumn, caused an increase of the air-filled porosity in the topsoil, and consequently increased respiration and suppressed methane production and emission (Knorr et al., 2008). In a boreal fen both primary production as respiration were enhanced by dry and hot conditions, and remained a strong sink for carbon (Flanagan and Syed, 2011). In a field experiment in a temperate, poor fen both water level dropdown and warming increased net ecosystem respiration, and the combination of both treatments had also positive synergetic effect (Samson et al., 2018). In this experiment the extreme hot days contributed strongly to monthly net ecosystem respiration. The effect of drying and subsequent rewetting on ecosystem respiration was small in a mesocosms experiment. This was attributed to most respiration occurred in the uppermost and soil layer, which stayed moist and aerated, and autotrophic respiration, that contributed 55 to 65% to ecosystem respiration, was only weakly affected by drought (Knorr et al., 2008). Because these findings are contrasting for fen ecosystems, the effects of the extreme dry and hot summer in our field study remains unclear. Possibly stronger aeration and high soil temperature could have accelerated the microbial decomposition of belowground litter more in undrained and rewetted fens then in drained. The later fens are also in normal meteorological years are exposed to strong water level dropdowns. Therefore, the extreme meteorological conditions might have an equalized the pattern of belowground biomass loss for the hydrological statuses. The same might also apply to vascular plant aboveground in rewetted fens that was equal high to the production in drained fens.

4.4 Implications of rewetting for peat formation

We quantified production and decomposition of plant material at multiple soil depths along a wide range of fens in undrained, rewetted, and drained states across Europe, and set it into relation to a broad range of abiotic and biotic parameters. This allowed us to generate geographically broad insights about the effects of fen peatland rewetting. An important outcome is that rewetted, formerly drained fens have a higher aboveground vascular plant biomass production than undrained fens. Moreover, the vertical pattern, but not the scale, of belowground production and decomposition is similar between rewetted and undrained fens. Given the finding in our study, which is corroborated by others (Zak et al., 2008), that P availability is positively correlated with decomposition, suppressing high P availability appears to be important for restoring peat accumulation in rewetted fens. For this, rewetting with long and deep inundation of degraded, P-rich peatlands should be avoided, as this creates eutrophic conditions with productive, tall helophyte vegetation lasting for several decades (Kreyling et al., 2021; Zak and Mcinnes, 2022). Low-nutrient availability after rewetting may quickly be achieved by topsoil removal (10 to 40 cm) (Emsens et al., 2015). This strategy is recommended for peatlands with a high risk of P mobilization from the soil upon rewetting, and can keep P mobilization low (Zak et al., 2017). However, the effects of this strategy on decomposability of fresh root and rhizome litter and potential for renewed peat formation are not clear yet, and therefore need further research. A long-term strategy might be a slow rise of the water table, as proposed by (Zak and Mcinnes, 2022). This method is also most likely to prevent strong P eutrophication and enhance the revitalisation of peat-forming vegetation and mire-typical biodiversity.

Author contribution

Investigation was designed and investigation was carried out by AK, CA, EP, ES, FT, HS, JK,, IJ, JF, LK, RD, WE, WK and YL, and data curation by AK, CA, ES, LK and RD. JK and TH contributed for mayor part to the statistical methodology, and together with CA also to development of software. Writing and visualization was done by CA, JK, FT and TH, while the other co-authors contributed to reviewing the manuscript.

Conflicts of Interest

The authors declare no conflicts of interest.

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