Fine-root biomass production and its contribution to organic matter accumulation in sedge fens under changing climate

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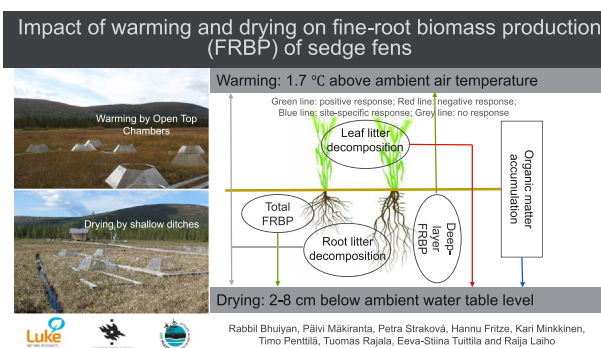[a] Natural Resources Institute Finland (Luke), Box 2 (Latokartanonkaari 9), FI-00791 Helsinki, Finland
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HIGHLIGHTS

- Most of sedge fen biomass is below ground, being important for carbon accumulation.
- Ingrowth cores and litterbags were used to assess fine-root production and decay.
- Drying increased total production while warming shifted production to deeper layers.
- Warming did not affect decay rates, drying decreased sedge leaf decay.
- Responses of organic matter accumulation depended on site.

GRAPHICAL ABSTRACT

Impact of warming and drying on fine-root biomass production (FRBP) of sedge fens

Warming: 1.7 °C above ambient air temperature

Green line: positive response; Red line: negative response; Blue line: site-specific response; Grey line: no response

Warming by Open Top Chambers

Drying by shallow ditches

Leaf litter decomposition

Total FRBP

Root litter decomposition

Deep-layer FRBP

Organic matter accumulation

Drying: 2–8 cm below ambient water table level

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ABSTRACT

Climate change may affect the carbon sink function of peatlands through warming and drying. Fine-root biomass production (FRBP) of sedge fens, a widespread peatland habitat, is important in this context, since most of the biomass is below ground in these ecosystems.

We examined the response of fine-root biomass production, depth distribution (10 cm intervals down to 60 cm), chemical characteristics, and decomposition along with other main litter types (sedge leaves, *Sphagnum* moss shoots) to an average May-to-October warming of 1.7 °C above ambient daily mean temperature and drying of 2–8 cm below ambient soil water-table level (WL) in two sedge fens situated in Northern and Southern Boreal zones. Warming was induced with open top chambers and drying with shallow ditching. Finally, we simulated short-term organic matter (OM) accumulation using net primary production and mass loss data.

Total FRBP, and FRBP in deeper layers, was clearly higher in southern than northern fen. Drying significantly increased, and warming marginally increased, total FRBP, while warming significantly increased, and drying marginally increased, the proportional share of FRBP in deeper layers. Drying, especially, modified root chemistry as the relative proportions of fats, wax, lipids, lignin and other aromatics increased while the proportion of polysaccharides decreased. Warming did not affect the decomposition of any litter types, while drying reduced the decomposition of sedge leaf litter. Although drying increased OM accumulation from root litter at both fens, total OM accumulation decreased at the southern fen, while the northern fen with overall lower values showed no such pattern.

Our results suggest that in warmer and/or modestly drier conditions, sedge fen FRBP will increase and/or be allocated to deeper soil layers. These changes along with the altered litter inputs may sustain the soil carbon sink function through OM accumulation, unless the WL falls below a tipping point.

1. Introduction

Fens, where sedges are the plant functional type that dominates the plant community, element cycles, and peat accumulation, are common habitats among northern peatlands (e.g., Bernard et al., 1988). Around 90 % of the plant biomass in boreal sedge fens is below ground (Sjörs, 1991; Saarinen, 1996, 1998) and consequently, understanding their fine-root biomass dynamics is crucial. The peat – and thus the soil carbon (C) store – in these sites consists mainly of sedge root and rhizome remains. In this dynamic system, annual root litter inputs and their decomposition significantly contribute to the rate of soil C accumulation. However, the accumulation of C in peatlands is sensitive to both weather and climate conditions at different time scales (e.g., Saarnio et al., 2007). Current trends and climate models suggest that climate change, at global mean temperature increase of 1.5–2 °C, may result in stronger warming in the northern region where peatlands are common (e.g., Kjellström et al., 2018). Predictions concerning changes in precipitation are less robust; however, warming is expected to increase evapotranspiration (Helbig et al., 2020) and lead to lowered soil water-table levels (WL) in peatlands (Roulet et al., 1992; Berg et al., 2009). Despite their importance for sedge fen functioning, studies of fine-root biomass production (FRBP) and decomposition are still scarce. Especially, the impacts of climate change on these deserve attention.

Most of the knowledge on the impacts of climate warming on FRBP in fens is based on mesocosm experiments (Weltzin et al., 2000, 2001; Bridgham et al., 2008). While aptly capturing the responses of specific plant communities to changes in abiotic conditions, mesocosm studies generally fail to include some biotic factors, such as dispersal of nearby species, that may shape community responses under field conditions. The so far only field study on the impact of warming on fen root dynamics, finding no significant effects (Mäkiranta et al., 2018), was based on one sampling in ecosystems still likely to be evolving after the treatment imposition (Updegraff et al., 2001; Wiedermann et al., 2007). As the sedge vegetation is dependent on the high WL and the related lack of shading by trees (Laine et al., 1995), drying is likely to have a stronger impact on fen vegetation than warming (Weltzin et al., 2001; Mäkiranta et al., 2018). Under field conditions, drying generally leads to increasing contribution of shrubs to community composition and biomass production (e.g., Berg et al., 2009; Mäkiranta et al., 2018). For a forested peatland, Malhotra et al. (2020) found greatly increased shrub root growth due to warming, but concluded that the response was rather to drying caused by the warming treatment than the warming per se. Consequently, assessment on the impact of climate change on fen FRBP calls for a field study covering several years to examine how the rooting patterns evolve in time, and considering the impacts of both warming and drying. We hypothesized that both warming and drying will increase the FRBP, drying more than warming.

Apart from biomass production, decomposition is the other major factor controlling soil organic matter accumulation and C balance. Temperature, moisture, and litter quality are generally the primary factors controlling litter decomposition rates (Silver and Miya, 2001; Hobbie, 2005; Laiho, 2006). In sedge fens, the typically high WL may be expected to exert a strong constraint. WL drawdown or drying generally has a direct positive effect on litter decomposition rates in fens (Straková et al., 2012). Drying thus has the potential to affect soil C balance and peat accumulation even if vegetation composition and litter inputs are not altered. Warming may further increase the decomposition rates. Earlier studies suggested that climate warming enhances peat organic matter decomposition (Dorrepaal et al., 2009; Fenner and Freeman, 2011; Jassey et al., 2013). In sedge fens, drying, especially combined with warming, increases ecosystem respiration (Laine et al., 2019); however, the possible impacts of warming under different WL scenarios on decomposition have so far not been directly evaluated. As drying improves the environmental conditions for aerobic decomposers, we hypothesized that drying will accelerate litter decomposition, and that root decomposition rate would decrease with depth in the soil profile.

Warming and drying may affect the organic matter accumulation not only through changed overall production and decomposition rates, but also through the vertical distribution of FRBP. The vertical distribution may change either due to species change, as, e.g., shrub fine roots may be constrained to a narrower depth range than those of wetland sedges (Proctor and He, 2019), or within the same plant community as a response to changed conditions (Murphy and Moore, 2010). A detailed view on the response of the vertical distribution of FRBP to warming and drying is needed for predicting the cycling and accumulation of C and nutrients. Roots growing deep into anoxic water-logged peat may be disproportionally important for C accumulation, especially (Saarinen, 1996). Earlier evidence suggests that drying may result in somewhat more superficial root production in bog-type peatlands that are characterized by woody plants (Murphy et al., 2009). We hypothesized that warming will not change the depth distribution of FRBP in sedge fens but drying will lead to more FRBP in deeper soil layers.

In addition to direct impacts of warming and drying, changes in organic matter chemistry may affect decomposition rates. The impact of litter quality has been suggested to be stronger than drying impacts on decomposition rates in peatlands (Straková et al., 2012). Infrared spectroscopy methods provide information about the presence, character and abundance of chemical bonds or functional groups of a given sample (e.g., Rewald and Meinen, 2013). Recently, such methods have been shown to be a useful tool for estimating the chemical composition of root materials (Straková et al., 2020). We hypothesized that both warming and drying will alter the different chemical quality of the produced fine-root biomass, drying more profoundly than warming as it is accompanied by some changes in the contributions of different plant species (Mäkiranta et al., 2018).

The aim of this study was to quantify fine-root biomass production (FRBP) and its contribution to organic matter accumulation in sedge fens under changing climate. To address our general aim, we first i) assessed the impacts of warming under two WL scenarios, wet and moderately drier, on FRBP and its depth distribution over three years. Next, we assessed ii) the chemistry of the FRB produced under the different experimental conditions utilizing FTIR spectroscopy, and iii) the decomposition rates of sedge fine roots compared to sedge leaves and *Sphagnum* moss under the different conditions. Those steps made it possible to iv) quantify how different vegetation components contribute to soil organic matter accumulation in short term.

2. Materials and methods

2.1. Study sites

Two experimental sites were established in 2008 in the boreal fens Lakkasuo and Lompolojänkkä. The southern fen Lakkasuo is located in southern Finland in Orivesi municipality (61°48′ N 24°19′ E). The northern fen Lompolojänkkä is located in northern Finland in Kittilä municipality (68° N 24°12′ E). In the southern fen, during the study period (2011–2013), the mean annual temperature and precipitation were ca. 4.6 °C and 746 mm, respectively, and the accumulative temperature sum (with a 5 °C threshold) was ca. 1378 degree days. The corresponding values for the northern fen were 0.2 °C, 650 mm and 884 degree days, respectively.

Both sites were wet minerotrophic sedge fens, and overall showed similar vegetation structure in terms of the occurrence and proportions of
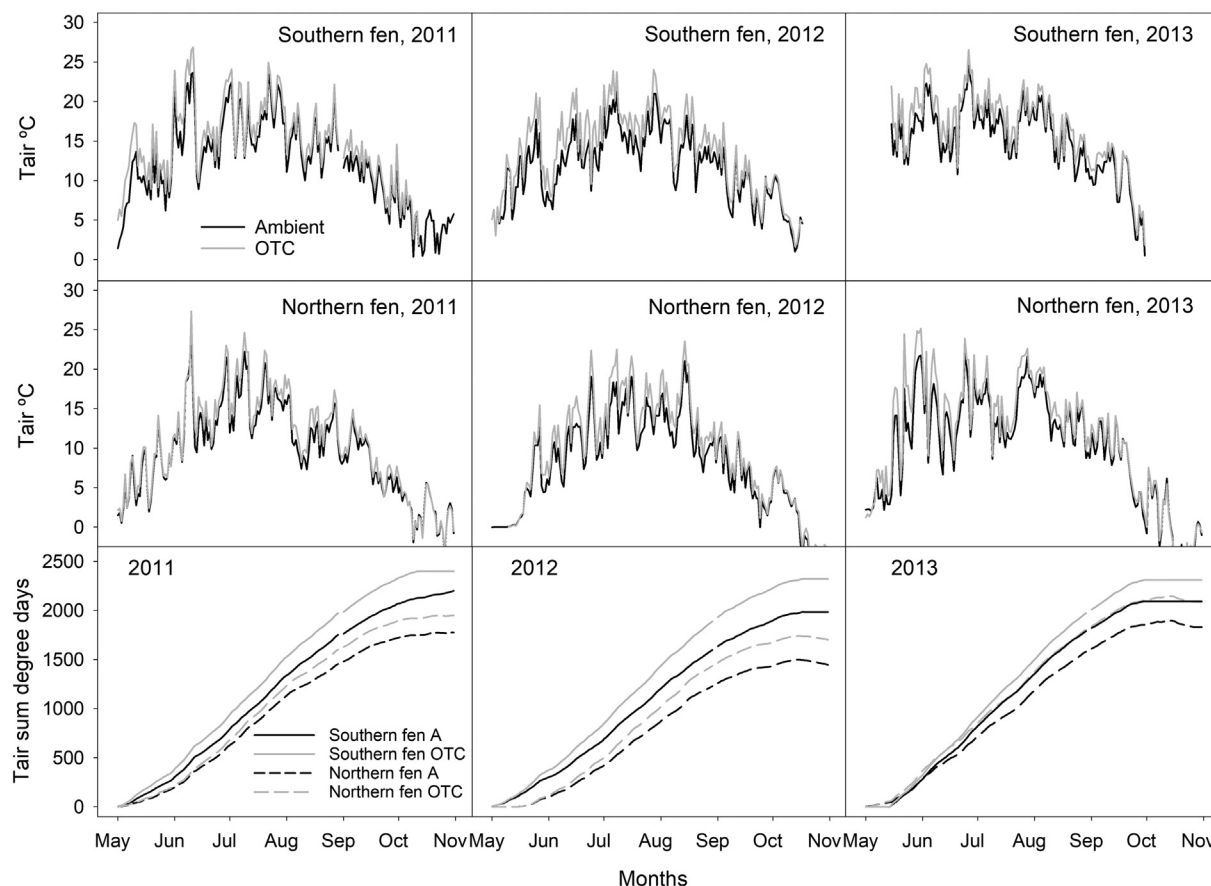
Fig. 1. Daily mean air temperature (Tair, °C) and air temperature sum (Tair sum in degree days, 5 °C threshold) at 15 cm height above ground under ambient (A) and warmed (OTC) conditions at the southern and northern fens from May to October 2011–2013. Warming was done passively using open top chambers (OTCs).

different plant functional types (see Mäkiranta et al., 2018 for details). However, there were also some differing patterns in their vegetation. In both sites, the field layer was characterized by sedges, *Carex lasiocarpa*[1] (especially in the southern fen), *C. rostrata* (especially in the northern fen), *C. chordorrhiza* and *C. limosa*. Both sites also shared some dwarf shrubs, *Andromeda polifolia* and *Vaccinium oxycoccos* (more abundant in the northern fen), and the herb *Menyanthes trifoliata*. Additionally, in the northern fen the horsetail *Equisetum fluviatile* and the herb *Comarum palustre* were present. In the moss layer, *Sphagnum papillosum* and *S. flexuosum* were abundant in the southern fen with small patches of *S. fallax, S. subfulvum* and *S. subnitens*, while in the northern fen the moss layer was overall patchier and consisted mainly of *S. fallax, S. riparium* and *S. flexuosum*, along with some *S. jensenii*.

2.2. Experimental design

We followed a split-plot experimental design to test the main and interactive impacts of warming and drying on FRBP (see details in Peltoniemi et al., 2015, 2016; Mäkiranta et al., 2018). For obtaining two water-level (WL) regimes: wet (ambient) and dry (drying treatment), drying had been induced by digging shallow ditches approximately 25–30 cm deep around the drying plots in early May 2008 at the southern fen and in June 2008 at the northern fen.

Three pairs of subplots within each WL regime (plot) had been established; one of the subplots acted as a control (ambient temperature) and the other was given a warming treatment. The warming of air and surface soil was obtained passively with hexagonal open top chambers (OTC)

(Marion et al., 1997; Hollister and Webber, 2000). The OTCs were made of clear plastic sheet, 60 cm tall, and each side panel was 76 cm long at the bottom (max. diagonal distance of 131 cm). The side panels of the OTCs were inclined to 60 % and placed on 10 cm tall supports, which allowed ventilation of air space and reduced disturbance to the soil surface. Our ingrowth core study (2010–2013) was started two years after the onset of the experiment, allowing the ecosystems some time to respond to the different treatments. However, full adaptation of the vegetation to the changed conditions may not yet have taken place during that time (e.g., Wiedermann et al., 2007).

To measure the temperature in the soil (5 and 15 cm below soil or *Sphagnum* moss capitula surface) and air (15 cm above the surface), automatic temperature data loggers were placed in each WL regime with and without OTC. The temperatures were monitored every 2 h. WL loggers were installed in both the wet and the dry plot. During the monitoring period (from May to October in 2011–2013), the average daily air temperature (Tair) above 15 cm of soil surface increased from 13 °C in the ambient plot to 15 °C in the OTC plot at the southern fen (Fig. 1). At the northern fen the average daily air temperature increased from the ambient 9.2 °C to 10.6 °C under the OTC (Fig. 1). This was reflected in the temperature sum (Tair, sum of all daily temperatures above 5 °C) that was approximately 252 and 228 degree days higher, or 112 % and 114 % of ambient, under the OTCs in the southern and northern fens respectively (Fig. 1).

The OTC also slightly affected the soil temperature during the monitoring period in both sites; the average daily soil temperature at 5 cm depth was approximately 0.4 °C higher under OTC at both fens (13.6 and 10.2 °C under OTC at the southern and northern fen, respectively; Figs. S1 and S2). At 15 cm depth, no difference in soil temperature (10.4 °C) could be observed between ambient and warmed plots at the northern fen (Fig. S3). However, at the southern fen the average daily soil temperature

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[1] Plant names follow WFO (2021).

at 15 cm was approximately 0.5 °C higher under OTC (13.4 °C). Drying did not affect the soil temperature at either 5 or 15 cm depth (Figs. S1, S2 and S3).

Water-table levels in the sites varied both within and between years, and the within-year patterns differed to some extent between sites (Fig. 2). The average growing season WL in the wet/control plot of the southern fen varied from 6 cm (2013) to 13 cm (2011), and that of the northern fen from 5 cm (2013) to 11 cm (2011). The measured drying effect was 7–8 cm in the southern fen, and 0–3 cm in the northern fen. All in all, the northern fen is generally wetter than the southern fen but in late summer 2012 this reversed temporarily. It should be noted that the WL measured from loosely surface-anchored dipwells do not necessarily reflect the full extent of drying, as the peatland surface changes along with changes in the water storage (e.g., Roulet, 1991; Fritz et al., 2013).

2.3. Ingrowth cores

To estimate the annual FRBP we used the ingrowth core method as described by Laiho et al. (2014) and Bhuiyan et al. (2017) to harvest the FRB produced over one, two, and three years. The cores were made of polyester fabric with a mesh size approximately 1 mm × 1 mm, and had an initial diameter of 3.2 cm and effective length of 60 cm. The cores were filled with deep-horizon sedge (*Carex*) peat, to exclude the possibility of having fresh live root remains in the substrate. The peat was chosen so that it mimicked the soil quality of the sites.

For each of the three annual recoveries, we installed two replicate cores in each subplot of the two WL regime plots: wet (ambient) and dry (drying) in October 2010. Thus, altogether 36 cores were installed in both WL regimes totalling 72 cores, half of which received no temperature manipulation (ambient) and the other half received artificial warming (OTC). The first annual set of 12 cores per plot was recovered in autumn 2011, followed by the second recovery in October 2012 and the final recovery in October 2013.

The recovered cores were divided into subsamples at 10 cm intervals starting from the surface: 0–10 cm, 10–20 cm, 20–30 cm, 30–40 cm, 40–50 cm and 50–60 cm. The top and bottom diameters (two crosswise measurements) and exact length of each subsample were recorded. Total roots, including both live and dead roots and rhizomes, inside the segments were recovered and gently washed with clean water. They were predominantly of ≤0.5 mm diameter, with occasional rhizomes of ≤2 mm diameter, and

were here all considered as fine roots (e.g., Finér et al., 2011). For technical reasons, dead roots were not possible to separate from live roots and hence total roots are reported. Dead roots inside the ingrowth cores represent production otherwise similarly to live roots but their mass may yield an underestimate as some decomposition (mass loss) may have taken place (see Bhuiyan et al., 2017). The roots were oven-dried to constant mass at 40 °C and then weighed. The area of the cores was calculated using the final diameters. The initial diameter was not used because our methodology involves the idea that the cores, installed in the autumn, adjust to their environment before the onset of root growth, and their diameter will be modified by the pressure from the ambient wet peat.

2.4. Analyses of FTIR-derived root chemistry

We assessed the root chemistry using FTIR (e.g., Straková et al., 2020). For these analyses, we utilized the roots of the second incubation year, and to provide sufficient material (≥0.10 g of dry root) for analysis the roots of 10–60 cm layers were combined. The samples were then powdered with an oscillating ball-mill. The infrared spectrum of each sample was measured using a Bruker VERTEX 70 series FTIR spectrometer (Bruker Optics, Germany) equipped with a horizontal ATR (Attenuated Total Reflectance) sampling accessory. Powdered samples were inserted directly on the ATR crystal and a MIRacle high-pressure digital clamp was used to achieve an even distribution and contact between the sample and crystal. Each spectrum consisted of 65 averaged absorbance measurements between 4000 and 650 cm^{-1}, with 4 cm^{-1} resolution.

2.5. Decomposition experiment

We applied the litterbag method (e.g., Straková et al., 2012) to analyze the mass loss of sedge (*Carex rostrata*) roots in comparison to the mass loss of sedge leaf and moss (*Sphagnum fallax*) shoot litter over a two-year incubation period (three-year period for the northern fen). These litter types were chosen as they represent the main biomass production components in boreal sedge fens (e.g., Mäkiranta et al., 2018). For the sedge root litter, whole living plants were collected from the experimental sites and cultivated in containers filled with expanded clay and water over the growing season of 2009. The root systems were then harvested, cleaned, and air-dried at room temperature (20 °C) in the early autumn. Senesced sedge leaves and moss shoot litter were harvested from the experimental sites in
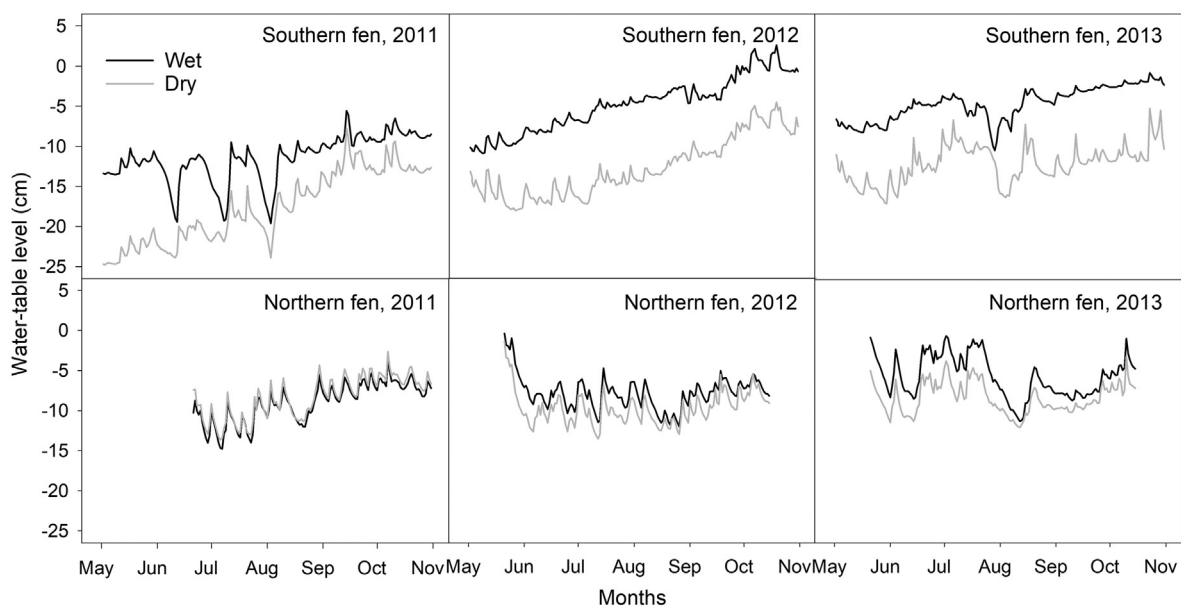

Fig. 2. Daily mean soil water-table level (WL, cm below the surface) in the two WL regime plots, Wet and Dry, at the southern and northern fens from May to October 2011–2013.

the early autumn of 2009. We collected the moss litter by cutting a 3–5 cm thick layer beyond the moss capitula with scissors, excluding both the upper green and the lower, already decomposing, layers. The collected litter was further sorted, and any green or visually decomposed parts were removed. These litter materials were also air-dried at room temperature (20 °C). Subsamples of each litter material were dried at 105 °C to determine their dry matter contents.

For preparing the litterbags, we used the same polyester fabric with a mesh size of approximately 1 mm × 1 mm as for the ingrowth cores. This mesh size allows small mesofauna typical of the sites (Silvan et al., 2000) to enter the bags. For each separate litterbag, 0.2–0.45 g (air dry mass) of root litter, 1–2 g of leaf litter, or 0.6–1 g of moss litter was weighed. The root litterbags were prepared to cover the depth range of 0–30 cm, with three separate 10-cm segments. Three litterbags of each litter type were prepared for each annual recovery in each site and subplot (WL regime and warming treatment condition). Site-specific materials were used.

The litterbags were installed in late September 2009 in the northern fen, and late October 2009 in the southern fen. The bags were moistened with the surface water in each site before installation. The sedge root litterbags were installed vertically to cover the depth of 0–30 cm, and the leaf litterbags were installed at the mire surface in the native sedge leaf litter layer. The moss shoot litterbags were installed inside the patches of this moss species, in the zone 3–5 cm below the capitula. Subsets of the litterbags were annually recovered in late September in the northern fen, and late October or early November in the southern fen. After each recovery, the litterbags were transported to a laboratory where their contents were cleaned by removing any additional (ingrowth) materials as well as possible, air-dried at room temperature, and weighed to determine the remaining air-dry mass. Subsamples were dried at 105 °C to determine the dry matter contents for each litter type.

2.6. Data analysis

2.6.1. Effects of warming and drying on FRBP

We applied a mixed-effect linear regression model to quantify the impact of warming and drying on the total FRB recovered from the ingrowth cores using the three-year data. The use of the three-year data allowed us to account for potential time-dependent patterns following the application of the treatments. Drying (wet vs dry), warming (ambient vs warmed), site, length of incubation (years) and their interactions were treated as fixed effects. To account for the lack of replicates at the Drying-level of the split-plot design, we added a random intercept term for each subplot.

The full model, including all interactions, for the total biomass of an ingrowth core of Site (s), Drying (d), Warming (w), Subplot (j) and Replicate (i) at recovery year t was defined as

$$
\begin{aligned}
\log(biomass_{sdwjit}) = \mu_0 &+ \beta_s + \beta_d + \beta_w + \beta_t + \\
&\beta_{sd} + \beta_{sw} + \beta_{st} + \beta_{dw} + \beta_{dt} + \beta_{wt} + \\
&\beta_{sdw} + \beta_{sdt} + \beta_{swt} + \beta_{dwt} + \\
&\beta_{sdwt} + \\
&\zeta_{sdwj} + \epsilon_{sdwjit} \\
\zeta_{sdwj} &\sim N\left(0, \sigma_\zeta^2\right) \text{ i.i.d.(Intra−subplot correlation)} \\
\epsilon_{sdwjit} &\sim N\left(0, \sigma^2\right) \text{ i.i.d.(Residual error)}
\end{aligned}
\tag{1}
$$

where

$biomass_{sdwjit}$ = the outcome variable at logarithmic scale for a particular subplot and replicate

β = Fixed effect regression coefficient

ζ_{sdwj} = Random effect coefficient for subplot; are assumed to be independent and identically distributed (i.i.d.) for different j

ϵ_{sdwjit} = Residual error for case j in group i and also assumed to be i.i.d.

σ_ζ^2 = Variance of random subplot effect

δ^2 = Residual variance.

The model was fitted using the *nlme* package in R software. The goodness of the fitted model was evaluated by performance metric ICC (Intra-class Correlation Coefficient) using the *performance* package in R (Table S1a–e), as well as by visual inspection of random effect structure (distribution of variance) of the model (Fig. S4a–e), predictions (fitted vs observed values) of the model (Fig. S5a–e) and residuals (errors) of the model (Fig. S6a–e).The estimated effect results of the model were reported as ANOVA table with different significance levels, e.g., p < 0.001, p < 0.05 and p < 0.01 (Table S2a–e).

2.6.2. Depth distribution of FRBP

The mixed-effect linear regression model (as in Eq. (1)) restricted our analysis when applying to the whole depth-wise root biomass data. Inclusion of depth variable caused complexity, e.g., multicollinearity in the fixed effects of the model. Thus, to assess the treatment effect on the depth distribution of the FRB recovered from the ingrowth cores, we fitted the root depth distribution pattern to an asymptotic equation described by Gale and Grigal (1987) and Jackson et al. (1996):

$$Y = 1 - \beta^d \tag{2}$$

where Y is the cumulative fraction of fine roots (a proportion between 0 and 1) found in the different layers starting from the soil surface to the depth d in centimeters, and β is the estimated distribution parameter. The values of β can range from 0.1 to 1, where value 0.1 indicates that all root biomass is at the topmost layer, and the value 1 that root biomass extends to the deepest layer. The β values were calculated individually for each ingrowth core using SYSTAT software. We then applied the mixed model for the root distribution parameter (β) using the *lme* package in R, as described above for FRB, to analyze the response of the root depth distribution (in terms of coefficient β) to warming and WL treatments.

2.6.3. FTIR-derived root chemistry

Variation in the FTIR-derived root chemistry for different sites, depths and treatments was analyzed by redundancy analysis (RDA). To correct for differences in the amplitude and baseline between different sample runs, we used standard normal variate transformation and de-trending. The transformed infrared absorbance data were used as response variables. Either site, depth (0–10 cm and 10–60 cm), treatment (warming, drying) or a combination of these (Wet-Ambient, Wet-Warmed, Dry-Ambient, Dry-Warmed) were used as explanatory variables. The spectral transformations were done using the Unscrambler software (Camo Process AS; Oslo, Norway) and RDA in Canoco 5 (Microcomputer Power, USA). The assignment of the FTIR absorption bands to chemical compounds was done as in Straková et al. (2020).

2.6.4. Litter mass loss

Linear mixed model was used, similar to the one used for FRB, to test if warming, drying, length of incubation period (two-year incubation period), depth (for root litter only), and their interaction had significant effects on litter decomposition of each litter type, using the mass loss data.

2.6.5. Simulation of organic matter accumulation

For estimating the accumulation of fresh organic matter into the soil, and the contributions of sedge fine-root litter versus above-ground plant materials (sedge leaf and moss litter), we performed a simple simulation using production (net primary production) and decomposition values. We assumed that standing biomass of each plant material is not changing over the simulation period, and thus, biomass production equals litter input. The simulation period was two years, as our decomposition data covered that time. We used the identified FRP "best estimates" for annual fine-root inputs based on the method described in Bhuiyan et al. (2017) and the aboveground production values for sedges and mosses from Mäkiranta et al. (2018) as annual above-ground inputs. These were then expected to decompose at the measured rates, and the remaining masses were summed up at the end of year two. Total organic matter accumulation

(OM$_{accu}$) from litter input (L) and decomposition (D) at different incubation periods was estimated as

$$OM_{accu} = ((L–L*D_1) − (L − L*D_1)*D_2) + (L − L*D_1) \qquad (3)$$

where L is the annual litter input (g m^{-2} yr^{-1}) and equal to biomass production, D_1 and D_2 are the mass loss rates (%) after year 1 and 2, respectively.

The input and mass loss data could not be individually matched, as the ingrowth cores and litterbags were placed in different spots around the subplots to avoid disturbance caused by recoveries, and further their number of observations per subplot differed. As a result, the potential differences of organic matter accumulation between the sites and the treatments could not be analyzed and only the average patterns are presented.

3. Results

3.1. Treatment effects on total FRBP

Across the incubation years and treatment plots, the total FRB in the ingrowth cores (0–60 cm) ranged between 118 and 698 g m^{-2} and 39–491 g m^{-2} at the southern and northern fen, respectively (Fig. 3). The variation of FRB between the sites was highly significant (p = 0.001, Table S2a). FRB in the ingrowth cores increased systematically over the whole 3-year study period (p $<$ 0.000, Table S2a, Fig. 3). Drying significantly increased the FRB (p = 0.046, Table S2a, Fig. 3). FRB in the northern fen, specifically, was systematically higher in the dry plots than wet plots (Fig. 3) as also indicated by a significant site-drying interaction (Table S2a, Fig. 3). Warming had a marginal main effect (p = 0.096) on the FRB. The warming effect was most evident in the southern fen after three-year incubation (Fig. 3).

3.2. Depth distribution of FRBP

Fine-root biomass depth distribution expressed as β (Eq. (2)) varied significantly among the sites (Table S2b, Fig. 4), indicating that the southern fen had proportionally more biomass production in deeper layers (β ranged between 0.91 and 0.94) compared to the northern fen (β ranged between 0.81 and 0.93). Warming showed a clear effect on the depth distribution, leading to proportionally more FRBP in deeper layers (Table S2b, Fig. 4), while drying had a marginal main effect (p = 0.096). There were also marginal interactions indicating site-specific drying and warming effects (p = 0.051, Table S2b). After two- and three-year incubation, a clear drying effect was evident in the northern fen.

3.3. FTIR-derived chemistry of FRB

The FTIR-derived chemistry of the produced FRB differed between the two fens (p = 0.002) and between the surface (topmost 0–10 cm) and deeper (10–60 cm) peat layers (p = 0.002) (Table S3, Fig. 5). The depth effect was more pronounced in the southern fen, as indicated by the greater distance between the centroids of the two depth classes in Fig. 5a. Roots in the topmost layer of the southern fen were characterized by higher intensities of absorption bands assigned to recalcitrant compounds (lignin and other aromatics, fats, wax, and lipids) while the roots of the northern fen and deeper peat layers of the southern fen had higher intensities of polysaccharide absorption bands (Fig. 5b).

Overall, warming had no significant effect on the chemical structure of FRB (Table S3), although in the topmost peat layer (0–10 cm), warming of the wet plots caused the root chemical structure to become more similar to the roots of the dry plots in both sites (Fig. 6a, b). Concurrently, drying had a clear effect on the chemistry of roots as the relative proportions of fats, wax, lipids, lignin and other aromatic compounds increased while the proportion of polysaccharides decreased. In the topmost layer, drying explained 25 % of the variation in root chemistry in both sites (Table S3, Fig. 6a, b). The strongest effect of drying on root chemistry was observed in deeper peat layers of the northern fen, where drying explained 50 % of the variation, whereas in the southern fen no drying effect could be detected in the deeper peat layers (Table S3, Fig. 6c, d).

3.4. Litter decomposition

The mass remaining after one year of decomposition of sedge root, sedge leaf and moss shoot litter ranged between 48 and 51 %, 69 and 82 % and 63 and 83 %, respectively, at the southern fen, and 65 and 70 %, 67 and 76 % and 76–89 %, respectively, at the northern fen. During the second year, mass loss generally decreased or even ceased, especially at the northern fen (Table S2c, Fig. 7). Additional data available for third year at northern fen showed clearly decreasing mass for roots in the upper 0–10 cm as well as for the surface litters.

Decomposition rates of sedge roots and moss shoot were significantly, and of sedge leaves marginally, lower in the northern fen (Table S2c–e) than southern fen. Neither warming nor drying affected the decomposition of sedge roots or moss shoot litter over two years. However, drying slowed the decomposition of sedge leaf litter, especially in the northern fen (Table S2d, Fig. 7). Further, the sedge root mass loss over two years did not depend on the depth position (0–10 cm, 10–20 cm and 20–30 cm soil layers) (Table S2c, Fig. 7).

3.5. Organic matter accumulation and the contributions of different plant materials

In the southern fen, the Wet-Ambient treatment showed the highest simulated organic matter accumulation and the Dry-Ambient the lowest (Fig. 8). The net total accumulation over 2 years was 603, 393, 280 and 283 g m^{-2} yr^{-1} for Wet-Ambient, Wet-Warmed, Dry-Ambient and Dry-Warmed treatments, respectively. In the northern fen, in contrast,
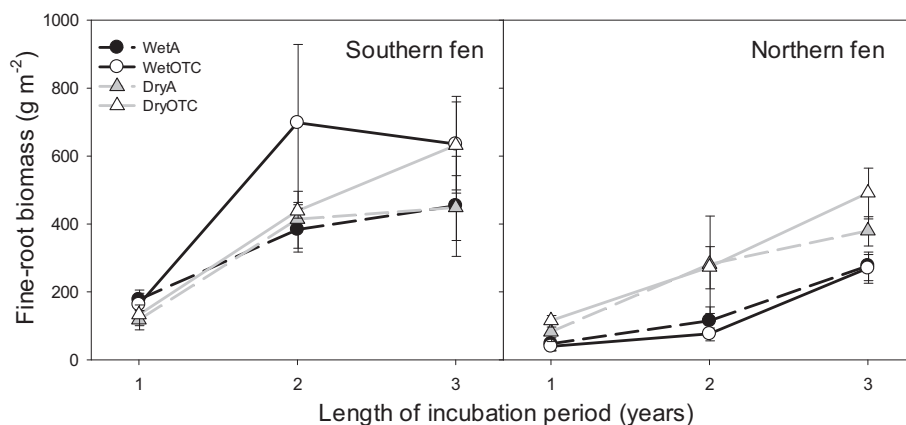

Fig. 3. Mean fine-root biomass recovered from ingrowth cores incubated for 1–3 years under Wet-Ambient (WetA), Wet-Warmed (WetOTC), Dry-Ambient (DryA), and Dry-Warmed (DryOTC) treatments. The ingrowth cores extended down to 60 cm depth from the peatland surface. All incubations started in 2010. Error bars show the standard error of mean.
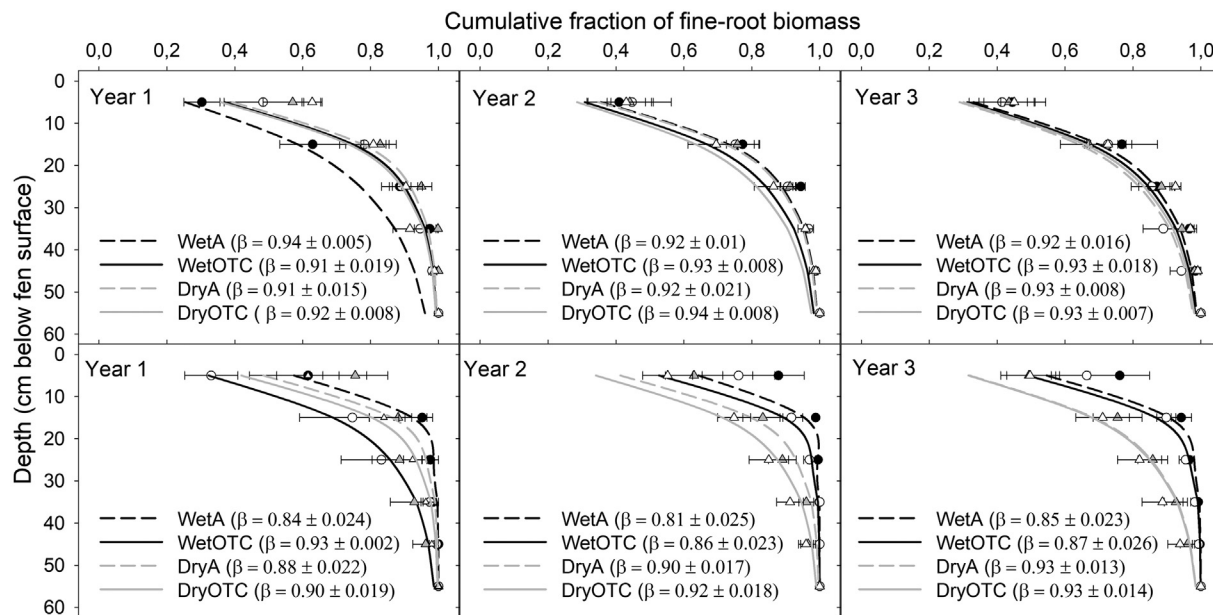
Fig. 4. Mean cumulative fraction of fine-root biomass produced over three years in the different 10-cm depth layers under Wet-Ambient (WetA; closed circle), Wet-Warmed (WetOTC; open circle), Dry-Ambient (DryA; closed triangle) and Dry-Warmed (DryOTC; open triangle) treatments, in the southern fen (top panels) and northern fen (bottom panels). Error bars show the standard error of mean. The lines are regression lines (Eq. (2): $Y = 1 - \beta^d$, where β is the fitted parameter). Larger values of β indicate a larger fraction of roots in deeper soil and smaller values of β indicate a larger proportion of roots near the soil surface.

the Dry-Warmed treatment showed the highest accumulation and the Wet-Warmed the lowest, the values being 279, 230, 299 and 330 g m^{-2} yr^{-1} for Wet-Ambient, Wet-Warmed, Dry-Ambient and Dry-Warmed, respectively.
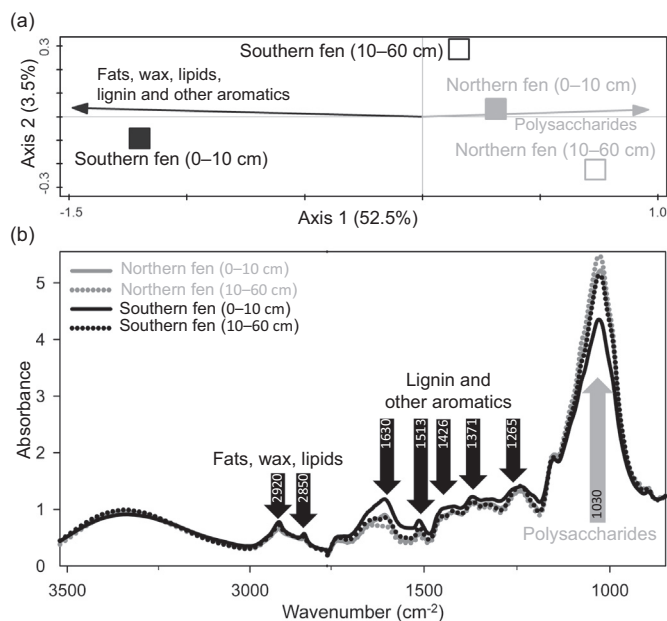

Fig. 5. (a) Redundancy analysis (RDA) of the FTIR absorbance data showing variation in the chemistry of the produced fine-root biomass between the two sites and the two sampling depth ranges, 0–10 cm and 10–60 cm below the fen surface. (b) FTIR spectra of the root biomass. The black arrows point to wavenumbers that showed positive correlation with the first axis in panel a (associated chemical compounds thus showed higher concentrations in the roots of the southern fen, especially in the 0–10 cm layer). The gray arrow points to wavenumbers that showed a negative correlation with the first axis in panel a (associated chemical compounds thus showed higher concentrations in the roots of the northern fen and deeper soil layers). Roots recovered from ingrowth cores that were incubated for two years were used in the analysis.

Under ambient conditions, moss contributed the highest proportion (62 %) of total litter accumulation in the southern fen, which dramatically decreased across treatment plots to as low as 14 % under the Dry-Warmed treatment (Figs. 8, S7). Simultaneously, the contribution of sedge roots increased from 20 % under ambient conditions up to 44 % in the Dry-Warmed treatment. The sedge leaf contribution ranged between 18 and 42 % across the treatments. On average, in the southern fen moss litter accumulation was highest (40 %) followed by sedge roots (32 %).

On the other hand, in the northern fen, sedge leaves contributed the most (57 %) and moss the least (15 %) to the total litter accumulation under ambient conditions (Figs. 8, S7). However, the contribution of sedge leaves decreased across the treatments to as low as 35 % in the Dry-Ambient treatment. Drying increased the contribution of sedge roots irrespective of the warming treatment (45 % in both Dry-Ambient and Dry-Warmed) as compared to ambient conditions (28 %). On average, in the northern fen sedge leaf accumulation was highest (45 %) followed by sedge roots (36 %).

4. Discussion

4.1. Effect of warming and drying on total FRBP and vertical distribution of FRBP

4.1.1. Effect of warming and drying on total FRBP

Our study provides a unique in-situ warming and drying experiment on evaluating sedge fen fine-root biomass production (FRBP) and its contribution to short-term soil organic matter accumulation. In sedge fen habitats, FRBP and decomposition are critical for sustaining the peat soil that consists almost completely of sedge root and rhizome remains.

We observed that FRBP in these fen ecosystems was affected more by moderate drying than warming, supporting our hypothesis. Interestingly, the northern fen showed a stronger FRBP response, although our direct observations of the soil water-table level (WL) indicated only very minor WL drawdown at that site, especially during the locally particularly wet year 2011 (see Lohila et al., 2016). The northern fen was overall wetter and had lower peat density than the southern fen, and, consequently, we suggest that the almost nonexistent WL drawdown as indicated by the WL measurements was partly caused by subsidence of the fen surface
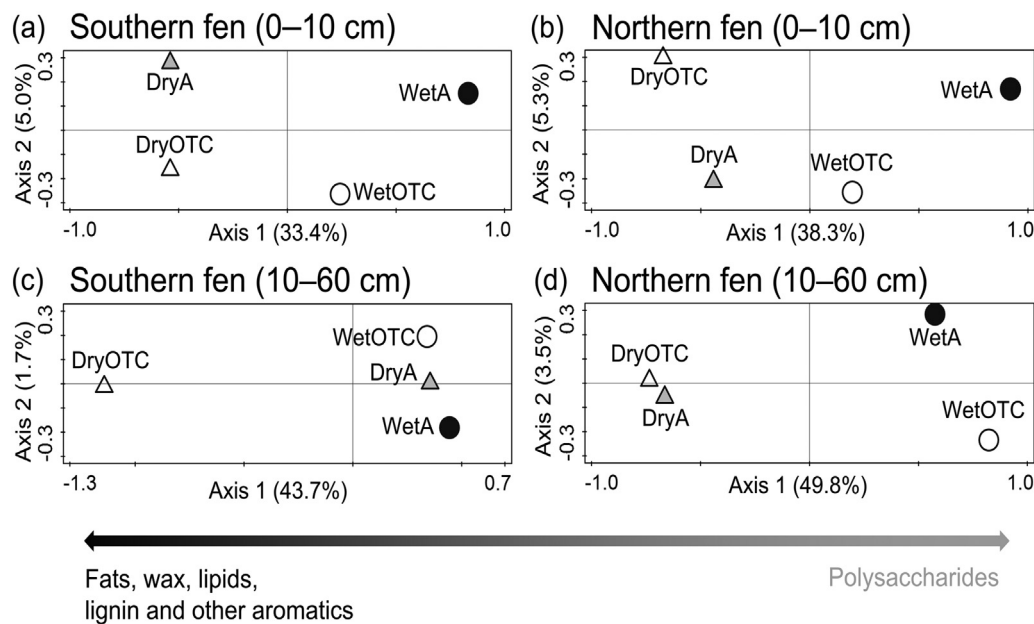
Fig. 6. Redundancy analysis (RDA) of the FTIR absorbance data showing the effects of Wet-Ambient (WetA), Wet-Warmed (WetOTC), Dry-Ambient (DryA) and Dry-Warmed (DryOTC) treatments on the chemistry of fine-root biomass in the (a), (b) 0–10 cm soil layer and (c), (d) in the 10–60 cm soil layer. Roots recovered from ingrowth cores that were incubated for two years were used in the analysis.

(e.g., Laiho and Pearson, 2016) following the decrease in water storage caused by the small ditches (Kellner and Halldin, 2002; Waddington et al., 2010; Stofberg et al., 2015). Modest measured-WL responses to drying treatment some years after the onset of the experiment have also been reported in other studies (e.g., Strack et al., 2006). It is further possible that higher moss growth at the southern fen than northern fen (Mäkiranta et al., 2018) may have contributed to the different extent of measured WL drawdown between the sites. All these minor changes may contribute (e.g., Whittington and Price, 2006) to changes in the flow of the minerogenic waters that the plant community of the sites were adapted to, leading to changes in rooting patterns. Strack et al. (2006) showed that under very wet conditions sedges may benefit from a modest drying, supporting our results. We cannot think of any artefact that could have affected the dry plot of the northern fen specifically so that the measured response of FRBP would be an error. Our advice for further studies is that when changes in WL are in focus, the measurements of both the WL and the peatland surface should be from the start linked to a fixed reference point.

Our drying treatment was not designed to simulate drought, like has been done in some other impact assessments (e.g., Fenner and Freeman, 2011), but a realistic, modest (5–10 cm at most during the summer) but consistent lowering of the WL. Lowering of maximum 10 cm of WL in fens have earlier been shown to have modest impacts on vegetation composition and aboveground biomass and production in a time range corresponding to our study (Churchill et al., 2015; Mäkiranta et al., 2018). More extensive WL drawdown of 10–20 cm, however, has been observed to initiate a significant vegetation succession and species turnover in fens, and to enable tree encroachment (Kokkonen et al., 2019), which may ultimately induce dramatic changes in the ecosystem (Laine et al., 1995; Laiho et al., 2003). Warming tended to increase total FRBP in our study, but not up to a significant level. This may in part be linked to the minor impact of the OTCs on soil temperature. While the OTCs increased air temperature on average by 1.7 °C, the impact on soil temperature remained modest. Why the increased air temperature did not lead to increased soil temperature is probably because of the buffering effect of the inflowing ground water, and the low thermal conductivity of peat. Also in earlier peatland warming experiments (Sullivan et al., 2008; Chivers et al., 2009; Dorrepaal et al., 2009; Delarue et al., 2015) <1 °C increase in peat soil was observed. With such modest soil warming, it is uncertain whether soil organic matter decomposition and nutrient mineralization are

enhanced to the extent of affecting FRBP (Nadelhoffer et al., 1991; Hobbie, 1996; Schmidt et al., 1999; Weltzin et al., 2000; Xu et al., 2012). Our results indeed did not show enhanced decomposition, and neither did estimates of soil nitrogen mineralization from our sites (Tytti Sarjala, unpublished data) that did not show any consistent patterns across treatments and involved very high variation.

Another explanation for the lack of FRBP response to warming may be the large temperature differences between day and night (as high as 25 °C) observed in our sites in an earlier study (Mäkiranta et al., 2018). Sedge plants may already have adapted to such dramatic temperature swings that the 1.7 °C increment may not affect their root biomass production. This adaptation view is further supported by the lower temperature optimum (15–20 °C) for shoot and root growth of sedge plants in arctic ecosystems than in temperate ecosystem (25–30 °C; Chapin, 1983). Our study with multiyear data emphasizes the importance of considering the time effect in experiments that induce potentially long-term treatment impacts. While first-year data showed no patterns, or patterns that later disappeared, relative to the treatments, the drying effect at the northern fen clearly strengthened with time, and the possible warming effect emerged only during the third year. The marginally significant warming effect suggests that warming may increase FRBP also in our sedge fens in longer term.

The findings of our study are partly contrasting with the findings of some earlier studies. For instance, in a fen mesocosm study, Weltzin et al. (2000) observed that soil warming by 1.6–4.1 °C at 15 cm depth increased fine-root biomass by 66–84 %, while drying by 10–20 cm did not affect the root biomass. Malhotra et al. (2020) reported strongly increased shrub root growth in response to soil warming by +2–9 °C in a forested peatland site. The differences may result from our treatment levels being more moderate, reflecting the on-going climate change, while the stronger treatment levels may better reflect the situation after a heat wave or in further future. How the warming proceeds is critical: it has been suggested that high-level warming (+2.5 °C) may destabilize plant community biomass production while low-level warming (+1.5 °C) may be better tolerated (Quan et al., 2021). The results of Malhotra et al. (2020) also suggest that the more superficial shrub roots are more responsive to warming than the deep-growing sedge roots. In an arctic fen site, Greenland, Sullivan et al. (2008) reported increased fine-root biomass due to warming by OTCs. There the conditions were clearly colder than in our sites, and together with our findings of stronger treatment effects in the northern fen support
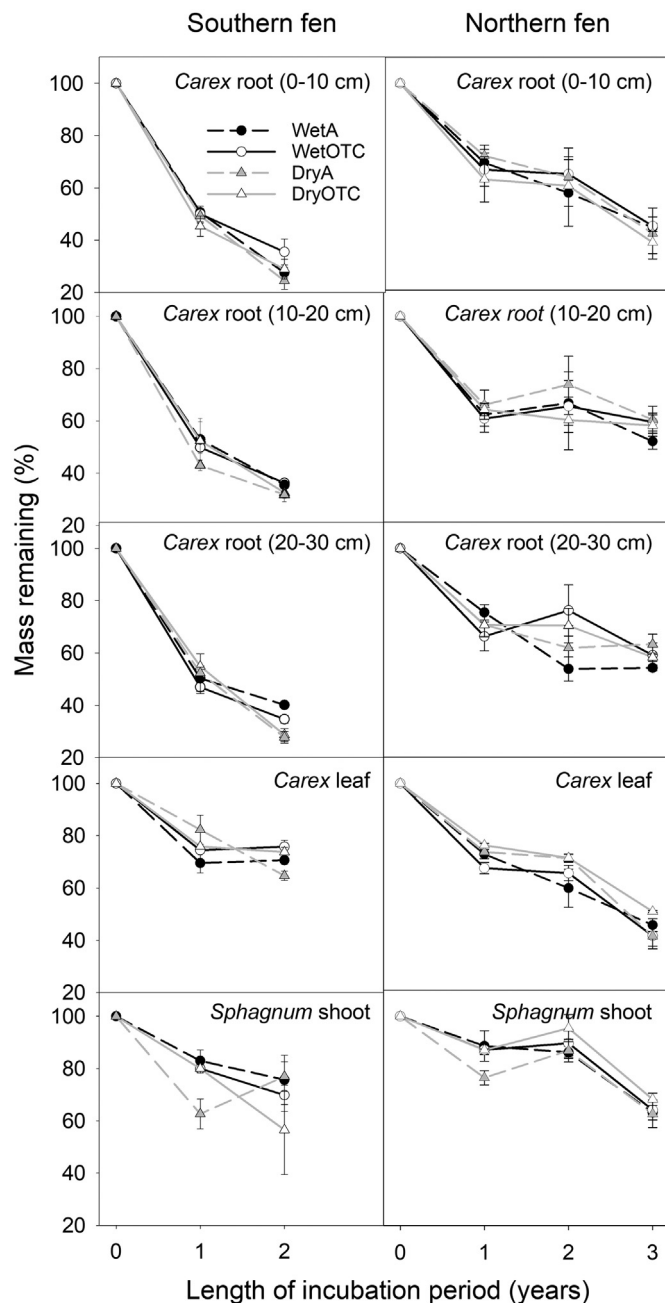
Fig. 7. Decomposition (% mass remaining, mean ± standard error) of sedge (*Carex rostrata*) root litter in three depths in the peat profile (0–10 cm, 10–20 cm and 20–30 cm), sedge (*Carex rostrata*) leaf litter incubated in the leaf litter layer on top of the fen surface, and moss (*Sphagnum fallax*) shoot litter incubated inside moss patches 3–5 cm below the moss capitula surface, under the Wet-Ambient (WetA), Wet-Warmed (WetOTC), Dry-Ambient (DryA) and Dry-Warmed (DryOTC) treatments in the northern and southern fens. Note that third year data were available only for northern fen.

the idea that fens are more responsive to climate change in their northernmost range.

4.1.2. Effect of warming and drying on vertical distribution of FRBP

Fine roots at the sites were initially distributed in the depth range studied (0–60 cm) in a different fashion, the southern fen showing proportionally more FRBP in deeper layers (higher β value) than the northern fen. It was unexpected that warming had a stronger effect on the depth distribution of FRBP than drying. Further, it was unexpected that a somewhat stronger drying at the southern fen did not affect the root
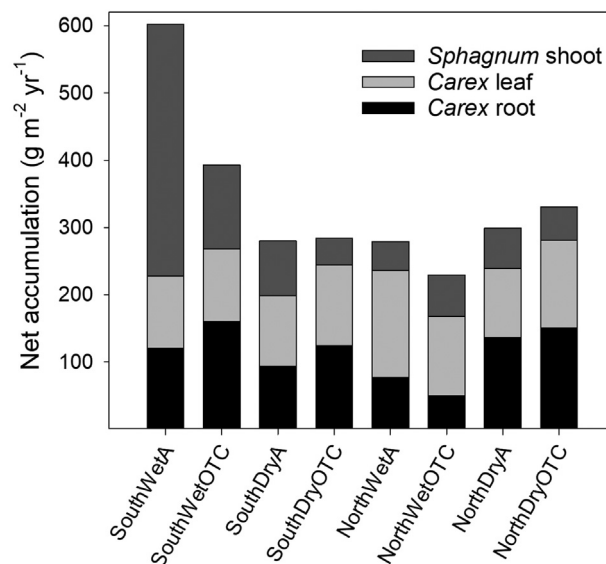

Fig. 8. Net accumulation of organic matter over a 2-year simulated period from sedge (*Carex rostrata*) root and leaf litter, and moss (*Sphagnum fallax*) shoot litter, under the different treatments at the southern and northern fens. A represents ambient temperature conditions and OTC warming with open top chambers.

depth distribution. Yet, it may simply result from more FRBP taking place in the deeper layers there to begin with. Mäkiranta et al. (2018) observed increased root production in deeper layers of forb and shrub, but not of sedge roots in the northern fen following drying. Sedges, in turn, increased their FRBP in the topmost 10 cm layer. The reasons behind these patterns remain unknown. In drier ecosystem types, more roots deeper down may be needed to harvest water (e.g., Liu et al., 2021), but this is not the case in our sites that were still quite wet after the drying treatment. Although our study did not identify the mechanisms for allocating more roots down to deeper layers, it suggests that such changes in sedge fens may be a direct response to climatic warming rather than moderate drying.

4.2. Effects of warming and drying on litter decomposition and FTIR-derived chemistry of FRB

In contrast to our hypotheses, warming and drying had no effect on sedge-root or moss litter decomposition rates in our experiment. Further, drying slowed sedge leaf litter mass loss, meaning that only the litter type that decomposes at the very top of the fen, in a layer that may be assumed to be oxic already under the wet conditions, responded to drying, and the response was the opposite to the expectation. This contrasts the commonly accepted paradigm that drying extends oxic conditions in soil and, consequently, enhances organic matter decomposition (e.g., Trettin et al., 1995; Thormann et al., 1999; Straková et al., 2012). Our results suggest that some factor that regulates decomposition, either biotic or abiotic, may have remained unfavorable following drying and warming.

Among the abiotic factors, WL and soil temperature are the most obvious regulators of decomposition. In our case, the changes in soil temperature were minor as discussed above. Also, even after drying in these very wet systems, WL remained quite high as compared to any terrestrial systems. The changes in our sites may have been too minor, especially relative to the seasonal variation, to induce significant responses. Still, one could have expected that both the moss litter and the topmost (0–10 cm) set of roots would have responded, if wetness and oxygen were the factor mainly limiting decomposition. Yet, our results align with the conclusion of Straková et al. (2012), based on cellulose decomposition, that the best environmental conditions for decomposition in peatlands are generally in moss patches and soil 0–10 cm layer (where we saw no response to treatments) and the worst in the surface litter layer of pristine wet plots (where we saw a negative response to drying).

It was most unexpected that the root litter lost similar amounts of mass over the 2-year decomposition period in the different depth positions. There was high spatial variation in year 2 in the deeper layers particularly at the northern fen, the mass-remaining values being in many cases higher than in year 1. This is an intuitively illogical, but an often-observed phenomenon in decomposition studies (e.g., Santelmann, 1992; Thormann and Bayley, 1997). Similar pattern, to some extent, was observed for the other litter types, and hampers comparisons. During the third year, mass loss had commenced again for all surface litters, but not for roots in the two deeper layers. The increasing mass may be caused by ingrowth of decomposer fungi or absorption of colloidal material from the soil or soil water by the decomposing material. Additionally, sampling of different litterbags from different spots annually contributes random variation to the estimates.

Overall, the mass losses observed in our study are in the ranges observed in other studies for corresponding litter types (e.g., Bartsch and Moore, 1985; Thormann et al., 2001; Limpens and Berendse, 2003; Moore et al., 2007).

4.3. Organic matter accumulation

The short-term soil organic matter accumulation potential estimated in our study summarizes the effects on both biomass production and decomposition rates. Estimates of the rates of recent organic matter accumulation for peatlands, particularly for sedge fens, are rare in the literature (Straková et al., 2012) that more often address long-term organic matter accumulation over centennial or millennial time scales (e.g., Turunen et al., 2002; Mäkilä and Goslar, 2008; Zhang et al., 2020). Long-term accumulation values often cover widely varying conditions, while short-term values may give some insight into the impacts of changing conditions. It should be noted that the majority of newly added material will decompose and not become part of the long-term C store (e.g., Young et al., 2019). Our findings indicated that the southern fen accumulated more organic matter than the northern fen (on average 130 and 95 g m^{-2} yr^{-1} respectively). These short-term values (about 50 % of biomass being C) are indeed very high as compared to long-term accumulation estimates. For instance, Turunen et al. (2002) and Zhang et al. (2020) reported average long-term carbon accumulation estimates of 15–17 and 72 g C m^{-2} yr^{-1} respectively for boreal sedge fens.

We could not perform significance tests between the fens, or the treatment plots and the results may be considered as indicative only. Yet, they allow us to compare net organic matter accumulation to independent CO_2 exchange data from the sites (Laine et al., 2019). Interestingly, different patterns were observed for the two fens with both methods. Consistent with the decreased net CO_2 uptake, we observed decreased net organic matter accumulation due to drying in the southern fen; both were further amplified by warming. This shows that even non-significant, minor changes may sum up to responses that are critical for the ecosystem functions. At the northern fen, the net CO_2 uptake remained stable (Laine et al., 2019), and we observed only minor variation in organic matter accumulation, even though the highest value was found for warming under drier conditions. The "success" of the northern fen seems to be largely due to the sustained or increased fine-root production. Laine et al. (2019) attributed the difference in the responses of the two fens to the small but potentially decisive differences in the WL between the two sites. While the northern fen still seems to be going strong following the treatment effects, the initially drier southern fen may be approaching a tipping point where more drastic changes in ecosystem structure and function are possible, especially if experiencing several successive drier years. In single years with warm and dry conditions, wet peatlands may turn into C sources due to increased decomposition induced by surface peat aeration (Alm et al., 1999; Bubier et al., 2003). However, if the drying is persistent enough to initiate hydroseral succession with fen-to-bog vegetation transition, it could lead to enhanced C sequestration (Tahvanainen, 2011; Loisel and Yu, 2013) as long as the transformed fen is still dominated by peatland vegetation, most importantly by *Sphagnum* carpet (Frolking et al., 2011; Turetsky et al., 2012).

Considering warming impacts in longer term, studies by Loisel and Yu (2013) and Charman et al. (2013) that utilized peat core stratigraphic analyses indicated overall increased long-term C accumulation in northern peatlands in response to warmer climate, where moisture is not a limiting factor. Gallego-Sala et al. (2018) also indicated more C accumulation at northern peatlands under future warmer climate conditions. These palaeo-ecological studies have predicted that in warmer climates, the increase in plant productivity will overcome increases in respiration at northern peatlands (Loisel and Yu, 2013; Charman et al., 2013; Gallego-Sala et al., 2018). In general, fen vegetation has shown peat-forming potential under highly variable (wet!) environmental conditions (e.g., Graf and Rochefort, 2009; Hinzke et al., 2021).

5. Conclusions

Our experimental study in sedge fens shows that with increasing temperatures, total fine-root biomass production does not change significantly, but the proportion of production in deeper soil layers increases. On the other hand, with lowering of the soil water-table level (drying), total fine-root biomass production increases significantly. Drying also reduces the decomposition of sedge leaf litter and modifies root chemistry regarding the relative proportions of fats, wax, lipids, lignin, polysaccharides and other aromatics. Together, this leads to different soil organic matter accumulation (SOM) patterns under changing environmental conditions. In a short-term simulation, our study shows that drying decreases total SOM accumulation. However, further studies are needed focusing on the effect of the evolving chemical change on decomposition rates, since root chemistry can largely influence root decomposition and thus SOM accumulation. In addition, longer-term decomposition results are needed to see how SOM accumulation will behave under different environmental conditions.

CRediT authorship contribution statement

Rabbil Bhuiyan: Methodology, Investigation, Formal analysis, Visualization, Writing - original draft; Päivi Mäkiranta: Methodology, Resources, Data curation, Writing - review & editing; Petra Straková: Methodology, Data curation, Formal analysis, Visualization, Writing - review & editing; Hannu Fritze: Funding acquisition, Project administration, Writing - review & editing; Kari Minkkinen: Funding acquisition, Writing - review & editing; Timo Penttilä: Conceptualization, Designing the study, Methodology, Writing - review & editing; Tuomas Rajala: Formal analysis, Visualization; Eeva-Stiina Tuittila: Funding acquisition, Writing - review & editing; Raija Laiho: Conceptualization, Designing the study, Methodology, Funding acquisition, Project administration, Resources, Supervision, Writing - original draft and revised versions of MS, review & editing.

Data availability

The FRBP, decomposition, and environmental data used in this paper are available at Zenodo, https://doi.org/10.5281/zenodo.7193829.

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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.159683.

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