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RESEARCH ARTICLE

Rewetting prolongs root growing season in minerotrophic peatlands and mitigates negative drought effects

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Abstract

1. Root phenology influences the timing of plant resource acquisition and carbon fluxes into the soil. This is particularly important in fen peatlands, in which peat is primarily formed by roots and rhizomes of vascular plants. However, most fens in Central Europe are drained for agriculture, leading to large carbon losses, and further threatened by increasing frequency and intensity of droughts. Rewetting fens aims to restore the original carbon sink, but how root phenology is affected by drainage and rewetting is largely unknown.
2. We monitored root phenology with minirhizotrons in drained and rewetted fens (alder forest, percolation fen and coastal fen) as well as its soil temperature and water table depth during the 2018 drought. For each fen type, we studied a drained site and a site that was rewetted ~25 years ago, while all the sites studied had been drained for almost a century.
3. Overall, the growing season was longer with rewetting, allowing roots to grow over a longer period in the year and have a higher root production than under drainage. With increasing depth, the growing season shifted to later in time but remained a similar length, and the relative importance of soil temperature for root length changes increased with soil depth.
4. *Synthesis and applications*. Rewetting extended the growing season of roots, highlighting the importance of phenology in explaining root productivity in peatlands. A longer growing season allows a longer period of carbon sequestration in form of root biomass and promotes the peatlands' carbon sink function, especially through longer growth in deep soil layers. Thus, management practices that focus on rewetting peatland ecosystems are necessary to maintain their function as carbon sinks, particularly under drought conditions, and are a top priority to reduce carbon emissions and address climate change.

KEYWORDS
carbon balance, growing season, minirhizotrons, peatlands, rewetting, root phenology, soil temperature, water table

1 | INTRODUCTION

Plant phenology, the timing of recurring life-history events, controls ecosystem processes that are crucial for the carbon storage function of peatlands, such as biomass production (Järveoja et al., 2020; Peichl et al., 2018). Peatlands are the most space-efficient terrestrial carbon sinks on the planet, storing about 20% of the global soil carbon pool on just 3% of the lands' surface (Joosten et al., 2016). Two thirds of European peatlands are minerotrophic peatlands, fens, in which peat is primarily formed by roots of vascular plants (Joosten et al., 2017; Succow & Joosten, 2001). The timing of root growth, that is, root phenology, strongly influences the timing of potential plant resource acquisition and carbon fluxes from roots into the soil (Finzi et al., 2015; McCormack et al., 2014). Altered root phenology can also drive large changes in root production in response to environmental changes, such as drought (Malhotra et al., 2020). However, despite the importance of root phenology, the majority of phenological studies focused only on the above-ground plant parts (Abramoff & Finzi, 2015), not taking into account that above- and below-ground phenology do not necessarily follow the same patterns (Abramoff & Finzi, 2015; Liu et al., 2022; Steinaker et al., 2010). Therefore, roots need to be explicitly considered in phenological studies to improve our general understanding of ecosystem processes related to carbon and nutrient cycling in peatlands.

Soil temperature is a strong driver of root growth in many seasonal ecosystems, thus, an increase in growing season length in temperate ecosystems is expected with warming (Keeling et al., 1996). However, in peatlands factors such as water table depth might be equally important (Joosten et al., 2017; Moore et al., 2007) or even override any temperature effects (Mäkiranta et al., 2018). The extent to which human influence, such as intensive land use and drainage, affects the importance of certain drivers of root growth is barely investigated. Here, studying root phenology in different depths is particularly important, as fluctuating water tables over the season might amplify the already prevailing differences in soil conditions with depth, such as soil moisture, oxygen content, bulk density and temperature (Jobbágy & Jackson, 2000). Plants can adapt their rooting depths to use emerging favourable conditions (Blume-Werry et al., 2019). Thus, identifying the response of root phenology to changes in water table and soil temperature at different depths is necessary to understand dynamic responses of peatlands to climate change.

Drainage of peatlands is widespread and turns them into carbon sources through enhanced decomposition (Joosten et al., 2016; Leifeld et al., 2019). In fact, 5% of total anthropogenic greenhouse gas emissions world-wide stem from drained peatlands and less than half of the peatlands in Europe are still accumulating peat (Leifeld et al., 2019; Tanneberger et al., 2017). Rewetting of drained peatlands may be a management option to lower emissions or even remove carbon from the atmosphere, but ecosystem consequences of rewetting are still largely unclear (Bonn et al., 2016; Joosten et al., 2016). Rewetting has far-reaching consequences in terms of plant and microbial composition, nutrient availability and soil characteristics, such as bulk density and pH (Lamers et al., 2015; Zeitz & Velty, 2002). As root production is an essential driver of peat formation in fens, estimating the effects of rewetting on root phenology will help us to better describe the consequences of restoration through rewetting of formerly drained fens on their carbon storage potential. A potential threat to the carbon storage potential even under rewetting, is the occurrence of long lasting droughts (Loisel et al., 2021). In 2018, Central Europe experienced one of the most extreme droughts recorded, with temperatures 3.3°C higher than the long-term average (April–October, compared to 1961–1990, Schuldt et al., 2020). These extreme climatic conditions are expected to occur more often in the future (IPCC, 2019), and it is thus important to understand its influence on root phenology.

Here, we studied root growth in different fen types: an alder forest, a percolation fen and a coastal fen, each in a drained and a rewetted state. We used minirhizotrons to estimate the start, end and length of the root growing season. We previously showed that these rewetted sites maintain higher root production at similar decomposition rates under drought conditions compared to the drained sites (Schwieger et al., 2021). Now we aimed to gain a deeper understanding on the underlying drivers of the observed high productivity by measuring root phenology under the same conditions and quantified net carbon balances. We hypothesized that (a) root growth happens later and longer due to the effect of higher soil water content dampening soil temperature effects and plant species composition changing to wetland specialists. We further expect that (b) the root growing season is prolonged in rewetted sites due to more favourable conditions under drought compared to the drained sites, and that (c) with increasing soil depth the growing season is shifted to later in the season as deeper soils warm later in spring and stay warm longer in autumn.

2 | MATERIALS AND METHODS

2.1 | Study sites

All study sites are located in north-eastern Germany (mean annual temperature: 8.8°C, mean annual precipitation: 565 mm, 1981–2010). The years 2015 to 2019 were about 2°C warmer and received with 450mm about 100mm less than average precipitation (Deutscher Wetterdienst). The study sites and the experimental set-up are described in detail in Jurasinski et al. (2020)

and Schwieger et al. (2021). In brief, we studied three different fen types: alder forest, percolation fen, and coastal fen. Of each type, we studied a drained site and one that has been rewetted for ~25 years after being drained for almost a century.

The two alder forest sites are stands of the same forest, a former natural alder swamp, that was drained for wood pasture in the end of the 18th century and subsequently used as production forest; one site was rewetted in 2003/2004 (Jurasinski et al., 2020). The two sites lie within the same basin and are about 3 km apart. The tree layer of the drained alder stand is characterized by *Alnus glutinosa* with a few individuals of *Fraxinus excelsior* L., while the understorey is dominated by herbaceous plants. The understorey of the rewetted alder stand is dominated by sedges, and *A. glutinosa* is the only tree species. The drained and rewetted lowland percolation fens are located in the hydrologically connected Lower Recknitz and Trebel Valley, respectively, *c.* 8 km apart. The drained percolation fen site is used as intensive grassland (Jurasinski et al., 2020) whereas the rewetted percolation fen (rewetted in 1997) is protected for nature conservation and not managed. The drained and rewetted coastal sites are about 200 m apart, on either side of a dike (rewetted by dike removal in 1993). Both are used for cattle grazing, and dominated by grasses. The rewetted site is occasionally flooded with brackish sea water during storm surges. See Supplements (see Table S1) for a detailed description of plant species at all sites.

For the study sites that are privately owned, we were granted access by the local communities and landowners. For sites located in landscape or nature conservation areas, permission was obtained from the local nature conservation authority of the district Vorpommern-Rügen. This study did not require ethical approval.

2.2 | Experimental set-up

Within each study site, a representative area with a size of 10 m × 35 m was fenced to exclude pasture and wild animals. Five plots (3 × 3 m) were evenly distributed in *c.* 10 m distance from each other inside the study area with three plots located at the north side and two plots located at the south side of a central boardwalk.

We compared six sites with replicates within each site but not for each fen type. Appropriate, rewetted replicates at the fen type level are not readily available. We selected study sites that were representative of each respective fen type in the broader region in terms of basic site characteristics, such as peat depth, degree of peat degradation and degree of drainage (Jurasinski et al., 2020; Schwieger et al., 2021). Furthermore, geostatistical analyses in fen peatlands in the region showed that spatial autocorrelation is almost absent (Koch et al., 2016; Koch & Jurasinski, 2015). Therefore, spatial replicates in the field can be seen as independent and their variation as being representative for the respective vegetation type. Based on these aspects, we describe our statistical results as comparisons between the six study sites, but see good reasons for them being representative for the respective fen types (see also Davies & Gray, 2015).

2.3 | Root phenology

We used minirhizotrons to monitor root phenology. Thereto, transparent tubes were installed at an angle of 45° in the soil to insert a root image scanner (CI-600 In-Situ Root Imager; CID Bio-science Inc.), taking *c.* 350° scans (image size: 21.6 × 19.6 cm) of the tube–soil interface and thus roots at three depths (0–15, 15–30 and 30–45 cm). The above-ground part of the tubes was wrapped with mirror foil to reduce thermal differences, taped and covered with a cap to exclude light from the tubes. Installation of the tubes took place in mid-August 2017 and measurements began in April 2018. As our study sites are very dynamic, fast-growing systems, we consider this time sufficient for recovery from the disturbance caused by the installation. Three minirhizotrons were installed within a distance of 1 m within each of the five plots at each of the respective sites, but one tube was damaged during the study, resulting in a total of 89 minirhizotrons (six sites × five plots × three tubes). In the rewetted coastal fen site, images could only be taken down to a depth of 30 cm for 10 tubes, due to hard mineral soil limiting the depth of minirhizotrons. This might have led to an underestimation of root length in these sites, as we cannot rule out the possibility of root growth into the mineral soil. We measured biweekly until 15 October 2018 and then monthly until 5 December 2018, resulting in 16 image sampling events.

We processed the sample images with our newly developed automated RootDetector (see methods S1 for a detailed description), which outputs binary images in which white pixels represent detected root objects and black pixels represent background or non-root objects (see Figure S1). We applied a topology-preserving thinning algorithm as implemented by the skeletonize function in scikit-image v. 0.17.1 to reduce the detected root objects to one pixel wide lines (see Figure S2). This was to avoid the patterns being dominated by large roots, as it is especially the fine roots that are important for carbon input into the soil due to their high turnover and exudation rates (Iversen et al., 2015). The output was converted into root length in mm cm^{-2}, given that root length is stronger related to root functionality (e.g. nutrient uptake) than mass (Freschet et al., 2020). We used root length as proxy for standing crop and to describe root phenology (i.e. increases and decreases in total root length over time). Soil movement and water table fluctuations sometimes led to light on images at the surface, which we excluded from analysis together with images affected by scanning errors (e.g. differences in contrast, stripes produced by the scanner bar), as these would likely have caused artefacts in root detection by the algorithm. This resulted in a total of 2,875 images of 21.6 cm × 19.6 cm for analysis.

2.4 | Growing season length

We used a quantitative approach to determine the root growing season (Radville et al., 2016). The start of the growing season was defined as day of the year (DOY) at which 10% of the maximum annual root length was reached, while the end of the growing season was defined as DOY at which 90% of the maximum annual root length was reached. We decided to calculate 90% of the maximum root length instead of 100% to exclude the possibility of very few roots determining the observed patterns (Blume-Werry et al., 2016). We narrowed down to the exact date when 10% and 90% of maximum annual root length was reached by using a linear model to interpolate between two measurement dates. To determine which environmental variables (i.e. soil temperature, water table, fen type, management type) explain changes in root length standing crop over time best, we defined changes in root length as any increase and decrease in root length since the previous sampling event. To normalize irregular sampling intervals, changes in root length were expressed as the change in root length per day (mm/d).

2.5 | Carbon balance

We measured the exchange of carbon gases (i.e. CO_2, CH_4) biweekly using transparent and opaque closed chambers on five permanently installed collars per site (Köhn et al., 2021). Based on the data gathered from October 2017 to September 2019, we derived the two consecutive annual exchange balances of CO_2 and CH_4 per site using artificial neural network models (Huth et al., 2022). Using the average annual balances per site, we summed up the resulting CO_2-C and CH_4-C values to derive annual carbon balances (see Table S2).

2.6 | Abiotic parameters

Precipitation data were recorded at weather stations less than 1 km distance from each study site. Soil temperature data were collected at 15-minute intervals at 5 cm, 15 cm and 30 cm depth by nine loggers per site (HOBO, Onset Computer Corporation). Air temperature was recorded at each site in 2 m height (CR300, Campbell Scientific Ltd.) averaged over 30 min.

Groundwater table relative to soil surface was recorded at 15-min intervals in a slotted PVC pipe using a CS456 pressure transducer connected via an SDI-12 sensor to a CR1000 data logger (Campbell Scientific Ltd.) at the alder forest sites, by Dipper-PT loggers for the two percolation fen sites and the drained coastal fen, and by a Baro-Dipper and a Dipper-APT logger (SEBA Hydrometrie GmbH & Co. KG) for the rewetted coastal fen site. Gaps in water table data recording for the rewetted alder forest site between 23 August and 27 October 2018 resulted from water tables below - 70 cm, which exceeded the reach of the groundwater pipe at this site (Figure 1).

2.7 | Data analysis

We used R version 4.0.2 (R Core Team, 2020) for all statistical analyses and visualizations (R package GGPLOT2, version 3.2.1). We tested for differences in root length between the fen types, between management (i.e. drained, rewetted), between depths and their interactions over time with a repeated measure linear mixed-effect model ANOVA (R package LMERTEST, version 3.1-0; and NLME, version 3.1-137). We used fen type, management, depth and time (i.e. day of the year of sampling) as interacting fixed effects, and tubes nested within plot as a random factor (three minirhizotron tubes per plot per site). To test for significant differences in root length within the fixed effects at the $\alpha = 0.05$ level, we used the criterion of whether or not two 83% confidence intervals overlap (Payton et al., 2003). To estimate differences in the start, end and length of the growing season, we used a linear mixed-effect model ANOVA for the above mentioned fixed effects except of time. For each model, we plotted the residuals with normal q–q plots and residual versus fitted values to graphically test the assumptions of normality and homogeneity of variance. When necessary, data were log- or square root-transformed to meet the assumptions. In case of the growing season end, the data were rank-transformed, resulting in a nonparametric test. A Tukey's HSD test (R package EMMEANS, version 1.4.1) was used for the response variables start, end and length of the growing season to test for differences within fen type, management and depth.

We used the second-order Akaike information criterion (AICc, R package MuMIn, version 1.43.17) to estimate the best-fit model that explains the greatest amount of variation in root length changes using the fewest possible explanatory variables (i.e. water table, soil temperature, management, fen type). The model with the lower AIC score was expected to strike a balance between its ability to fit the dataset and its ability to avoid over-fitting the dataset (Akaike, 1974). Afterwards, we estimated the marginal R^2 for describing the proportion of variance explained by the fixed factor(s) alone. These tests were performed for the soil depths 0–15, 15–30 and 30–45 cm separately to test for differences in the importance of abiotic factors for root length changes in different depth. Effects were considered significant at $p < 0.05$.

3 | RESULTS

3.1 | Root length

Root length was highest in the percolation fens, three times higher than in the alder forest, which had the lowest root length ($F = 53.1$, $p < 0.001$). Root length was higher in the rewetted than in the drained sites ($F = 4.4$, $p = 0.039$, Table 1). This was mainly caused by large differences in root length between the drained and rewetted percolation fen, while root length did not differ between the drained and rewetted alder stands and coastal fens (Fen type × Management: $F = 22.1$, $p < 0.001$; Figure 1). Root length changed over time ($F = 82.4$, $p < 0.001$) and also whether the root lengths differed between the management types depended on the time of the season (Management × Time: $F = 15.0$, $p < 0.001$). From July onward root length in the drained percolation fen started to decrease, while root length in the rewetted site stayed stable until the end of the measuring period resulting in a larger root length for the rewetted

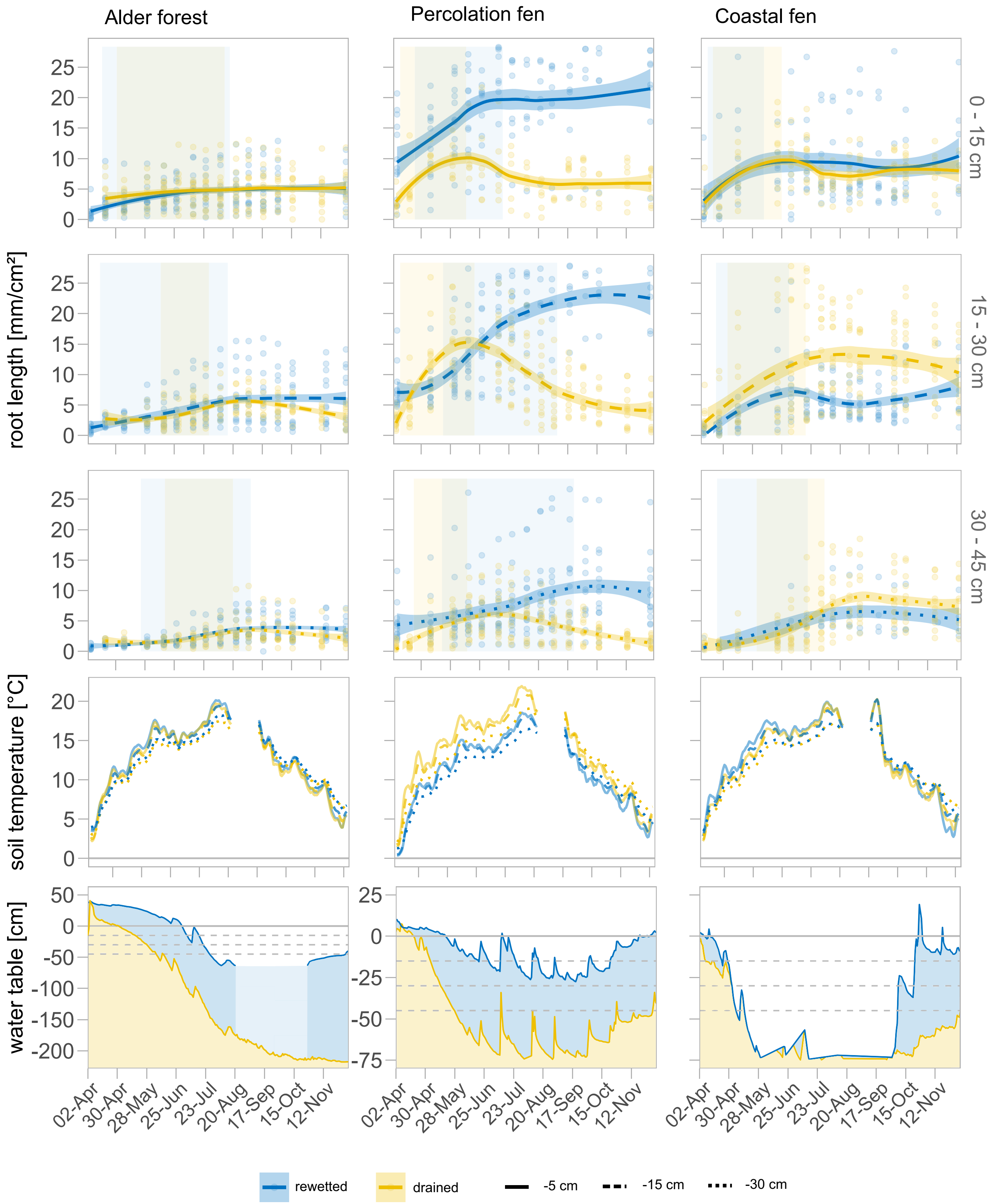

FIGURE 1 Root length (in mm/cm^2) over time in Alder forest, Percolation fen and Coastal fen in drained (yellow) and rewetted (blue) sites under the 2018 drought. Displayed are the soil depths 0–15 (solid), 15–30 (dashed) and 30–45 cm (dotted) for root length and soil temperature. Vertical ribbons highlight the calculated growing season length. Water table depth (in cm) for rewetted and drained sites, dashed grey lines indicate the soil depths in which root length was measured. Between 23 August and 27 October 2018, the water table in the rewetted alder forest site fell below −70 cm, exceeding the groundwater pipe at this site (white ribbon). Coloured bands show 83% confidence intervals to test for significant differences in root length between management type over time at the $\alpha = 0.05$ level.

percolation fen from July onwards. In the other two fen types root length differed only temporarily between management types (Fen type × Management × Time: $F = 15.0$, $p < 0.001$, Figure 1).

Root length was highest in the upper soil layers (0–15 cm) and decreased with soil depth ($F = 1022.4$, $p < 0.001$; Figure 1). This decrease in root length with depth was more pronounced in the drained sites. Here, root length differed between all three depths, whereas root length in rewetted sites did not differ significantly between the upper and the middle soil layer (0–15, 15–30 cm) in the percolation fen and the alder stand, and for the middle and the deepest soil layer (15–30, 30–45 cm) in the costal fen (Fen type × Management × Depth: $F = 14.6$, $p < 0.001$; see Figure S5).

TABLE 1 ANOVA results for root length in different fen types (Alder forest, percolation fen, coastal fen), management types (drained, rewetted), depths (0–15, 15–30, 30–45 cm) and over time (16 sample events from 4 April 2018 to 5 December 2018), and their interactions.

Fixed effects	*df*	*F*	*p*
Fen type	2	53.1	**<0.001**
Management	1	4.4	**0.039**
Depth	2	1,022.4	**<0.001**
Time	15	82.4	**<0.001**
Fen type × Management	2	22.1	**<0.001**
Fen type × Depth	4	80.5	**<0.001**
Management × Depth	2	4.3	**0.014**
Fen type × Time	29	5.4	**<0.001**
Management × Time	15	15.0	**<0.001**
Depth × Time	30	4.6	**<0.001**
Fen type × Management × Depth	4	14.6	**<0.001**
Fen type × Management × Time	25	15.0	**<0.001**
Fen type × Depth × Time	58	1.5	**0.013**
Management × Depth × Time	30	2.3	**<0.001**
Fen type × Management × Depth × Time	46	2.2	**<0.001**

Note: Values in bold indicate significant differences ($p \le 0.05$).

Root length increased simultaneously with warming soils in spring in all sites, except the drained alder stand (Figure 1). Root length increased in spring even under waterlogged conditions and did not decline as water tables rose in autumn in the rewetted sites. Except for the drained percolation fen, we detected almost no decline in root length towards the end of the year, despite of a much earlier estimated end of the growing season, that is, no growth was detected, but also no root loss.

3.2 | Root growing season

In general, roots in the rewetted sites started to grow, that is, observed increase in root length, significantly earlier (DOY 119 ± 3.0; mean ± SE) than in the drained sites (DOY 124 ± 4.6; $F = 4.7$, $p = 0.034$; Figure 2, Table 2). This was not the case for the percolation fens, where the growing season started 45 days earlier in the drained site than in the rewetted site (Type × Management: $F = 39.4$, $p < 0.001$, Figure 2). However, the end of the growing season was only significantly different between managements for the percolation fens (HSD Tukey: $p < 0.001$) where the growing season ended 72 days later than in the drained site. In contrast, the end of the growing season did not depend on management in the alder forest and coastal fen (Type × Management: $F = 13.0$, $p < 0.001$).

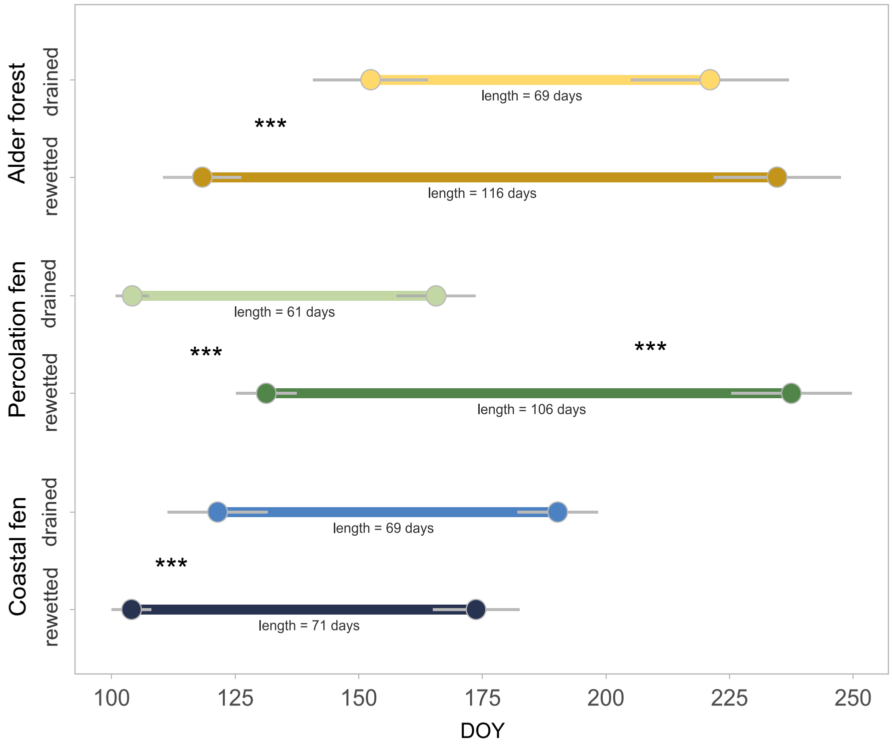

FIGURE 2 Root growing season length in drained and rewetted Alder forest, Percolation fen and Coastal fen under the 2018 drought. Circles mark the start and end of growing season averaged over depth (0–15, 15–30, 30–45 cm). Grey bars show 83% confidence intervals to test for significant differences in start and end of growing season at the $\alpha = 0.05$ level. Asterisks indicate significant differences in start (left) and end (right) of the growing season between the management types respectively (***$p < 0.001$).

TABLE 2 ANOVA results for start, end and length of the root growing season in different fen types (Alder forest, Percolation fen, Coastal fen), management types (drained, rewetted), depths (0–15, 15–30, 30–45 cm) and their interactions.

		Start		End		Length	
Fixed effects	*df*	*F*	*p*	*F*	*p*	*F*	*p*
Fen type	2	18.7	**<0.001**	19.1	**<0.001**	6.1	**0.004**
Management	1	4.7	**0.034**	10.1	**0.002**	39.1	**<0.001**
Depth	2	30.9	**<0.001**	4.9	**0.010**	0.0	0.989
Fen type × Management	2	39.4	**<0.001**	13.0	**<0.001**	8.7	**<0.001**
Fen type × Depth	4	1.3	0.290	1.2	0.332	3.4	**0.015**
Management × Depth	2	0.5	0.597	2.6	0.083	5.6	**0.006**
Fen type × Management × Depth	4	5.7	**<0.001**	2.1	0.097	2.5	0.053

Note: Values in bold indicate significant differences ($p \leq 0.05$).

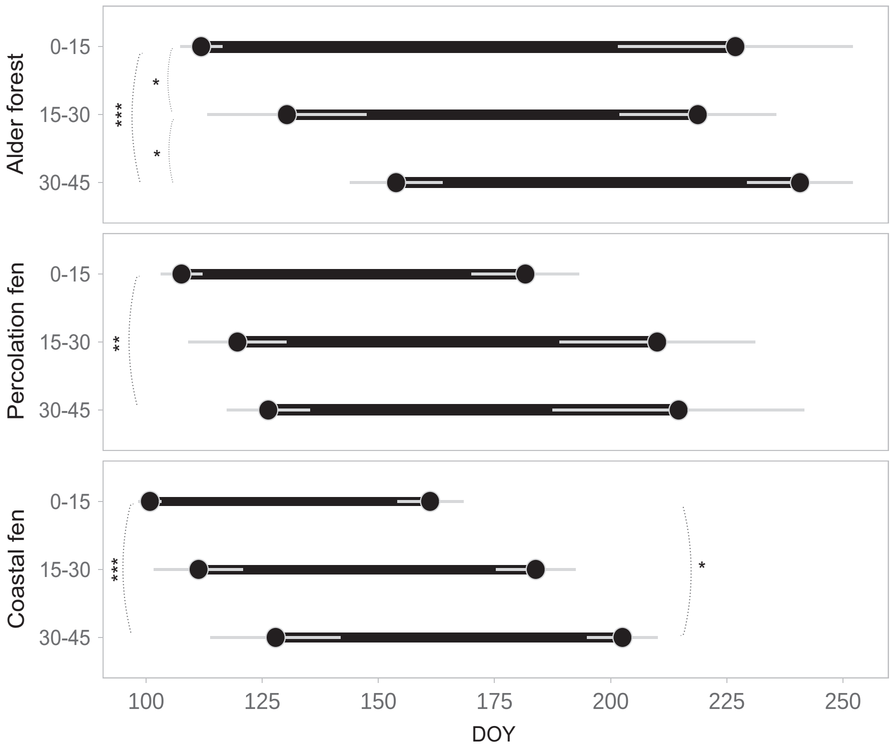

FIGURE 3 Root growing season length for the soil depths 0–15, 15–30 and 30–45 cm in the fen types Alder forest, Percolation fen and Coastal fen under the 2018 drought. Grey bars show 83% confidence intervals to test for significant differences in start and end of growing season between the depths at the $\alpha = 0.05$ level. Asterisks indicate significant differences in start (left) and end (right) of growing season between the soil depths (***$p < 0.001$, **$p < 0.01$, *$p < 0.05$).

Overall, the growing season was 1 month longer in the rewetted sites (100 ± 4.8 days) than in the drained sites (66 ± 3.9 days; $F = 39.1$, $p < 0.001$). Growing season in the rewetted percolation fen was 42%, and in the rewetted alder stand 41% longer than in their drained counterpart. However, there was no difference in growing season length between the two coastal fen sites (Type × Management: $F = 8.7$, $p < 0.001$).

The start of the growing season differed significantly between all three depths (0–15, 15–30, 30–45 cm), while the end of the growing season differed only between the upper (0–15 cm) and deepest soil layer (30–45 cm). With deeper soil depths, the growing season started and ended later (start: $F = 31.0$, $p < 0.001$; end: $F = 4.9$, $p = 0.010$; Figure 3). However, this was a mere shift in time, as we found no difference in growing season length with soil depth (Table 2).

Start and end of the growing season differed between fen types (start: $F = 18.7$, $p < 0.001$, end: $F = 19.1$, $p < 0.001$). Growing season in the coastal fens was the shortest (70 ± 3.0 days; $F = 6.1$, $p = 0.004$), while the growing season length in the percolation fens (85 ± 6.0 days) and in the alder stands (96 ± 7.9 days) did not differ from each other.

3.3 | Drivers of root length changes

The best-fit model of root length changes for the 0–15 cm soil layer included the parameters soil temperature, water table, fen type and management type with their interaction effects, explaining 53% of the variation of root length changes (Table 3). The next-best-fit model for the depth 0–15 cm includes only the parameters soil temperature, water table and fen type, which explained 49% of the variation in root length changes. The best-fit models for the 15–30 and 30–45 cm soil layers included the parameters soil temperature, management type and fen type with their interaction effects. The fixed effects explained 33% of the variation in root length changes for the depth 15–30 cm and 26% of variation in 30–45 cm (Table 3).

3.4 | Carbon balance

During the dry and warm study period, all sites showed a positive carbon balance. Rewetted sites, however, lost considerably less carbon in the percolation fen (−366.4 g m^{-2} year^{-1}) and slightly less in the coastal fen (−30.4 g m^{-2} year^{-1}; see Table S2 for details).

4 | DISCUSSION

The root growing season was up to 1 month (34 days) longer in the rewetted than in the drained fens. This extension of the growing season, rather than a higher growth rate, can explain the overall higher root productivity in response to rewetting under drought conditions measured previously (Schwieger et al., 2021) and the positive effect on carbon balance (see Table S2). With increasing depth, the beginning and end of the growing season shifted later in time, resulting in an overall similar length of the growing at the different depths despite. The relative importance of soil temperature for changes in root length increased with increasing soil depth.

4.1 | Extension of root growing season with rewetting

As we expected, drained and rewetted sites differed in their phenology, which was expressed by shifts in the start and end, but also in the length of the growing season depending on the fen type. We measured a significantly longer root growing season with rewetting in two of three cases. These results support our assumption that, under drought conditions, rewetting promotes plant growth by providing sufficient soil moisture conditions compared to the drained sites. The longer growing seasons are linked to increased carbon storage (see Table S2; Churkina et al., 2005; Dragoni et al., 2011; Keenan et al., 2014). Furthermore, our results suggest that the previously reported higher annual productivity of these rewetted fens under drought (Schwieger et al., 2021) was driven by an extension of the growing season. While it was a carbon source in the dry year, the percolation fen has accumulated *c.* 106 g C m^{-2} year^{-1} since rewetting in 1997 (Mrotzek et al., 2020).

The observed differences in phenology between the drained and rewetted sites may not be rooted in the management per se, but rather caused by differences in plant functional types between the sites (Mäkiranta et al., 2018). Different plant functional types or species may respond differently to interannual variability in resource

TABLE 3 Marginal R^2 (R^2_m) and conditional R^2 (R^2_c) for root length changes with the tested fixed effects soil temperature in °C (soil T, recorded in respective depth to root length changes), water table depth in cm, management type (drained, rewetted) and fen type (Alder forest, Percolation fen and Coastal fen).

	0–15 cm			15–30 cm			30–45 cm		
Model parameters (fixed effects)	R^2_m	R^2_c	AICc	R^2_m	R^2_c	AICc	R^2_m	R^2_c	AICc
Soil T × water table × management × fen type	**0.53**	**0.67**	**−4157**	0.49	0.63	−4707	0.30	0.66	−5065
Soil T × management × fen type	0.49	0.71	−4069	**0.33**	**0.48**	**−4736**	**0.26**	**0.64**	**−5213**
Water table × management × fen type	0.47	0.61	−4096	0.33	0.48	−4548	0.18	0.55	−4944
Soil T × water table × fen type	0.49	0.71	−4100	0.45	0.66	−4629	0.29	0.67	−5035
Soil T × water table × management	0.11	0.42	−3886	0.11	0.42	−4469	0.10	0.57	−4963
Management × fen type	0.21	0.36	−4061	0.22	0.35	−4638	0.14	0.50	−5071
Soil T × fen type	0.23	0.38	−4076	0.24	0.39	−4667	0.19	0.54	−5124
Soil T × management	0.02	0.35	−4028	0.05	0.38	−4621	0.06	0.55	−5105
Water table × fen type	0.45	0.64	−4067	0.28	0.44	−4501	0.15	0.50	−4910
Water table × management	0.09	0.42	−3886	0.05	0.34	−4432	0.02	0.49	−4898
Soil T × water table	0.11	0.42	−3888	0.06	0.38	−4436	0.06	0.55	−4938
Soil T	0.01	0.35	−4030	0.00	0.34	−4596	0.05	0.54	−5105
Water table	0.11	0.43	−3889	0.02	0.33	−4421	0.01	0.49	−4897
Management	0.01	0.35	−4023	0.01	0.34	−4595	0.01	0.48	−5062
Fen type	0.20	0.35	−4064	0.19	0.34	−4635	0.13	0.49	−5076

Note: Models with the lowest AICc for the respective depths are highlighted in bold.

supply and climatic constraints (McCormack et al., 2014). Plants in all the drained sites, such as forbs and grasses, are adapted to drained soils but not necessarily to drought. The rewetted sites, however, are generally dominated by graminoids (i.e. Poaceae and Cyperaceae), which are adapted to high and prolonged water tables. Their special adaptations, such as aerenchyma, permit root growth deep into waterlogged conditions (Voesenek et al., 2006). In fact, root length in the depths 45–60 cm in the graminoid-dominated rewetted percolation fen was twice as high as in the drained counterpart (see Table S3), and water tables in the rewetted percolation fen did not drop below −25 cm during the growing season (Figure 1). Thus, roots still reached water saturated soil layers in the rewetted sites. The root system of the drained sites and the rewetted coastal fen, however, experienced a lowering of the water table of −75 cm and deeper during most of the year (Figure 1). As a result, the growing season in the drained sites was significantly shorter than in the rewetted sites. Clearly, rewetting is not only beneficial for peat formation and climate change mitigation during 'normal' weather conditions, but also may help alleviate drought stress and thus maintain a higher production/decomposition ratio under drought conditions—driven by an extension of the root growing season.

Interestingly, we found no decrease in root length in four of six sites at the end of the year despite of decreasing soil temperatures in autumn. This suggests that even if the season of active growth (i.e. increase in root length) ended, many of the roots are living (and presumably functional) for a majority of the year, contributing to ecosystem carbon and nutrient fluxes. The stagnation of the root length might also indicate that as many roots were decomposed as produced in this time.

4.2 | Abiotic factors driving changes in root length in different depths

As expected, the root growing season was shifted later in the season with increasing depth, while growing season length did not change with depth (Figure 3). This offset of growth with a later start, but also a later end of the growing season with increasing soil depth is likely related to dampened temperature dynamics (Figure 1). The model that included both, soil temperature and water table described root length changes best in the upper soil layer (0–15 cm), while with deeper soil depth the relative importance of water table decreased (Table 3). While differences in species composition are most likely still the main determinant of root length changes, these results imply that soil temperature is important when predicting root phenology at depth. As water was either present (rewetted sites) or absent (drained sites) in deeper soil layers, it fluctuated in the upper soil layers of the rewetted sites, thus, the relative importance of soil temperature might have increased with depth. Changing controls of root phenology with increasing depth might be linked to such changes in soil properties (Jobbágy & Jackson, 2000), but also to different rooting depths between species, and thus a change in 'species composition' with depths. The fact that the length of the growing season at deeper depths remains the same, even though the factors determining root length changes are changing, shows that the potential for carbon sequestration also in deeper soil layers might be high. More so because colder and wetter conditions with increasing soil depth are ideal to promote the accumulation of organic matter and trap the carbon in the soil.

An earlier start in the root growing season was detected for the rewetted alder forest and costal fen, despite waterlogged conditions in spring, most likely because the prevailing plant species are adapted to flooding. In the rewetted percolation fen and alder forest, the growing season was clearly linked to soil warming in spring and ended shortly after soil temperatures peaked in the end of August (Figure 1). In contrast to that, root length changes were less affected by soil temperature in the drained counterparts. The drained sites experienced a water table drawdown up to −45 cm, which resulted in a significantly earlier end of the growing season even before maximum soil temperatures where reached. It appears that the plant communities in the drained sites (and the rewetted coastal site) were less able to cope with the drier soils and that those conditions overrode the generally positive effects of temperature on root length changes, whereas plants on the rewetted sites even maintained their high productivity in the dry and warm summer of this year. Mäkiranta et al. (2018) also showed that in boreal sedge-dominated fens, increase in temperature alone affected root production and phenology less than water-level drawdown. Drought stress has also been shown to inhibit root growth and can cause root production to shift to more favourable, in this case wetter, times of the year (Hendrick & Pregitzer, 1997; Joslin et al., 2000). Furthermore, root production can also be related to the previous year precipitation (Withington et al., 2021). In contrast to the alder forests and percolation fens, the water table in the rewetted coastal fen is highly dependent on sea levels, with water tables above soil surface twice during storms and flooding, in October and November 2018. Root phenology, therefore, strongly resembles that of the drained coastal fen except for the slight increase in root length at the end of the year.

Since anoxia from high water tables is the main driver of peat accumulation, increasing droughts in the future seriously threaten their carbon sink function (Loisel et al., 2021). Our results might not reflect the long-term consequences of continuing summer droughts, including possible changes in plant composition to drought-adapted species, thus, further studies on the effects of changing climate and land use on root phenology are crucial.

5 | CONCLUSIONS

Our results underline the high potential of rewetting peatlands to support their carbon sink function even under drought. A longer growing season with rewetting enhances root production and allows for longer carbon sequestration in form of root biomass. Root growth in deeper soil depth especially may promote carbon sequestration, as soils remain anoxic even under drought conditions, which impedes the decomposition of organic matter. Rewetting drained peatlands is thus crucial to turn them from carbon sources back to carbon sinks—an important step to addressing climate change.

AUTHORS' CONTRIBUTIONS

S.S., G.B.-W. and J.K. conceived the study; S.S. did the fieldwork and statistical analyses with advice from J.K.; B.P., A.G. and U.F.v.L. provided the algorithm to automatically digitize the raw scans; G.J. and D.K. provided carbon balance data; S.S., G.B.-W. and J.K. interpreted the results; S.S. led the writing of the manuscript with the contribution of G.B.-W., J.K. and B.P.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.0gb5mkm3p (Schwieger et al., 2022).

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REFERENCES

Abramoff, R. Z., & Finzi, A. C. (2015). Are above- and below-ground phenology in sync? *New Phytologist*, *205*, 1054–1061.

Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, *19*, 716–723.

Blume-Werry, G., Milbau, A., Teuber, L. M., Johansson, M., & Dorrepaal, E. (2019). Dwelling in the deep – Strongly increased root growth and rooting depth enhance plant interactions with thawing permafrost soil. *New Phytologist*, *223*, 1328–1339.

Blume-Werry, G., Wilson, S. D., Kreyling, J., & Milbau, A. (2016). The hidden season: Growing season is 50% longer below than above ground along an arctic elevation gradient. *New Phytologist*, *209*, 978–986.

Bonn, A., Allott, T., Evans, M., Joosten, H., & Stoneman, R. (2016). *Peatland restoration and ecosystem services: Science, policy and practice*. Cambridge University Press.

Churkina, G., Schimel, D., Braswell, B. H., & Xiao, X. (2005). Spatial analysis of growing season length control over net ecosystem exchange. *Global Change Biology*, *11*, 1777–1787.

Davies, G. M., & Gray, A. (2015). Don't let spurious accusations of pseudoreplication limit our ability to learn from natural experiments (and other messy kinds of ecological monitoring). *Ecology and Evolution*, *5*, 5295–5304.

Dragoni, D., Schmid, H. P., Wayson, C. A., Potter, H., Grimmond, C. S. B., & Randolph, J. C. (2011). Evidence of increased net ecosystem productivity associated with a longer vegetated season in a deciduous forest in south-Central Indiana, USA. *Global Change Biology*, *17*, 886–897.

Finzi, A. C., Abramoff, R. Z., Spiller, K. S., Brzostek, E. R., Darby, B. A., Kramer, M. A., & Phillips, R. P. (2015). Rhizosphere processes are quantitatively important components of terrestrial carbon and nutrient cycles. *Global Change Biology*, *21*, 2082–2094.

Freschet, G. T., Roumet, C., Comas, L. H., Weemstra, M., Bengough, A. G., Rewald, B., Bardgett, R. D., De Deyn, G. B., Johnson, D., Klimešová, J., Lukac, M., McCormack, M. L., Meier, I. C., Pagès, L., Poorter, H., Prieto, I., Wurzburger, N., Zadworny, M., Bagniewska-Zadworna, A., … Stokes, A. (2020). Root traits as drivers of plant and ecosystem functioning: Current understanding, pitfalls and future research needs. *New Phytologist*, *232*, 1123–1158.

Hendrick, R. L., & Pregitzer, K. S. (1997). The relationship between fine root demography and the soil environment in northern hardwood forests. *Écoscience*, *4*, 99–105.

Huth, V., Günther, A., Bartel, A., Gutekunst, C., Heinze, S., Hofer, B., Jacobs, O., Koebsch, F., Rosinski, E., Tonn, C., Ullrich, K., & Jurasinski, G. (2022). The climate benefits of topsoil removal and Sphagnum introduction in raised bog restoration. *Restoration Ecology*, *30*. https://doi.org/10.1111/rec.13490

IPCC, Shukla, P. R., Skea, J., Calvo Buendia, E., *et al.* (2019). Climate change and land: An IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems. In press. Retrieved from https://www.ipcc.ch/srccl/cite-report/

Iversen, C. M., Sloan, V. L., Sullivan, P. F., Euskirchen, E. S., McGuire, A. D., Norby, R. J., Walker, A. P., Warren, J. M., & Wullschleger, S. D. (2015). The unseen iceberg: Plant roots in arctic tundra. *New Phytologist*, *205*, 34–58.

Järveoja, J., Nilsson, M. B., Crill, P. M., & Peichl, M. (2020). Bimodal diel pattern in peatland ecosystem respiration rebuts uniform temperature response. *Nature Communications*, *11*, 4255.

Jobbágy, E. G., & Jackson, R. B. (2000). The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological Applications*, *10*, 423–436.

Joosten, H., Sirin, A., Couwenberg, J., Laine, J., & Smith, P. (2016). The role of peatlands in climate regulation. In *Peatland restoration and ecosystem services: Science, policy and practice* (p. 66). Cambridge University Press.

Joosten, H., Tanneberger, F., & Moen, A. (2017). *Mires and peatlands of Europe: Status, distribution and conservation*. Schweizerbart Science Publishers.

Joslin, J. D., Wolfe, M. H., & Hanson, P. J. (2000). Effects of altered water regimes on forest root systems. *New Phytologist*, *147*, 117–129.

Jurasinski, G., Ahmad, S., Anadon-Rosell, A., Berendt, J., Beyer, F., Bill, R., Blume-Werry, G., Couwenberg, J., Günther, A., Joosten, H., Koebsch, F., Köhn, D., Koldrack, N., Kreyling, J., Leinweber, P., Lennartz, B., Liu, H., Michaelis, D., Mrotzek, A., … Wrage-Mönnig, N. (2020). From understanding to sustainable use of peatlands: The WETSCAPES approach. *Soil Systems*, *4*, 14.

Keeling, C. D., Chin, J. F. S., & Whorf, T. P. (1996). Increased activity of northern vegetation inferred from atmospheric CO_2 measurements. *Nature*, *382*, 146–149.

Keenan, T. F., Gray, J., Friedl, M. A., Toomey, M., Bohrer, G., Hollinger, D. Y., Munger, J. W., O'Keefe, J., Schmid, H. P., Wing, I. S., Yang, B., & Richardson, A. D. (2014). Net carbon uptake has increased through warming-induced changes in temperate forest phenology. *Nature Climate Change*, *4*, 598–604.

Koch, J., Siemann, A., Stisen, S., & Sheffield, J. (2016). Spatial validation of large-scale land surface models against monthly land surface temperature patterns using innovative performance metrics: Spatial validation of distributed models. *Journal of Geophysical Research: Atmospheres*, *121*, 5430–5452.

Koch, M., & Jurasinski, G. (2015). Four decades of vegetation development in a percolation mire complex following intensive drainage and abandonment. *Plant Ecology & Diversity*, *8*, 49–60.

Köhn, D., Günther, A., Schwabe, I., & Jurasinski, G. (2021). Short-lived peaks of stem methane emissions from mature black alder (*Alnus glutinosa* [L.] Gaertn.) – Irrelevant for ecosystem methane budgets? *Plant-Environment Interactions*, *2*, 16–27.

Lamers, L. P. M., Vile, M. A., Grootjans, A. P., Acreman, M. C., van Diggelen, R., Evans, M. G., Richardson, C. J., Rochefort, L., Kooijman, A. M., Roelofs, J. G. M., & Smolders, A. J. P. (2015). Ecological restoration of rich fens in Europe and North America: From trial and error to an evidence-based approach. *Biological Reviews*, *90*, 182–203.

Leifeld J, Wüst-Galley C, & Page S. (2019). Intact and managed peatland soils as a source and sink of GHGs from 1850 to 2100. *Nature Climate Change 9*: 945947, 945, 947.

Liu, H., Wang, H., Li, N., Shao, J., Zhou, X., van Groenigen, K. J., & Thakur, M. P. (2022). Phenological mismatches between above- and belowground plant responses to climate warming. *Nature Climate Change*, *12*, 97–102.

Loisel, J., Gallego-Sala, A. V., Amesbury, M. J., Magnan, G., Anshari, G., Beilman, D. W., Benavides, J. C., Blewett, J., Camill, P., Charman, D. J., Chawchai, S., Hedgpeth, A., Kleinen, T., Korhola, A., Large, D., Mansilla, C. A., Müller, J., van Bellen, S., West, J. B., … Wu, J. (2021). Expert assessment of future vulnerability of the global peatland carbon sink. *Nature Climate Change*, *11*, 70–77.

Mäkiranta, P., Laiho, R., Mehtätalo, L., Straková, P., Sormunen, J., Minkkinen, K., Penttilä, T., Fritze, H., & Tuittila, E. S. (2018). Responses of phenology and biomass production of boreal fens to climate warming under different water-table level regimes. *Global Change Biology*, *24*, 944–956.

Malhotra, A., Brice, D. J., Childs, J., Graham, J. D., Hobbie, E. A., Vander Stel, H., Feron, S. C., Hanson, P. J., & Iversen, C. M. (2020). Peatland warming strongly increases fine-root growth. *Proceedings of the National Academy of Sciences of the United States of America*, *117*, 17627–17634.

McCormack, M. L., Adams, T. S., Smithwick, E. A. H., & Eissenstat, D. M. (2014). Variability in root production, phenology, and turnover rate among 12 temperate tree species. *Ecology*, *95*, 2224–2235.

Moore, T. R., Bubier, J. L., & Bledzki, L. (2007). Litter decomposition in temperate peatland ecosystems: The effect of substrate and site. *Ecosystems*, *10*, 949–963.

Mrotzek, A., Michaelis, D., Günther, A., Wrage-Mönnig, N., & Couwenberg, J. (2020). Mass balances of a drained and a rewetted peatland: On former losses and recent gains. *Soil Systems*, *4*, 16.

Payton, M. E., Greenstone, M. H., & Schenker, N. (2003). Overlapping confidence intervals or standard error intervals: What do they mean in terms of statistical significance? *Journal of Insect Science*, *3*, 1–6.

Peichl, M., Gažovič, M., Vermeij, I., de Goede, E., Sonnentag, O., Limpens, J., & Nilsson, M. B. (2018). Peatland vegetation composition and phenology drive the seasonal trajectory of maximum gross primary production. *Scientific Reports*, *8*, 8012.

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Radville, L., McCormack, M. L., Post, E., & Eissenstat, D. M. (2016). Root phenology in a changing climate. *Journal of Experimental Botany*, *67*, 3617–3628.

Schuldt, B., Buras, A., Arend, M., Vitasse, Y., Beierkuhnlein, C., Damm, A., Gharun, M., Grams, T. E. E., Hauck, M., Hajek, P., Hartmann, H., Hiltbrunner, E., Hoch, G., Holloway-Phillips, M., Körner, C., Larysch, E., Lübbe, T., Nelson, D. B., Rammig, A., … Kahmen, A. (2020). A first assessment of the impact of the extreme 2018 summer drought on central European forests. *Basic and Applied Ecology*, *45*, 86–103.

Schwieger, S., Kreyling, J., Couwenberg, J., Smiljanić, M., Weigel, R., Wilmking, M., & Blume-Werry, G. (2021). Wetter is better: Rewetting of minerotrophic peatlands increases plant production and moves them towards carbon sinks in a dry year. *Ecosystems*, *24*, 1093–1109.

Schwieger, S., Kreyling, J., Peters, B., Gillert, A., Freiherr von Lukas, U., Jurasinski, G., Köhn, D., & Blume-Werry, G. (2022). Data from: Rewetting prolongs root growing season in minerotrophic peatlands and mitigates negative drought effects. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.0gb5mkm3

Steinaker, D. F., Wilson, S. D., & Peltzer, D. A. (2010). Asynchronicity in root and shoot phenology in grasses and woody plants. *Global Change Biology*, *16*, 2241–2251.

Succow, M., & Joosten, H. (2001). *Moorkunde*. E. Schweizerbart'sche Verlagsbuchhandlung.

Tanneberger, F., Tegetmeyer, C., Busse, S., & Barthelmes, A. (2017). The peatland map of Europe. *Mires and Peat*, *19*, 1–17.

Voesenek, L. A. C. J., Colmer, T. D., Pierik, R., Millenaar, F. F., & Peeters, A. J. M. (2006). How plants cope with complete submergence. *New Phytologist*, *170*, 213–226.

Withington, J. M., Goebel, M., Bułaj, B., Oleksyn, J., Reich, P. B., & Eissenstat, D. M. (2021). Remarkable similarity in timing of absorptive fine-root production across 11 diverse temperate tree species in a common garden. *Frontiers in Plant Science*, *11*, 11.

Zeitz, J., & Velty, S. (2002). Soil properties of drained and rewetted fen soils. *Journal of Plant Nutrition and Soil Science*, *165*, 618–626.

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