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The effects of glucose addition and water table manipulation on peat quality of drained peatland forests with different management practices

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Abstract

Peatlands are globally significant C storage because waterlogged conditions slow down organic matter (OM) decomposition. Changes in the water table (WT) because of global warming or drainage, consecutive vegetation succession, and enhanced root exudation causing priming may transform peatlands from C sinks to sources. We studied how glucose addition, WT, and forest harvesting affect the chemical composition of peat and decomposition rate by incubating peat columns collected from drained clear-cut (CC) and forested (FD) peatlands. Columns were divided into high or low WT, and half were labeled with ^{13}C to study the priming effect on peat decomposition and peat chemical quality. We measured CO_2 fluxes, peat OM, and water quality. There was no detectable priming effect after glucose addition. Lowering of the WT led to increased CO_2 efflux, which during the measurements averaged between 39 and 291 μg m^{-2} s^{-1}. Low WT also decreased the proportion of water-soluble OM in CC areas but not in FD areas. The proportion of recalcitrant OM in surface peat was higher in forest than in clear cut. Forest management also affected the quality of dissolved OM in soil water, with CC showing higher concentrations

Abbreviations: CC, clear-cut; DOC, dissolved organic carbon; DON, dissolved organic nitrogen; EC, electric conductivity; FD, forest with ditches; OM, organic matter; WT, water table.

of recalcitrant compounds. Decomposition and OM quality were governed by forest management practices and WT manipulation. In the future, the C sink capacity of forested peatlands will be regulated by changes in WT level, forest management, and quality of OM.

1 | INTRODUCTION

Peatlands are a globally significant C storage that contains approximately one-third of the global soil C (Gorham, 1991; Turunen et al., 2002). Peat accumulates when litter input exceeds its decomposition rate under waterlogged conditions. Whether a peatland acts as a C sink or source is determined by the balance between C inputs and outputs. Because peat is formed of dead plants of various stages of decomposition, the quality of peat depends on the initial quality of the plant residues, concentrations of easily accessible carbohydrates, and the quality changes with proceeding decomposition (Straková et al., 2010). The peat decomposition rate depends on abiotic conditions such as water table (WT) and soil temperature (Minkkinen et al., 2018), chemical composition (Straková et al., 2010), and microbial community (Wang et al., 2021). Because of high WT, pristine peatlands usually act as C sinks (Amesbury et al., 2019; Rydin & Jeglum, 2013).

The WT level on peatlands may be affected by global warming, which is pronounced in high latitudes (IPCC, 2013). Increased evapotranspiration following warming may lead to the lowering of WT (Rouse et al., 1997). Many pristine peatland areas have also been drained for forestry, agriculture, or peat extraction especially in northern Europe (Päivänen & Hånell, 2012). In the Baltic Sea drainage basin, approximately half of the total 19.5 million ha peatland area has been drained for forestry (Piirainen et al., 2017). Peatland WT lowering, whether caused by global warming or drainage, causes drastic changes in the C turnover of peatlands by increasing the thickness of the oxic layer (Lohila et al., 2011), which favors decomposition and release of C as CO_2 instead of anoxic methane (CH_4) production. This enhanced peat decomposition increases C emissions as well as nutrient and dissolved organic carbon (DOC) exports to watercourses (Finér et al., 2021). On the other hand, because of the increased forest growth following the drainage (Laurén et al., 2021) and shifts in vegetation pattern, increased litter and fine root production may further affect the decomposition rate through the addition of readily decomposable leaf and root litter and root exudates (Waldo et al., 2021), resulting in the so-called priming effect (Murphy et al., 2009).

Priming describes a process where the addition of new, easily decomposable labile organic matter (OM) leads to changes in the decomposition rate of older, recalcitrant soil organic matter (SOM) (Fontaine et al., 2003; Kuzyakov, 2010). As a result of the labile C addition, the decomposition of old SOM may increase (positive priming) or decrease (negative priming) (Kuzyakov et al., 2000). The direction of priming depends on nutrient availability, soil type, and plant and microbial attributes (Bastida et al., 2019; Lloyd et al., 2016; Razanamalala et al., 2018). Because of the various possible drivers, the priming effect may vary between different ecosystems. Consequently, the existence of the priming effect and the complex causes behind it have so far remained elusive (Fontaine et al., 2003). The majority of priming experiments so far have been conducted in mineral soils and not much is known about the priming effect on peatlands (Basiliko et al., 2012), though recent years have shown an increase in these studies (Basiliko et al., 2012; Gavazov et al., 2018; Linkosalmi et al., 2015; Waldo et al., 2021). For example, Yan et al. (2022) and Gavazov et al. (2018) studied root-induced priming on pristine peatlands, showing a positive priming effect on peat decomposition. Further, Waldo et al. (2021) reported selective positive priming of C compounds in the peat of a bog. On the contrary, Linkosalmi et al. (2015) detected no positive priming effect on drained peatlands with differing fertility. These studies show that the priming effect on peatlands is not straightforward and there remains a demand for further studies. Specifically, the combined effects of priming and WT fluctuations in peatlands are poorly understood.

The effects of priming and WT lowering on peat C balance depend also on peat quality and site fertility. Low productivity peatland sites tend to remain C neutral or C sinks after drainage, while the fertile sites tend to turn into C sources (Ojanen et al., 2014). This is because nutrient status and consequent vegetation composition determine the initial quality of peat. The peat quality in turn is further modified by decomposition, which is controlled by the WT level. In drained forested peatlands, the C cycle is also affected by the forest harvesting causing WT fluctuations. Harvesting, drainage, and priming effect may also increase the leaching of C (Joensuu et al., 2001; Mäkiranta et al., 2012; Nieminen et al., 2021), which has a significant influence on the aquatic ecosystems. The changes in vegetation patterns following drainage could induce a positive priming effect, leading to increased release of C from peat to runoff. High C concentrations in the runoff cause brownification of downstream water bodies (Kritzberg et al., 2020; Nieminen et al., 2021).

Therefore, interactions between the priming and WT should be considered in the evaluation of peatland C fluxes.

While the priming effect (Basiliko et al., 2012; Linkosalmi et al., 2015; Waldo et al., 2021), and especially the greenhouse gas fluxes, have on peatlands been studied actively (Amesbury et al., 2019; Korkiakoski et al., 2020; Lohila et al., 2011; Moore & Knowles, 1989; Ratcliffe et al., 2020), comprehensive studies connecting priming, WT, and forest management are scarce. Therefore, in this study we applied glucose addition and WT manipulation in a peat column experiment to simulate priming and WT changes. The peat columns were collected from drained peatland forest sites under clear-cut (CC) and uncut (FD) forest areas. Consequently, our study combines the mechanisms of WT manipulation, priming of SOM decomposition, and forest management practices to study their interlacing effects on OM quality. We hypothesized that (a) the addition of glucose decreases the proportion of recalcitrant OM in peat and increases CO_2 emissions via priming, (b) priming increases concentrations of DOC and dissolved organic nitrogen (DON)/DOC ratios because of enhanced decomposition, (c) priming is more pronounced in CC forests because the input of tree root exudates has ceased, and (d) high WT reduces priming because a shortage of oxygen limits the decomposition of old OM in peat.

Core Ideas

- Glucose addition did not induce positive priming of OM in forested peatlands.
- Decreased water table level lead to increased CO_2 fluxes from peat.
- Forest management affected both peat OM and water quality.

2 | MATERIALS AND METHODS

2.1 | Site description

The study area is located in Paroninkorpi of Janakkala, southern Finland (61.01° N, 24.75° E), which is an experimental setting for long-term field experiments for testing the effects of different forest management practices on forest C balance, greenhouse gas emissions, and water quality (e.g., Laurila et al., 2021). The area belongs to the boreal forest zone with an annual mean temperature of 4.7 °C and annual precipitation of 638 mm. The area is a drained, herb-rich peatland (Laine, 1989), dominated by Norway spruce [*Picea abies* (L.) H. Karst.]. The Carex peat layer is >1.5 m thick. The main ditches were dug in the 1940s, and the ditch network was complemented at the beginning of the 1960s. The ground vegetation consists mostly of shrubs [bilberry *Vaccinium myrtillus* (L.) and alpine cranberry (*V. vitis-idaea* L.)], mosses {red-stemmed feathermoss [*Pleurozium schreberi* (Brid.) Mitt.] and peat moss (*Sphagnum* spp.)}, sedge (*Carex* spp.), and forbs {wood sorrel (*Oxalis acetocella* L.) and oak fern [*Gymnocarpium dryopteris* (L.) Newman]}.

The study area is divided into experimental plots (random factorial design) of which, half are covered by forest ($n = 5$) and half were clear-cut ($n = 5$) in 2017 (Figure 1). The size of the plots varied between 1,000 and 2,000 m^2. The basal area of the tree stand on uncut sites was 21–30 m^2 ha^{-1}. A total of 32 undisturbed peat columns including surface vegetation and their roots were collected using plastic cylinders (16-cm diam., 50 cm depth) in February 2020. At the time of collection, the WT level on CC peatland forest was, on average, −36 cm and −41 cm on FD. Half of the 32 peat columns were from CC and half were from FD plots. Peat columns were stored in the water content they had upon collection and in dark at 4 °C until the experiment started.

In May 2020, the peat columns were placed outside without a cover, exposing them to rainfall. At the onset of the experiment, half of the columns were adjusted to high WT (10 cm below the peat surface) and the other half to low WT (30 cm below the peat surface) by deionized water (pH = 5.5), and the WT was maintained throughout the experiment by adding water when necessary. Half of the columns from each WT and forest management (CC or FD) were treated by adding ^{13}C-labeled glucose (D-Glucose-1-^{13}C; Sigma Aldrich) mixed with unlabeled glucose [D-(+)-Glucose, Sigma Aldrich]. The glucose mixture used for ^{13}C-labeling contained 1.4% of ^{13}C-labeled glucose and 98.6% of unlabeled glucose, resulting approximately to a d^{13}C-value of 270. The glucose mixture was given in a water solution to half of the columns every week over the experiment. The amount of C given as glucose corresponded to 212 g C m^{-2} divided over 4 mo from June through September 2020, which equals to ∼33% of the C assimilated in photosynthesis per year in a boreal forest (Ilvesniemi et al., 2009). The amount of C added as glucose represented 1.5% of total C stored in the uppermost 25 cm of peat. Hypothetically the amount of added C could have formed 42% of C respired over 4 mo. The treatments, therefore, resulted in a mixture of high or low WT columns with or without ^{13}C label in two different forest managements, and the number of replicates in each of these groups was four. The treatments are shown in more detail in Table 1.

2.2 | CO_2 flux measurements

The soil respiration (CO_2 flux) was measured from the peat columns four times during the incubation experiment. The first CO_2 flux measurement was conducted at the end of

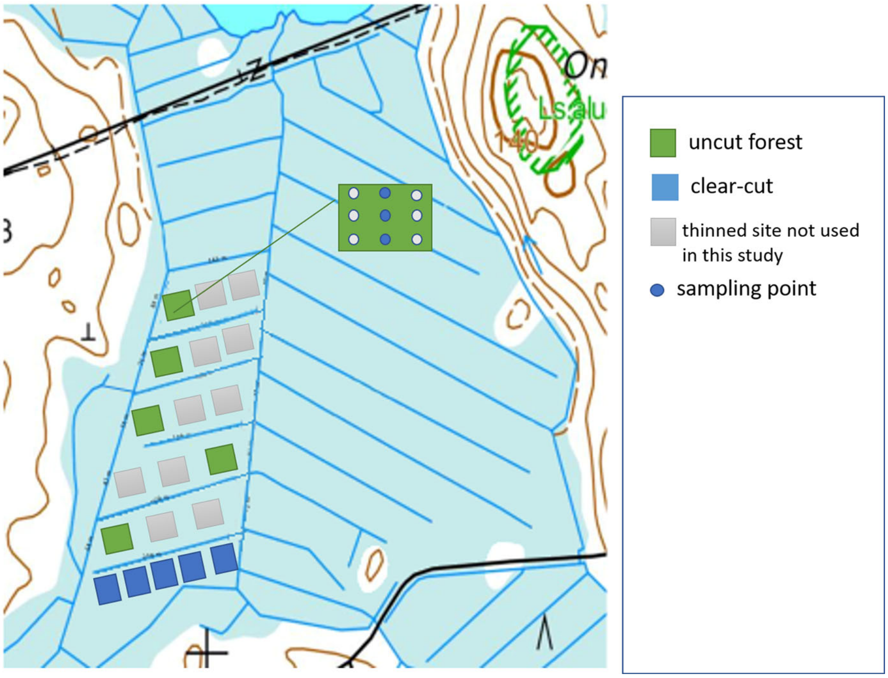

FIGURE 1 The experiment set up in Paroninkorpi drained peatland sites. Figure modified from Palviainen et al. (2022)

TABLE 1 Measured peat characteristics: Mean ± SEM $\delta^{13}C$ of peat samples in different treatments, mean total C and N contents, C/N ratios, and ground vegetation biomass (mosses and vascular plants)

Layer	Management	Water level	Glucose	$\delta^{13}C$	C	N	C/N ratio	Ground vegetation
				‰	———%———			kg m^{-2}
A	Clear cut	High	Yes	−14.7 ± 5.7	49.4 ± 0.7	1.79 ± 0.1	27.7 ± 1.3	1.3 ± 0.4 a
		Low		4.2 ± 20 a	50.1 ± 0.2	1.65 ± 0.2	31.1 ± 3.1	0.6 ± 0.2
		High	No	−28.1 ± 0.6 b	47.1 ± 2.1	1.72 ± 0.1	27.8 ± 2.4	0.4 ± 0.2
		Low		−24.4 ± 0.9	48.5 ± 0.9	1.70 ± 0.2	30.1 ± 4.0	0.3 ± 0.2
	Forest with ditches	High	Yes	−8.1 ± 5.6	51.3 ± 0.5	1.90 ± 0.1	27.2 ± 1.3	0.5 ± 0.2
		Low		−4.9 ± 4.6	48.3 ± 1.2	2.20 ± 0.3	23.2 ± 3.5	0.6 ± 0.3
		High	No	−26.6 ± 1.5	60.0 ± 10.6	2.66 ± 0.5	23.0 ± 2.2	0.4 ± 0.2
		Low		−27.7 ± 0.3	50.9 ± 1.1	2.10 ± 0.0	24.3 ± 1.1	0.2 ± 0.1 b
C	Clear cut	High	Yes	−27.9 ± 0.1	54.9 ± 0.4	1.97 ± 0.1	28.0 ± 1.5	–
		Low		−21.4 ± 6.7	52.2 ± 1.6	1.91 ± 0.1	27.6 ± 1.7	–
		High	No	−28.2 ± 0.1	54.4 ± 0.2	1.75 ± 0.0	31.1 ± 0.8	–
		Low		−28.0 ± 0.2	54.4 ± 0.7	1.85 ± 0.1	29.4 ± 1.3	–
	Forest with ditches	High	Yes	−28.2 ± 0.3	54.8 ± 0.3	2.16 ± 0.1	25.7 ± 1.8	–
		Low		−28.3 ± 0.2	54.9 ± 0.6	2.11 ± 0.2	26.7 ± 2.6	–
		High	No	−27.9 ± 0.3	52.6 ± 1.2	2.12 ± 0.2	25.7 ± 3.0	–
		Low		−25.1 ± 3.5	52.5 ± 0.3	2.26 ± 0.3	24.6 ± 3.8	–

Note. The A and C layers denote the peat sampled from the top (0–10 cm) and bottom (40–50 cm) of the peat columns, respectively. Letters in denote statistical differences between treatments in question, when no letters are given, no differences were observed.

May after WT manipulation and before the first addition of ^{13}C-labeled glucose in June. The next three CO_2 flux measurements were performed in July, August, and September always a week after the addition of ^{13}C-labeled glucose. During the flux measurement, a chamber was set on top of the soil columns carefully without damaging the vegetation. The chamber ($h = 0.21$ m and Ø $= 0.17$ m) was covered with aluminum foil to prevent photosynthesis. A small fan was set inside the chamber to ensure air circulation, and the CO_2 concentration was measured with a nondispersive infrared CO_2 probe (GMP343, Vaisala Oyj). Relative humidity and temperature were measured using a humidity and temperature sensor (HMP75, Vaisala Oyj). The sensor measured at 15 s intervals for 5 min. The flux was obtained using the following equation (modified from Pihlatie et al., 2013):

$$F = \frac{\mathrm{d}c}{\mathrm{d}t}\frac{MVT}{V_\mathrm{m}tA} \tag{1}$$

where F is the flux (μg m^{-2} s^{-1}), M is the molar mass of the gas (g mol^{-1}), V_m ideal gas volume (0.00224 m^3 mol^{-1}), T is 273.51 K, t is chamber temperature (K), V is the chamber volume (m^3), and A is the basal area of the chamber (m^2). Term dc/dt is the rate of change in gas mixing ratio (ppm s^{-1}) and is estimated by fitting a linear model into the time series of gas mixing ratio. After the CO_2 flux measurements with CO_2 probe, the $\delta^{13}CO_2$ of the respired CO_2 was measured by taking air samples at intervals of 0, 5, 15, and 30 min from the chamber with 50 ml polypropylene syringes (BD Plastipak). These were injected into 12-ml pre-evacuated glass exetainers (Labco Ltd.) flushed with N_2. The gas samples were analyzed with Isotopic Analyzer (Picarro G2201-I, Picarro Inc.).

2.3 | Peat quality analysis

Peat-quality-related analyses were performed at the end of the experiment. The peat columns were dissected into two layers: 0–10 and 40–50 cm referred to as A and C layers, respectively. From dissected layers, subsamples were collected for peat quality analysis. Peat decomposition degree on von Post scale of these samples varied between 5 and 8 in the A layer and 5 and 10 in the C layer. Before further analysis, visible roots were removed from the samples and samples were oven dried (40 ˚C). Following this, peat samples were ground to homogenize the material. A chemical fractionation was used for the determination of peat OM quality: peat was extracted into water (sugars, low levels of fatty acids, and protein remains), ethanol (waxes, fats), sulfuric acid hydrolysable (hemicellulose, cellulose), and nonhydrolysable (Klason lignin and humified material) fractions (Berg & McClaugherty, 2008; Trofymow & CIDET Working Group, 1998). The fractionation was performed by extracting peat samples in pure water, ethanol, and sulfuric acid (H_2SO_4) following the methods of Karhu et al. (2010) and Berg and Ekbohm (1991). Samples were first extracted with water by sonicating the peat–water mixture in a water bath for 90 min and filtered (Whatman paper filter for water [pore size < 2 μm] and corresponding glass-fiber filters for ethanol and acid extraction). Filtered samples were oven dried at 105 ˚C, and weighed with an analytical scale. The water-soluble fraction was determined as mass loss of pre- and postextracted samples. The following ethanol extraction was performed accordingly with pure ethanol. Finally, the samples were extracted in 72% sulfuric acid. The acid solution was sonicated for 60 min and the solution was diluted to 2.5%. The samples were then autoclaved for 60 min at 125 ˚C, filtered, and rinsed with ultrapure water and oven dried as before. For determination of the proportions of each fraction, the peat OM content was determined as a loss on ignition (550 ˚C, 3 h). The different fractions are expressed as a percentage of total OM and can roughly be connected to OM pools characterized by their turnover times: active pool (sugars), slow pool (waxes, fats, cellulose), and very slow and stable pool (lignin) (Bot & Benites, 2005).

Carbon and nitrogen concentrations and isotopic ^{13}C were analyzed from peat samples from the two separated layers. Before analysis, the samples were ground into a fine powder, and 3 mg of the powder was weighed into tin boats. These were analyzed in an elemental analyzer (FlashEA 1112 Series, Thermo Fischer Scientific) coupled to an isotope ratio mass spectrometer (DELTA plusXP, Thermo Electron Fischer Scientific). Isotopes were measured so that we would be able to track the success of the labeling and values are presented in Table 1. The isotopic values are expressed as δ^{13}C per mil (^{13}C/^{12}C ratios) in relation to international reference standards (Peedee Belemnite for ^{13}C/^{12}C) as described in Aaltonen et al. (2019).

2.4 | Porewater analysis

Water samples were collected into 50-ml plastic syringes (BD Plastipak) via a thin plastic tube (connected to rhizon, Rhizosphere Research Products) inserted into the soil column (10 cm from the bottom) every month at the same time interval as CO_2 measurements. After water collection, samples were filtered through syringe filters (0.45 μm) and stored at −21 ˚C. The DOC and total dissolved nitrogen concentrations were measured from samples that were acidified with phosphoric acid before analyzing them with thermal oxidation coupled with infrared detection (Multi N/C 2100, Analytik). Spectral absorbance of the water samples was analyzed by a UV-1800 (UV-VIS spectrophotometer, Shimadzu) from wavelength 200–800 nm with 1 nm acquisition step at low speed by a 10-mm pathlength quartz cell. The samples for spectral analysis were diluted so that their absorbance

TABLE 2 Water-quality-related measurements from peat columns. The table shows the division of peat columns to different treatments, mean (±standard error of the mean) pH, dissolved organic carbon (DOC) concentrations, specific UV absorbance (SUVA), ratio of the absorbances at 465 and 665 nm (E4/E6), and electrical conductivity (EC) of four measurement times. Glucose denotes ^{13}C-labeled glucose addition. Management indicates areas with clear cut (CC) and drained uncut forest (FD). Water level indicates high or low water level in peat columns during the experiment

Management	Water level	Glucose	pH	DOC	SUVA	E4/E6	EC
				mg L^{-1}	L mg m^{-1}		S m^{-1}
CC	High	Yes	4.3 ± 0.2	135 ± 12	5.1 ± 0.2	7.4 ± 0.6	31.6 ± 3.1
	Low		4.5 ± 0.1	127 ± 10	4.7 ± 2.2	7.1 ± 0.6	31.1 ± 3.0
	High	No	4.3 ± 0.0	149 ± 10	4.6 ± 0.3	8.3 ± 0.6	37.9 ± 1.8
	Low		4.3 ± 0.0	140 ± 14	4.8 ± 0.2	8.1 ± 1.1	35.7 ± 2.9
FD	High	Yes	4.6 ± 0.2	151 ± 18	4.5 ± 0.1	7.8 ± 0.8	44.5 ± 4.7
	Low		5.0 ± 0.2	103 ± 7	4.7 ± 0.1	7.3 ± 0.8	36.1 ± 3.1
	High	No	4.5 ± 0.1	139 ± 16	4.4 ± 0.2	7.9 ± 0.8	42.3 ± 2.6
	Low		4.5 ± 0.1	185 ± 20	4.6 ± 0.2	8.1 ± 0.9	53.6 ± 3.6

was <1.5. Electric conductivity (EC) and pH were also measured from the collected water by Multiline P4 (WTW) conductometer (SCHOTT).

Based on spectral data, we determined three DOC quality-related factors: specific UV absorbance measured at 254 nm wavelength ($SUVA_{254}$), ratio of the absorbances at 465 and 665 nm (E4/E6), and ratio of the absorbances at 250 and 365 nm (E2/E3). The $SUVA_{254}$ is often used to characterize DOC quality in stream waters and is expressed as C specific absorbance at 254 nm divided by DOC concentration (Rostan & Cellot, 1995). The E4/E6 ratio relates to the molecular size of humic substances (Peuravuori & Pihlaja, 1997). The values of the E4/E6 ratio are typically <5 for humic acids, while fulvic acids range from 6 to 8 (Peuravuori & Pihlaja, 1997). The E2/E3 (Peacock et al., 2014), on the other hand, relates inversely to molecular size (Ågren et al., 2008; De Haan, 1993). The mean values for DOC, E4/E6, $SUVA_{254}$, pH, and EC during the measurement period are presented in Table 2.

2.5 | Statistical analysis

We used variance component analysis in linear mixed effect models to study the effect of forest management, WT and glucose addition on CO_2 fluxes, peat OM fractions, and water quality. The data was grouped according to the possible treatment combinations resulting in three different models (Equations 2–4), where management, WT, and glucose addition (and possible cross-effects) were fixed factors and the sampling plot was a random term containing the residual. If the fixed effects were not significant, the model was dropped from the further analysis. When a significant effect was detected, the data was split into those remaining two groups, and multiple comparisons were conducted between these groups (plot remaining as random). This allowed a more precise comparison. The mixed models were conducted with R using the lme4 package (Bates et al., 2015) and multiple comparisons of means were performed with Tukey's HSD post hoc test. The normality of data sets was checked with qqplots. Organic matter fractions presented as percentage values were arcsine transformed to meet the criteria of the tests. The initial models were as follows:

$$X = \text{glucose} + \text{management} + \text{glucose}^{*}\text{management} + \text{plot} \tag{2}$$

$$X = \text{glucose} + \text{water}_1 + \text{glucose}^{*}\text{water}_1 + \text{plot} \tag{3}$$

$$X = \text{management} + \text{water}_1 + \text{management}^{*}\text{water}_1 + \text{plot} \tag{4}$$

where X is the dependent factor (CO_2 flux, peat OM fraction, E2/E3 ratio or dissolved C/N ratio), glucose is the glucose addition (0 or 1), management is the clear cut or forest, water is the WT level (low or high), glucose × management (or glucose × water_1, water_1 × management) is the possible cross-effect of the fixed factors and plot is the random effect of the sampling plot. This allowed assessing the different treatments separately. Factors that showed no significant effect were left out, and data was grouped by treatments that had a significant effect.

3 | RESULTS

Glucose addition had no apparent effect on the measured CO_2 fluxes ($p > .05$) according to the initial mixed effect models, while WT management resulted in some differences. Therefore, for simplicity, the data was grouped by WT

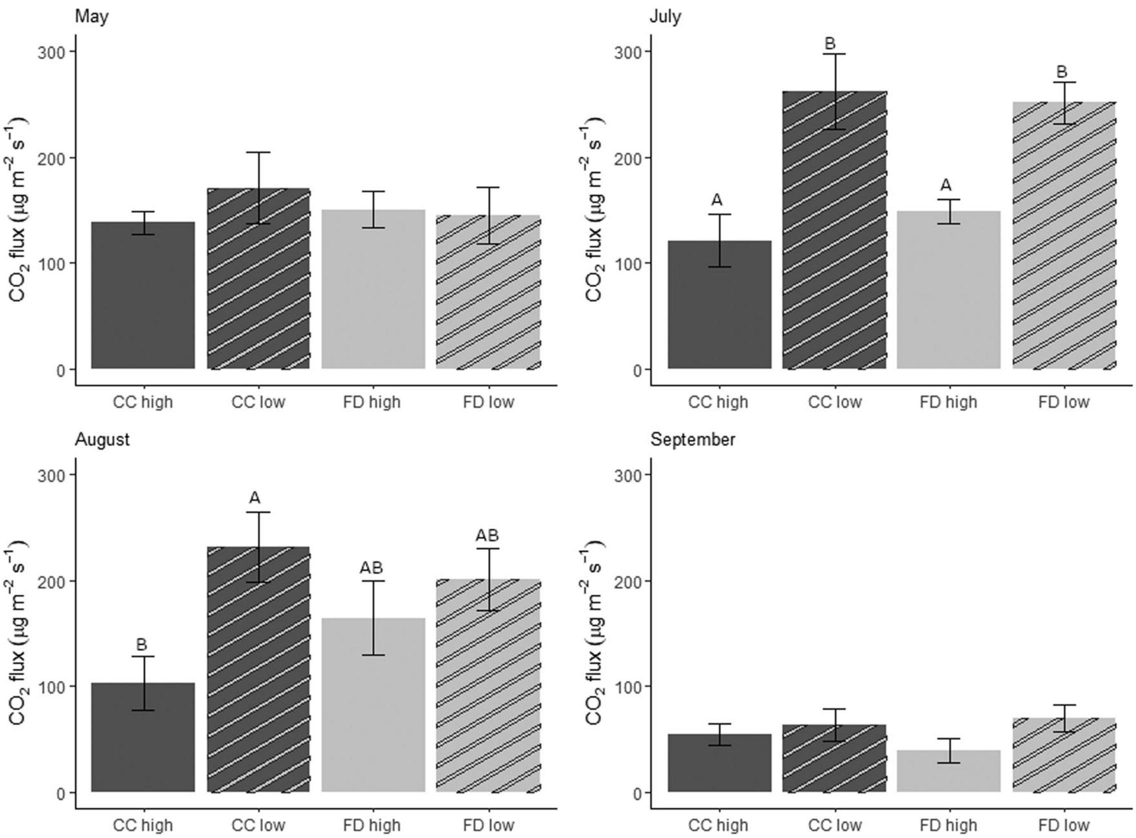

FIGURE 2 Mean (±standard errors of the mean) CO_2 fluxes measured from peat columns grouped by water table depth and management. Capital letters indicate statistical differences among treatments, with the same letter denoting no differences. When no letters are shown, no significant differences were detected between any treatments during that measurement time

level and management regardless of glucose addition and are, from this point on, presented grouped by these two treatments in figures and results. During the measurements, the average CO_2 fluxes of the treatment groups ranged from 39 to 291 µg m^{-2} s^{-1}. The measurements of ^{13}C values from the respired CO_2 failed because of technical reasons with the analyzer; therefore, only total CO_2 fluxes were considered in further data analyses. The CO_2 fluxes also varied seasonally within treatments: fluxes measured in September were overall significantly lower ($p < .05$) than earlier in the experiment likely because of lower temperatures. When data was grouped by forest management and WT level (Figure 2), CC and FD with low WT had higher fluxes than treatments with high WT ($p \leq .02$) in July. In August, CC with low WT still had higher CO_2 flux than CC with high WT ($p = .02$). During May and September, there were no differences between treatments.

Also, OM fractions were not affected by glucose addition ($p > .05$) and data was again grouped only by WT level and forest management. Most of OM in the A and C layers consisted of insoluble material (54–79%), while the smallest fraction was ethanol soluble (0.4–7%). In the water-soluble fraction, differences were found between WT levels, while in other fractions, the differences were between forest managements (Figure 3). In the A layer, CC with a high WT level had a proportionally higher water-soluble fraction than CC with low WT ($p < .001$), while CC with low WT had a lower ethanol-soluble fraction than other treatments ($p < .002$). In acid-soluble fractions, CC with a low WT had a higher fraction than FD with high WT ($p < .05$). In the insoluble fraction, FD with high WT had a higher fraction than CC with high WT ($p < .05$). In the C layer, the only significant difference was that CC with a low WT level had a smaller water-soluble fraction than other treatments. The total C content and C/N ratio in peat did not differ between treatments ($p > .05$). The peat ^{13}C values showed that glucose addition was more prominent in the upper peat layer and less apparent in the bottom.

Glucose treatment did not affect water quality ($p > .05$). The DOC concentrations (Table 1) varied between 23 and 313 mg L^{-1}, and there were no differences between the treatments ($p > .05$). Also, the spectral data showed no differences in $SUVA_{254}$ (varying between 2.1 and 5.3) and E4/E6 ratio (varying between 4 and 21) between any of the treatments ($p > .05$) as was also the case with pH and EC. The DOC, $SUVA_{254}$, E4/E6 ratio, pH, and EC, in general, showed no

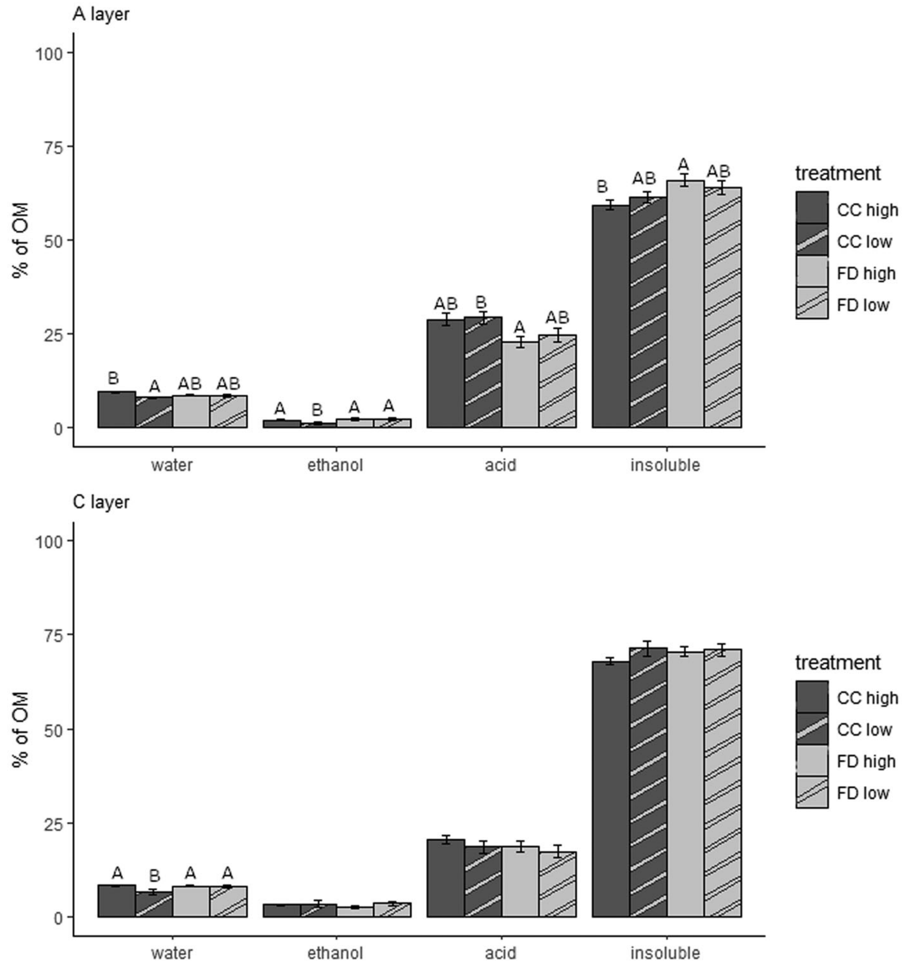

FIGURE 3 The soluble fractions of peat organic matter (OM) to water, ethanol, sulfuric acid, and remaining insoluble OM fraction presented as percentage of total OM content of peat. Error bars show the standard error of mean. Capital letters indicate statistically significant differences within the same fraction (e.g. water soluble) among the treatments, with the same letter denoting no differences. When no letters are shown, no significant differences were detected between any treatments during that measurement time. CC, clear cut; FD, forest with ditches

significant changes with time (within treatments) barring a few exceptions—CC and FD with high WT showed higher E4/E6 ratios in May and July than in August. The EC values for CC with high WT were significantly lower in May than in August, and for CC with low WT significantly lower in May than in July.

The E2/E3 ratios varied between 4 and 6 during the measurements (Figure 4). In May, both CC treatments had lower E2/E3 ratios than FD with low WT ($p < .05$). In July, only CC with high WT differed from FD treatments, and by August and September, difference remained only between CC and FD with high WT. The E2/E3 ratio showed no particular variation with growing season within treatments—only FD with low WT had greater ratios in May than in August and September ($p < .05$). Further, the dissolved C/N ratio in treatments varied between 12 and 70. During May and July, the dissolved C/N ratios showed no differences (Figure 5), but during the last two measurements, CC with low WT had higher values than FD with low WT. The C/N ratio remained steady throughout the season within treatments, with only CC with high WT showing higher ratios in May than in any of the later measurements.

4 | DISCUSSION

In this study, we aimed to determine if glucose addition induces decomposition of recalcitrant OM while simultaneously increasing CO_2 emissions in forested peatlands. Additionally, we studied whether ex situ WT manipulation and in situ forest clear cutting cause differences in CO_2 fluxes and peat OM quality. Based on our results, glucose addition appeared to have little effect on the CO_2 production and OM and water quality of peat. Thus, our hypotheses regarding the effects of glucose addition on the decomposition of recalcitrant OM in peat and DOC concentrations were not supported. Rather, the detected differences seem to relate more to WT and especially the forest clear cutting.

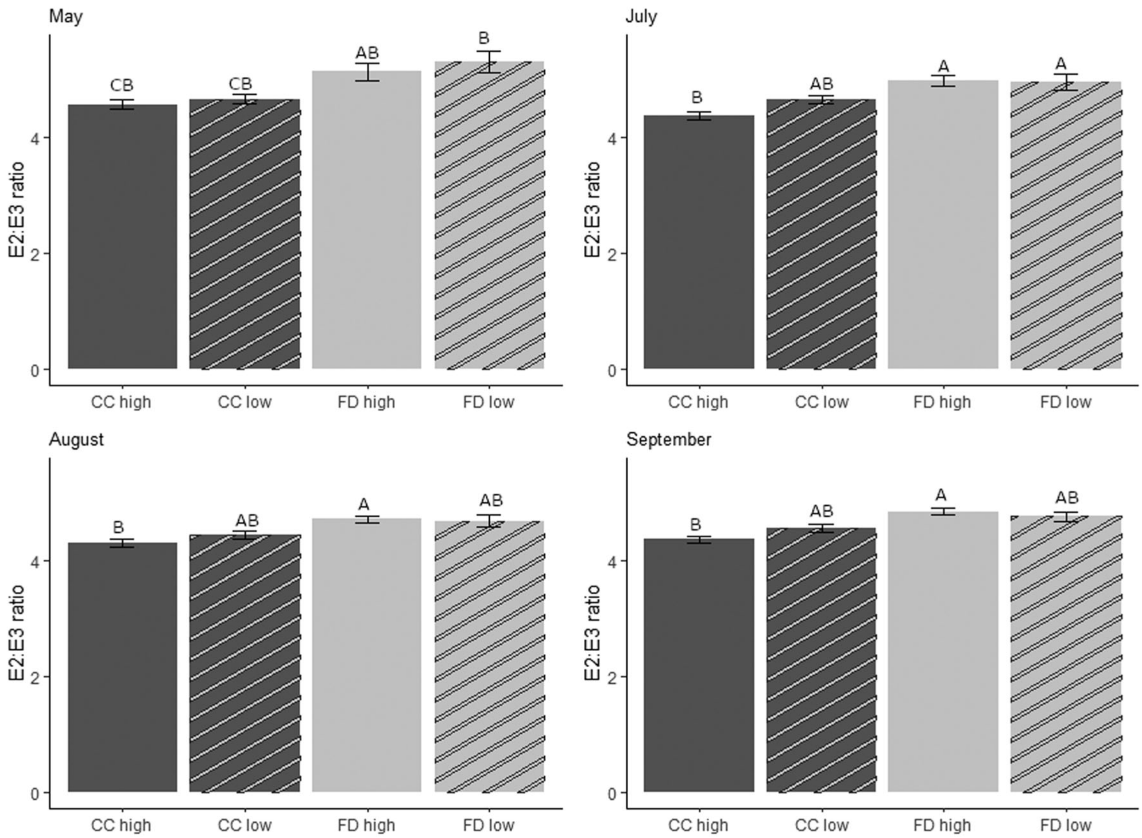

FIGURE 4 The mean ratio of the absorbances at 250 and 365 nm (E2/E3) of different treatments during each measurement time. Error bars show the standard error of the mean. Capital letters indicate statistical differences among treatments, with the same letter denoting no differences. When no letters are shown, no significant differences were detected between any treatments during that measurement time. CC, clear cut; FD, forest with ditches

We hypothesized that higher WT would limit the priming effect, but either of the high or low WT manipulations showed no positive priming with glucose addition. The initial draining of our study site had been carried out several decades ago, meaning that the effects of drainage on peat and the following succession of vegetation has modified the peat qualities already for decades, making the manipulations used in this column study short lasting in comparison. Thus, the peat decomposition perhaps was more determined by these prevailing conditions. The peat appeared fairly decomposed and the majority of OM was formed by recalcitrant fraction, which might affect the possibility of priming. Priming-related studies on peatlands do not yet seem to form a clear consensus of how or if peat quality affects priming; for example, while positive priming has been detected on nutrient-poor bogs (Walker et al., 2016), another study found no evidence of priming on either nutrient-poor or nutrient-rich sites (Linkosalmi et al., 2015). Yet, different soil types may have varying thresholds for substrate additions that will induce priming (Liu et al., 2017). Priming may also be dependent on OM content and C/N ratio, at least in mineral soils (Razanamalala et al., 2018). For example, Bastida et al. (2019) noted that soils with high OM content were less likely to show a positive priming effect as microbial communities in these soils are adapted to high input of C from vegetation. Contrastingly, soils with low C content may be more receptive to priming. Also, soil water content plays a part: in drier soils with aerobic conditions, the aerobic bacteria may support positive priming, whereas anaerobic microorganisms may be associated with negative priming (Bastida et al., 2019; Ding et al., 2018), which has been connected to anaerobic conditions (Santruckova et al., 2004).

In peatlands, WT level has been shown to affect rhizosphere priming: positive priming appeared at −40 cm WT level and negative at −20 cm (Yan et al., 2022). Given that a previous study determined that peatland fertility classes did not seem to affect the possibility of priming (Linkosalmi et al., 2015) and that WT depths in our study were −30 and −10 cm, it could be speculated that lack of positive priming was caused by relatively higher WT levels in our study compared with Yan et al. (2022). It must also be noted that the priming effect is a complex phenomenon (Fontaine et al., 2003) and results still vary on to what extent it exists (e.g., Linkosalmi et al., 2015; Walker et al., 2016; Yan et al., 2022).

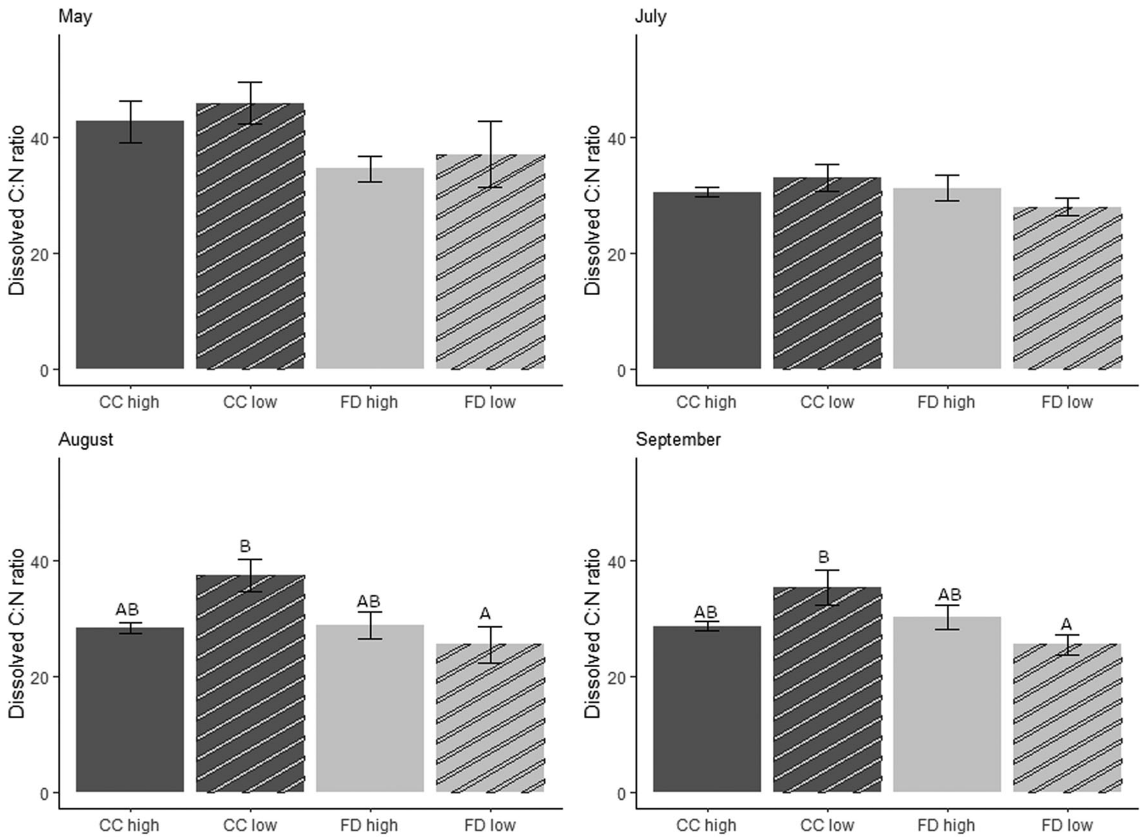

FIGURE 5 Mean dissolved C/N ratio in water extracted from peat columns during different measurement times. Error bars show the standard error of the mean. Capital letters indicate statistical differences among treatments, with the same letter denoting no differences. When no letters are shown, no significant differences were detected between any treatments during that measurement time

The CO_2 fluxes indicated dependence on WT; CC with high WT showed lower fluxes than CC (July and August) and FD with low WT (July). During July, FD with high WT had lower fluxes than FD with low WT. The lack of differences in May and September are likely connected to overall seasonal variations in flux rates. Higher CO_2 production with a lower water table has been reported in previous studies (Gorham, 1991; Kluge et al., 2008; Waddington & Price, 2000) and is connected to a thicker aerated peat layer, which allows the decomposition by aerobic microbes and possible CH_4 oxidation. In addition, lowering the WT level leads to changes in vegetation pattern, and for this reason, the WT level induced changes in CO_2 fluxes are also connected to the vegetation dynamics. In natural conditions, peatlands become more aerated when drained, but clear cutting of the tree stand leads to temporal rising of WT level when the transpiring canopy is removed (Leppä et al., 2020). In our experiment, the WT difference of 20 cm was high enough to affect the CO_2 production as was also found by Yan et al. (2022). Some other studies have reported minimal or no change in CO_2 production following WT lowering, appointing this to lack of easily oxidizable OM (Ellis et al., 2009; Updegraff et al., 2001). These varying results most likely arise from peatlands having different fertilities and vegetation cover. Though, whether the managed peatland forest is a sink or source of C depends on the WT level (Moore & Knowles, 1989), the production rate is also affected by OM quality.

The peat OM quality also showed some dependence on WT; CC with high WT had proportionally higher water- and ethanol-soluble fraction than CC with low WT (A layer), but such difference was not detected between high and low FD treatments. The difference in water-soluble fraction appeared also in the C layer where no other differences were found. In the acid-soluble and insoluble fractions, the differences were observed more between forest management types than different WT levels, the acid-soluble fraction being higher in the A layer of the CC than the respective layer in the FD. The effect of WT level on the size of the water-soluble fraction is understandable, as higher WT advances the release of labile C from the peat surface. In this way, it appears that the fast-cycling C pools (water soluble) are affected by WT level, which may fluctuate relatively fast, while slowly cycling C pools (acid and insoluble) are more affected by the management type that controls the amount and quality of litter input in the peatland forest on a long timescale (Ellis et al., 2009).

Upon clear cutting, there is first a large input of fresh litter and wood debris in the soil, which increases the amount of soluble fractions. The most easily decomposable compounds, such as sugars, starch, and lipids, are consumed by soil biota shortly after CC followed by cellulose and later lignin whose decomposition may take years to decades (Liski et al., 2005). This could also be reflected in our study areas where the amount of acid-soluble fraction was on average higher in the surface peat (A layer) at the CC with low WT compared with FD with high WT, while deeper in the peat (C layer), such differences were not observed (Figure 3). During the first years following clear-cutting, the depletion of the labile fraction leads to enrichment of more recalcitrant compounds in peat (Kalbitz, 2001) before new vegetation reappears on the site. Peatlands with different fertility also have varying OM qualities. Litter quality on pristine peatlands governed by *Sphagnum* species is poor (Dorrepaal et al., 2005), but easily soluble matter may accumulate because of anoxic conditions (Straková et al., 2011) and be readily available for decomposers after drainage. While the most labile OM fraction in peat is depleted following WT lowering (Gao et al., 2014) and more recalcitrant are left behind (Kalbitz et al., 2003), it could be expected that proportions of these fractions change with vegetation succession and litter accumulation as well as with forest management practices. Indeed, it has been noted that in time, the direct effects of drainage on peat OM quality become overruled by indirect effects of vegetation composition and quality (Laiho, 2006; Straková et al., 2010). In our experiment, CC areas had proportionally higher acid-soluble and lower insoluble fractions than FD, denoting relatively higher amounts of cellulose and hemicellulose compounds and lower amounts of lignin-type material in CC areas. While we expected that priming would be pronounced on CC areas because of reduced production of root exudates and increased input of woody debris, we did not observe such an effect. Part of this could be explained by the pioneer species already growing on the sites providing a new source of labile OM.

Glucose addition did not seem to increase DOC concentration or change the dissolved C/N ratio. Instead, the E2/E3 ratio and dissolved C/N ratio were affected by forest management. The CC management had, in general, lower E2/E3 ratios than FD. The E2/E3 ratio is inversely related to molecular size (Ågren et al., 2008; De Haan, 1993), denoting that the water collected from peat columns of CC management had molecules with greater molecular size than the water from FD. Thus, the clear cutting appears to have led to an input of more complex, and thus recalcitrant, compounds to water. Similarly, Ågren et al. (2008) have found that leaching from wetland contains higher molecular weight compounds than leaching from a forested area. Also, other studies found that C leaching from peatlands tends to have more aromaticity than C leaching from forest soils (Ågren et al., 2008; Kalbitz et al., 2003; Tipping et al., 1999). Though this cannot be straightforwardly connected to our experiment, the conditions in clear-cut peatland forest (transpiring canopy removed) are hydrologically closer to a pristine than forested peatland. The more complex compounds of DOC from the CC area indicate longer decomposition time, that is, the compounds may be carried along the continuum of land and aquatic ecosystems for a long time before being consumed and thus may translocate far from their origin. This increased complexity of DOC from CC areas could perhaps be connected to the relatively higher acid-soluble OM fraction in CC, both of which could be affected by cutting residues remaining on the site. In addition, the CC management showed, though somewhat inconsistently, higher dissolved C/N ratios than FD toward the end of the growing season. This could indicate preferential leaching of C from CC compared with N or limitation of N pools in CC management.

We conclude that our results did not support the hypothesis of a priming effect affecting the decomposition of more recalcitrant OM in peat or increased DOC concentrations. The lack of positive priming after glucose addition may be connected to the limitation of decomposition because of high water content or the C-rich peat material as found in other studies (Bastida et al., 2019; Linkosalmi et al., 2015; Razanamalala et al., 2018). Priming may not occur in fertile peatlands, as the decomposition is most likely not limited by C. Therefore, decomposition was regulated by a more profound effect of WT level manipulation and forest management type, which governed the peat OM decomposition rates and quality. Our results highlight the complexity of interacting factors affecting OM decomposition in peatlands affected by WT fluctuations and differing successional stages. The results indicate that the leaching of easily soluble OM and decomposition are induced by WT fluctuations, while the slowly cycling OM pool is more affected by the vegetation patterns affected by management or successional stage following changed WT level. The release of C to the atmosphere and watersheds from forested fertile peatlands during global warming will most likely be regulated by changes in WT level and quality of OM, which, in turn, governed by global-warming-induced WT fluctuations and changing vegetation patterns.

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AUTHOR CONTRIBUTIONS

Heidi Aaltonen: Data curation; Visualization; Writing-original draft. Xudan Zhu: Data curation; Formal analysis; Writing-review & editing. Rikta Khatun: Formal analysis; Investigation; Writing-review & editing. Annamari (Ari)

Laurén: Conceptualization; Funding acquisition; Methodology; Project administration; Writing-review & editing. Marjo Palviainen: Conceptualization; Funding acquisition; Methodology; Project administration; Resources; Writing-review & editing. Mari Könönen: Data curation; Investigation; Validation; Writing-review & editing. Elina Peltomaa: Data curation; Methodology; Validation; Writing-review & editing. Frank Berninger: Conceptualization; Funding acquisition; Investigation; Methodology; Project administration; Resources; Supervision; Writing-review & editing. Kajar Köster: Conceptualization; Funding acquisition; Investigation; Writing-review & editing. Anne Ojala: Conceptualization; Funding acquisition; Project administration; Resources; Writing-review & editing. Jukka Pumpanen: Conceptualization; Funding acquisition; Methodology; Project administration; Resources; Supervision; Writing-review & editing.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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