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RESEARCH ARTICLE

Evidence for older carbon loss with lowered water tables and changing plant functional groups in peatlands

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Abstract

A small imbalance in plant productivity and decomposition accounts for the carbon (C) accumulation capacity of peatlands. As climate changes, the continuity of peatland net C storage relies on rising primary production to offset increasing ecosystem respiration (ER) along with the persistence of older C in waterlogged peat. A lowering in the water table position in peatlands often increases decomposition rates, but concurrent plant community shifts can interactively alter ER and plant productivity responses. The combined effects of water table variation and plant communities on older peat C loss are unknown. We used a full-factorial 1-m^3 mesocosm array with vascular plant functional group manipulations (Unmanipulated Control, Sedge only, and Ericaceous only) and water table depth (natural and lowered) treatments to test the effects of plants and water depth on CO_2 fluxes, decomposition, and older C loss. We used $\Delta^{14}C$ and $\delta^{13}C$ of ecosystem CO_2 respiration, bulk peat, plants, and porewater dissolved inorganic C to construct mixing models partitioning ER among potential sources. We found that the lowered water table treatments were respiring C fixed before the bomb spike (1955) from deep waterlogged peat. Lowered water table Sedge treatments had the oldest dissolved inorganic ^{14}C signature and the highest proportional peat contribution to ER. Decomposition assays corroborated sustained high rates of decomposition with lowered water tables down to 40 cm below the peat surface. Heterotrophic respiration exceeded plant respiration at the height of the growing season in lowered water table treatments. Rates of gross primary production were only impacted by vegetation, whereas ER was affected by vegetation and water table depth treatments. The decoupling of respiration and primary production with lowered water tables combined with older C losses suggests that climate and land-use-induced changes in peatland hydrology can increase the vulnerability of peatland C stores.

KEYWORDS
carbon fluxes, climate change, ecosystem respiration, histosol, mixing models, radiocarbon

1 | INTRODUCTION

Peatlands are estimated to hold around 30% of soil organic carbon (C) globally, although the true amount may be even higher (Nichols & Peteet, 2019; Yu, 2012). Cold and hypoxic conditions coupled with *Sphagnum* moss traits constrain decomposition relative to primary productivity over millennia in northern peatlands, resulting in a net accumulation of organic matter (Piatkowski et al., 2021; van

Breemen, 1995; Wieder et al., 2006). The strength of the peatland C sink is predicted to decrease with future climate change as increased respiration rates outpace attendant primary production gains (Gallego-Sala et al., 2018; Piao et al., 2008). While sudden disturbance events such as wildfire and land-use change rapidly affect peatland C stores, long-term alterations in temperature, water balance, and dominant plant functional groups also make peat C more vulnerable to loss (Hopple et al., 2020; Loisel et al., 2021; Wilson et al., 2016).

Increases in the average depth to water table are one of the most important determinants of peatland C emissions to the atmosphere (Evans et al., 2021) and are closely linked with plant community changes. Lower water tables consistently increase ecosystem respiration (ER) in the short term, but whether these increases are compensated for by primary production depends on plant community changes (Bubier et al., 2003; Chimner et al., 2017; Juszczak et al., 2012; Laiho, 2006; Riutta et al., 2007; Zhong et al., 2020). Hypoxic conditions below the water table depress peatland decomposition rates, indicating that persistent labile organic material in peatland C sinks may be readily decomposed when not waterlogged (Laiho, 2006), especially in colder northern sites (Verbeke et al., 2022). Hydrology influences redox conditions, gas diffusion, and nutrient availability (Holden, 2005). Moisture, temperature, and nutrient changes are linked to changing plant species and abundances (Munir et al., 2015; Weltzin et al., 2003; Wieder et al., 2019), which in turn affect rooting zone depth (Armstrong et al., 1991), enzymatic profiles (Romanowicz et al., 2015; Wiedermann et al., 2017), and reduction–oxidation potential (Kane et al., 2019). Rhizosphere effects from vascular plants can also promote decomposition (Chanton et al., 2008; Fontaine et al., 2007), particularly when the depth to water table increases (Yan et al., 2022). Through these mechanisms, the direct and indirect effects of lower water tables and changing plant communities can interactively affect peatland C stores.

While rapid changes in surface peat C storage have been observed with changes in water table depth and attendant plant functional group shifts (Bridgham et al., 2008), the effect of this interaction on the stability of deeper, older C is unknown. The loss of old C under climate change is currently underrepresented in global models relative to changes in plant productivity and near-surface decomposition (Gallego-Sala et al., 2018), but strong evidence exists for potential respiration loss from this previously stable pool with warming or shifts toward vascular plant dominance (Gavazov et al., 2018; Hardie et al., 2009; Hicks Pries et al., 2015; Hopple et al., 2020; Walker et al., 2016; Wilson et al., 2021). Heterotrophic peat decomposition and old C loss can be primed by fresh inputs from vascular graminoid and shrub roots (Gavazov et al., 2018; Walker et al., 2016). A temperature and plant functional type peatland manipulation found that water table changes incidental to the study design did not directly alter the ^{14}C content of ER (Walker et al., 2016) but Pegoraro et al. (2020) found that moisture and temperature were co-drivers of ER radiocarbon age in thermokarst features with warming and drying treatments. The combined effects of vegetation changes and water table depths on older C stores remain unexplored.

To investigate the interactive effects of water table depth and changing plant communities on the age and origin of peatland ecosystem C respiration, we initiated a manipulative mesocosm experiment (Peatland Experiment at the Houghton Mesocosm Facility, PEATcosm). We applied water table depth (lowered and natural) and vascular plant functional group (PFG; unmanipulated Control, Sedge only, and Ericaceous only) treatments in a full factorial design with four replicates of each treatment. Previous analysis in this experiment established that the lowered water table treatment induced subsidence and lowered net peat accumulation, particularly in Sedge vegetation plots (Potvin et al., 2015). We have also seen that lowered water tables combined with aerenchymatous sedge roots accumulated more oxidized dissolved organic matter relative to other treatments, indicating a key pool of organic electron acceptors (Kane et al., 2019). Taken together with important microbial community shifts, alteration in water table depth and PFGs may be driving changes in key mechanisms of decomposition and C retention (Lamit et al., 2021).

Due to the bomb pulse of radiocarbon in the atmosphere during the 20th century, it is possible to gain detailed information about the age of respired C in ER based on its $\Delta^{14}C$ signature (Schuur et al., 2016). We measured the $\Delta^{14}C$ of ER in an outdoor mesocosm without the use of intermediate molecular sieves, which can introduce a source of fractionation (Egan et al., 2014). The $\Delta^{14}C$ signature of ER represents a mixture made up of contributions from several potential CO_2 sources. Mixing models are a framework for estimating the proportional contribution of defined sources to the whole-ecosystem ER based on the isotopic signatures of potential sources. We estimated the contribution of key source pools to ER to draw conclusions on the origin and age of respiration: from dissolved inorganic C (DIC), bulk peat C above the water table position, and plants. Unlike previous mixing model approaches to determine older C loss in peatlands, we have delineated source pools based on the position of the water table rather than age. This allowed us to account for the large differences in $\delta^{13}C$ and $\Delta^{14}C$ between bulk peat and DIC caused by fractionation from methanogenesis processes (Chasar et al., 2000; Wilson et al., 2021) and diffusional fractionation against heavier isotopes from DIC. Our models were run separately for natural and lowered water table treatments with source pool structures tailored to account for the specific depth increments of peat above and below the water table in each treatment at the time of radiocarbon measurement. Before running models, we determined if the defined pool contained pre-bomb spike C. To aid in the interpretation of our mixing model results, we also analyzed trends in growing season decomposition along the depth profile and ecosystem methane emissions at the time of radiocarbon analyses.

Previous studies in our mesocosms and similar peatland ecosystems have seen a decrease in sedge biomass with water table drawdown and strong positive relationships between gross primary production (GPP) and ER (Bubier et al., 2003; Potvin et al., 2015; Zhong et al., 2020). We, therefore, hypothesized that (H1a) GPP will

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be highest in the lowered water table Ericaceous and Control treatments and (H1b) that ER will respond in a similar pattern as GPP.

We also hypothesized that (H2a) the contribution of above-water table peat C (compared with plants or DIC) to ER would be higher in lowered water treatments relative to natural water table treatments due to oxygen availability based on depth to water table and subsequent shifts in redox chemistry. We would correspondingly see (H2b) a more enriched ER $\Delta^{14}C$ with lowered water tables as more respiration would be expected from areas beneath the more contemporary top layers of the peat profile that contain higher amounts of bomb spike C. (H2c) Sedge treatments will have a higher contribution from DIC due to the presence of aerenchymatous roots (Armstrong et al., 1991) that provide O_2 below the water table and have been shown to increase the pool of organic terminal electron acceptors (Kane et al., 2019). While we did not divide our source pools based on age, we were able to conclude whether treatments were inducing the loss of older C based on whether the source pools of the corresponding natural or lowered water table mixing model contained pre-bomb spike $\Delta^{14}C$ signatures (Table 1).

2 | MATERIALS AND METHODS

2.1 | Study site and experimental design

In 2010, we harvested 24 intact 1-m^{-3} peat monoliths from an oligotrophic peatland in Meadowlands, MN, USA (47.07278° N, 92.73167° W) and transported them to the Mesocosm Facility at the USDA Forest Service Northern Research Station Forestry Sciences Laboratory in Houghton, MI, USA (47.11469° N, 88.54787° W) as previously described in detail (Potvin et al., 2015). The Mesocosm Facility is comprised of 24 Teflon-coated stainless-steel bins housed in a climate-controlled underground tunnel and exposed to ambient outdoor conditions at the surface. Each bin was insulated along the vertical surfaces to prevent lateral thermal gradient formation while facilitating the vertical temperature gradient that characterizes peat profiles. The most common moss species in the experimental units were *Sphagnum fuscum* (Schimp.) Klinggr, *S. magellanicum* Brid., *S. rubellum* Wilson, and *Polytrichum strictum* Brid. Dominant vascular plants included the Ericaceae *Vaccinium oxycoccos* L., *Kalmia polifolia* Wangenh., and *Chamaedaphne calyculata* (L.) Moench., and the sedge *Carex oligosperma* Michx. Full information on vegetation changes induced by treatments can be found in Potvin et al. (2015), but unmanipulated Control plots did lose *C. oligosperma* cover between 2010 and 2013. Moss cover decreased in response to lowered water tables, particularly *Sphagnum* spp., with *S. rubellum* responding negatively to lowered water tables.

Beginning in 2012, we initiated a full-factorial randomized complete block manipulation of water table depths and vegetation types ($n = 4$). We manipulated water tables to reflect either "natural" (average seasonal profiles) or "lowered" (drought seasonal profiles) water table regimes comprised of seasonally-varying water table depths informed by a 45-year water table record from the Marcell Experimental Forest (USDA Forest Service) near the peat harvest location in northern Minnesota. Desired water depths were achieved using a combination of artificial rainwater, rain-out shelters, and outflow from the acrotelm-catotelm boundary, as seasonally appropriate. On average, water tables in the lowered table treatment were 20 cm deeper than in the natural treatment (see Haynes et al., 2017 for hydrograph data). The PFG treatments included three levels: unmanipulated ("Control"), all Ericaceae removed ("Sedge"), or all sedges removed ("Ericaceous"). To initiate treatments, we removed all aboveground and, when possible, belowground plant material. Some Ericaceous root structures and deep Sedge roots were not removed but were expected to die back over time. If belowground biomass could not be removed in a way that minimized disturbance, plants were instead clipped at the base of the stem. Treatments were maintained weekly during the growing season. Water level depth was monitored using submersible vented pressure transducers (Grainger 2HMC7) deployed in PVC pipe wells (see Potvin et al., 2015). More information on the peat collection, facility, and experimental manipulations can be found in Potvin et al. (2015) and Haynes et al. (2017).

2.2 | CO_2 and CH_4 flux measurements

We measured CO_2 and CH_4 fluxes in each mesocosm eight times in the 2014 growing season (May–October), as previously described

TABLE 1 Mean, standard deviation (SD), and sample size (*n*) of each source pool defined for the mixing model

Source	Water table	$\delta^{13}C$ mean (‰)	$\delta^{13}C$ SD (‰)	$\Delta^{14}C$ mean (‰)	$\Delta^{14}C$ SD (‰)	*n*
Plants	Lowered and natural	−28.0	1.6	19.8	3.1	9
DIC	Lowered	−3.1	1.9	5.5‡	13.1	2
	Natural	−1.8	0.6	70.9	15.8	11
Bulk peat (0–20 cm)	Lowered	−28.1	0.5	77.9	23.8	10
Bulk peat (20–30 cm)	Lowered	−27.2	0.4	201	92.0	5
Bulk peat (0–10 cm)	Natural	−28.7	0.5	56.2	6.9	5

Note: As separate lowered and natural water table treatment models were run, we indicate for which model each source was tailored. The source pool with a contribution from pre-bomb spike material is marked with a ‡. Plants values are derived from the contemporary Schauinsland observatory data set. Bulk peat values were measured at the inception of the experiment and DIC values were obtained from porewater at the time the $\Delta^{14}C$ of ecosystem respiration was measured (July 2014).

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in Tucker et al. (2022). All CO_2 flux measurements were made with an EGM-4 infrared gas analyzer (IRGA; PP Systems) using static chamber techniques. For net ecosystem production measurements, we placed a clear chamber (620 1 volume) securely onto the bin. Headspace within the chambers was mixed with two standard CPU fans. To measure ER, an opaque shroud was placed over the chamber such that no light entered the chamber during the measurement period. All rates of GPP and ER are expressed in μmol CO_2-C m^{-2} s^{-1}, where we calculated GPP as the negative value of net ecosystem production plus ER.

We measured CH_4 emissions from each mesocosm using opaque chambers (400 1 volume) with similar CPU fans to mix the headspace within the chamber. Chambers were sealed for approximately 40 min, during which time headspace CH_4 concentrations were measured five times using a field portable flame ionization detector (FID; Inficon-Photovac MicroFID), which was directly plumbed to each chamber (cf. Sánchez et al., 2017). The microFID would pull ~60 ml of air directly from the chamber and provide a stabilized concentration reading at each interval. Methane measurements were evaluated here only as an independent check on the relative anaerobic decomposition environment. Here, we present methane emissions measured in each bin on a date closest to the radiocarbon measurements (July 21st, 2014).

2.3 | Cellulose decomposition assay

To assess rates of decomposition on a common substrate representative of plant material, we weighed dried cellulose paper (Whatman 1001–929 Quantitative Filter Paper 11 μm Grade 1, 600 mm^2) and inserted each paper into an 80 μm nylon mesh bag. We placed a bag at 10 cm intervals along a birch rod in the first week of June 2014. Each mesocosm bin received two rods. Rods were retrieved in the first week of August, and papers were removed from the bag, dried at 55°C, and weighed. The percent mass loss was calculated as ([initial mass−final mass]/initial mass) × 100.

2.4 | Radiocarbon sample collection

In 2014, the third growing season after the initiation of the experimental treatments, eight bins were selected for radiocarbon analysis of respired CO_2 and DIC. Two mesocosms were chosen from each treatment combination (e.g., two bins with "Sedge" and "Lowered" water table treatments), excluding the unmanipulated treatment. Bins were randomly selected from the stratified design across all experimental blocks and sampled from July 17 to 20, 2014.

To collect respired CO_2, we placed the 100 × 100 × 40 cm silicone-sealed opaque chambers used for CH_4 measurements over the mesocosm bins. We taped the chamber to create an airtight seal to the rim of the mesocosm. The chamber was in a closed loop with an IRGA (described above as in CO_2 flux measurements) to monitor headspace CO_2 levels. To scrub the chamber headspace of ambient air, we used another closed loop with a pump (3.74 m^3 h^{-1}; 115 VAC oil-less, Cole Parmer #EW-07061-60) connected to two 5.1 cm diameter columns, each containing 400 g fresh Soda Lime (Indicating Type 4–8 Mesh Baker Analyzed ACS #3448-05-cs). We circulated chamber air through the Soda Lime to remove atmospheric CO_2 for 2 h, which brought the headspace CO_2 down from ambient to approximately 130 ppm. This effectively replaced the headspace with scrubbed air 18 times. At the end of the scrubbing period, we recorded the CO_2 concentration, disconnected the pump lines, and allowed CO_2 to accumulate in the chamber until a concentration of approximately eight times (>1000 ppm) initial scrubbed concentration was achieved in the static chamber (cf. Egan et al., 2014). A purpose-built air CO_2 capture apparatus (6 1 volume) consisting of an airtight stainless-steel cylinder outfitted with an internal battery-operated CPU fan was also connected in a closed loop with the flux chamber (Figure S1). The apparatus was connected in line with an IRGA and a 25 mm diameter (31.9 ml volume) water trap with Drierite desiccant ($CaSO_4$) and a stainless steel cold trap (length of 25 cm, 49 ml volume). We verified the CO_2 concentration within the apparatus, and then the attached cold trap was lowered into a dewar filled with liquid nitrogen (N_2) to trap CO_2; the CPU fan situated above the trap ensured a homogenous pool of CO_2 within the apparatus. After 10 min we sealed the trap, disconnected it from the apparatus, and immediately transferred it in the dewar to the USDA Northern Research Station radiocarbon facility on site and connected it to a vacuum line for CO_2 purification (removal of non-condensables) and transfer to evacuated glass tubes to be sealed for conversion to graphite. In effect, this on-site capture of whole-ecosystem respired CO_2 negated the need for an intermediate molecular sieve trap system that could introduce ^{14}C fractionation (Egan et al., 2014). The air capture apparatus was flushed with N_2 between measurements. Purified CO_2 was then graphitized with an iron powder catalyst (99.99%) in a method modified from Vogel et al. (1984). Graphite targets were sent to the Lawrence Livermore National Laboratory in Berkeley, CA, USA, for analysis on an accelerator mass spectrometer. The $\delta^{13}C$ was calculated on splits of the same sample based on the permil ratio of $^{13}C/^{12}C$ relative to the international standard Vienna Peedee belemnite. Radiocarbon values were normalized to a $\delta^{13}C$ of −25‰ using the measured $\delta^{13}C$ to account for mass-dependent fractionation and 2014 was the year of measurement for decay corrections. To obtain $DI^{14}C$, 60 ml of porewater from 10 cm depth regions centered at 20, 40, and 70 cm below peat surface (15–25 cm, 35–45 cm, and 65–75 cm) from the same bins as selected for respiration $^{14}CO_2$ were collected and placed in pre-evacuated 125 ml glass serum bottles via septa. The collections were made through pre-installed micropiezometers made of ultra-high-density polyethylene casing with inner Teflon tubing, where each depth represented 10 cm centered around the three depths stated above, and each level was flushed before collection. In lowered water table bins, collections were only made at 70 cm due to the position of the water table falling below the other collection zones. After shaking for 5 min and standing for a 5-min standardized equilibration time, 10 ml

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of headspace air was removed, purified, graphitized, and analyzed for radiocarbon following the same procedure described above.

We measured the $\delta^{13}C$ and $\Delta^{14}C$ of bulk peat from five of the 24 peat monolith harvest locations at the onset of the experiment from the 10–20, 20–30, 50–60, and 70–80 cm depth increments as previously described in detail (Potvin et al., 2015). To obtain the samples, a 10 cm^3 block of peat for each depth increment was removed from the face of the remaining peat after the monolith to be installed in the mesocosm facility was removed from the ground, which may help alleviate some transport of newer materials from the surface to depth with coring. Samples were ground and then processed for ^{14}C measurement, as above. Spatial variation in $\Delta^{14}C$ profiles can exist even on a small spatial scale within the same peatland (Hardie et al., 2007), but we did not see large differences between the five profiles collected here (see Potvin et al., 2015, where the standard error associated with each depth increment $\Delta^{14}C$ mean was less than 20‰).

2.5 | Mixing models

At the time of radiocarbon measurements, the average water table depths in lowered and natural water table treatments were 13.1 and 36.5 cm from the surface, respectively. We observed a large difference in $\delta^{13}C$ of DIC versus bulk peat, indicating that respiration from above or below the water table could not be effectively substituted for one another in a mixing model apportioning ER (see Table 1, Figure 1). The potential heterotrophic source pools in our mixing models were, therefore, defined as either above or below the water table rather than by radiocarbon age or depth. We ran separate mixing models for natural and lowered water tables so that the source signatures we fed into the model could reflect the amount of peat exposed above the water table and apparent treatment-induced differences in DI^{14}C signatures (see Figure S2). Separating DIC and above-water table bulk peat rather than pooling by age/depth of C also allowed us to account for diffusional fractionation in porewater CO_2 by applying a trophic discrimination factor of 4.4‰ (O'Leary, 1988).

We used three- (natural water tables) or four-source (lowered water tables) two isotope (^{14}C and ^{13}C) mixing models created in *MixSIAR* (Stock et al., 2018) to determine the relative contribution of plants, DIC, and bulk peat to total ecosystem respired CO_2 in a framework that allows for the inclusion of fixed effects. We aimed to keep the number of source pools low to avoid increasing the bias toward generalist solutions to our models. While each model was originally run with three sources, the lowered water table model convergence statistics were poor, likely due to the very large standard deviation in bomb-spike peat from 0–30 cm beneath the surface. Based on the data spread, we opted to split the peat pool by depth in the lowered water model, with one pool representing 0–20 cm ("Peat [Shallow]") and a second pool representing 20–30 cm from the surface ("Peat 20–30 cm").

All radiocarbon values are expressed as $\Delta^{14}C$ (‰, Schuur et al., 2016). The oldest DIC sample was dated to 1954 (Reimer & Reimer, 2022). This likely reflects a mixture of fresh plant root inputs and much older peat rather than material from 1954

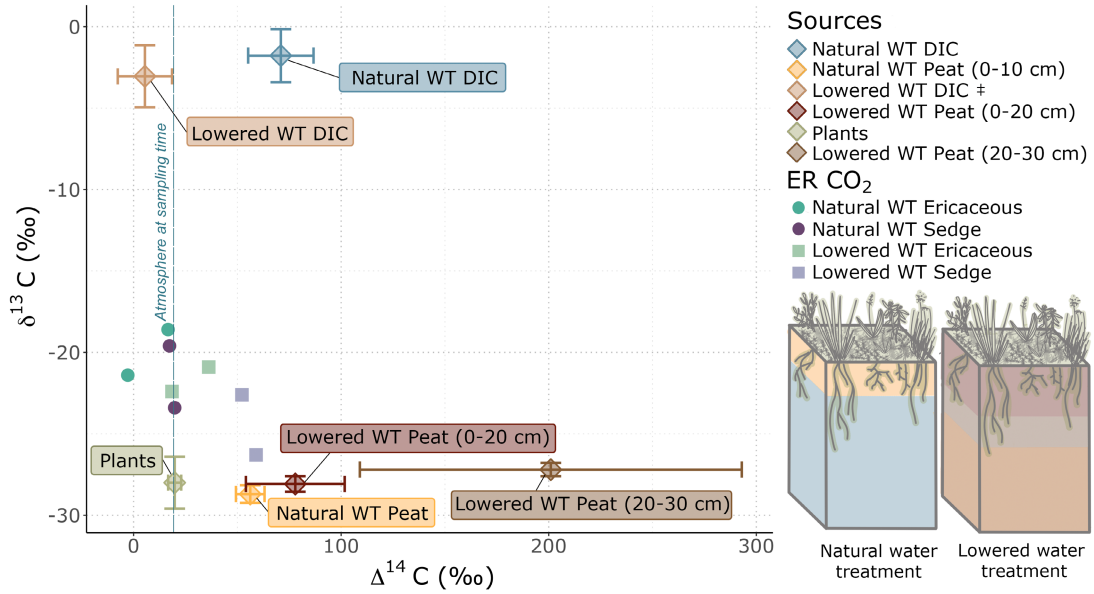

FIGURE 1 Isotopic signatures of source pools (labelled diamonds) and mixtures (circles and squares) from the mixing models to apportion the relative contribution of each source pool in ecosystem respiration (ER). Error bars on source diamonds are standard deviations. The fill color of the source diamonds corresponds to the mesocosm diagrams in the lower right corner. Pore water values originate from either the natural or lowered water table (WT) treatments, where natural water porewater CO_2 (DIC) was sampled at 20, 40, and 70 cm beneath the peat surface and lowered treatments porewater was sampled at 70 cm (the only location where it was present). Plant values were based on atmospheric $\Delta^{14}CO_2$ during the 2013 and 2014 growing seasons. ‡Symbol indicates contribution to source from pre-bomb spike material. DIC, dissolved inorganic C. [Colour figure can be viewed at wileyonlinelibrary.com]

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exclusively. Using that logic, age assumptions throughout are based on whether $\Delta^{14}C$ signatures were below the 2014 atmosphere to indicate "older" materials, as we could logically conclude that these samples contained material from the upslope or before the bomb spike in atmospheric ^{14}C around 1955 (Andrews et al., 2016; Hua et al., 2021). Within the framework of the mixing models we assumed that if the source pool contained older C based on its signature, and that source pool then contributed to the measured ER signatures, we could conclude that both PFG treatments within the water table treatment were inducing the loss of older C.

We determined the mean and standard deviation of porewater DIC $\delta^{13}C$ and $\Delta^{14}C$ across PFGs at lowered and natural water table treatments (Figure 1, Table 1). Natural water table treatment DIC measurements were made at 20, 40, and 70 cm beneath the surface using the pre-installed piezometers described above. Lowered water table DIC measurements were only made at 70 cm, as the water table in those bins at the time of measurements was below 40 cm. Past research has established that porewater DIC $\Delta^{14}C$ values track those of dissolved organic carbon substrates for microbial respiration but differ significantly from bulk peat values (Chasar et al., 2000; Wilson et al., 2021).

We used the average and standard deviation of measured $\Delta^{14}C$ of the atmosphere in the 2013 and 2014 growing season from the Schauinsland observatory for the plant-associated and recent litterfall respiration signature (Hua et al., 2021). The assumption that plant respiration matches the atmospheric signature appears robust in past studies (Hicks Pries et al., 2013, 2015). We used averages of measured vegetation $\delta^{13}C$ to approximate the $\delta^{13}C$ plant respiration signature. Some fractionation of ^{13}C occurs both between plant organs and between plants and respiration, but the scale of these fractionation events is generally less than 2‰ (Bowling et al., 2008; Werth & Kuzyakov, 2010).

We averaged bulk peat $\delta^{13}C$ and $\Delta^{14}C$ for lowered and natural water table treatments based on the depth of peat that was above water at the time of the experiment (0–10 cm in natural water table treatments, 0–20 and 20–30 cm in lowered water table treatments). Due to the scale of the original depth increments in the bulk peat $\Delta^{14}C$ measurements, a small portion of peat above the water table could not be accounted for in any source pool. The peat 30–35 cm below the surface in the lowered water table treatment and the 10–13 cm depth increment in the natural water table treatment were exposed at the time of radiocarbon measurements. However, as water tables frequently changed within a range during the growing season, that level of precision is unlikely to have a strong effect on the models. We also cannot account for changes that may have been induced in the first years of treatment.

A Markov chain Monte Carlo method was used to assign proportional contributions to the mixture samples (ER) based on a normal distribution of each source pool derived from the means and standard deviations where the sample size is accounted for in the scaling parameter of the mean (Ward et al., 2010). We did not provide value ranges to guide the proportions of the model, as prior research has shown large variations in the contribution of our sources to ER (Hardie et al., 2009; Hicks Pries et al., 2013). We ran one model for each water table treatment, with each run containing both Sedge and Ericaceous data under the fixed effect of PFG and a process error term times a residual error term. One ER sample from the natural water table Ericaceous treatment did fall well outside of the isotopic space defined by its sources. As our data set is already small, we opted to include this sample. Models were run with three chains of 3,000,000 in length, a burning of 200,000, and a thin of 100. The Gelman–Rubin diagnostic, a measure of model convergence, identified all variables as below the threshold of 1.05, with zero variables greater than 1.01, in both models. The Geweke Diagnostic identified one out of three chains in the natural water table model as containing variables outside the desired range, but this statistic did not improve or worsen in models with longer or shorter chain lengths. In the lowered water table model with four sources, all chains had zero variables outside ±1.96. These diagnostics indicated that there was very weak evidence for model non-convergence.

2.6 | Statistical analysis

All statistical analyses were performed in R Studio 1.2.1335 using R version 3.6.1 (R Core Development Team, 2018). Data manipulation and visualization were accomplished using tidyr packages *dplyr* and *ggplot2* (Wickham et al., 2019). To test for differences among treatments in the seasonal means of GPP and ER, we used a linear mixed effects model in *lme4* 1.1-21 (Bates et al., 2015) with fixed effects water table depth (natural and lowered), PFG (Sedge, Ericaceous, or Control), and the interaction between them with a random effect of mesocosm bin to account for repeated measures of the same experimental unit. Throughout the manuscript, the language of evidence is used (Muff et al., 2021). To avoid the pitfalls associated with assigning an alpha value, we instead refer to results as on a spectrum of evidence ranging from very strong evidence to no evidence (Muff et al., 2021). Differences in the mass loss for cellulose decomposition ($n = 48$) were also tested using a mixed model with the same fixed- and random-effects structure with an added fixed effect of depth interacting with the experimental treatments. In the decomposition model, the random effect of the mesocosm bin is to account for the non-independence of multiple rods from the same bin rather than repeated measurements across time. A two-way ANOVA with fixed effects of water table depth, PFG, and the interaction between them was conducted to test for the interaction between water table and PFG effects in $DI^{14}C$ ($n = 17$), ER CO_2 $\Delta^{14}C$ ($n = 8$), and CH_4 emissions ($n = 24$). As all DIC values were treated as a single source pool in mixing models, we did not include a fixed effect of depth of measurement in the $DI^{14}C$ model. All model residuals were visually inspected using the check_model() function in the *performance* package and model results were displayed through the *ggeffects* package (Lüdecke, 2018; Lüdecke et al., 2021).

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3 | RESULTS

3.1 | Ecosystem respiration, gross primary production, and methane emissions

There were strong effects of both PFG and water table on rates of ER, but no interactive effect (Table 2). The natural water table treatment respired less CO_2 compared with lowered water table treatments (Figure 2a, p = .004). Sedge treatment plots respired less CO_2 than either Control or Ericaceous plots (p = .013 and .084, respectively). There was strong evidence that the PFG treatment affected GPP, and no evidence for an effect of water table depth or an interaction between the two experimental manipulations (Table 2). Strong statistical evidence suggested Sedge plots had a lower GPP compared with Control and Ericaceous plots (p = .003 and .037, respectively), which were similar to one another (p = .634, Figure 2b). Water table was a strong determinant of methane emissions, where natural water tables had higher emissions (F = 29.26, df = 1, p < .001), while PFG had no effect (F = 1.68, df = 2, p = .217), and there was no evidence for an interaction between water table and PFG (F = 0.92, df = 2, p = .418).

TABLE 2 ANOVA table of mixed models where the structure of the mixed model (including random and fixed effects) appears above the output values for ecosystem respiration (ER) and gross primary production (GPP). An interaction between plant functional group (PFG) and water table treatment are the fixed effects of each model

Fixed effect	*F* value	Degrees of freedom	*p*
ER ~ (1|bin) + PFG × water table			
PFG	5.436	2	.005
Water table	11.228	1	<.001
PFG × water table	0.124	2	.883
GPP ~ (1|bin) + PFG × water table			
PFG	8.19	2	.003
Water table	0.45	1	.511
PFG × water table	0.30	2	.744

3.2 | Radiocarbon values and mixing models

The $\Delta^{14}C$ of ER was affected by water table (F = 16.24, df = 1, p = .010) and vegetation treatment (F = 7.82, df = 1, p = .038, Figure 4a). There was no statistical evidence for an interaction between water table and PFG treatment, and the interaction term was removed from the model. Natural water table Sedge treatment ER most closely resembled the atmospheric $\Delta^{14}C$ at the time of sampling. Lowered water table Sedge treatments had the highest $\Delta^{14}C$ signature and Natural water table Ericaceous plots the lowest.

Dissolved inorganic ^{14}C (Figure 1, Figure S2) was strongly affected by water table treatment (F = 49.6, df = 1, p < .001) but not by PFG treatment (F = 0.8, df = 2, p = .470). There was no statistical evidence for an interaction between water table and PFG treatment, and the interaction term was removed from the model. Measured $DI^{14}C$ was highest in natural water table Sedge treatments across all depths (Figure S2). Both lowered water table PFG treatments had $DI^{14}C$ signatures that indicated inputs from before or immediately after the bomb spike. The $\delta^{13}C$ of DIC was more enriched compared with plants, bulk peat, and ER CO_2 (Figure 1).

In the mixing models, the mean contribution of plants in all treatments was between 40–70%, with higher plant contribution means in natural water table treatments relative to lowered water table treatments (Figure 4b). Shallow peat (0–20 cm) had a large contribution to ER with lowered water tables, particularly in the Sedge

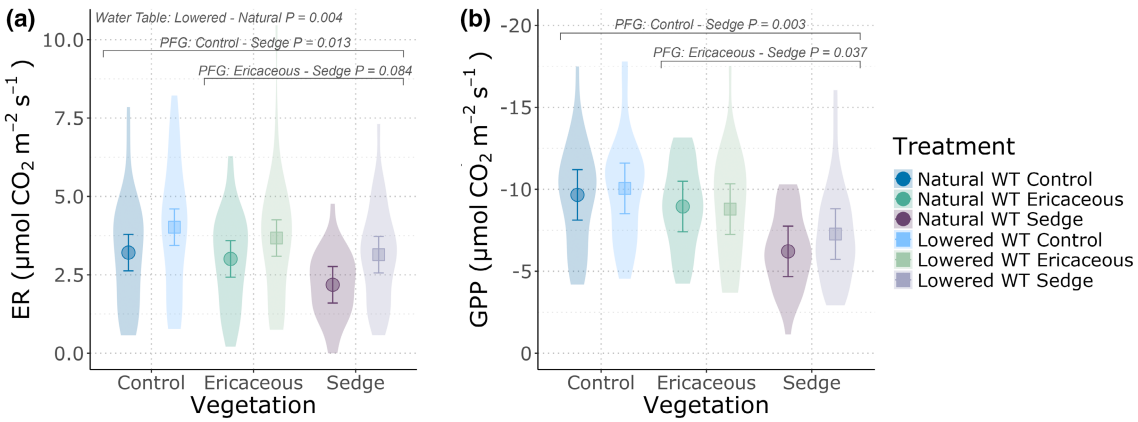

FIGURE 2 Model means (points) and 95% confidence intervals (error bars) for ecosystem respiration (a) and gross primary production (b) for all mesocosm treatments in the 2014 growing season. Violin plots in the background show the spread of the underlying data in the model. Ecosystem respiration is represented by positive numbers, whereas gross primary production values are negative. Note the switch in the *y*-axis orientation in panel (b), where the directionality is inverted for ease of interpretability. For ER, there was strong evidence that Sedge treatments were respiring less than both Control and Ericaceous treatments (p = .013 and .084, respectively). Lowered water treatments also had higher respiration rates than natural water table bins (p = .004). Rates of GPP were also lower in Sedge plots than Control and Ericaceous plots (p = .003 and .037). ER, ecosystem respiration; GPP, gross primary production; WT, water table [Colour figure can be viewed at wileyonlinelibrary.com]

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TABLE 3 ANOVA table of mixed models interpreting mass loss values from the cellulose decomposition experiment where the structure of the mixed model (including random and fixed effects) is in the first row. An interaction between plant functional group (PFG), water table treatment, and depth of cellulose paper beneath the peat surface are the fixed effects of each model

Mass loss ~ (1|bin) + PFG × water table × depth			
Fixed effect	***F* value**	**Degrees of freedom**	***p***
PFG	0.687	2	.500
Water table (WT)	13.746	1	.002
Depth	67.194	7	<.001
PFG × WT	0.497	2	.634
PFG × depth	4.381	14	<.001
WT × depth	18.402	7	<.001
PFG × WT × depth	1.053	14	.490

treatment (Figure 4b). Summed together, deeper (20–30 cm) and shallow (0–20 cm) peat in lowered water table bins contributed 30.9% and 39.4% of respired CO_2 in Ericaceous and Sedge plots, respectively. The peat source pool in the natural water table bins represented a smaller volume of peat (0–10 cm) and accounted for less than 15% of ER in both PFG treatments. Deeper peat (20–30 cm) in lowered water table treatment plots accounted for less than 10% of ER (Figure 4b). Compared with Ericaceous plots within the same water table treatment, Sedge plots had a lower contribution from DIC (33.1% to 21.3% in natural water treatments, 28.7% to 16.4% in lowered water treatments, Figure 4b). The DIC pool in the lowered water table mixing model had a source pool containing pre-bomb spike C (Table 1).

3.3 | Cellulose decomposition

The interactions between cellulose paper depth and water table as well as cellulose paper depth and PFG had strong effects on decomposition as measured by cellulose mass lost over the growing season (Table 3). There was no three-way interaction, so pairwise comparisons were made at each depth across the water table and PFG (Tables S2 and S3). There was strong evidence that Sedge plots had less mass loss at the surface compared with Control and Ericaceous plots in the top 10 cm of peat (Figure 5, Table S1, Sedge–Control $p < .001$ and Sedge-Ericaceous $p = .012$). Otherwise, there was no evidence for differences among PFG treatments at each depth (Table S1). There was also no evidence of a contrast between masses lost in the top 10 cm of peat between natural and lowered water tables, but strong evidence of higher rates of decomposition in lowered water table plots from 10–40 cm of depth (Table S2, Lowered-Natural 10–20 cm $p < .001$, 20–30 cm <0.001, 30–40 cm $p = .033$). While not explicitly included in statistical modeling, there is a visual trend in decomposition related to the transition from modern (post-1955) to pre-bomb spike (before 1955) bulk peat age, particularly in lowered water treatments (Figure 5).

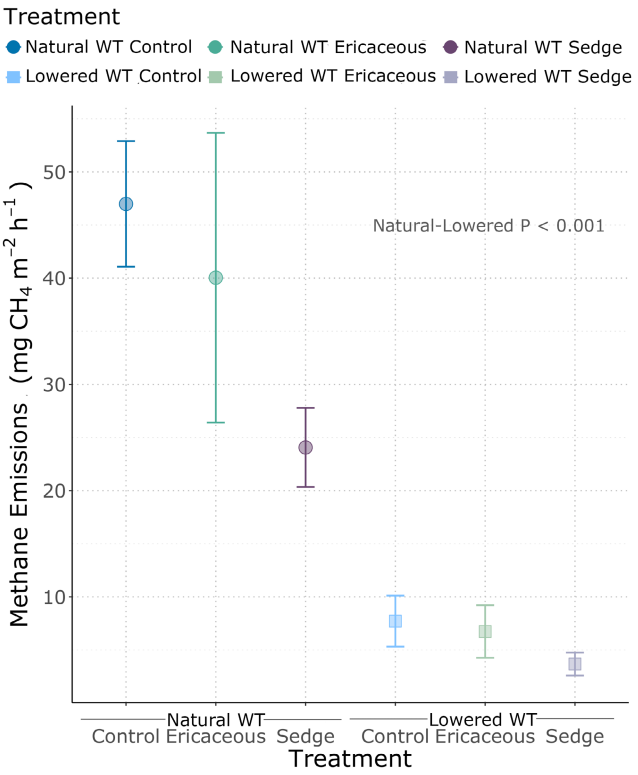

FIGURE 3 The panel shows methane emissions means and standard errors as measured contemporaneously with radiocarbon assays (July 21). Colors of points and error bars correspond to treatments. WT, water table [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

4.1 | Loss of older C from saturated peat with lowered water tables

While the $\Delta^{14}C$ of respired CO_2 increases with lowered water tables, multiple lines of evidence together indicated that older C (before 1955) was being released to the atmosphere in mesocosms with the lowered water table regime, especially when sedges were the dominant vascular PFG. The oldest C respired in lowered water table treatment plots came from below the water table. Contributions from DIC with pre-1955 $\Delta^{14}C$ signatures made up more than 15% of total ER in lowered water table Sedge plots and almost 30% of the total in Ericaceous plots (Figure 4b). The 70 cm DI^{14}C measurements taken in natural and lowered water table plots putatively represented a similar age of bulk peat, and yet we found dissolved CO_2 in the lowered water table treatment was much more depleted relative to the natural water table mesocosms (Figure S2). The signature from the lowered water table Sedge plots was relatively older (below 0‰), indicating a higher contribution from pre-1955 materials (Figure S2). We can conclude that the lowered water table treatments were inducing the decomposition of C fixed before the bomb spike. While the lowered Ericaceous water tables had a potentially higher proportional contribution from older DIC, the age of the DIC was older in the lowered water table Sedge plots.

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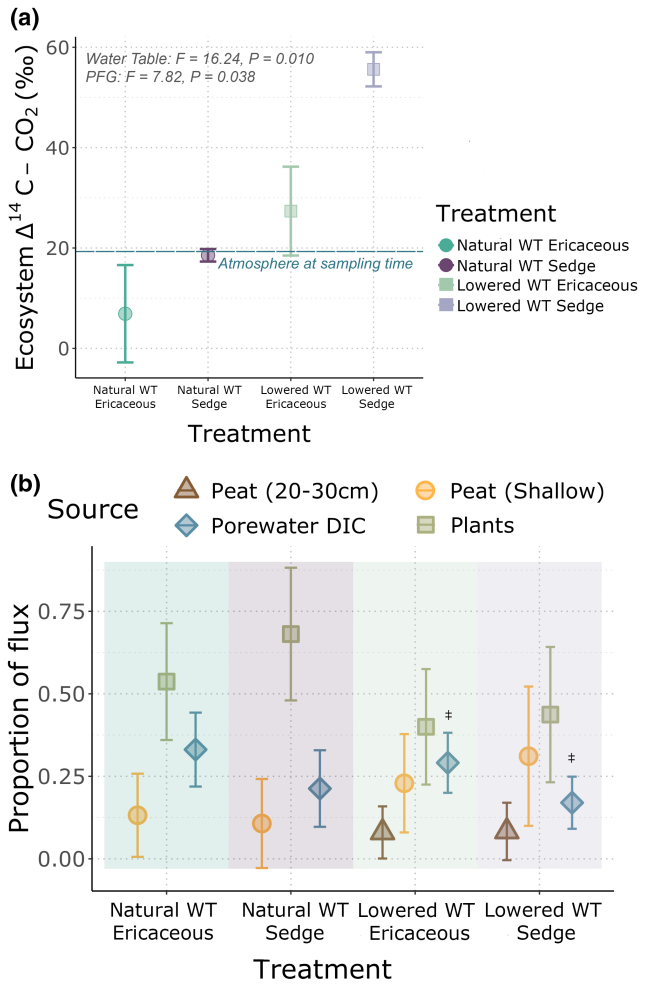

FIGURE 4 The top panel (a) shows the measured $\Delta^{14}C$ (mean and standard deviation) of ecosystem respiration as measured in mesocosms. The blue line at 19.2‰ indicates the atmosphere at sampling time. Black brackets show pairwise contrasts when p value was <0.1. Mixing model results (b) show the predicted mean (points) and standard deviation (error bars) of each source's proportional contribution to ecosystem flux. Background colors correspond to treatment group (see legend in panel a). ‡Above a source indicates contribution to source from pre-bomb spike material. DIC, dissolved inorganic C; WT, water table [Colour figure can be viewed at wileyonlinelibrary.com]

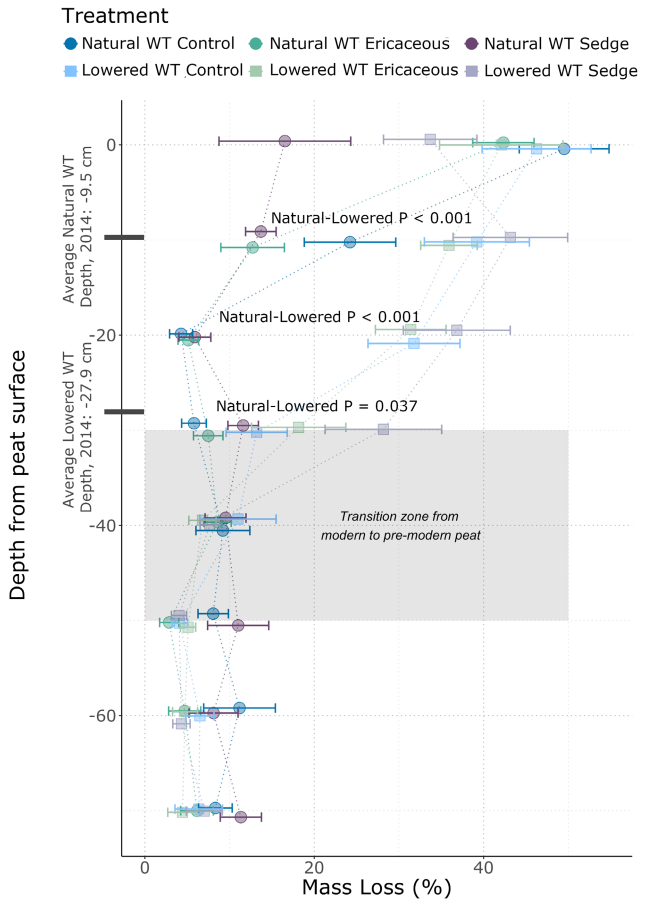

FIGURE 5 Mass of cellulose papers lost over a 3-month incubation by treatment. Small jitter added to points for visual differentiation. Each listed depth represents the top depth of the 10 cm increment, that is, the points at −20 cm represent the 20–30 cm depth increment. The only effect ($p < .1$) pairwise comparison between plant functional group treatments at each depth was 0–10 cm (Control–Sedge $p < .001$, Ericaceous–Sedge $p = .012$, see Table S2). WT, water table [Colour figure can be viewed at wileyonlinelibrary.com]

4.2 | Large changes in decomposition patterns

Perhaps as notable as the loss of older C with a lowering of the water table was the increase in rates of decomposition in the top 30 cm of peat, which was reflected in the growing proportion of peat respiration relative to plants (Figure 4b) and by patterns in the mass loss of cellulose (Figure 5). While decomposition is not considered to be linear with depth in peatlands, surficial peat (typically in the top 10 cm) consistently has the highest decomposition rates (Moore et al., 2007; Wieder, 2001), particularly when decomposition materials are collected from depth and reflect the true level of humification, unlike fresh material (Belyea, 1996). A primary or secondary peak in decomposition rates can also be seen near the water table depth variation zone, and the absence of this peak in our results may indicate sufficient hydrological connectivity to the surface to prevent decomposition rates slowing due to a lack of moisture (Laiho, 2006). We observed no peak in decomposition in either treatment within the zone of water table depth variability. A parallel but longer-running cellulose decomposition assay in the same experimental plots saw an even stronger effect of water table driving higher rates of decomposition in lowered water treatment plots (Wiedermann et al., 2017).

The mixing models provided evidence of a shift in decomposition trends with depth even with humified substrate deeper in the peat profile. We found strong support for H2c, as the higher $\Delta^{14}C$ of lowered water table Sedge plots corresponded with the highest contribution from bomb-spike peat from that treatment in the mixed models (see Table 1, Figure 4b). The contribution of peat (both Shallow and Deep together, 0–30 cm) accounted for 70% of heterotrophic respiration from the bins. Although not ecologically likely, if we were to assume that the contribution of each source to ER is roughly proportional to the volume of peat either above and

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below the water table (i.e., the mesocosm volume in the lowered water table treatments was 35% unsaturated peat and 65% below the water table, so peat contributions to heterotrophic respiration will be ~35% of heterotrophic respiration), lowered water table Sedge peat contribution to ER exceeded its expected amount by 35%. Unsurprisingly, all treatments surpass the anticipated volumetric contribution of bulk peat respiration, but the natural water table Ericaceous, natural water table Sedge, and lowered water table Ericaceous treatments exceeded expectations by less than 25%. Overall, we found strong support for our hypothesis (H2a) that lowered water table treatments would lead to higher peat-derived contributions to ER.

4.3 | Partitioning peat and plant respiration

Past studies that have partitioned sources of ER between autotrophic and heterotrophic respiration have generally found that plant contributions make up between one third to two thirds of total respiration depending on when in the growing season the measurement was taken (Crow & Wieder, 2005; Hicks Pries et al., 2013; Pegoraro et al., 2020; Riutta et al., 2007). The contrast we saw in plant contributions to respiration between natural and lowered water table plots represents a shift where heterotrophic respiration dominates over autotrophic respiration in lowered water table treatments even at the height of the growing season. As litterfall respiration from recent growing seasons was putatively included in the plant pool rather than the peat pool, our models may overestimate "autotrophic" contributions and underestimate heterotrophic contributions. As such, the plant pool may better be considered the "recently fixed" C pool. Both water table and PFGs are known to change the structure of microbial communities in these mesocosms, particularly at the 20–30 cm depths (Lamit et al., 2021). Low water table experimental treatments in fens have been associated with more fungal lignocellulose degraders in the peat (Rupp et al., 2021). Some respiration ascribed to "peat" in our mixing models may well be due to plant-associated microbial activity. Differences in root-associated fungal communities between PFGs are documented to interact with water table changes, as well as other plant functions, and may contribute to a vascular plant priming effect of the peat decomposition (Gavazov et al., 2018; Lamit et al., 2021; Rupp et al., 2021).

We found no support for our hypothesis (H2b) that DIC would be a larger contributor to ER in Sedge plots relative to Ericaceous plots within water table treatments. We instead found the opposite, where respiration in Ericaceous plots had a larger contribution from DIC relative to Sedge plots within water table treatments (Figure 4b). It seems unlikely that methanogenesis in lieu of CO_2 production can explain our results since PFG did not have a strong effect on rates of methane emission (Figure 3). In some ecotypes, the rooting depth of *C. oligosperma*, is concentrated in the top 30 cm of the peat profile but has the potential to reach at least 60 cm in drained peat (Strack et al., 2006), and visually reached the bottom of the mesocosm in our experiment. Previous research in the PEATcosm experiment and elsewhere suggests that these rooting zones can accumulate oxidized organic compounds, increasing the pool of electron acceptors (Agethen et al., 2018; Kane et al., 2019). Measurements of DI^{14}C were made only at 70 cm of depth in lowered water table mesocosms due to the specifications of the pre-installed piezometers and the water table depth at the time of measurement. Therefore, the DIC source pool in our lowered water table model may underrepresent DIC from 35–65 cm in depth, an area, which would be likely to see sedge rhizosphere-induced changes. It is possible that the contribution of DIC in Sedge plots was minimized in our model due to the absence of DIC measurements within the rooting zone. The movement of the water table through the aerenchymatous rooting zone can further propel decomposition and CO_2 production above the water table through "redox pumping" (Brouns et al., 2014; Gao et al., 2019). Sedges may have had a greater impact on the contribution of the above-water peat pool as opposed to the DIC pool, as is borne out in the lowered water table Sedge plots (see Figure 4b). In natural water table plots, the output of CO_2 from the 40–60 cm zone beneath the water table may still be underestimated in our mixing models, which is supported by the relatively high cellulose decomposition rates associated with natural water Sedge treatments below 50 cm (Figure 5).

The large degree of enrichment in ^{13}C between bulk peat and DIC we observed may be associated with acetoclastic or hydrogenotrophic methanogenesis (Garnett & Hardie, 2009; Neumann et al., 2016). Natural water table Ericaceous treatments had the most enriched DI^{13}C signature and the highest rate of methane emissions at the time of measurement (see Table 1, Figure 3). Past studies in PEATcosm have identified hydrogenotrophic methanogens as an indicator taxa in the natural water table treatments (Lamit et al., 2021). Future studies on the Δ^{14}C of CH_4 in conjunction with water table depth may reveal a source of older C in natural water table mesocosms that was not measured in this study; however, DI^{14}C has been shown to be representative of methane age (Chanton et al., 2008).

The relatively depleted Δ^{14}C signature of ER in natural water table Ericaceous plots indicated the potential mixing of pre-bomb spike C, but with no apparent source as neither above water peat nor DIC included pre-bomb spike C. It is possible that the snapshot style measurement of porewater DI^{14}C was not representative of all potential values or that Ericaceous microbial partners are occasionally accessing an older recalcitrant C pool.

4.4 | Respiration changes decoupled from primary production

We found higher rates of GPP in Ericaceous and Control plots relative to Sedge plots, which is partially in support of our hypothesis (H1a) that Control and Ericaceous plots will fix more C. Surprisingly, water table treatment had no effect on rates of CO_2 uptake even in the presence of plant communities expected to respond positively to lowering of water tables (Bubier et al., 2003), which does not support the portion of H1a that predicted that lowered water

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tables would increase GPP with Ericaceous or Control vegetation. Although past vegetation manipulations and natural observations have often found that sedges have high primary production relative to other vegetation types, *C. oligosperma* may be less productive than other species that dominate in sedge fens (Radu & Duval, 2018; Strack et al., 2006). The lower *Sphagnum* spp. biomass in lowered water table plots compared with natural water table plots (Potvin et al., 2015) did not appear to have a strong effect on overall rates of GPP. While S. rubellum in particular was negatively impacted in the lowered water table plots, the shifting species composition was unlikely to have a strong impact on rates of photosynthesis. *Sphagnum rubellum* and *S. fuscum* are part of the same subsection within *Sphagnum*, share similar environmental preferences, and have similar photosynthetic rates (Bengtsson et al., 2016).

In line with previous findings, a lowered water table increased ER (Bubier et al., 2003; Chimner et al., 2017; Juszczak et al., 2012; Zhong et al., 2020). We found no support for the second part of our hypothesis (H1b) that ER and GPP would respond in similar ways to our treatments. Unlike GPP, ER was strongly affected by water table and PFG (Table 2, Figure 2a). The decoupling of trends relating ER and GPP was largest in the lowered water table Sedge treatment, which had low rates of GPP without correspondingly low rates of ER. The same trend toward a decoupling of GPP and ER can be seen in the lowered water table Control and Ericaceous plots. We can expect the increases in ER in lowered water tables are linked with the proportional increase in heterotrophic contributions to ER CO_2 found in the lowered water table mixing models.

The loss of older C alone does not indicate a shift from sink to source in peatland C dynamics. However, the loss of older C in lowered water table treatments below the water table and the shift in shallow peat decomposition patterns indicated two pathways by which decomposition could overtake primary productivity in the future. Even at the height of the growing season, we found evidence that heterotrophic sources accounted for more respiration than autotrophs. This effect was especially pronounced in the Sedge plots, which may be due to oxygenation through aerenchymatous roots, changing microbial communities, root exudates, or a combination of these factors. The decrease in *Sphagnum* spp. cover in lowered water table treatments, and thus the loss of *Sphagnum* traits that help to preserve decomposition patterns, interacting with changing substrate quality and microbial communities as previously observed in the experiment, may also play a role in C losses (Lamit et al., 2021; Potvin et al., 2015). Some changes due to a decrease in the water table may be offset by accompanying subsidence and increases in peat bulk density, and the experiment presented here is most relevant to short-term changes. However, predictions that peatlands will remain a net C sink through this century rely on the assumption of offsetting increases in decomposition with production and the inert status of older, deeper peat layers (Gallego-Sala et al., 2018; Noon et al., 2022). Here, we saw evidence for a decoupling of production and respiration in lowered water table treatment plots and the loss of pre-bomb spike C, suggesting that these assumptions may not be valid with drainage, land use change, or plant species shifts.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

https://doi.org/10.1594/PANGAEA.942789, Radiocarbon of ecosystem respired CO_2 and DIC in PEATcosm array. Other PEATcosm data sets in Pangaea: https://doi.org/10.1594/PANGAEA.878268; https://doi.org/10.1594/PANGAEA.902313. Temporary access to the main dataset can be found at https://doi.pangaea.de/10.1594/PANGAEA.942789.

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