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Response of the peatland carbon dioxide sink function to future climate change scenarios and water level management

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Abstract

Stress factors such as climate change and drought may switch the role of temperate peatlands from carbon dioxide (CO_2) sinks to sources, leading to positive feedback to global climate change. Water level management has been regarded as an important climate change mitigation strategy as it can sustain the natural net CO_2 sink function of a peatland. Little is known about how resilient peatlands are in the face of future climate change scenarios, as well as how effectively water level management can sustain the CO_2 sink function to mitigate global warming. The authors assess the effect of climate change on CO_2 exchange of south Swedish temperate peatlands, which were either unmanaged or subject to water level regulation. Climate chamber simulations were conducted using experimental peatland mesocosms exposed to current and future representative concentration pathway (RCP) climate scenarios (RCP 2.6, 4.5 and 8.5). The results showed that all managed and unmanaged systems under future climate scenarios could serve as CO_2 sinks throughout the experimental period. However, the 2018 extreme drought caused the unmanaged mesocosms under the RCP 4.5 and RCP 8.5 switch from a net CO_2 sink to a source during summer. Surprisingly, the unmanaged mesocosms under RCP 2.6 benefited from the warmer climate, and served as the best sink among the other unmanaged systems. Water level management had the greatest effect on the CO_2 sink function under RCP 8.5 and RCP 4.5, which improved their CO_2 sink capability up to six and two times, respectively. Under the current climate scenario, water level management had a negative effect on the CO_2 sink function, and it had almost no effect under RCP 2.6. Therefore, the researchers conclude that water level management is necessary for RCP 8.5, beneficial for RCP 4.5 and unimportant for RCP 2.6 and the current climate.

KEYWORDS

bog, climate chamber-based mesocosm experiment, drought, net ecosystem exchange, representative concentration pathway, vascular plant

1 | INTRODUCTION

Peatlands are one of the largest carbon storage areas in the biosphere (Yu, 2012), holding a carbon pool equivalent to around half of the current atmospheric carbon pool (Gorham, 1991). A high water table and the consequent anoxia along with low soil temperature and low pH are key causes of low decomposition of organic matter and accumulation of carbon in peatlands (Laiho, 2006). However, there is a growing concern that peatlands in many regions may change from carbon sinks to carbon sources in the face of global change (Fenner & Freeman, 2011; Ise et al., 2008; Loisel et al., 2021). This is especially a concern for temperate regions, which contain a significant share of the world's degrading peatlands (that lose carbon), and in addition stand out as being intensively utilized by humans (Leifeld & Menichetti, 2018). Thus, whereas most of the global peat carbon stock is in boreal and polar wetlands, the fate of temperate peatland carbon is of particular relevance in the face of climate change.

Higher temperatures influence the carbon dioxide (CO_2) release from fungal and microbial activity (Asemaninejad et al., 2018) as well as CO_2 uptake by plant photosynthesis, which are both mainly thermophilic processes (Frolking et al., 2001; Poorter et al., 2012; Weltzin et al., 2000). Increased temperatures elevate the primary production of plants in peatlands until the point where temperature becomes a stress factor (Weltzin et al., 2000); for example, up to 27°C in the case of *Sphagnum* spp. (Johansson & Linder, 1980). Besides direct effects of temperature, warming can indirectly affect peatlands through alterations in water level and associated oxygen (Buttler et al., 2015; Laine, Mäkiranta, et al., 2019; Munir et al., 2015). Due to the combined positive effects of warming and oxygenation, a substantial increase in heterotrophic respiration has been observed in peatlands when elevated temperature has been accompanied by water level drawdown (Laine et al., 2019; Samson et al., 2018; Zhong et al., 2020).

Elevated temperature along with a more frequent occurrence of extremes such as floods and droughts as well as changes in nutrient regime may shift plant composition (Dieleman et al., 2015; Walker et al., 2006). Change in cover and composition of dominant plant functional groups (ericoid [*Erica*-like]) dwarf shrubs, graminoids (herbaceous with a grass-like morphology) and bryophytes (moisture-loving non-vascular land plants) in peatlands has consequences for the CO_2 flux (Kuiper et al., 2014; Ward et al., 2009; Zhao et al., 2017). Lower *Sphagnum* productivity can be expected as a result of climate-change-induced water stress (Bragazza et al., 2016; Kuiper et al., 2014). Furthermore, global warming will increase vascular plant productivity (graminoids and ericoid shrubs; Heijmans et al., 2008; Ward et al., 2009), thereby maintaining the peatland CO_2 sink role. However, it is not clear whether the expansion of vascular plants producing more degradable litter can preserve the peatland sink role in the long term (Del Giudice & Lindo, 2017; Robroek et al., 2016).

Water level management has been regarded as an important climate change mitigation strategy as it can regulate net CO_2 exchange and sustain peatland natural net CO_2 sink role (Beyer et al., 2021; Leifeld et al., 2011; Salimi et al., 2021). However, estimates of water level management efficiency for climate change mitigation do not take into account how future climate change will change the sink function of peatlands (Beyer et al., 2021). In addition, there is a need to understand the effectiveness of water level management in the face of more frequent and severe climatic extreme events. There is a risk that drought severity can hinder climate change mitigation goals for managed peatlands (Harris et al., 2006). Furthermore, little is known about how restored and intact peatlands respond to the altered temperature and hydrology under future climate change scenarios (Günther et al., 2020; Loisel et al., 2021).

Ultimately, these altered factors will drive a shift in plant functional types, and it is not yet clear how the new plant composition will respond to climate perturbations (Kuiper et al., 2014; Munir et al., 2015; Sulman et al., 2010). Therefore, studying the response of plant communities to climate change along with extreme events in both managed and unmanaged peatlands is critical to understand the trend of net ecosystem CO_2 exchange (Salimi et al., 2021).

Since 2017, the authors are performing continuous experiments with mesocosms; peatland samples obtained from an ombrotrophic (rain-fed) bog in southern Sweden located within climate chambers. In this study, researchers simulated different representative concentration pathway (RCP) future climate scenarios for the experimental bog mesocosms for the first time. The authors also simulate the current climate scenario based on the hydrological years (starting from the first of October) 2017, 2018 and 2019. These climate data were simulated within the experiment in 2018, 2019 and 2020, respectively. It should be noted that 2018 was recorded in Scania (Skåne in Swedish), Sweden, as the warmest and driest summer since 1950. The year 2019 had the second warmest summer, but rather typical precipitation. The authors also examined the effect of water level management in all climate scenarios.

The aim is to understand the impact of different levels of climate change (current and future RCP climate scenarios including RCP 2.6, RCP 4.5 and RCP 8.5) and water level management on the CO_2 sink function of peatlands. The researchers hypothesize that (a) the sink function of unmanaged mesocosms decreases from the coldest (current) to the warmest (RCP 8.5) climate scenario and that (b) water level management enhances the sink function of the system comparing to the unmanaged systems under all climate scenarios.

2 | MATERIALS AND METHODS

2.1 | Mesocosm experimental setup

The peatland samples were collected from an ombrotrophic bog called Fäjemyr, which is located in the province of Scania (latitude of 56°15′N, longitude of 13°33′E and altitude of 140 m). The samples were extracted using spades and shovels from the top layer of the peatland and were placed directly in glass tanks (30 cm in length; 22 cm in width; 24 cm in height) in the field. The peatland mesocosms consist of 20 cm of the top bog vegetation community with some young peat at the bottom.

All mesocosms were representative of the wider sampling site and comprised an approximately equal proportion of dominant plant types in Fäjemyr: dwarf shrubs (*Calluna vulgaris* and *Erica tetralix*), sedges (*Eriophorum vaginatum*) and *Sphagnum* spp. (*S. magellanicum* and *S. rubellum*; Lund et al., 2012).

The researchers randomly distributed 16 peatland mesocosms into four climate chambers (four mesocosms per chamber). Moreover, the four mesocosms in each climate chamber were split into two managed and two unmanaged systems (two replicates for each group). The team managed the water level for the managed mesocosms and skipped the water level adjustment for the unmanaged ones (see water level management section) to understand how water level adjustment can change the response of peatlands in terms of respiration, net ecosystem exchange (NEE), gross primary production (GPP) and climate scenario (Salimi et al., 2021).

Four climate chambers were used to simulate four different climate scenarios for peatland mesocosms: one current climate scenario as a control, and three future potential climate scenarios. The climate chambers allowed for an accurate and dynamic climate scenario simulation for the mesocosms by applying four different climate variables of temperature, precipitation, relative humidity and radiation simultaneously (Salimi et al., 2021).

2.2 | Climate scenario simulation within climate chambers

To derive better and more realistic estimates of CO_2 fluxes (Salimi et al., 2021), simulations of radiative forcing climate scenarios have been conducted in this study. To create future climate scenarios for the climate chambers, hourly data of 10 different regional climate models (RCM) were collected from the Rossby Centre of the Swedish Meteorological and Hydrological Institute (SMHI; Table S1). The data for the RCM were collocated for different potential future climate scenarios, which are based on different radiative forcing target levels predicted for the future (Anno 2100) and are released by the Intergovernmental Panel on Climate Change (IPCC; AR5; IPCC, 2007). According to an IPCC's fifth assessment report (AR5; IPCC, 2007), there are four different scenarios, which are called RCP2.6, RCP4.5, RCP6 and RCP 8.5 (Van Vuuren et al., 2011). In this project, the data of the RCMs were collected for RCP 2.6, RCP 4.5 and RCP 8.5 (Table S1) to simulate low, moderate and extreme future climate change scenarios in the climate chambers (Figure 1). The data were collected for the domain Scania County located in southern Sweden. The four climate variables temperature, humidity, radiation and precipitation were used to simulate the different scenarios within the climate chambers dynamically (Figure S1). Hourly data of these variables for the present climate scenario (2016–2019 data from Malmö A station) were downloaded from SMHI (http://opendata-download-metobs.smhi.se/explore/) for climate scenario simulations.

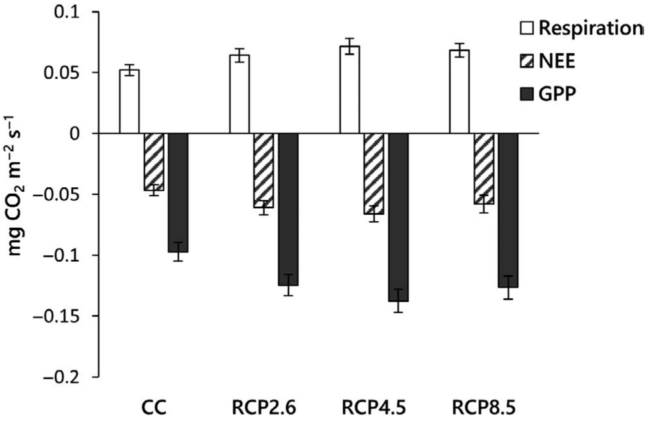

FIGURE 1 Average of respiration, net ecosystem exchange (NEE) and gross primary production (GPP) for all mesocosms (both managed and unmanaged) under different climate scenarios (current climate [CC] and representative concentration pathways [RCP] 2.6, RCP 4.5 and RCP 8.5)

Since there is uncertainty regarding all RCM outputs, no specific RCM was used for creating the climate scenarios, instead the delta change approach was employed to include all existing RCM to reduce uncertainty. In this method, the difference between the output of each RCM for the last 30 years of the century (2069–2098) and the historical data of the same models for the same number of years (1976–2005) has been estimated. The results were then averaged across all RCM models for all RCP, and, subsequently, the estimated differences (for temperature) and ratios (for precipitation, relative humidity and radiation) were calculated for each month resulting in monthly delta change coefficients. The estimated monthly delta change coefficients were applied to the hourly observation data of Malmö station to obtain the future climate scenario values. The 3-hourly values for temperature, relative humidity and radiation were calculated and used for the climate change scenario simulation in the chambers.

To simulate current and future climates, the team used the four climate chambers KK 750 (Pol-Eko-Aparatura; https://www.pol-eko.com.pl/model/climatic-chambers-kk/climatic-chamber-kk-750/). These chambers were equipped with a phytotronic system to regulate temperature and humidity. Each chamber was also supplied with a fluorescent lamp 840 (daylight) for day and night simulation. Both illumination intensity and duration were controlled by the chamber as well. The climate chamber regulates the temperature from −10 to +60°C with the light switched-off, and from 0 to +50°C with the light on. The chambers are equipped with an ultrasonic humidifier, which has to be supplied with deionized water to provide the required humidity in the chambers. There is also an air flap and a ventilator in each chamber to allow for a stable condition in terms of air extraction and circulation. The climate chambers are remotely programmable allowing the user to regulate the temperature and relative humidity, as well as radiation at a 3-h resolution. Precipitation simulation was conducted manually on a weekly basis.

2.3 | Water level management

Precipitation was simulated for all mesocosms in all chambers on a weekly basis based on precipitation data from the created climate scenarios (explained above). Rainwater was gathered from nearby greenhouse glass roofs and manually added to the top surface of the mesocosms, where it infiltrated into the peatland soil. The water level in the mesocosms was regulated to prevent adverse effects of mesocosm floods or drought stress on the carbon sink function of the mesocosm. The water levels between 10 (±0.5) and 18 (±0.5) cm (from the bottom of the tank) were considered as acceptable thresholds for mesocosms to provide all types of plants with water for photosynthesis and avoid nutrient loss due to flooding as they can boost the rate of photosynthesis.

Water level management was carried out either by adding water from the storm water pond called Lake (Sjön Sjön in Swedish), which is located on the campus of the Faculty of Engineering at Lund University, to the mesocosms when the water level dropped to less than 10 cm due to evapotranspiration or by removing excess water (runoff or management outflow) from the mesocosms, when the water level exceeded 18 cm. Water was added for management purposes to the top surface of the mesocosms while excess water was removed from the vertical standing pipe located in the center of each mesocosm where in a practical application the outflow of the mesocosm would be collected. For the unmanaged mesocosms, laboratory workers skipped the water adjustment procedures. It follows that rainwater simulated on the basis of climate scenario predictions was the only inflow to the unmanaged mesocosms. Therefore, some mesocosms encountered extreme events such as drought and flooding (maximum 4 cm above the top soil).

2.4 | Flux measurements and calculations

The CO_2 fluxes of the peatland mesocosms were measured at a monthly time step inside all climate chambers. The EGM-5 Portable CO_2 Gas Analyzer (PP Systems) was used to measure the concentration of CO_2 in the closed chamber. The analyzer was connected to a 36-L transparent Plexiglas static measurement box.

The measurement box was equipped with a circulation fan to homogenize the air inside the box. For each measurement, the measurement box created a closed ecosystem over each mesocosm located in the climate chamber. During all measurements, the following parameters were recorded: mesocosm water level, soil temperature and approximate volume of vegetation in the chamber. To measure the volume of the total air that contributed to the CO_2 flux in the chamber, the air-filled porosity of the mesocosm had to be measured.

Carbon dioxide concentrations were measured over time for both day and night to estimate the NEE of the mesocosm (day measurement) and then the ecosystem respiration (night measurement), respectively. The GPP, which is an indication of photosynthetic uptake, can be calculated by subtracting respiration from the NEE. A negative value represents CO_2 uptake (CO_2 sink) into the ecosystem and a positive value indicates CO_2 release to the atmosphere (CO_2 source).

The CO_2 concentration (ppm) was measured inside the measurement chamber for 180 s. The flux of CO_2 was calculated using Equation (1) assuming that 1 kg mol^{-1} of gas (equals 44.01 kg of CO_2) occupies a volume of 22.41 m^3 at standard conditions for a temperature of 0°C and at a pressure of 1013.25 mbar.

$$\text{Flux} = b \times \frac{p}{1013.25} \times \frac{273}{273 + T_{\text{air}}} \times \frac{44.01}{22.41} \times \frac{V}{A} \times 10^{-2}, \tag{1}$$

where the Flux is presented in mg CO_2 m^{-2} s^{-1}; b indicates the slope (ppm s^{-1}) determined by linear regression of CO_2 concentration (ppm) change inside the measurement chamber over time (s); $p/1013.25$ is the correction of barometric pressure with p measured in mbar; $273/273 + T_{\text{air}}$ is the correction for air temperature in the chamber with T_{air} measured in °C; 44.01 kg/22.41 m^3 is the molar volume and ideal gas constant at standard temperature and pressure (0°C and 100 kpa); V is the volume (cm^3) of the measurement chamber and A is the inner surface area (cm^2) of the chamber; and the remaining term (10^{-2}) is a unit conversion factor.

2.5 | Plant analysis

The mesocosms were analyzed for different plant functional type (*Sphagnum* spp., dwarf shrubs and sedges) coverage at the start of the experiment in July 2017 (July), and the following years including 2018 (August), 2019 (July) and 2020 (September). The unbiased estimates of the areal covers of each plant functional type were analyzed. A 15 × 11 grid with a cell size of 2 cm times 2 cm was superimposed on each mesocosm for subsequent plant species analysis. The presence or absence of each species at each grid intersection was noted. The coverage of each plant functional type was calculated relative to the tank area as a percentage.

2.6 | Statistical analysis

A one-way ANOVA has been used to find the significant differences between different climate variables under different climate scenarios. The Tukey's test was then used to assess pairwise differences. The Sen's (1968) slope estimator was applied to the current climate data to examine whether there is a significant trend for the climate variables under different climate scenarios over the experimental period.

The team used a mixed-effects model to test the significant effect of different climate scenarios, water level management as well as their interactions on respiration, NEE and GPP responses over time. Climate scenarios and water level management were considered as the main effects in this model. The strength of the mixed-effects model is that the term random effect is incorporated into the model. As samples (mesocosms) were randomly collected from the peatland (Fäjemyr) and assigned randomly to four climate scenarios, the replicates (mesocosms) were defined as random effects in the model. Moreover, time expressed as season was involved as a random effect as well (Bolker et al., 2009). The results of the model were explored to assess if it met the assumptions; that is, that residuals have a normal distribution and constant variance. For multiple comparison analysis, the Bonferroni adjustment test (Sokal & Rohlf, 1995) was conducted as a post hoc analysis to determine the statistically significant differences between the managed and unmanaged systems under different climate scenarios. A two-way ANOVA was used to analyze the effect of different climate scenarios, water level management and their interactions on the distribution different plant functional types (*Sphagnum* spp., dwarf shrubs and sedges). The Bonferroni adjustment test was used for the multiple comparisons. For all tests in this study, the significance level was set to $p < 0.05$.

3 | RESULTS

3.1 | Climate variables under different climate scenarios

Sen's slope estimator results revealed no significant ($p > 0.05$) trend for the annual and monthly time series of all climate variables except radiation, which showed a significant ($p < 0.05$) increasing trend in April over the experimental period. All Sen's slope values for the time series have been shown in Table S2. These results are valid for all climate scenarios as the future climate scenarios have been generated from the current climate scenario applying the delta change coefficients. Therefore, the trends of all future climate scenarios follow the current climate scenario. A multiple comparison (Tukey's test) between the climate scenarios showed that all climate scenarios were significantly different ($p < 0.05$) from each other in terms of temperature (Figure S2b). There was an increasing trend from the current climate toward RCP 8.5. The differences between the annual average temperature of the future climate scenarios RCP 2.6, RCP 4.5 and RCP 8.5 relative to the current climate (control scenario) were 1.8 ± 0.52, 2 ± 0.43 and 3.2 ± 0.75°C, respectively (Figure S1b).

There was neither a significant difference ($p > 0.05$) in relative humidity between the current climate scenario and RCP 2.6, nor between RCP 4.5 and RCP 8.5. Nevertheless, both the current climate scenario and RCP 2.6 had a significantly ($p < 0.05$) lower relative humidity than RCP 4.5 and RCP 8.5 (Figure S2c). Although precipitation showed an increasing trend from the colder scenario (the current climate) to the warmest climate scenario (RCP 8.5), no significant difference ($p > 0.05$) was identified between the four climate scenarios (Figure S2d). Radiation showed a decreasing trend from the coldest scenario (the current climate) to the warmest climate scenario (RCP 8.5; Figure S2a). The current climate had significantly ($p < 0.05$) higher radiation than RCP 4.5 and RCP 8.5, but not RCP 2.6. Moreover, there were no significant ($p > 0.05$) differences in radiation between all future climate scenarios (Figure S2a).

3.2 | Effect of climate scenario, water level management and their interaction on respiration, NEE and GPP

The results of the 2-year climate change simulation showed no statistically significant effect of climate scenario on NEE or its components (GPP and respiration). The effect of water level management was significant ($p = 0.013$) on NEE, but not significant for respiration and GPP ($p > 0.05$).

The respiration ranged from 4×10^{-7} to 0.3 mg CO_2 m^{-2} s^{-1}. The lowest seasonal average of respiration (0.0023 mg CO_2 m^{-2} s^{-1}) was noted for winter 2019 for the managed mesocosms under the current climate scenario and the highest seasonal average of respiration (0.16 mg CO_2 m^{-2} s^{-1}) was recorded for summer 2019 in the managed mesocosms under RCP 2.6 (Figure 2a). The Bonferroni test did not show significant differences between the respiration of managed and unmanaged mesocosms for different climate scenarios (Figure 3a). However, the respiration in the managed mesocosms was 1.8 times more than in the unmanaged ones for RCP 8.5 (Figures 3a and 4a). There was a small difference between the respiration of managed and unmanaged mesocosms under RCP 4.5 (Figures 3a and 4a). The ratio of managed to unmanaged mesocosm respiration was 0.6 and 0.7 for RCP 2.6 and the current climate scenario, respectively (Figures 3a and 4a).

Gross primary production ranged from −0.48 to 0.023 mg CO_2 m^{-2} s^{-1}. The lowest seasonal average of GPP (−0.280 mg CO_2 m^{-2} s^{-1}) was noted for summer 2019 for the managed mesocosms under RCP 8.5, whereas the highest seasonal average of GPP (−0.003 mg CO_2 m^{-2} s^{-1}) was recorded for winter 2019 for the managed mesocosms under the current climate scenario (Figure 2c,d). No significant (Bonferroni test; $p > 0.05$) differences were found between the GPP of the managed and unmanaged mesocosms for different climate scenarios (Figure 3c). The highest average of GPP (lowest average of photosynthesis) was noted for the unmanaged mesocosms subjected to RCP 8.5 followed by the managed mesocosms for the current climate scenario (Figures 3c and 4b). The ratio of GPP for the managed to the unmanaged mesocosm showed that the effect of water level management is more critical for the warmest climate scenario: RCP 8.5 had a ratio of 2.8 compared to the ratio of, for example, RCP 4.5, which was only 1.5 (Figure 4b). Surprisingly, the effect of water level management did not improve the rate of GPP in the managed mesocosms for RCP 2.6 and the current climate scenario, as the ratio of GPP for the managed to unmanaged mesocosms regarding RCP 2.6 and the current climate were 0.8 and 0.7, respectively (Figure 4b).

Net ecosystem exchange ranged from −0.420 up to 0.084 mg CO_2 m^{-2} s^{-1} over 2 years. The lowest seasonal average of NEE (−0.170 mg CO_2 m^{-2} s^{-1}) was noted for autumn 2019 regarding the managed mesocosms under RCP 8.5 while the highest seasonal average of NEE (0.040 mg CO_2 m^{-2} s^{-1}) was recorded for summer 2019 concerning the unmanaged mesocosms under RCP 8.5 (Figure 2e,f). The highest average of NEE (lowest average of CO_2

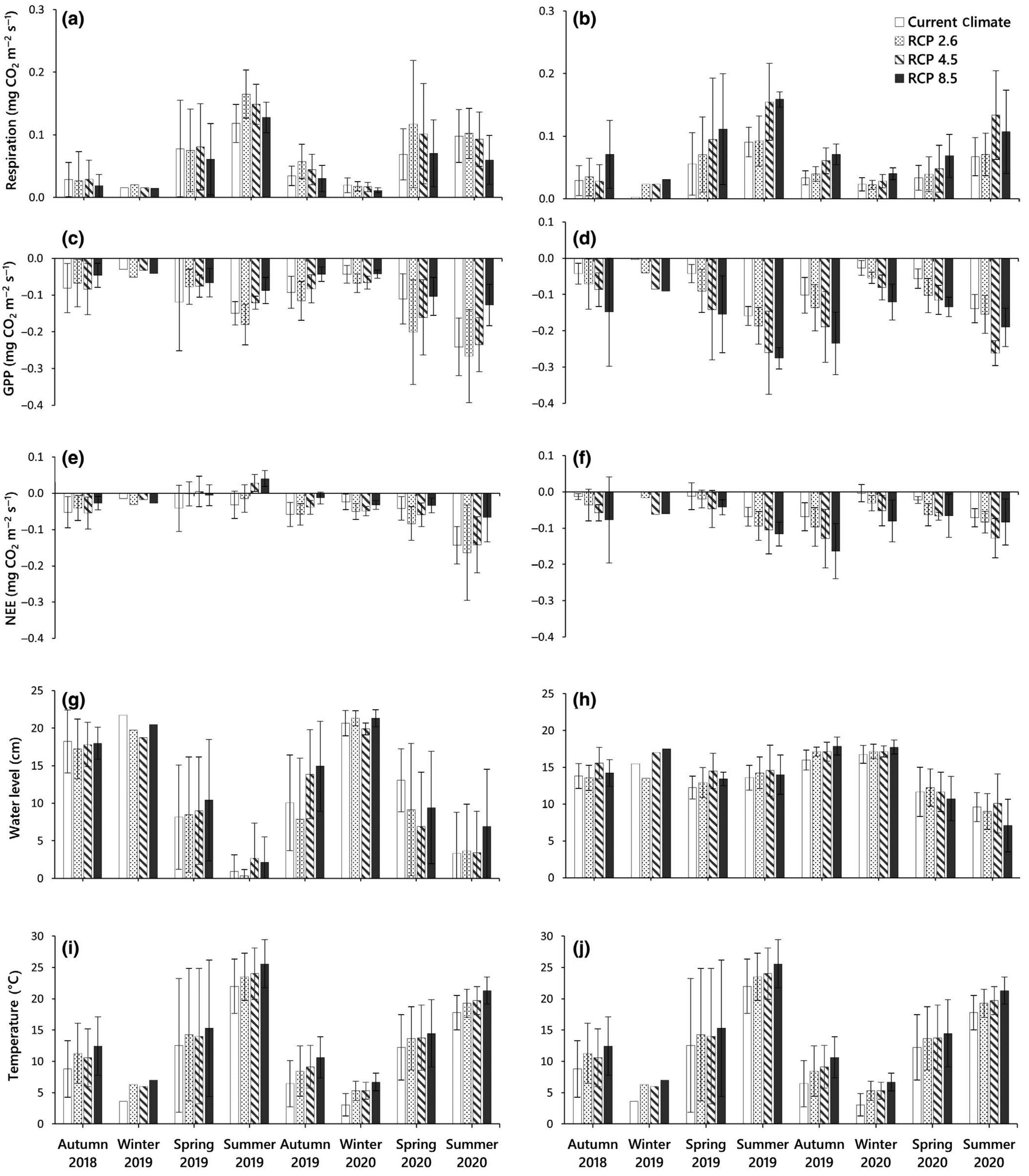

FIGURE 2 Seasonal averages for respiration, gross primary production (GPP), net ecosystem exchange (NEE), water level and temperature of managed and unmanaged mesocosms under different climate scenarios (current climate and representative concentration pathways [RCP] 2.6, RCP 4.5 and RCP 8.5) are illustrated over period of experiment from 2019 to 2020

uptake) was recorded for the unmanaged mesocosms under RCP 8.5 followed by the managed mesocosms under the current climate scenario. Moreover, the results of the Bonferroni test showed a significant difference (p = 0.041) between the NEE average of the managed and unmanaged mesocosms under the climate scenario RCP 8.5 (Figure 3e). The ratio of managed mesocosm NEE to the unmanaged mesocosm NEE was the highest for RCP 8.5 (5.8) followed by RCP 4.5 (2.1), RCP 2.6 (1.1) and CC (0.6; Figure 4c).

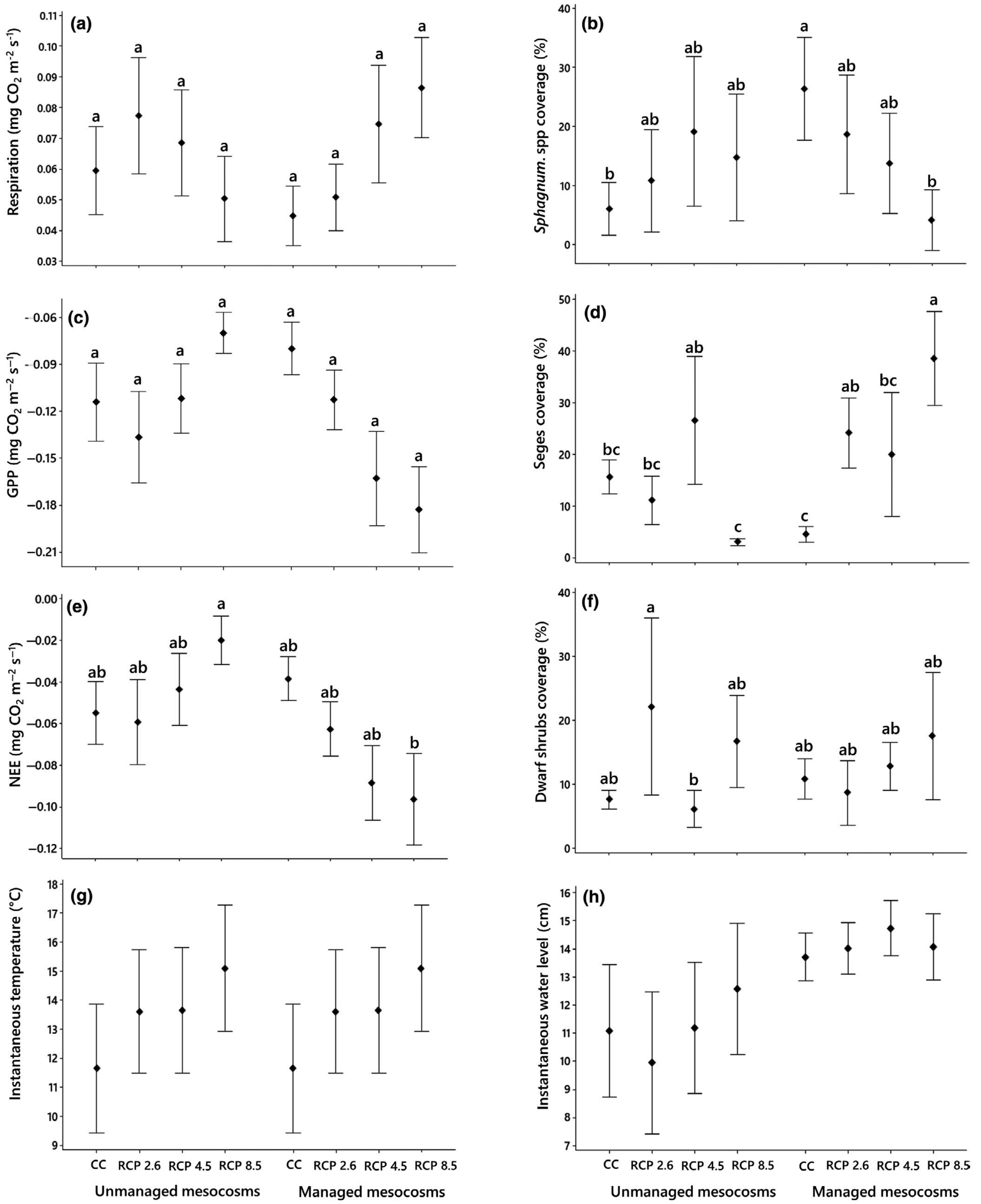

FIGURE 3 (a) Respiration means; (b) *Sphagnum* spp. coverage means; (c) gross primary production (GPP) means; (d) sedges coverage; (e) net ecosystem exchange (NEE) means; (f) dwarf shrubs coverage; (g) instantaneous temperature; and (h) instantaneous water level for managed and unmanaged mesocosms under different climate scenarios (current climate [CC] and representative concentration pathways [RCP] 2.6, RCP 4.5 and RCP 8.5). Means that do not share a superscripted letter are significantly different at $\alpha = 0.05$ (Bonferroni adjusted significance test). Note: The significant difference test was only performed for the responses (a–f) and not for the environmental parameters (g and h)

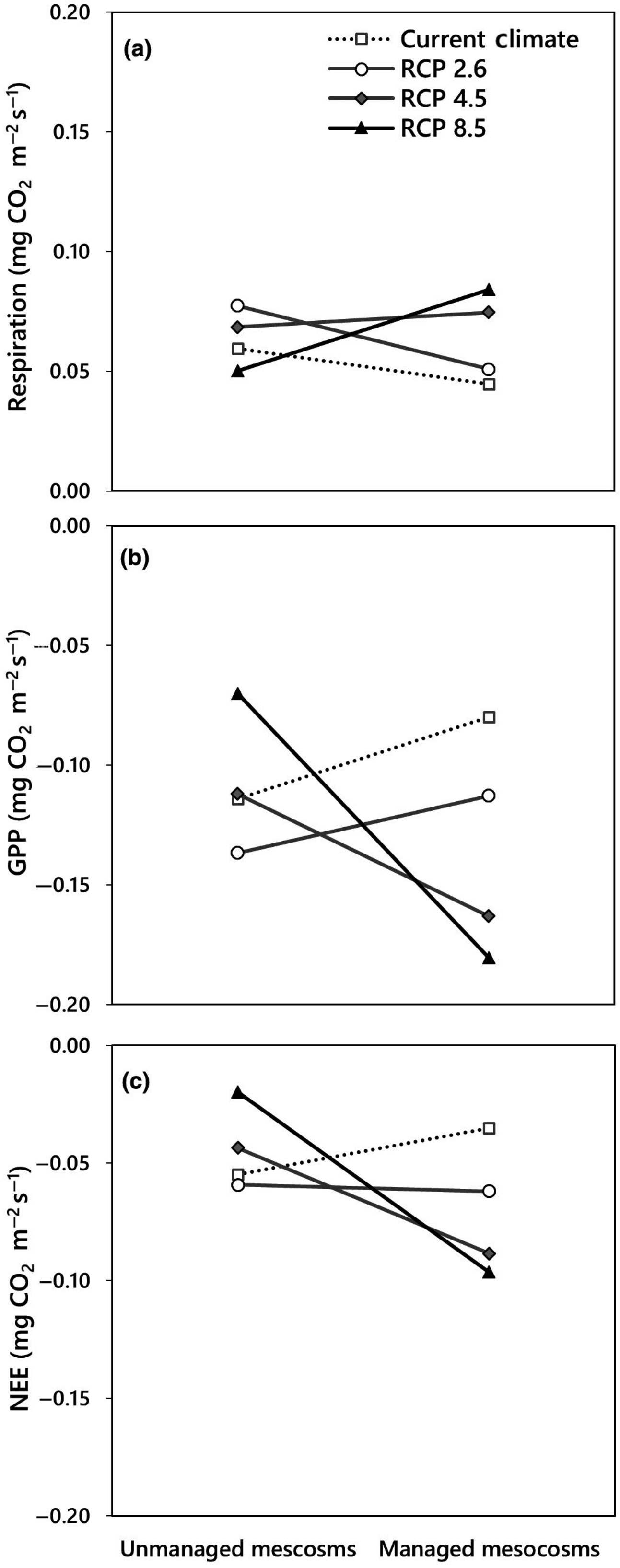

FIGURE 4 The responses of (a) respiration; (b) gross primary production (GPP) and (c) net ecosystem exchange (NEE) to the interactive effect of climate scenarios (current climate and representative concentration pathways [RCP] 2.6, RCP 4.5 and RCP 8.5) and water level management (managed and unmanaged mesocosms) are shown as mean values in the interaction plots

The interactive effect of water level management and climate scenario was significant for all measured variables: NEE ($p = 0.013$), GPP ($p = 0.014$) and respiration ($p = 0.018$). Comparison of the managed and unmanaged mesocosms revealed that the interactive effect of water level management and climate change resulted in greater variability of NEE, GPP and respiration in the managed mesocosms (Figure 4). The authors found an inverse interactive effect of water level management and climate change on GPP and respiration; that is, GPP and respiration showed a decreasing trend from the unmanaged mesocosms to the managed mesocosms under RCP 4.5 and RCP 8.5, whereas this trend was increasing for RCP 2.6 and the current climate scenario.

Regarding NEE, the interactive effect of water level management and climate change caused the managed mesocosms to have a lower NEE rate than the unmanaged ones under RCP 4.5 and 8.5. However, NEE between the managed and unmanaged mesocosms had no substantial change under RCP 2.6, and the current climate showed an increasing trend from the unmanaged to managed system in contrast to other climate scenarios.

3.3 | Impact of climate change, water level management and their interaction on plant distribution

The results of a two-way ANOVA showed that the effect of climate scenario ($F = 19.27$, $p < 0.001$), water level management ($F = 18.96$, $p < 0.001$) and their interaction ($F = 52.59$, $p < 0.001$) was statistically significant for *Sphagnum* spp. The coverage of *Sphagnum* spp. decreased gradually for both the current and future climate scenarios, but the decline was more drastic for RCP 8.5 (Figure 5a). The significant effect of water level management caused a significantly higher ($p < 0.05$) coverage of *Sphagnum* spp. in the managed compared to the unmanaged mesocosms under the current climate scenario (Figure 3b). The alleviation effect of water level management was the greatest for the current climate (Figures 5a and 3b).

The effect of climate scenario ($F = 39.11$, $p < 0.001$), water level management ($F = 74.32$, $p < 0.001$) and their interaction ($F = 123.81$, $p < 0.001$) was statistically significant for *E. vaginatum*. *E. vaginatum* (hare's-tail cotton grass) increased over time in all managed mesocosms subjected to future climate scenarios, but not for the current climate scenario (Figure 5c). The increase was drastic for the managed mesocosms concerning the scenario RCP 8.5 (Figures 3d and 5c). All unmanaged mesocosms have undergone a gradual increase in *E. vaginatum* coverage, with the exception of those for RCP 8.5, which have experienced a decline (Figures 3d and 5c).

The effect of climate scenario ($F = 25.60$, $p < 0.001$) as well as climate scenario and water level management interaction ($F = 27.02$, $p < 0.001$) were found to be significant for dwarf shrubs. Dwarf shrubs increased its coverage significantly in the unmanaged systems for the RCP 2.6 ($p > 0.05$) compared to other managed and unmanaged systems for the other climate scenarios and considerably for the managed and unmanaged system under the RCP 8.5 scenario (Figures 3f and 5b). However, the authors observed a decline in these systems

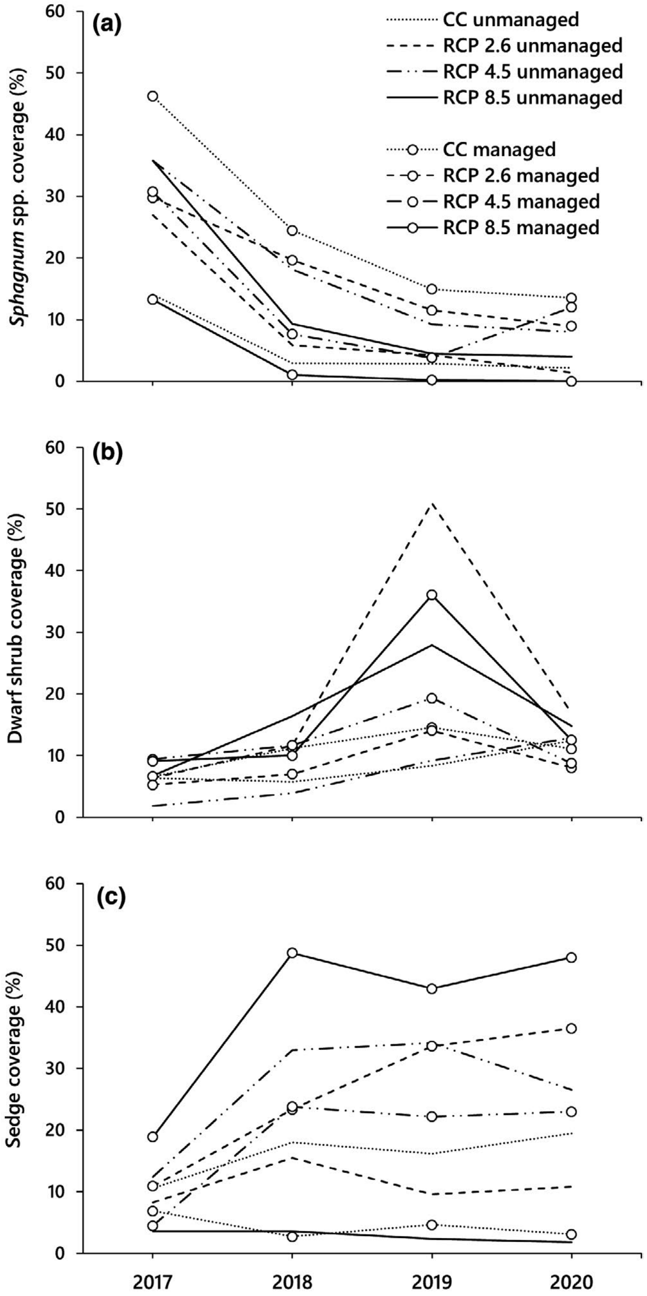

FIGURE 5 Changes in coverage of plant functional types including (a) *Sphagnum* spp.; (b) dwarf shrubs and (c) sedges over the entire period of the experiment. CC, current climate; RCP, representative concentration pathway

for 2020 (Figure 5b). Gradual increases in both managed and unmanaged systems for the other scenarios were not substantial.

4 | DISCUSSION

4.1 | Key interactions

The authors demonstrated that warmer future climate scenarios alone cannot trigger a significant shift in peatland ecosystem sink function (Figures 1 and 3e). However, water availability (water level management), particularly in interaction with temperature (climate scenario), may play an important role in changing the CO_2 sink function of peatlands (Figure 4c). These findings are novel, yet in line with previous studies (Lohila et al., 2011; Sullivan et al., 2008), which emphasize the critical interactive impact of temperature and wetness on GPP and respiration response as either factor alone. Furthermore, the team realized that this interactive effect is essential in shifting plant composition, which is a key factor in determining the response of net CO_2 ecosystem exchange of peatlands subject to global warming and the resulting decrease in water level (Moore et al., 2002; Weltzin et al., 2003).

4.2 | Effect of climate scenarios on the CO_2 sink function of unmanaged mesocosms

The authors expected that the unmanaged system would be the largest CO_2 sink under the current climate scenario, with the lowest temperature, sufficient water level and less water stress during drought. However, this was not the case (Figures 2e and 3e). The team speculates that lower temperatures in this climate scenario could reduce plant productivity and vascular plant expansion, and thus CO_2 uptake (Dieleman et al., 2015; Weltzin et al., 2001). The team found that unmanaged mesocosms under RCP 2.6 had the best CO_2 sink function instead (Figures 2e and 3e), despite having the lowest water level during the growing season during summer and autumn 2019 (Figures 2g and 3h). This finding implies that a slightly higher temperature for RCP 2.6 could induce CO_2 uptake through increased photosynthetic capacity of plants in the unmanaged mesocosms, especially dwarf shrubs, which had the greatest coverage (Figures 3f and 5b). This increased photosynthetic capacity could offset the highest rate of respiration, resulting in the largest CO_2 sink for this scenario. Other studies (Breeuwer et al., 2010; Potvin et al., 2015; Weltzin et al., 2003) also reported an increased NEE of CO_2 as a result of higher temperature and lower water level. They indicated that a lower water level could improve oxygen supply to plant roots and nutrient availability, which are the factors that can lead to a higher vascular plant productivity (Ratcliffe et al., 2019; Walker et al., 2015) and also higher respiration rates (Ise et al., 2008).

A lower CO_2 sink function under the warmer climate scenarios RCP 4.5 and RCP 8.5 was observed as predicted (Figures 2e and 3e). Possibly, a lower CO_2 sink would be in part due to a higher rate of decomposition and respiration during drought (Figure 2a) as a result of higher temperature (Bubier et al., 2003; Davidson & Janssens, 2006). In addition, a lower CO_2 sink function seems to be associated with the gradual decrease in plant GPP, which declined due to the drought of 2019 and high temperatures in 2019 and 2020 during the growing seasons, over the course of the experiment (Figures 2c and 5).

In general, findings demonstrated that under future climate scenarios, all unmanaged systems will continue to serve as CO_2 sinks throughout the experiment period (Figures 2e and 3e). However, under the stress of drought, the unmanaged systems under RCP 4.5

and RCP 8.5 lost their photosynthetic efficiency and switched to becoming CO_2 sources (Figures 2e and 6). The unmanaged system under RCP 2.6 could have a stronger net CO_2 sink function compared to the ones under other future climate scenarios and be able to act as CO_2 sinks even during droughts (Figures 2e and 6), owing to a boosted dwarf shrub primary production. These results support the findings by Wu and Roulet (2014), who modeled both fens and bogs, and found that bogs are less sensitive to the future IPCC climate scenarios (A1B, A2, B1 and Commit) until 2100. They indicated that bogs might still be a carbon sink up to 2100 for almost all future climate scenarios through an enhanced GPP, but that their sink role will be reduced relative to baseline fluxes under the present climate conditions.

4.3 | Impact of drought on the CO_2 sink function of unmanaged mesocosms

The unmanaged mesocosms in both current climate and RCP 2.6 scenarios preserved their sink function during the 2019 drought (Figures 2e and 6), suggesting less drought tension under these scenarios due to lower temperature (Figures 2i and 6), even at zero water level (Figure 6). In accordance to this finding, Parmentier et al. (2009) noted that when the water content of the soil is adequate for plant activity, CO_2 flux is less sensitive to the water level status. Furthermore, Ratcliffe et al. (2019) suggested that the resistance of the dominated vegetation group to lower water levels was a critical factor in maintaining the resilience of CO_2 sink efficiency within peatlands.

The high rate of CO_2 uptake in the unmanaged system under RCP 2.6 decreased during the extreme and long drought of 2019 (end of May–July), but the systems maintained their CO_2 sink function (Figure 6). In the following summer of 2020, when the plants were not under drought stress, the rate of CO_2 uptake increased due to the recovery of plants (particularly dwarf shrubs) to the extent that they were the largest CO_2 sink compared to all other managed and unmanaged systems in other climate scenarios (Figures 2e and 6). Reduced sensitivity of shrubs to the hydrology (Bragazza et al., 2013; Ratcliffe et al., 2019) and elevated sensitivity to temperature has been reported in other studies (Dieleman et al., 2015; Munir et al., 2015; Radu & Duval, 2018) as appears to be happening for the unmanaged mesocosms under RCP 2.6 in this study. Furthermore, Flanagan and Syed (2011) noted that nearly equal increases in photosynthesis and respiration of an ecosystem exposed to climate change can keep the system balanced in terms of net CO_2 ecosystem exchange. Thus, with a slightly warmer climate such as RCP 2.6, increased photosynthesis offset higher respiration, and the negative effects of drought are compensated in subsequent years with normal precipitation.

The severe drought in 2019 caused unmanaged mesocosms under the RCP 4.5 and RCP 8.5 scenarios to switch temporarily from sinks to sources (Figures 2e and 6). Vascular plants respond to drought, physiologically and structurally, to minimize water loss, and this causes a major decrease in the photosynthetic efficiency of unmanaged mesocosms under RCP 4.5 and RCP 8.5 scenarios (Cai et al., 2010). In addition, the exposure of these mesocosms to severe droughts under these two climate scenarios resulted in *Sphagnum* spp. mortality (Figure 5a) and a consequent shrinkage and subsidence of the top surface of the mesocosms (Dieleman et al., 2015; Leifeld & Menichetti, 2018a, 2018b).

In line with the findings of this study, Lund et al. (2012) confirmed a shift from sink to source during a long and early drought during the growing season in Fäjemyr, where the mesocosms in this study were sampled, which could have an adverse influence on canopy

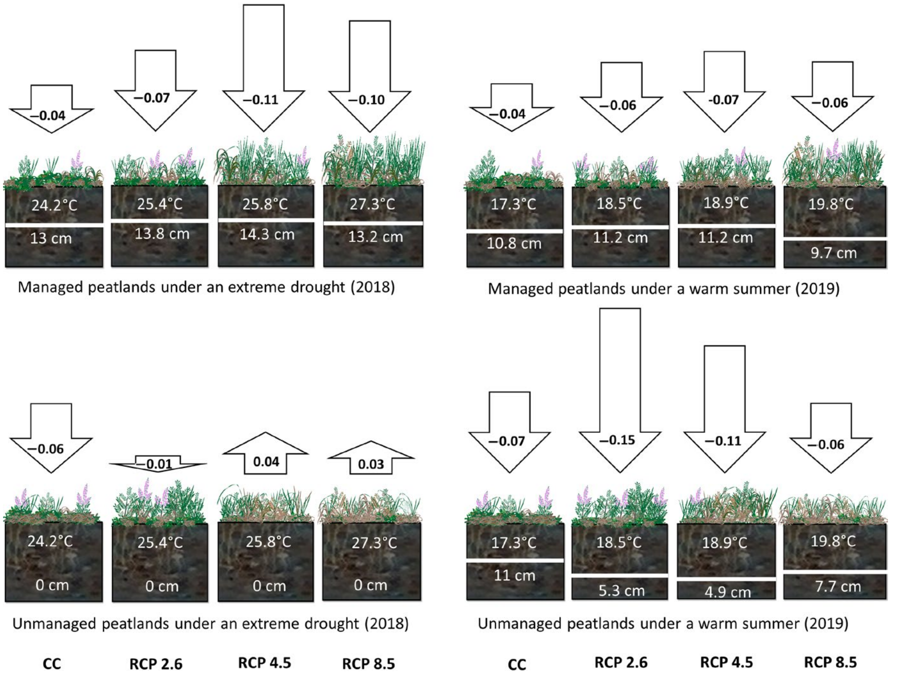

FIGURE 6 Magnitude of carbon dioxide sink function of peatland mesocosms under different climate scenarios (current climate and representative concentration pathways [RCP] 2.6, RCP 4.5 and RCP 8.5) during the warmest months (May, June and July) for two extreme summers in 2018 and 2019 (real time) simulated in 2019 and 2020 in the experiment respectively. The values indicate net ecosystem exchange; the net CO_2 sink has been expressed as a negative value while the net CO_2 source expressed as a positive value. Water level averages are shown by white lines and the values underneath them. The temperature averages indicate the temperatures within the climate chambers

development and thus reduce the system GPP. Thus, water stress may have a more serious impact on plant functionality in warmer climates indicated by RCP 4.5 and RCP 8.5 during drought.

Both unmanaged systems under RCP 4.5 and RCP 8.5 recovered from the drought and returned to the carbon sink state during the subsequent autumn rains (Figure 2e). These findings are supported by Kuiper et al. (2014) showing a rapid recommence of CO_2 uptake after rewetting the mesocosms. However, they reported that the mesocosms without ericoids could recover faster. In comparison, in this study, more or equal CO_2 uptake by the mesocosms with relatively more ericoid plants (e.g. RCP 2.6 scenario) was noted (Figure 6). Moreover, Jassey and Signarbieux (2019) documented that boreal systems benefited from transitional warming-induced photosynthesis, but highlighted the vulnerability of ecosystems to extreme warming and drought that can have lasting consequences. In this study, during the summer of 2020, unmanaged mesocosms under the RCP 8.5 scenario have lost some of their sink function relative to the other climate scenarios (Figures 2e and 6). The unmanaged mesocosms under RCP 8.5 have undergone irreversible changes for plants such as *Sphagnum* spp. and sedges (Figure 5a,c), which slightly diminished the photosynthetic efficiency (Figure 2c) and they could not recover as efficient as the ones for the RCP 2.6 and RCP 4.5 scenarios (Figures 2e and 6). In line with the results in this study, Buttler et al. (2015) reported that *Sphagnum* moss coverage of an ombrotrophic peatland decreased in response to an interactive impact of warming and reduced soil wetness due to a change in their moss structure affecting its moisture-holding capacity (Dorrepaal et al., 2004). Therefore, for extreme scenarios such as RCP 8.5, natural recovery of peatlands from drought may be unlikely.

The recovery of the carbon sink function of unmanaged mesocosms during the growing season of 2020 (after the drought of 2019) can be due the capacity of these systems to establish more productive plant communities (vascular plants). It was surprising that the unmanaged system could recover to the extent that a year after the drought, they showed a greater sink capacity compared to the managed systems (Figures 2e,f and 6). This can be attributed to the introduction of nutrients (Shaver et al., 1992) into the unmanaged system as a result of the litter decomposition during the drought of 2019. These nutrients were available to plants in the following growing season and boosted their growth rate (Laiho, 2006; Munir et al., 2015; Straková et al., 2012). Shaver et al. (1992) documented that higher CO_2 sequestration rates in plant biomass can occur in nutrient-limited northern peatlands, as higher temperatures can increase nutrient mineralization, making it available for vascular plants. The crucial impact of vascular plants on net CO_2 assimilation in peatlands was also found in other studies (Kuiper et al., 2014; Laine et al., 2012; Ward et al., 2013). However, a further group of studies has stated that an increase in vascular plant coverage can stimulate soil microbes by providing labile carbon, which can mobilize additional energy from the decomposition of relatively old organic matter (Fontaine et al., 2007; Schmidt et al., 2011).

4.4 | Interactive effect of climate change and water level management on the CO_2 sink function of managed mesocosms

The authors found that the response of peatland is a function of the interaction of climate change and water level management. At different circumstances, each of them may play a more or less prominent role. For example, the team observed that NEE and its components (absolute values for NEE and GPP) for the managed system followed the sequence of the climate scenarios (Figure 3a,c,e,g). This implies a strong association of the system to temperature, when the water level was virtually constant for the managed systems. Moreover, when water was continuously available for the managed system, lower temperatures during the 2020 growing season caused lower rates of carbon uptake compared to the 2019 growing season with about 4–5°C higher temperature (Figure 6). In comparison to the unmanaged systems, the trend of NEE and its components (GPP and reversed respiration) followed the trend of water level (Figure 3a,c,e,h). In accordance with the authors' observation, Bubier et al. (2003) revealed that the water table position within a peatland was the strongest control on respiration during a dry summer, whereas surface peat temperature could explain most of the respiration variability during a wet summer.

The authors found that the effect of water level management differed depending on the climate scenario. They demonstrated that water level management could not enhance the photosynthetic capacity of the mesocosms under the current climate scenario and RCP 2.6 (Figure 4b). This finding contradicts the idea that increasing the water level will promote CO_2 uptake (Karki et al., 2016; Swenson et al., 2019). However, in both cases, the managed mesocosms had a lower respiration than the unmanaged ones (Figure 4a), but they still had a lower and nearly equivalent CO_2 sink power (Figure 4c). In general, higher water levels under the current climate scenario could only result in slightly higher primary production of *Sphagnum* spp. (Chaudhary et al., 2018) compared to the unmanaged mesocosms (Figure 3b). Since the coverage of vascular plants, particularly dwarf shrubs, did not increase notably (Figures 3f and 5b), the team could not have observed an improvement in sink function of the managed systems (Munir et al., 2015; Ward et al., 2013) relative to the unmanaged ones under the current climate scenario and RCP 2.6.

Water level management had the greatest positive impact on the sink function of mesocosms under RCP 8.5 followed by RCP 4.5 (Figure 4e) by stimulating the growth of vascular plants (sedges and dwarf shrubs) during the growing season over the 2-year experiment (Figure 5b,c; Beyer et al., 2021). Other studies showed a lower NEE (higher CO_2 uptake) in the restored areas after rewetting compared to drained peatlands (Karki et al., 2016; Planas-Clarke et al., 2020; Schimelpfenig et al., 2014; Swenson et al., 2019). For example, Nugent et al. (2018) indicated that internal hydrological controls can strengthen the stability and strong carbon sink function of peatlands during summer drawdowns. As a result, in warmer climates, particularly during drought, water level management can have a profound impact on maintaining the sink function of peatlands.

The authors observed a marginal decline in the sink function of managed mesocosms under RCP 8.5 from 2019 to 2020 (Figure 2f). This is due to a gradual decrease in productive vascular plant coverage (Figure 5b,c), because of high temperatures over 2 years. These results were expected, in particular, for sedges, which are an arctic-boreal plant group that does not benefit from a long-term extreme warm climate as the one simulated for RCP 8.5. In comparison, continuous growth of sedges in managed mesocosms under RCP 4.5 was observed (Figure 5c), indicating more pleasant conditions for this plant functional type (Olefeldt et al., 2017). In agreement with the results in this article, Dieleman et al. (2015) reported an abundance of vascular plants, especially graminoids (up to 15 times more), at a temperature increase of +4°C compared to ambient temperatures. The results indicate that, while water level management can significantly improve the sink role of managed mesocosms, decreased tolerance of vascular plants (especially graminoids) to higher temperatures during longer warm seasons can reduce water level management efficiency under the warmest climate scenario (RCP 8.5) in the long term.

Overall, the authors highlight the beneficial effects of water level management on plant GPP and sink function of the wetland systems under warmer climate scenarios. They are likely to cope with the adverse impact of climate change and widespread droughts in the future (Beyer et al., 2021; Dai, 2013; Nugent et al., 2018; Wilson et al., 2016). In agreement with results discussed in this paper, Jarveoja et al. (2018) found in their partitioning study that the daily variations in NEE were primarily regulated by plant productivity and the dynamics in respiration were mainly determined by plants rather than by microbial respiration. Although this study emphasizes the important role of plant productivity, which can be manipulated by water level management, a gradual decrease in GPP for a warmer climate scenario like RCP 8.5 could be expected over the long term even with active water level management. However, to meet the Paris Agreement target (i.e. limiting the rise in global temperature to well below 2°C), the peatlands at risk need to be rewetted to reduce the emission of too much CO_2 (Günther et al., 2020).

5 | CONCLUSIONS AND RECOMMENDATIONS

The CO_2 sink function of peatlands is largely controlled by plant functional types. The plant population proportions shift over time in response to climate change, and that this shift can cause uncertainty in the ecosystem response as it might vary considerably depending on both the magnitude of climate change and the severity of management actions.

The effect of climate scenarios on NEE and its components (GPP and respiration) depends upon whether the system is managed or unmanaged in terms of water level regulation. Temperature was the main driver for the sink function, when the water is almost equally available to the managed wetland systems. However, for the unmanaged systems, the lowest water level was associated with the largest sink. This unexpected result is due to the differential impacts of drought on various climate scenarios, plant succession and vegetation photosynthetic capacity. For example, systems impacted on by the RCP 2.6 scenario combined with low temperature will experience less drought stress, and vascular plants will benefit from the extra nutrients provided by more oxic conditions caused by drought, boosting the CO_2 sink function. In comparison, plants in warmer climate scenarios experience higher drought stress for RCP 4.5 and 8.5 and will lose a large amount of photosynthetic capacity.

The authors conclude that changes in vegetation communities on the peat top surface play a great role in the CO_2 flux of the peatland ecosystem. This was revealed by comparing GPP and respiration of both managed and unmanaged mesocosms during the growing seasons (spring and summer) between 2019 and 2020. The unmanaged mesocosms under RCP 8.5 had the lowest respiration and photosynthesis rates. These findings are surprising as one might expect that the higher rate of respiration from RCP 8.5 is due to exposure to more extreme drought (2019) and higher temperatures (2020) compared to other climate scenarios. The researchers therefore concluded that the lowest respiration for RCP 8.5 can be attributed to the mortality of the plants (mainly sedges and *Sphagnum* spp.), because of the stress factor of higher temperature and drought. This might have an adverse irreversible consequence for RCP 8.5, but not for other future climate scenarios.

The significant difference between the managed and unmanaged systems under RCP 8.5 implies the necessity of water level management for this scenario. In addition, the positive impact of water level management for the RCP 4.5 scenario was evident as well. Although the advantageous impact of water level management has been demonstrated for warmer climate scenarios in this experiment, the impact of plant succession, dominance of plants with higher decomposition sensitivity as well as change in microbial community on the carbon sink function of peatlands is not clear for the long term, and the experiments supported by large-scale field trials should be continued to assess these influences.

Water level management, according to the findings of this and other studies, is an effective method for mitigating climate change. Referring to the observed trend of NEE in response to the interaction of climate change and water level management, the team concludes that water level management is necessary for RCP 8.5, beneficial for RCP 4.5 (particularly during drought), and not essential for RCP 2.6 and the current climate.

In this study, a critical impact of plant functional type on peatland CO_2 sink function was noted. Therefore, the authors recommend that a new experimental setup be established to investigate the impact of different plant functional types on CO_2 emission and water availability. In such a future study, plant functional types need to be regarded as a treatment (independent variable) affecting the CO^2 emission and water availability of peatland ecosystem as the response (dependent variable).

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CONFLICT OF INTEREST

None.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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