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Effects of climate warming on *Sphagnum* photosynthesis in peatlands depend on peat moisture and species-specific anatomical traits

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Abstract

Climate change will influence plant photosynthesis by altering patterns of temperature and precipitation, including their variability and seasonality. Both effects may be important for peatlands as the carbon (C) sink potential of these ecosystems depends on the balance between plant C uptake through photosynthesis and microbial decomposition. Here, we show that the effect of climate warming on *Sphagnum* community photosynthesis toggles from positive to negative as the peatland goes from rainy to dry periods during summer. More particularly, we show that mechanisms of compensation among the dominant *Sphagnum* species (*Sphagnum fallax* and *Sphagnum medium*) stabilize the average photosynthesis and productivity of the *Sphagnum* community during summer despite rising temperatures and frequent droughts. While warming had a negligible effect on *S. medium* photosynthetic capacity (A_{max}) during rainy periods, A_{max} of *S. fallax* increased by 40%. On the opposite, warming exacerbated the negative effects of droughts on *S. fallax* with an even sharper decrease of its A_{max} while *S. medium* A_{max} remained unchanged. *S. medium* showed a remarkable resistance to droughts due to anatomical traits favouring its water holding capacity. Our results show that different phenotypic plasticity among dominant *Sphagnum* species allow the community to cope with rising temperatures and repeated droughts, maintaining similar photosynthesis and productivity over summer in warmed and control conditions. These results are important because they provide information on how soil water content may modulate the effects of climate warming on *Sphagnum* productivity in boreal peatlands. It further confirms the transitory nature of warming-induced photosynthesis benefits in boreal systems and highlights the vulnerability of the ecosystem to excess warming and drying.

KEYWORDS
climate change, extreme events, net photosynthesis, phenotypic plasticity, soil water content, *Sphagnum fallax*, *Sphagnum magellanicum*, temperate and boreal ecosystem, trait plasticity

1 | INTRODUCTION

Northern ecosystems currently experience an unprecedented era of climatic changes. All historical records have witnessed important increase in air temperature during the past decades that are likely to exceed 2°C on average by the end of the century (Marcott, Shakun, Clark, & Mix, 2013). Along with warming, observational data further evidenced interannual and seasonal variability in precipitation patterns (Fischer & Knutti, 2016; Groisman et al., 2005; Wang et al., 2017). Most detectable changes are the increase of the frequency and intensity of heavy precipitation and drought events (Dai, 2013; Fischer & Knutti, 2016; Martin, 2018). Global

and regional climate models showed that more heavy precipitation episodes often lead to longer period of continuous dry days (Allan & Soden, 2008) at the expense of light and moderate precipitation (Dai, 2011; Ljungqvist et al., 2016; Sherwood & Fu, 2014). It is, therefore, crucial that we increase our understanding of the potential impact of future climate changes on northern ecosystems, as warming and precipitation variation are expected to cause dramatic shifts in their structure and composition (Bjorkman et al., 2018; Elmendorf et al., 2012), with potential global consequences.

Northern ecosystems contain nearly half of the world's belowground carbon (C). As major soil C stock (Yu et al., 2011), peatlands are expected to contribute to the majority of warming-induced soil C loss over the next century (Crowther et al., 2016). Plant photosynthesis strongly affects C balance of peatlands (Frolking et al., 1998), which in turn influence regional and global climates (Booth et al., 2012; Peichl et al., 2018). More particularly, photosynthesis of peat-forming mosses (*Sphagnum* spp.) strongly influence below-ground C storage (Bengtsson, Granath, & Rydin, 2016). Nearly 16% of the annual net C fixed through photosynthesis by *Sphagnum* mosses is stocked belowground as peat (Laiho, 2006), corresponding to a net C accumulation of ca. 40 g m^{-2} year^{-1} in wet years (Roulet et al., 2007). Understanding the sensitivity of *Sphagnum* photosynthetic metabolism to temperature and precipitation changes thus emerges as the most important need for better predicting the consequences of climate changes on C balance in northern ecosystems.

Whether northern peatlands will continue to function as C sink in a warmer and drier climate is currently uncertain (Gallego-Sala et al., 2018; Jassey et al., 2018; Laine et al., 2019; Walker, Ward, Ostle, & Bardgett, 2015; Wang, Richardson, & Ho, 2015). Rising temperatures may increase *Sphagnum* photosynthesis and biomass production in wet and cool season where low temperatures can hinder plant growth (Buermann et al., 2018; Buttler et al., 2015; Robroek, Limpens, Breeuwer, & Schouten, 2007). However, recent studies also provide evidence that earlier and warmer springs may lead to less plant productivity during the subsequent summer and autumn, especially in northern ecosystems (Buermann et al., 2018). While warmer springs may favour plant biomass production through the development of larger leaves (Hudson, Henry, & Cornwell, 2011), spring warmth may have a profound impact on plant productivity during the late season through the build-up of water deficits (Aerts, Cornelissen, & Dorrepaal, 2006).

More heavy, but less frequent precipitation events will strongly influence *Sphagnum* microhabitats during the growing season with deeper water tables and drier surface conditions. *Sphagnum* mosses lack stomata and water-conducting tissues, making their C uptake through photosynthesis strongly dependent on water level depth (Robroek et al., 2007; Robroek, Schouten, Limpens, Berendse, & Poorter, 2009). Capillary rise usually provide water from the water table to the *Sphagnum* capitulum (i.e. apical and living part of *Sphagnum* moss) when the water table is shallow (Ketcheson & Price, 2014). In case of a deep water table, capillary rise strongly decreases (McCarter & Price, 2012), and so does the *Sphagnum* C uptake. Intense summer droughts leading to deep water table are thus

expected to significantly reduce *Sphagnum* C uptake (Robroek et al., 2009). However, quick rainfall events during drought period may counteract the negative effects of drought on moss C uptake (Nijp et al., 2014). Nevertheless, the precipitation-dependent effects on *Sphagnum* C uptake may strongly rely on the water retention capacity of the *Sphagnum* species and their tolerance to droughts. Given the high degree of climate sensitivity of peatland species to either cool or warm climates (Robroek et al., 2017), the intrinsic properties, such as anatomical traits, of dominant *Sphagnum* species are likely to determine the response of peatlands to climate warming in terms of C accumulation (Bengtsson et al., 2016; Laine et al., 2019; Mazziotta, Granath, Rydin, Bengtsson, & Norberg, 2019). Such understanding is urgently needed to predict future trajectories for peatlands under climate change and improve management strategies, global climate models and climate-change mitigation actions.

Here, we took advantage of a 5 year experimental warming setup in a mountain peatland (The Forbonnet peatland; Jassey et al., 2013) to examine the response of *Sphagnum* photosynthesis to warming and precipitation variability. More particularly, during summer 2013, we quantified the photosynthetic capacity of the two most abundant *Sphagnum* species (*Sphagnum medium* and *Sphagnum fallax*) which have different climate sensitivity (Robroek et al., 2017). We further related their photosynthesis performances to characteristic anatomical traits of water retention capacity. Our overarching hypothesis is that effects of climate warming on *Sphagnum* photosynthesis depend on *Sphagnum* moisture conditions. *Sphagnum* species will probably experience both positive and negative effects of climate warming on photosynthesis. We expect positive effects when *Sphagnum* water content is relatively large, but negative effects when the *Sphagnum* mat is dry (<60% water content; Robroek et al., 2009). Nevertheless, we expect that the negative effect of warming in combination with drought will be less dramatic for the species with favourable traits for drought resistance than for the drought-sensitive species.

2 | MATERIAL AND METHODS

2.1 | Field site description, climate manipulation and climatic indices

We conducted the experiment at the Forbonnet peatland located in the Jura Mountains, France (46°49′35″N, 6°10′20″E, alt. 840 m). Mean annual precipitation is ca. 1,700 mm and mean monthly temperatures in January and July are −1.4 and 14.6°C, respectively (meteorological data from the Scientific Research Station). Lawn and hummock microhabitats characterize the peatland surface. In the lawns, *S. fallax* (H. Klinggr.) dominate the moss layer, while in hummocks, *S. medium* (Limpr.; *S. magellanicum* Brid. according to the former classification) and *S. fallax* are the co-dominant moss species (Buttler et al., 2015). Ericoid dwarf shrubs *Calluna vulgaris* (L.), *Vaccinium oxycoccus* (L.), *Andromeda polifolia* (L.) and the two graminoids *Eriophorum vaginatum* (L.) and *Carex rostrata* (Stokes.) characterize the vascular plant community.

In April 2008, three open-top-chambers (OTC; height 50 cm, basal diameter 250 cm) and three control (intact) plots were equally installed in each microhabitat (in total six OTCs, six control plots). In each plot, air temperature (10 cm above the *Sphagnum* surface) was recorded continuously every 30 min using thermocouple probes linked to a Campbell data-logger (CR-1000 Campbell). Overall, OTCs significantly increased mean air temperature in spring and summer by up to ca. 1.3°C. We did not find any difference in light intensity at the *Sphagnum* capitula level between control plots (1,509 ± 27 μmol of photons m^{-2} s^{-1}) and the OTCs (1,496 ± 21 μmol of photons m^{-2} s^{-1}). More details on the OTC effect on air and soil temperature can be found in Delarue et al. (2011) and Jassey et al. (2015). Furthermore, precipitation at the site was continuously monitored using sensors connected to the data-logger. We quantified changes in daily heavy precipitation in the period 2009–2013 using percentile of daily precipitation (Fischer & Knutti, 2016). We first calculated average daily precipitation percentiles of all days (dry and wet) in the period 2009–2013 as a reference. We then binned the summer daily precipitation (June–September period) for each year according to the percentiles defined in the reference period, and observed frequency of occurrence of heavy precipitation (90th–99.9th percentiles), so that for example, 5% of all days fall in the bin 90th–95th percentiles. We further quantified the number of drought events during summer in the period 2009–2013. Any period with a minimum of three consecutive days without precipitation were considered as a drought event. We observed the frequency of occurrence of drought events greater than or equal to 3, 5, 6, 8, 10 and 14 consecutive days without precipitation for each summer between 2009 and 2013. Finally, we calculated a drought index (DI) based on a standardized precipitation evapotranspiration index (SPEI; Vicente-Serrano et al., 2010) to estimate drought severity in summers 2009–2013. We used the FAO-56 Penman-Monteith equation implemented in the *spei* R package to calculate atmospheric evaporative demand (ETo) each month based on average daily minimum and maximum temperatures, average daily temperature, average daily relative humidity, solar radiation, wind speed, latitude and altitude (Vicente-Serrano et al., 2010). SPEI was then calculated as precipitation minus ETo over the June–September period using *spei* R function. We used the reverse of SPEI values as a DI (Prugh et al., 2018), such that DI = −1 × SPEI. Positive DI values indicate an increase of aridity while negative DI values indicate the opposite.

2.2 | Sample collection

In 2013, we collected samples of *S. fallax* (both in hummocks and lawns) and *S. medium* (only in hummocks) for photosynthesis measurements at three different times during the growing season (Figure 1): (a) at the beginning of the summer (late June); (b) after frequent summer drought events (early September); and (c) after heavy precipitation (late September). For each campaign of measurements and in each plot, *Sphagnum* mosses were sampled at four permanently marked spots (ca. 3–5 shoots per spot). The permanent marked spots were placed to avoid any border effect from the OTC which could have decreased the amount of precipitation received by mosses. At the end of the growing season, we further collected *Sphagnum* mosses in every plot (ca. 20 shoots of fresh *Sphagnum*) to capture the integrative effect of 2013 climate on their leaf anatomical traits (see below). All collected *Sphagnum* shoots were cut at 1 cm from the top capitula; that is, *Sphagnum* capitula plus about half centimetre of stem according to the size of the capitulum. The term '*Sphagnum* capitula' is used hereafter for simplicity and to denote that we focused on top living segments of *Sphagnum* mosses only.

2.3 | Photosynthetic capacity, C and nitrogen content

We measured *Sphagnum* photosynthetic capacity (A_{max}) on three to five (depending of the size) *Sphagnum* capitula in order to fill the entire area of the chamber used for the measurements. A_{max} (maximum net CO_2 assimilation rate) was measured with an open-path infrared gas analyser (IRGA) system connected to a 2.5 cm^2 PLC-6 chamber (CIRAS-2; PP-Systems) under optimum conditions for light (i.e. 1,200 μmol of photons m^{-2} s^{-1}, which was previously determined in

FIGURE 1 Climatic conditions in the experiment in 2013. (a) Averaged temperature anomalies (daily mean temperature in warmed plots—daily mean temperature in control plots) and daily precipitation recorded in the experiment in 2013 and for the reference period 2009–2012. Red arrows represent the dates when samples were collected. (b) Frequency of drought events in 2009–2013 calculated as number of days without precipitation >3 (short drought event) to >14 (long drought event)
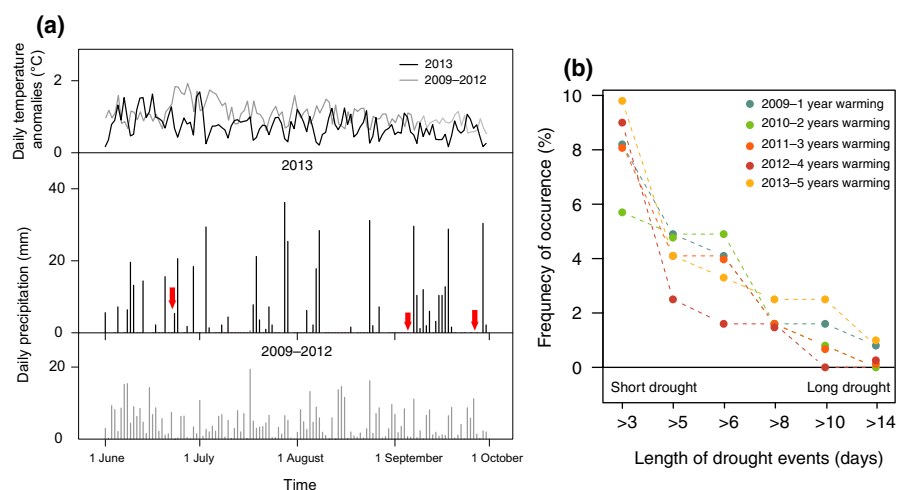
the field), temperature (20 ± 1°C), CO_2 concentration (380 ± 2 ppm) and relative air humidity ranged between 60% and 70%, maintaining a vapor-pressure deficit (VPD) <1 kPa. Immediately after measurements, *Sphagnum* capitula fresh weight was determined, and then capitula were freeze-dried to constant weight (DW). A_{max} was expressed per unit dry weight as mg of CO_2 per gram of DW per hour (mg g^{-1} hr^{-1}). The freeze-dried capitula from each date and plot were homogenized in a ball mill, and analysed for their C and nitrogen (N) concentrations using an elemental analyser (DELTA V Advantage; Thermo Scientific). Furthermore, health of photosystem II (PSII) was assessed through leaf chlorophyll a fluorescence emission using a pulse-modulated Fluorescence monitoring system (PAM-2500; Heinz Walz GmbH). According to Maxwell and Johnson (2000), we measured the maximum PSII efficiency (F_v/F_m) on fresh capitula after 30 min of dark adaptation using 2030B leaf-clip holders (Heinz Walz GmbH).

To estimate the capacity of *S. fallax* to recover from extreme dryness (see Section 3), we performed rewetting response curves. We sampled *S. fallax* capitula with a water content of ca. 20% in four OTC plots (two lawns and two hummocks). We measured A_{max} as described above; that is, several capitula per measurement were used to fill the chamber. We rewatered the capitula in a water cup for 15 min to simulate extreme rain events following drought periods recorded on site (see Figure 1). The capitula were thus submerged in water and reached their maximum water holding capacity after few minutes. Following rewetting, we measured A_{max} every 15 min for an hour on the same capitula. No rewetting response curves were performed on *S. medium* as this species did not suffer from extreme drought in our site (see Section 3).

2.4 | *Sphagnum* productivity

We estimated *Sphagnum* productivity in each plot by multiplying their net CO_2 assimilation rate (A_{max}; mg C g^{-1} hr^{-1}) to total species frequency in each plot and the dry mass of capitula per square centimetre (g/cm^2). First, we measured *Sphagnum* species frequency at peak biomass using the point intercept method in 50 × 50 cm subplots (Buttler et al., 2015). We used a Plexiglas frame with adjustable legs placed above a permanently marked subplot. A 20 holes ruler was moved along 20 different positions so as to obtain 400 measuring points on a regular grid. A metal pin (1 mm diameter) was lowered through each hole in the ruler and each contact of the pin with *Sphagnum* surface was recorded. Then, we divided the average dry mass of *Sphagnum* capitula measured in each plot by the respective species frequency. By doing so, we obtained the productivity of each *Sphagnum* species for each plot, expressed as mg C cm^{-2} hr^{-1}. We then summed *Sphagnum* productivity per plot (*S. fallax* + *S. medium* in hummocks and *S. fallax* in lawns) to estimate the cumulative productivity over the summer and at each sampling date.

2.5 | *Sphagnum* anatomical traits

We characterized the potential resistance of *S. fallax* and *S. medium* to drought using a suite of six anatomical traits: diameter, height and volume of the capitulum, net water content at water saturation of the capitulum, number of hyaline cells in tissues (i.e. empty dead cells storing water) and surface (in μm^2) of the hyaline cells. In total, 120 individuals of *S. fallax* and *S. medium* were collected in the plots to estimate the volume of the capitula (mm^3) by measuring their height and diameter using a precise ruler. Then, we used the same samples to quantify the net water content at water saturated of the capitula for both species. Capitula were watered until they reached their maximum water retention capacity. Excess of water was removed by allowing water to flow naturally after removing capitula from water. Then, individual capitula were weighted water-saturated and dried after 3 days at 80°C. The net water content at water saturated of each individual was thus expressed in grams of water per gram of dry mass (g H_2O_2/g dm). At the cellular level, we randomly took 10 *Sphagnum* leaves from 10 capitula and prepared microscopic slides. We quantified the number of hyaline cells in tissues (number of hyaline cells per mm^2), and their surface (length × width; μm^2) using a light microscope connected to a camera (LEICA ICC50 HD). Ten photographic grips on three individuals of each species were observed (in total 60 pictures), and cell measurements made using the LEICA suite software.

2.6 | Numerical analyses

All data were tested for normality and transformed if necessary. We used linear mixed effects models to test the effects of warming, drought and microhabitat on *Sphagnum* photosynthesis (A_{max}), fluorescence (F_v/F_m), productivity, water content and C and N concentrations in capitula while accounting for the temporal repeated measurements in each plot on the three dates. All models were fitted including plots nested with date as a random effect on the intercept to correct for the inflation of the residual degrees of freedom that would have occurred if we were using repeated measurements as true replicates. The *nlme* package in R was used to run these models (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2019; R Core Team, 2019). As a proxy for drought, we used the total amount of precipitation at the site 2 weeks before each sampling campaign to estimate the intensity and frequency of drought. Similar models were used to test the response of *Sphagnum* photosynthesis to precipitation percentiles. The response of *S. fallax* A_{max} to rewetting over time was tested using linear mixed effects models with time as a fixed effect and plot nested with time as a random effect on the intercept.

3 | RESULTS

3.1 | Micrometeorology

Overall, daily mean air temperature in OTCs during summer 2013 was 0.75°C (0.2–1.6°C) higher than in the control plots ($p < .05$). Although this warming effect was significant, its intensity was lower than the 2009–2012 period (ca. –1°C; Figure 1a). The number of warming anomalies higher than 3°C was indeed three times lower in 2013 (23 days) than in 2009–2012 (on average 75 days). Similarly, precipitation patterns in summer 2013 strongly differed from 2009 to 2012 despite similar

amount of summer precipitation (2013 = 535 mm; 2009–2012 = 550 mm on average; Figure 1a). Moreover, higher drought index in 2013 compared to 2009–2012 confirms that summer 2013 was drier than years before despite similar precipitation amounts (Figure S1). Precipitation in summer 2013 were characterized by a higher frequency of drought events compared to 2009–2012, especially long droughts (i.e. >8 days; Figure 1b). Nevertheless, precipitation records also showed that heavy and very heavy precipitation were more frequent in summer 2012 and 2013 when compared to the period 2009–2011 (Figure S2).

3.2 | *Sphagnum* C, N and water contents

At the beginning and the end of summer 2013, *S. fallax* and *S. medium* water content reached about 90%, both in control and warmed plots. Repeated drought events during summer 2013 reduced the water content of *S. fallax* (−20%, $p < .001$; Table 1) and *S. medium* (−15%, $p < .01$; Table 1) in control plots, although such decrease was more pronounced for *S. fallax* (Figure 2a–c). We found that warming exacerbated the negative effects of summer droughts on *S. fallax* water content with an even sharper decrease of its water content (−75%, $p < .001$; Figure 2a,b; Table 1) while no effect was found on *S. medium* water content ($p = .19$; Figure 2c; Table 1). Neither droughts nor warming influenced C content of either *Sphagnum* species (ca. 460 mg/g dw in both species (Tables 1 and 2). While *S. medium* N content remained stable along with drought and warming, N content in *S. fallax* capitula decreased with drought by 20% in each microhabitat respectively ($p < .01$; Tables 1 and 2).

3.3 | Response of *Sphagnum* photosynthesis and productivity to drought and warming

In general, *S. medium* had a higher maximum net CO_2 photosynthetic rate (A_{max}, 1.69 mg C g^{-1} dw hr^{-1} in controls) than *S. fallax* (0.78 mg C g^{-1} dw hr^{-1} in controls; Figure 2d–f), while their maximum PSII efficiency (F_v/F_m) values, relating to the integrity of the chlorophyll,

were similar (ca. 0.65; Figure 2g–i). Repeated droughts during summer strongly reduced A_{max} of *S. fallax* ($p < .001$; Table 1) and *S. medium* ($p < .05$; Table 1) in controls by 73% and 58% respectively (Figure 2d–f). However, F_v/F_m values of both species were not influenced by drought in control conditions (Figure 2g–i). Rising temperatures had contrasting effects on A_{max} according to *Sphagnum* species. While *S. medium* photosynthesis did not respond to higher temperatures (Figures 2f and 3a; Table 1), the warming treatment had a markedly different effect on A_{max} of *S. fallax* when mosses were either dry or wet (Figures 2d,e and 3b; Table 1). When *S. fallax* moisture was high (mostly 50th and 75th percentiles), warming increased A_{max} by 40% on average (Figure 3b), but whenever substantial moisture deficit occurred (25th percentile), warming decreased *S. fallax* A_{max} by 45% on average. Due to an interaction between warming and drought, *S. fallax* A_{max} even switched from CO_2 assimilation to CO_2 respiration (negative values of A_{max}) in warmed plots (Figures 2d,e, and 3b). Similarly, F_v/F_m of *S. fallax* in warmed plots strongly differed from controls under drought ($p < .001$, Figure 2g,h; Table 1) and dropped below 0.4 in both microhabitats.

Over the summer, cumulative *Sphagnum* community productivity (both species were pooled) was similar in control and warmed plots with ca. 0.09 mg C cm^{-2} hr^{-1} (Figure 4a). This similarity was despite significant variations of *Sphagnum* community productivity according to precipitation amounts (warming × drought: $F_{1,13} = 0.24$; $p = .64$; Figure 4b). More particularly, we found that differential responses of both *Sphagnum* species to warming and/or warming × drought maintained *Sphagnum* community productivity in warmed plots at the end of the growing season. While drought × warming suppressed *S. fallax* productivity (−50%; warming × drought: $F_{1,13} = 5.2$; $p < .05$), we found that warming increased its productivity (+47%) under wet conditions, and thus offset drought-induced loss (Figure 4a). Also important was the resistance of *S. medium* productivity to drought × warming conditions ($F_{1,13} = 0.23$; $p = .64$) that compensated the loss of *S. fallax* productivity under such conditions (Figure 4b,d). On the opposite, the higher productivity of *S. fallax* under wet and warmer conditions compensated the decrease of *S. medium* productivity (Figure 4).

TABLE 1 Summary of models of treatment and environmental effects on *Sphagnum* A_{max}, F_v/F_m, water content (WC), nitrogen (N) and carbon (C) contents in capitula. F and P indicate F-statistics and p values respectively. R^2 corresponds to the adjusted R^2 of the full model

| Source of variance	A_{max}		F_v/F_m		WC		N		C	
	F	p	F	p	F	p	F	p	F	p
Sphagnum fallax (n = 36)										
Warming (W)	0.007	.94	36.7	<.001	25.4	<.001	0.05	.82	0.63	.45
Precipitation (P)	51.1	<.001	57.3	<.001	133.6	<.001	10.2	.004	0.86	.37
W × P	4.3	.049	37.8	<.001	42.2	<.001	0.04	.9	0.11	.75
Habitat × W × P	1.1	.31	0.23	.65	0.06	.81	0.7	.4	0.93	.36
R^2	0.65		0.81		0.86		0.25		0.018	
Sphagnum medium (n = 18)										
Warming (W)	1.2	.34	0.2	.67	0.6	.48	0.8	.43	0.09	.78
Precipitation (P)	8.6	.01	0.05	.83	15.1	.003	2.1	.18	0.93	.36
W × P	0.03	.86	0.4	.55	1.9	.2	1.0	.35	0.02	.9
R^2	0.41		0.05		0.53		0.23		0.07	
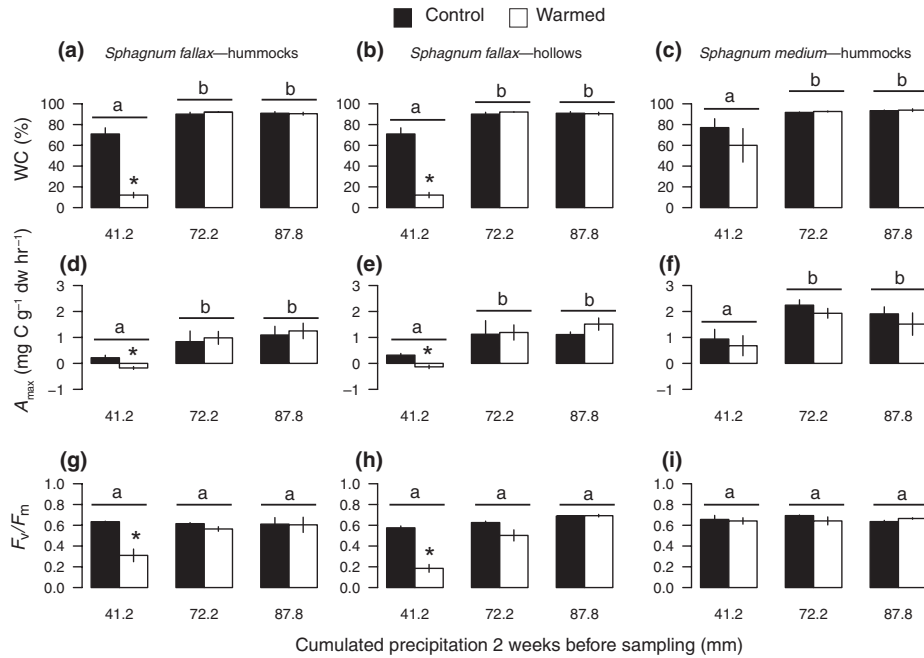
FIGURE 2 Photosynthetic characteristics and water content measured in *Sphagnum fallax* (n = 36; hummocks and lawns) and *Sphagnum medium* (n = 18; hummocks only). (a–c) Water content (%) in *Sphagnum* capitula. (d–f) Maximum net CO_2 assimilation rate (A_{max}) of *Sphagnum* mosses. (g–i) *Sphagnum* maximum efficiency of photosystem II system (F_v/F_m). Letters indicate significant differences at $p < .05$ among periods of cumulated precipitation (linear mixed effect models; see Table 1 for details). Asterisks indicate significant differences at $p < .05$ among control and warmed treatments (linear mixed effect models; see Table 1 for details)

TABLE 2 Summary of anatomical traits of *Sphagnum fallax* and *Sphagnum medium*

	S. medium hummocks		*S. fallax* hummocks		*S. fallax* hollows	
	Mean	SD	Mean	SD	Mean	SD
Morphological traits						
Capitulum diameter (mm; n = 90)						
Control	9.9 a	0.75	4.3 a	0.4	4.2 a	0.3
Warmed	8.9 a	0.45	4.3 a	0.1	3.6 a	0.2
Capitulum height (mm; n = 90)						
Control	6.3 a	0.34	2.9 a	0.2	2.9 a	0.2
Warmed	4.5 b	0.33	3.1 a	0.2	2.7 a	0.2
Capitulum volume (mm^3; n = 90)						
Control	2,824 a	450	287 a	57	254 a	49
Warmed	1,593 b	213	287 a	61	169 a	27
Water holding capacity of capitulum (n = 48; g H_2O_2/g dw)						
Ambient	35 a	0.8	22 a	2.1	26 a	1.9
Warmed	36 a	4.1	26 a	4.3	25 a	0.7
Cellular traits						
Number of hyaline cells (mm^{-2}; n = 60)	1,734	56	2,077	132	n.a.	n.a.
Area of hyaline cells (µm^2; n = 60)	629	24	440	20	n.a.	n.a.
Width of chlorocystes (µm; n = 60)	4.4	0.4	3.2	0.3	n.a.	n.a.

Letters indicate significant differences among warming treatments at $p < .05$ (linear mixed effect models).
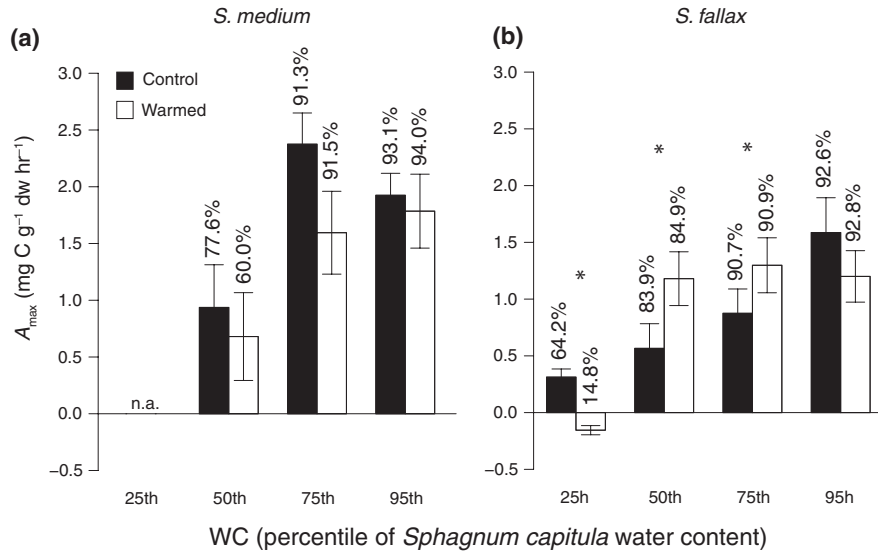
FIGURE 3 *Sphagnum* photosynthesis according to *Sphagnum* capitula water content. Mean maximum net CO_2 assimilation rate ($A_{max} \pm SEM$) of (a) *S. medium* and (b) *S. fallax* in control (black) and warmed (white) treatments compared during periods that ranged from dry to wet conditions. Periods represent *Sphagnum* water content within treatments across all measurements, from dry to wet, that are the 25th, 50th, 75th and 95th wettest percentiles of *Sphagnum* capitula water content for each species and treatment. The percentiles occurred on nearly identical sampling dates in both treatments. Per cent values on the top of bars represent the averaged *Sphagnum* capitula water content within a percentile. They are all similar among treatments, except for the 25th percentile of *Sphagnum fallax* that was drier in warmed plots than in ambient plots. Asterisks indicate significant differences between treatments at $p < .05$ in the same percentile category
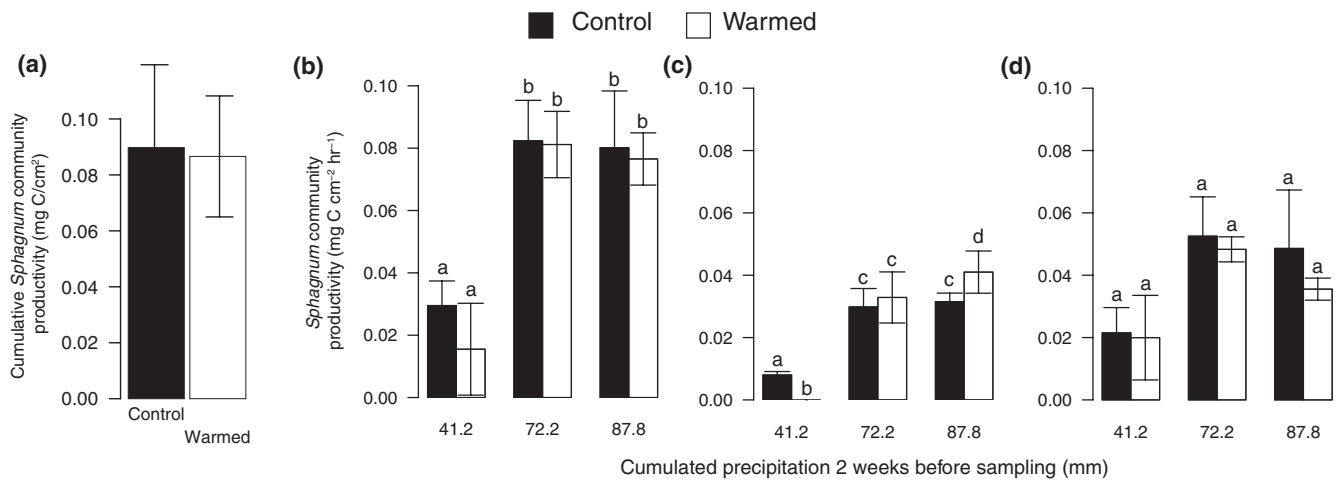

FIGURE 4 Response of *Sphagnum* community productivity to warming (*Sphagnum fallax* and *Sphagnum medium* productivities were pooled). (a) Cumulative *Sphagnum* community productivity for the period June–September 2013 in control (black) and warmed (white) treatments. (b) *Sphagnum* community productivity at each sampling date (represented by cumulative precipitation 2 weeks before sampling) in control and warmed treatments. (c, d) *Sphagnum fallax* (hummocks and lawns pooled) and *S. medium* productivity at each sampling date respectively. Letters indicate significant differences among treatments and dates (linear mixed effects models)

3.4 | *S. fallax* response recovery to drought

Rewetting–response curves showed that *S. fallax* photosynthesis recovered quickly from extreme drought following rewetting, that is, within an hour. *S. fallax* photosynthesis linearly increased with time ($F_{1,15} = 69.9$; $p < .001$; Figure 5) to reach a plateau 45 min after rewetting. After 15 min of rewetting, *S. fallax* photosynthetic capacity was already twofold higher than its initial dry state. After an hour of rewetting, *S. fallax* photosynthesis was sevenfold higher than its initial dry stage with values equivalent to *S. fallax* in healthy conditions (Figure 5).

3.5 | *Sphagnum* water retention capacity

According to their anatomical traits, *S. fallax* and *S. medium* strongly differed in their capacity to hold water. *S. medium* water holding capacity was three times higher than *S. fallax*, thanks to a volume of capitulum eight times higher than *S. fallax* (Table 2). Although *S. fallax* had a higher number of hyaline cells (2,077 hyaline cells, mm^{-2}) than *S. medium* (1,734 hyaline cells, mm^{-2}), the capacity of *S. medium* hyaline cells to store water was 1.5 times higher than *S. fallax* (Table 2). *S. medium* was more efficient in holding water, suggesting a better
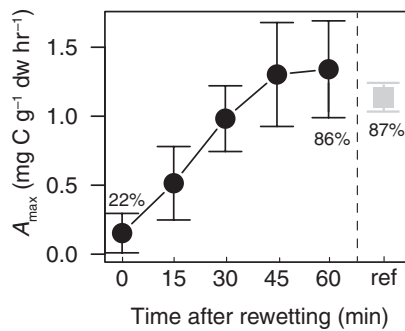
FIGURE 5 Response of the photosynthesis of dry *Sphagnum fallax* capitula to rewetting. Mean maximum net CO_2 assimilation rate ($A_{max} \pm SEM$) of *S. fallax* 0, 15, 30, 45 and 60 min after rewetting (black circles). *Sphagnum* capitula water content at the beginning (0 min) and the end of the rewetting (60 min) are indicated on the plot as percentage values. Grey square represents *S. fallax* A_{max} in control plots with a water content ≥85% as a reference

resistance to drought in term of CO_2 assimilation than *S. fallax* (Fig. S3). Furthermore, *S. fallax* anatomical traits were similar in both microhabitats, and warming and control treatments (Table 2). On the contrary, the size of *S. medium* capitula tended to shrink with warming, as showed by the reduction in capitula's height (–29%; $F_{1,4} = 8.7$; $p = .04$) and volume (–43%; $F_{1,4} = 2.5$; $p = .18$; Table 2) at the end of the growing season. We further found that the response of *Sphagnum* photosynthesis to warming in moist conditions was related to the magnitude of capitulum shrinkage ($p < .01$; Figure S4).

4 | DISCUSSION

Experimental manipulations of climate are essential to disentangling the mechanisms through which climate change will affect species performance and ecosystem processes. By combining an experimental climate warming experiment with the natural intensification of intermittency in precipitation, we were able to simulate a climate change consistent with most recent generations of climate models for northern Europe (Donat, Lowry, Alexander, O'Gorman, & Maher, 2016; Fischer & Knutti, 2016; Wang et al., 2017). Specifically, the increase of heavy precipitation events interrupted with longer, and subsequent more intense drought events in 2013 compared to 2009–2012 was consistent with simulations of future changes in precipitation patterns (Wang et al., 2017). However, despite these shifts in precipitation patterns, total *Sphagnum* primary productivity bore little change in warmed compared to control conditions at the end of the growing season. We showed that the effects of climate warming on dominant *Sphagnum* species productivity flipped from positive to negative as the bog transited from rainy to dry periods. In other words, low soil moisture reduced *Sphagnum* productivity, but most importantly, suppressed the benefits of climate warming on productivity in wet periods. These results highlight the role of compensation dynamic within *Sphagnum* community in stabilizing

its productivity in response to climate change, that is, the ability of species to compensate for the loss productivity when conditions are favourable (Cleland, Chuine, Menzel, Mooney, & Schwartz, 2007; Fu et al., 2019).

The response of both *Sphagnum* species was not consistent with the hypothesis that effects of experimental warming on photosynthesis would be positive during periods of high soil moisture. In rainy periods, warming had a negligible effect on *Sphagnum medium* photosynthetic capacity (A_{max}), whereas A_{max} of *S. fallax* increased by 40%. These findings indicate that the response of *Sphagnum* photosynthesis to temperature increase is not as straightforward as for other genus, like for example boreal trees (Reich et al., 2018). Previous findings showed contrasting effects of temperature on *Sphagnum* ecophysiology (Breeuwer, Heijmans, Gleichman, Robroek, & Berendse, 2009; Dorrepaal, Aerts, Cornelissen, Callaghan, & Van Logtestijn, 2004; Gerdol, 1995; Gunnarsson, Granberg, & Nilsson, 2004; Robroek et al., 2007). In addition to these previous studies, our results suggest that *Sphagnum* species stabilize their community productivity by differences in the magnitude of their responses to rising temperatures. More particularly, such differences may rely on species optimum temperature for photosynthesis as *S. fallax* seems to have its optimum photosynthesis around 30°C (Haraguchi & Yamada, 2011) and *S. medium* around 18°C (He, He, & Hyvönen, 2016). Unlike *S. fallax*, *S. medium* might have reached its maximum photosynthetic rate, explaining the negligible effects of warming on its photosynthesis. However, these previous studies used different protocols to establish the optimum temperatures for photosynthesis of both species, making this assumption wobbly. Furthermore, the average air temperature during the growing season was below 18°C, adding even more uncertainty on the fact that *S. medium* reached its maximum photosynthetic rate. Rather, our results suggest that environmental factors such as intermittence in precipitation and temperature seasonality influenced the underlying biochemical and anatomical determinants of photosynthesis of both *Sphagnum* species differently. We found that the etiolation of warmed *S. medium* capitula seemed to have hampered its ability to increase its photosynthesis. The shrinkage of capitula may have triggered specific adjustments in the leaf anatomical determinants of CO_2 fixation and/or transfer (Sáez, Cavieres, & Galmés, 2018), limiting photosynthetic CO_2 assimilation of *S. medium* under higher temperatures. Ultimately, although the exact mechanisms are unclear, our results suggest that *S. medium* has a lower phenotypic and functional plasticity than *S. fallax* and as such is unable to adapt its morphology to cope with rising temperatures. On longer term, *S. medium* growth might further suffer from warming as suggested by the constant lower values of A_{max} in warmed compared to ambient conditions (Figures 2 and 3).

As expected, and in accordance with previous research (Breeuwer et al., 2009; Laine, Juurola, Hájek, & Tuittila, 2011; Robroek et al., 2007, 2009), limited water availability caused adverse effects on *Sphagnum* photosynthesis (Figure 3). The maximum net photosynthesis decreased once capitulum water content reached 85%; especially *S. fallax* whose water holding capacity was lower than *S. medium*

(Figure S4). Nevertheless, both species maintained a minimum photosynthesis despite long and frequent droughts during summer. More relevant to our overarching hypothesis, the warming treatment had a markedly different effect on *S. fallax* compared to *S. medium* when precipitation was scarce. During drought periods (25th percentile of *Sphagnum* water content), *S. fallax* photosynthesis in warmed conditions switched from CO_2 fixation to CO_2 release, while *S. medium* had similar CO_2 assimilation rate as in control conditions (Figure 3). Collectively, lower *Sphagnum* water content and F_v/F_m are likely to have contributed to making the response of *S. fallax* photosynthesis to warming more negative than *S. medium* at low soil moisture. Exacerbated desiccation in warmed plots most likely damaged the thylakoid membranes of *S. fallax* as indicated by low F_v/F_m (Schwab & Heber, 1984), and, therefore, eliminated the potential benefits of elevated temperature on its photosynthetic performance. Despite identical desiccation in warmed plots, *S. medium* maintained a more stable water content, and then photosynthesis, thanks to its anatomical traits favouring water-holding (Figure S4). This indicates that species having structural characteristics that strengthen their resistance to drought may determine community productivity in extreme drought periods (Fry et al., 2018; Matias, Luis Quero, Zamora, & Castro, 2012) but not necessarily the community assemblage in the near future. Indeed, although *S. fallax* was less resistant to drought than *S. medium*, we found that its photosynthesis fully recovered from extreme desiccation (20% of maximum capitulum water content; Figure S3) after a rewetting equivalent to 85% of capitulum water content. Recovery from desiccation is highly variable among *Sphagnum* mosses (Clymo, 1973; Hájek & Beckett, 2008; Hájek & Vicherová, 2014; Schipperges & Rydin, 1998). However, *Sphagnum* mosses from Cuspidata section (i.e. *S. fallax*) have been shown to survive slow rates of desiccation (Wagner & Titus, 1984) because they harden in the early stages of dehydration by forming a cellular protection. Hardening avoids cell damages, such as degradation of chlorophyll and rupture of cell membranes, and allows *Sphagnum* to tolerate and recover from drought (Hájek & Vicherová, 2014). While *S. medium* can be sensitive to repeated extreme desiccations (Schipperges & Rydin, 1998), our results show that *S. fallax* photosynthesis, and most likely growth, promptly recover following rain drops, suggesting that this species could acclimate to frequent drought events.

Our results provide information on how precipitation may modulate the effects of climate warming on *Sphagnum* productivity in boreal peatlands. Climate models predict shifts in precipitation rainfalls with rising temperatures towards more intense heavy rains but longer dry spells (Trenberth et al., 2014). Thus, the observed responses to climate warming are likely to be indicative of responses to future climate warming in northern peatlands. Furthermore, climate warming is likely to extend the season of active photosynthesis in boreal systems where longer positive effects of warming on *Sphagnum* photosynthesis could help to offset the negative effects of drying on photosynthesis. Although the relative magnitude of such offsets will not be uniform according to species, our results show that *Sphagnum* community should continue to assimilate C over the growing season. This result counters the often implicit assumption that peatlands might turn into a C source instead of C sink under climate warming due to lower *Sphagnum* productivity (Nijp et al., 2015; Wu & Roulet, 2014; Zhao, Peichl, Öquist, & Nilsson, 2016). It rather corroborates the most recent model simulation and experiment of the peatland C sink with warming (Gallego-Sala et al., 2018; Laine et al., 2019). While our results are reassuring in showing that the natural peatland C sink may remain in future, none of the potential changes in vascular plant performance have been taken into account (Gavazov et al., 2018; McPartland et al., 2019; Rastogi et al., 2019). Vascular plants may differ from *Sphagnum* mosses in their sensitivity to rising temperatures and soil moisture (Buttler et al., 2015; Dieleman, Branfireun, McLaughlin, & Lindo, 2015; Mäkiranta et al., 2018; Rastogi et al., 2019), and exert powerful braking effects on potential benefits of climate warming on *Sphagnum* photosynthesis (Bragazza et al., 2016; Gavazov et al., 2018; Jassey et al., 2018).

In summary, our results have important implications for understanding why *Sphagnum* community may maintain ecosystem functioning when subject to future climate warming. We show that functional compensation among *Sphagnum* species, whereby one species increases while the other decreases its photosynthetic performance, is a mechanism underlying weak or absent effects of warming on *Sphagnum* community performance over the growing season. This indicates that an aggregate community process such as productivity can be stabilized by differences in the magnitude and timing of species responses to climate warming (Gonzalez & Loreau, 2009). This is important for peatland conservation as it confirms that peat bog functioning can be maintained if species pool is preserved or compensated by the arrival of species with similar climatic sensitivity (Lamentowicz et al., 2019; Mäkiranta et al., 2018; Robroek et al., 2017). Investing for improving the conservation of the full peat bog species pool appears as the highest priority in the mitigation of peatland impacts on climate change.

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