

Contrasting growth responses of dominant peatland plants to warming and vegetation composition

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Abstract There is growing recognition that changes in vegetation composition can strongly influence peatland carbon cycling, with potential feedbacks to future climate. Nevertheless, despite accelerated climate and vegetation change in this ecosystem, the growth responses of peatland plant species to combined warming and vegetation change are unknown. Here, we used a field warming and vegetation removal experiment to test the hypothesis that dominant species from the three plant functional types present (dwarf-shrubs: *Calluna vulgaris*; graminoids: *Eriophorum vaginatum*; bryophytes: *Sphagnum capillifolium*) contrast in their growth responses to warming and the presence or absence of other plant functional types. Warming was accomplished using open top chambers, which raised air temperature by approximately 0.35 °C, and we measured air and soil microclimate as potential mechanisms through which both experimental factors could influence growth. We found that only *Calluna* growth increased with experimental warming (by 20 %), whereas the presence of

dwarf-shrubs and bryophytes increased growth of *Sphagnum* (46 %) and *Eriophorum* (20 %), respectively. *Sphagnum* growth was also negatively related to soil temperature, which was lower when dwarf-shrubs were present. Dwarf-shrubs may therefore promote *Sphagnum* growth by cooling the peat surface. Conversely, the effect of bryophyte presence on *Eriophorum* growth was not related to any change in microclimate, suggesting other factors play a role. In conclusion, our findings reveal contrasting abiotic and biotic controls over dominant peatland plant growth, suggesting that community composition and carbon cycling could be modified by simultaneous climate and vegetation change.

Keywords *Calluna vulgaris* · Competition · *Eriophorum vaginatum* · Facilitation · Microclimate · Open top chambers · Peatlands · *Sphagnum*

Introduction

Given the dependency of the Earth's climatic and biological systems on the balance between terrestrial and atmospheric carbon (C) (Prentice et al. 2001; Friedlingstein et al. 2006), understanding the effects of climate change on ecosystem C cycling represents a major research challenge of the twenty-first century. It is becoming increasingly apparent that, while warming can directly impact C cycle feedbacks by modifying the balance between net primary production and ecosystem respiration (Davidson and Janssens 2006), indirect effects via changes in vegetation composition also play a significant role (Cornwell et al. 2008; De Deyn et al. 2008; Hooper et al. 2012; Ward et al. 2013). The potential for elevated temperature, and other global change phenomena, to alter the distribution of plants may

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thus have profound consequences for C dynamics in many biomes (Wardle et al. 2011; Metcalfe et al. 2011). Consequently, there is a need for consideration of not only direct effects of changing climate on ecosystem C cycling but also effects of simultaneous, longer-term, changes in vegetation (Bardgett et al. 2013).

Northern peatlands are central to this issue, being the largest but potentially most vulnerable C sink in the terrestrial biosphere (Dise 2009). Undamaged peatlands represent a sizable C sink because the low temperatures and high water tables therein limit microbial decomposition of organic matter, thus facilitating the long-term sequestration of C as peat (Billett et al. 2010). However, the disproportionate level of warming expected in high latitude regions where peatlands mainly occur is causing considerable concern because of its potential to directly stimulate rates of ecosystem respiration (Prentice et al. 2001; Dorrepaal et al. 2009). Coupled with this, there is growing recognition that vegetation change itself can act as a powerful regulator of peatland greenhouse gas fluxes, acting via the ecophysiological traits of dominant plant functional types (Dorrepaal 2007; De Deyn et al. 2008; Trinder et al. 2008). UK peatlands are typically dominated by three plant functional types, namely dwarf-shrubs, graminoids and bryophytes, which differ considerably in such traits. For instance, dwarf-shrubs and bryophytes construct tissue rich in secondary compounds that promote slow C turnover, whereas graminoids facilitate fast C turnover through rapid assimilation and transfer of newly fixed CO₂ (e.g. Trinder et al. 2008; Turetsky 2003; Ward et al. 2009). Consequently, warming-driven shifts in plant community composition, which are expected to favour shrubs (Walker et al. 2006; Gallego-Sala and Prentice 2012), may result in feedbacks to C dynamics due to increased representation of woody traits in the ecosystem. Despite the uncertainties this raises over the future C balance of peatlands, little is currently known about the influence of combined warming and changes in vegetation composition on the growth of dominant peatland plant species.

There are trends in high-latitude regions for warming to directly promote vascular plant growth (Rustad et al. 2001; Hudson et al. 2011; Elmendorf et al. 2012). However, the effect of warming on bryophytes, and in particular *Sphagnum* species, is less clear (e.g. Gunnarsson 2005; Aerts et al. 2006; Bu et al. 2011; Loisel et al. 2012). At the same time, *Sphagnum* mosses have been reported to exhibit control over vascular plant growth via competition for rain-borne nutrients (Turetsky 2003), and by regulating soil community structure (Jassey et al. 2013). Similarly, *Calluna vulgaris* (hereafter *Calluna*), an abundant dwarf-shrub in UK peatlands, can influence co-occurring species through its associations with ericoid mycorrhizae (Genney et al. 2000; Read et al. 2004). Dwarf-shrubs, graminoids

and bryophytes may also have contrasting effects on air and soil microclimate, which could subsequently impact plant growth. For example, species with low albedo can warm the vegetation layer by increasing heat transfer from the atmosphere (Blok et al. 2011b), whereas species with dense canopies may have a cooling effect by shading out direct sunlight (Myers-Smith et al. 2011). Species-specific rates of evaporation and evapotranspiration also influence heat loss from the soil, transferring heat from the surface into the vegetation layer (Groffman et al. 2001; Blok et al. 2011a). Nevertheless, the effects of different peatland plant functional types on air and soil microclimate are not well understood, and very little is currently known about the combined influence of warming and vegetation composition on the growth of dominant peatland plant species.

Here, we used a warming and plant functional type removal experiment (Ward et al. 2013), established on a blanket peat site in northern England, to test the hypothesis that dominant species from different plant functional types differ in their growth responses to combined warming and changes in vegetation composition. We also took corresponding measurements of near-surface air temperature, soil temperature and water table height to investigate these microclimatic variables as potential mechanisms through which experimental warming and changes in vegetation composition influence plant growth.

Materials and methods

Study site and experimental design

The study took place at Moor House National Nature Reserve, a 6,500-ha area of acidic ombrogenous blanket peat in the North Pennines, UK (54°65'N, 2°45'W; altitude 550 m). The climate is sub-arctic oceanic (Heal and Smith 1978), with a mean annual temperature of 5.8 °C and a mean annual precipitation of 2048 mm (UK Environmental Change Network; <http://www.data.ecn.ac.uk>). Air temperature (°C) and rainfall (mm) during the experimental period were representative of long-term trends at the study site, lying within 1 °C and 0.05 mm of the 2000–2013 growing season average, respectively (Fig. S1). Mean peat depth is 1.2 m, over which the vegetation is *Calluna vulgaris*–*Eriophorum vaginatum* blanket mire, *Empetrum nigrum* ssp. *nigrum* sub-community (M19b), as classified by the UK National Vegetation Classification (Rodwell 1991).

We used a fully factorial warming and plant functional type removal experiment established in 2009 (Ward et al. 2013). Briefly, the plant functional type removal treatment was implemented by hand-removing aboveground vegetation to create 1.5 m² plots containing none (bare), one or two plant functional types in all combinations of

dwarf-shrubs, graminoids and/or bryophytes. We maintained the plant functional type removal treatment by regular weeding to ensure that regrowth did not occur. A final control treatment was left fully vegetated with no plant removal, giving a total of eight different plant functional type combinations. Vegetation composition, as percentage cover of different plant functional types, was assessed non-destructively when treatments were established (Fig. S2). *Calluna* (99 %) and *Eriophorum* (99 %) dominate the dwarf-shrub and graminoid plant functional types, respectively, whereas the bryophyte plant functional type is dominated by *Sphagnum* (26 %) and feather moss species (38 %) (Ward et al., unpublished data). We superimposed a passive atmospheric warming treatment on half of the experimental plots to generate ambient and elevated temperature versions of each plant functional type combination. This resulted in a total of 16 treatments, which were replicated in four replicate blocks. The warming treatment was applied using open top chambers (OTCs) modified from the ITEX design to suit peatland vegetation (Marion et al. 1997; Ward et al. 2013), which were left in place throughout the year. While this approach can have confounding effects on climatic variables other than temperature, such as timing of snow melt (Marion et al. 1997; Bokhorst et al. 2013), it remains one of the most robust means of implementing warming treatments in remote field experiments (Walker et al. 2006; Bokhorst et al. 2013).

Plant growth measurements

Sampling took place at approximately 9-day intervals between April and September 2012, giving a total of 13 time points over the growing season. We measured above-ground growth of *Calluna*, *Eriophorum* and *Sphagnum*, representing the dwarf-shrub, graminoid and bryophyte plant functional types, respectively, in plots where they occurred. In order to get a plot-level representation of growth, we took repeated measurements from three individual plants for each species per plot; over four replicate blocks, this resulted in 12 measurements per species for every treatment combination and on every sampling date. We defined discrete tussocks and mats as separate plants for *Eriophorum* and *Sphagnum*, respectively, and defined isolated canopies as separate plants for *Calluna*.

Growth was assessed non-destructively by measuring tissue extension on the major growth axis of each species (Gimingham 1960; Clymo 1970; Wein 1973; Cornelissen et al. 2003). Destructive biomass sampling was not possible due to the long-term nature of the experiment and the slow regrowth of peatland plant species. For *Eriophorum*, we measured the total height of green leaf tissue from the tussock surface (Wein 1973; Cornelissen et al. 2003). For *Calluna*, we measured three evenly spaced terminal shoot

branches per individual plant canopy (area <40 cm²) and calculated the mean of these to generate a canopy-wide estimate of shoot growth for each plant (Gimingham 1960; Keuper et al. 2011; Dawes et al. 2011). These measurements were repeated on the same shoot branches at every time point. *Sphagnum* growth was determined using the crank-wire method (Clymo 1970). Specifically, for each individual, a wire with two opposing 90° bends was fixed to the moss surface such that one end protruded vertically from it and the middle section lay flat against it. *Sphagnum* growth was measured as a decrease in the length of protruding wire between sampling points.

To examine season-wide controls over plant growth, we determined total season growth rates (mm day⁻¹) for all individuals. This was calculated as the change in size, per day, between the largest size measurement and that of the first sampling point. To examine growth at higher resolution across the growing season, we also determined growth rates (mm day⁻¹) between every sequential pair of measurements (approximately 9-day intervals; hereafter ‘within-season growth’).

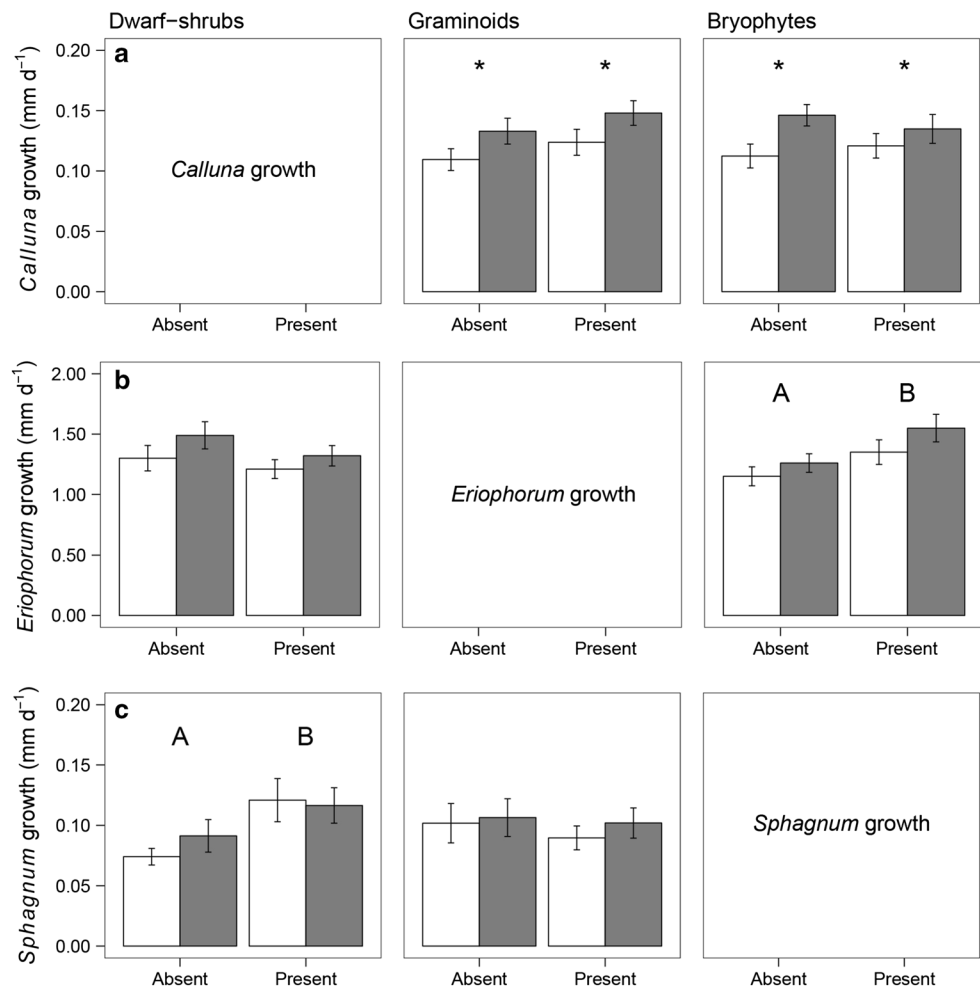
Air and soil microclimate measurements

To determine warming and plant functional type effects on abiotic conditions relevant to plant growth, we monitored air temperature (°C) at canopy height (10–30 cm depending on plant removal treatment), soil temperature (°C) at 5 cm below the peat surface, and water table height (cm below the surface) for the duration of the 5-month study period. Air and soil temperature were recorded using sensors (Lascar Electronics, Salisbury, UK) installed in blocks one to three, whereas water table height was recorded using sensors (Tru Track, Christchurch, New Zealand) installed in 1.5 m dipwells in the same blocks.

Statistical analysis

All data were processed and analysed in R (R Development Core Team 2013), using the packages ggplot2 (Wickham 2009), nlme (Pinheiro et al. 2013), plyr (Wickham 2011) and reshape2 (Wickham 2007). For all variables, we used linear mixed effects models (Zuur et al. 2010) to test for effects of experimental warming, the presence or absence of different plant functional types and their interactions over the growing season. Model assumptions were scrutinised using fitted values versus residuals plots and QQ plots; where necessary, models were refined to account for unequal variance between levels of explanatory variables (Zuur et al. 2010). We determined significance of fixed effects using single term deletions combined with likelihood ratio (LR) tests, retaining variables in models with $P < 0.05$, and used Tukey post hoc comparisons to test for

Fig. 1 Mean total season growth ($\text{mm day}^{-1} \pm 1\text{SE}$) of **a** *Calluna vulgaris*, **b** *Eriophorum vaginatum* and **c** *Sphagnum capillifolium* for plots subjected to an ambient (white bars) or elevated (shaded bars) warming treatment and the presence or absence of dwarf-shrubs (left panel), graminoids (centre panel) or bryophytes (right panel). Plant functional type (PFT) treatments are represented as the presence or absence of a given PFT, irrespective of other PFTs ($n = 8$). Within each panel, different letters indicate significant differences between PFT presence/absence, whereas an asterisk indicates a significant difference between warming treatments



differences between levels of significant factors containing more than two levels.

For growing-season temperature and water table height, we tested for effects of experimental warming, the presence or absence of different plant functional types, and all two-way warming \times plant functional type interactions, including a random intercept term for block nested in date. For total season plant growth, we tested for effects of experimental warming, the presence or absence of different plant functional types, and all two-way warming \times plant functional type interactions on total season plant growth, including a random intercept term for plant nested in plot nested in block to accommodate for multiple plants per plot. To investigate intra-seasonal controls over *Calluna* growth, we tested for effects of sampling date (categorical), experimental warming, the presence or absence of different plant functional types, and all two- and three-way interactions involving date on within-season growth data. Again, this included a random intercept term for plant nested in plot nested in block.

To investigate relationships between microclimate and plant growth, we used Pearson's product moment

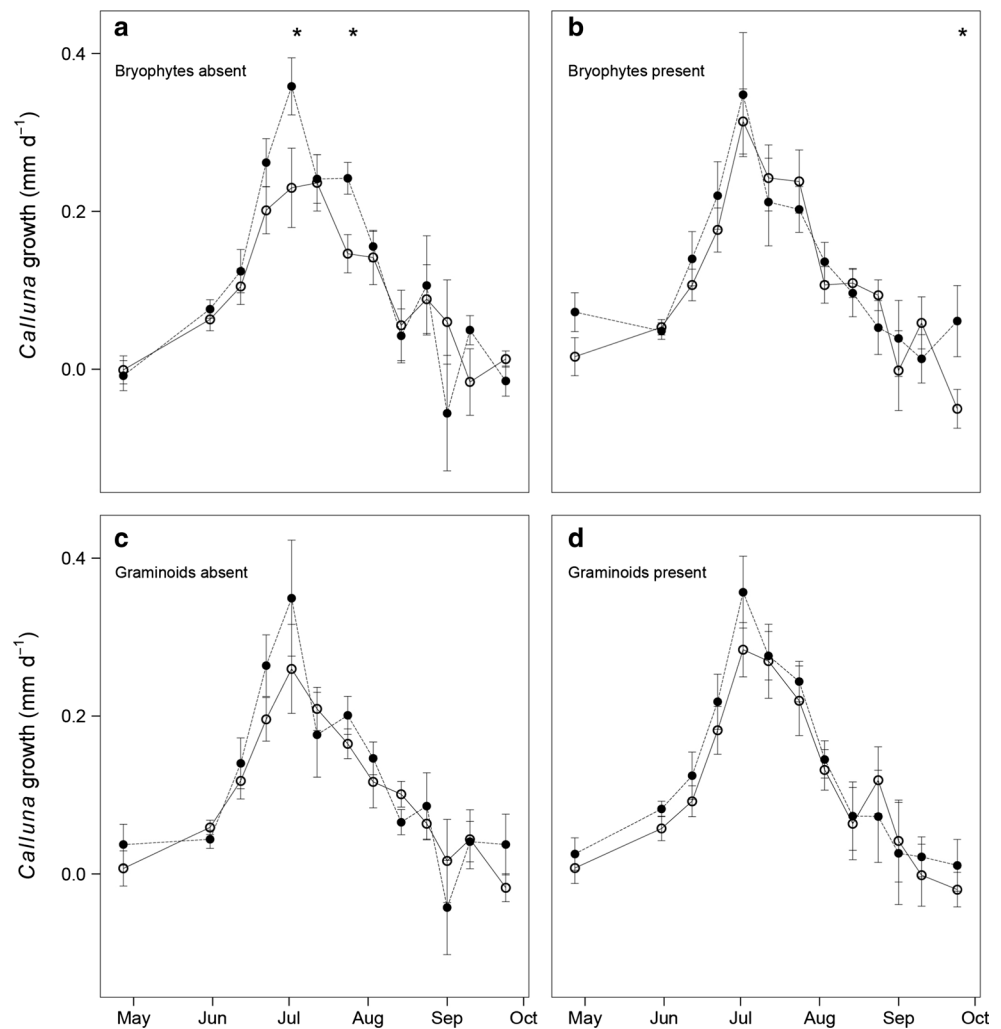
correlations to separately test for associations between air temperature, soil temperature, water table height and within-season plant growth. These were performed on within-season data from all plots and time points, irrespective of experimental treatments. Finally, we additionally isolated all within-season air temperature and *Calluna* growth data relating to the period of peak *Calluna* growth (June–July) and tested for effects of experimental warming, the presence or absence of bryophytes and their interaction on these variables using linear mixed effects models (as above).

Results

Plant growth

Calluna was the only species to respond significantly to experimental warming (Fig. 1), in that total *Calluna* growth over the growing season was approximately 20 % greater in warmed plots than in ambient temperature plots ($LR = 4.71$, $df = 1,7$, $P = 0.0300$). Warming effects on total

Fig. 2 Mean *Calluna vulgaris* growth ($\text{mm day}^{-1} \pm 1\text{SE}$) at 9-day intervals across the growing season for plots subjected to an ambient (*open circles; solid lines*) or elevated (*closed circles; dashed lines*) warming treatment and the **a** absence or **b** presence of bryophytes and **c** absence or **d** presence of graminoids. Plant functional type (PFT) treatments are represented as the presence or absence of a given PFT, irrespective of other PFTs ($n = 8$). For each PFT treatment and date, an *asterisk* denotes a significant difference between warming treatments (Tukey: $P < 0.05$)



season *Calluna* growth were consistent irrespective of the presence of graminoids (LR = 0.01, $df = 1,9$, $P = 0.9735$) or bryophytes (LR = 0.88, $df = 1,9$, $P = 0.3489$). However, examination of within-season growth data revealed that, at the height of the growing season, *Calluna* growth was significantly affected by the interaction between experimental warming and bryophytes (Fig. 2; warming \times bryophytes \times date: LR = 26.10, $df = 14,78$, $P = 0.0251$). Specifically, during peak growth for this species (June–July), warming increased *Calluna* growth by approximately 35 % when bryophytes were absent, but had no effect when bryophytes were present. In contrast, neither experimental warming nor its interactions with any plant functional type significantly influenced total season *Eriophorum* growth or total season *Sphagnum* growth (Table S1).

Vegetation composition significantly affected total season growth of *Eriophorum* and *Sphagnum*, but not total season *Calluna* growth (Fig. 1). Specifically, total season *Eriophorum* growth increased by approximately 20 % when bryophytes were present (LR = 6.36, $df = 1,10$,

$P = 0.0117$), but was not affected by the presence of dwarf-shrubs (LR = 1.69, $df = 1,10$, $P = 0.1930$). In contrast, total season *Sphagnum* growth increased by 46 % when dwarf-shrubs were present (LR = 6.04, $df = 1,11$, $P = 0.0140$), but was not affected by graminoids (LR = 0.01, $df = 1,11$, $P = 0.9334$). Neither graminoids (LR = 1.85, $df = 1,7$, $P = 0.1734$) nor bryophytes (LR = 0.02, $df = 1,7$, $P = 0.8936$) impacted total season *Calluna* growth at all.

Air temperature

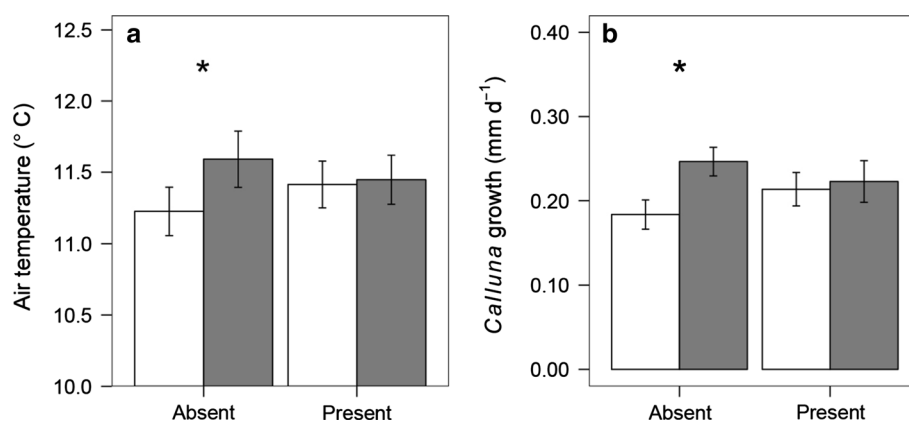
Across the whole growing season, experimental warming increased air temperature by 0.35 ± 0.03 °C (Table 1; LR = 98.25, $df = 1,15$, $P < 0.0001$), whereas dwarf-shrub presence reduced air temperature by 0.24 ± 0.04 °C (LR = 55.19, $df = 1,15$, $P < 0.0001$). Furthermore, warming had larger positive effects on air temperature when dwarf-shrubs were absent (LR = 23.81, $df = 1,18$, $P < 0.0001$). Neither graminoids (LR = 1.49, $df = 1,15$, $P = 0.2224$) nor

Table 1 Mean (± 1 SE) growing season air temperature ($^{\circ}\text{C}$), soil temperature ($^{\circ}\text{C}$) and water table height (cm below surface) for plots subjected to an ambient or elevated temperature treatment and the presence or absence of dwarf-shrubs, graminoids or bryophytes

Effect	Warming	Response		
		Air temperature	Soil temperature	Water table height
Dwarf-shrubs absent	Ambient	10.33 \pm 0.22 a*	9.33 \pm 0.22 a	-7.59 \pm 0.97 a
Dwarf-shrubs absent	Elevated	10.61 \pm 0.24 a*	9.12 \pm 0.22 a	-6.37 \pm 0.62 a
Dwarf-shrubs present	Ambient	10.34 \pm 0.22 b*	8.88 \pm 0.18 b	-7.07 \pm 0.29 b
Dwarf-shrubs present	Elevated	10.47 \pm 0.21 b*	9.07 \pm 0.18 b	-7.22 \pm 0.33 b
Graminoids absent	Ambient	10.43 \pm 0.23*	9.15 \pm 0.21 a	-5.56 \pm 0.27 a
Graminoids absent	Elevated	10.52 \pm 0.24*	9.09 \pm 0.21 a	-6.32 \pm 0.38 a
Graminoids present	Ambient	10.25 \pm 0.21*	9.00 \pm 0.19 b	-8.46 \pm 0.65 b*
Graminoids present	Elevated	10.54 \pm 0.22*	9.09 \pm 0.18 b	-7.26 \pm 0.48 b*
Bryophytes absent	Ambient	10.29 \pm 0.22*	9.16 \pm 0.22 a	-5.67 \pm 0.27 a*
Bryophytes absent	Elevated	10.61 \pm 0.24*	8.97 \pm 0.21 a	-4.54 \pm 0.35 a*
Bryophytes present	Ambient	10.38 \pm 0.21*	9.00 \pm 0.18 b	-8.38 \pm 0.66 b
Bryophytes present	Elevated	10.47 \pm 0.21*	9.18 \pm 0.19 b	-8.14 \pm 0.44 b

For each response variable, different lowercase letters indicate significant differences between plant functional type (PFT) treatments, whereas an asterisk indicates significant differences between warming treatments within PFT treatments (Tukey: $P < 0.05$)

Fig. 3 Effects of warming (ambient temperature *white bars*, elevated temperature *shaded bars*) and the presence or absence of bryophytes on mean **a** air temperature ($^{\circ}\text{C} \pm 1$ SE) and **b** *Calluna vulgaris* growth ($\text{mm day}^{-1} \pm 1$ SE) during peak *Calluna vulgaris* growth in June and July ($n = 8$). Within plant functional type treatments, significant warming effects are indicated by an asterisk (Tukey: $P < 0.05$)



bryophytes (LR = 1.44, $df = 1,15$, $P = 0.2308$), nor even their interactions with warming (Table S2), affected air temperature over the whole growing season. However, air temperature data relating to the period of peak *Calluna* growth (June–July) were significantly affected by the interaction between experimental warming and bryophytes (LR = 5.51, $df = 1,9$, $P = 0.0189$). Specifically, warming increased air temperature at this time by 0.36 ± 0.07 $^{\circ}\text{C}$ when bryophytes were absent, but had no effect when bryophytes were present. These responses matched those of *Calluna* growth during the same period (Fig. 3).

Correlations between air temperature and plant growth (Fig. 4a–c) revealed that *Calluna* growth was significantly and positively correlated with air temperature ($r = 0.15$, $df = 399$, $P = 0.0035$), when considered irrespective of any experimental treatment. This was not the case for *Eriophorum* ($r = -0.05$, $df = 239$, $P = 0.4660$) or *Sphagnum* growth ($r = -0.02$, $df = 305$, $P = 0.7490$).

Soil temperature

Experimental warming did not influence soil temperature across the whole growing season (Table 1; LR = 1.58, $df = 1,15$, $P = 0.2090$), nor did any interaction between experimental warming and different plant functional types (Table S2). However, the presence of dwarf-shrubs, graminoids or bryophytes significantly reduced soil temperature (dwarf-shrubs: LR = 127.69, $df = 1,15$, $P < 0.0001$; graminoids: LR = 40.28, $df = 1,15$, $P < 0.0001$; bryophytes: LR = 53.78, $df = 1,15$, $P < 0.0001$). Overall, the presence of dwarf-shrubs had the biggest influence, lowering soil temperature by 0.48 ± 0.05 $^{\circ}\text{C}$.

Correlations between soil temperature and plant growth (Fig. 4d–f) revealed that *Sphagnum* growth was significantly and negatively correlated with soil temperature ($r = -0.14$, $df = 241$, $P = 0.0336$), when considered

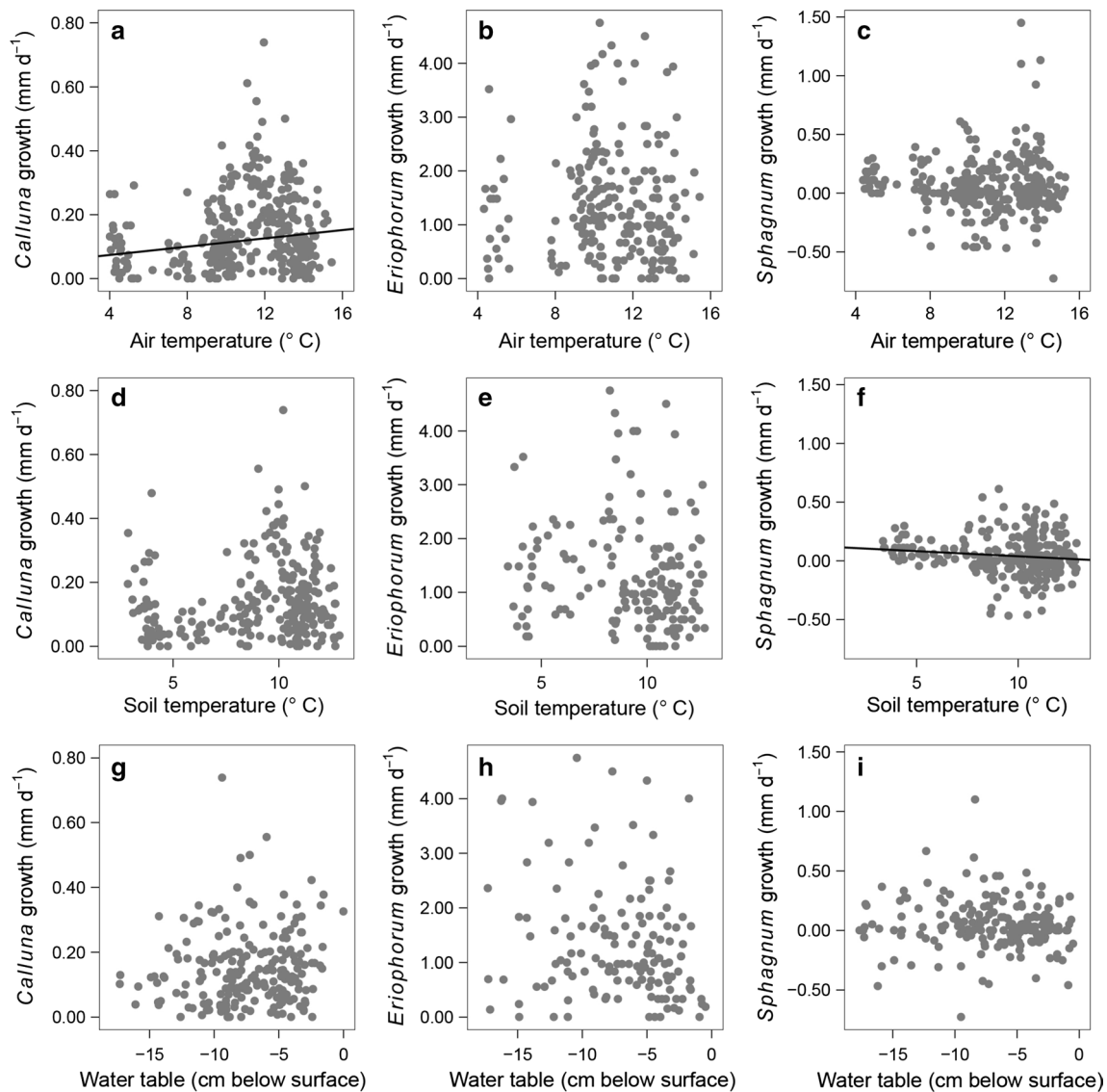


Fig. 4 Within-season correlations between growth (mm day^{-1}) of **a, d, g** *Calluna vulgaris*, **b, e, h** *Eriophorum vaginatum* or **c, f, i** *Sphagnum capillifolium* and **a–c** air temperature ($^{\circ}\text{C}$), **d–f** soil temperature

($^{\circ}\text{C}$) or **g–i** water table height (cm below surface). Trend-lines are shown for significant correlations (Pearson product moment correlations: $P < 0.05$)

irrespective of any experimental treatment. In contrast, neither *Calluna* ($r = 0.10$, $df = 289$, $P = 0.0965$) nor *Eriophorum* growth ($r = -0.13$, $df = 169$, $P = 0.0826$) were related to soil temperature.

Water table height

Bryophytes had the strongest effect of any plant functional type on water table height (Table 1; $\text{LR} = 59.56$, $df = 1,12$, $P < 0.0001$), lowering it by 3.10 ± 0.31 cm when present. By comparison, graminoids and dwarf-shrubs lowered water table height by 1.94 ± 0.33 and 0.17 ± 0.40 cm, respectively (graminoids: $\text{LR} = 15.55$,

$df = 1,12$, $P < 0.0001$; dwarf-shrubs: $\text{LR} = 5.42$, $df = 1,12$, $P = 0.0199$). While experimental warming did not affect water table height in isolation ($\text{LR} = 2.48$, $df = 1,12$, $P = 0.1154$), it had a small positive effect when either graminoids were present or bryophytes were absent, but was not modified by the presence of dwarf-shrubs (Table S2).

Correlations between water table height and plant growth (Fig. 4g–i) revealed that growth of *Calluna* ($r = 0.014$, $df = 241$, $P = 0.8280$), *Eriophorum* ($r = -0.04$, $df = 149$, $P = 0.6298$) and *Sphagnum* ($r = -0.09$, $df = 206$, $P = 0.2051$) was not significantly related to water table height.

Discussion

The aim of this study was to determine the combined effects of warming and vegetation composition on the growth of dominant peatland plants. We found that *Calluna*, the dominant dwarf-shrub, was the only species to respond to experimental warming, but that both *Eriophorum* and *Sphagnum* growth were affected by the presence of other plant functional types. Measurements were taken during a single growing season, so implications for long-term shifts in peatland plant community composition must be inferred with caution. Nevertheless, both climate and microclimate during this period were reflective of longer-term trends from this field site (Fig. S1; Ward et al. 2013, 2014), suggesting that growth responses could occur on an inter-annual scale. Ultimately, our findings show that growth responses to simultaneous climate and vegetation change differ between plant functional types within the peatland plant community.

The positive effect of experimental warming on *Calluna* growth is likely a direct effect of increased air temperature, a view supported by the positive correlation between air temperature (range across all plots within the growing season: 12 °C) and *Calluna* growth across all treatments (Fig. 4a). This finding is also consistent with other studies of arctic and peatland shrub species where positive effects of warming on their growth are reported (Chapin 1983; Myers-Smith et al. 2011; Elmendorf et al. 2012). However, in our study, it is striking that experimental warming promoted *Calluna* growth by 20 % (Fig. 1a), despite only increasing air temperature by 0.35 °C. This suggests that, in these peatlands, *Calluna* growth is highly sensitive to rising temperature. Given that *Calluna* is a dominant dwarf-shrub of northern peatlands (Grace and Marks 1978), and that it makes up over 70 % of the plant community of our study site (Fig. S2), even a modest 0.5 °C increase in atmospheric temperature (e.g. IPCC 2007) is likely to exacerbate its dominance in the longer term.

Although warming effects on *Calluna* growth were evident across the whole growing season, its response to experimental warming was dampened by the presence of bryophytes in the middle of the growing season (June–July). Bryophyte presence similarly negated warming effects on air temperature during this period (Fig. 3), implying that bryophytes have the potential to dampen warming effects on mid-season *Calluna* growth by regulating air temperature. Bryophytes have been shown to affect air and soil temperature by promoting evaporation from the soil surface (Blok et al. 2011a), which cools the soil and can transfer heat into the canopy (Groffman et al. 2001). It is possible that this process is occurring at this point in the growing season, since bryophytes lowered both soil temperature and water table height in this study. More work is

needed to fully explore this mechanism and its implications for plant community composition in the context of climate change.

We found that *Sphagnum* growth was positively affected by the presence of dwarf-shrubs (Fig. 1c). Dwarf-shrub presence also had the strongest negative effect of any treatment on soil temperature (Table 1), and we found a negative correlation between soil temperature and *Sphagnum* growth (Fig. 4f), irrespective of any experimental treatment (range across all plots within the growing season: 11 °C). Assuming that soil temperature is also reflective of temperature on the peat surface, these findings together suggest that dwarf-shrubs increase *Sphagnum* growth by promoting a cool microclimate. Such cooling was not, though, evident under experimental warming, revealing both the strong influence of dwarf-shrubs over soil temperature and the subtle influence of the warming treatment relative to the overall microclimatic variation present. Dwarf-shrubs are most likely to reduce surface and soil temperature by shading the understorey from direct sunlight (Myers-Smith et al. 2011), and this is especially true in this region due to the dense canopy of the dominant dwarf-shrub, *Calluna* (Grace and Marks 1978). However, documented responses of bryophyte growth to microclimate are inconsistent, with some studies reporting positive relationships with air temperature (Gunnarsson 2005; Aerts et al. 2006) and photosynthetically active radiation (Loisel et al. 2012), and others reporting positive effects of shading due to protection from desiccation (Murray et al. 1989). In this study, *Sphagnum* growth benefitted from dwarf-shrub cover, and we found no evidence that its responses to any factor were coupled to those of air temperature. Dwarf-shrubs also had only a minor influence over water table height, suggesting that bryophytes under the dwarf-shrub canopy do not experience an altered moisture regime. The fact that *Sphagnum* growth did not correlate with water table height adds support to this. Instead, our results suggest that vegetation effects on *Sphagnum* growth act via changes in soil temperature, although we cannot rule out the influence of other, unmeasured, microclimatic variables. Regardless of the mechanism, dwarf-shrub presence increased *Sphagnum* growth by almost 50 %, indicating that shifts in dwarf-shrub cover, for example driven by climate (Myers-Smith et al. 2011), may also influence the contribution of bryophytes (9 %; Fig. S2) to the plant community.

In contrast to other species, *Eriophorum* growth was positively affected by bryophyte presence (Fig. 1b), but these responses did not relate to any microclimatic variable. Furthermore, while the warming treatment in this study only increased air temperature by 0.35 °C, we found no associations between *Eriophorum* growth and air temperature (range across all plots within the growing season: 13 °C). This suggests that microclimate is not a major

factor regulating *Eriophorum* growth in this ecosystem, and is in agreement with previous studies examining *Eriophorum* growth, which have found it to be primarily nutrient limited (Kool and Heijmans 2009; Medina-Roldán and Bardgett 2012). The bryophyte plant functional type at our study site comprises 9 % *P. schreberi* (Ward et al., unpublished data), a feather moss that fixes atmospheric nitrogen (N) through symbiotic associations with cyanobacteria (DeLuca et al. 2002). While not studied here, bryophytes may consequently be facilitating *Eriophorum* growth in our study if *P. schreberi* improves access to N. It is unclear whether this mechanism alone would be sufficient to stimulate the 20 % increase in *Eriophorum* growth that occurred when bryophytes were present. Nevertheless, this effect was present even with a relatively low abundance of bryophytes in the plant community (9 %; Fig. S2), so it represents a powerful control over *Eriophorum* growth. Changes in bryophyte abundance, for example driven by shifts in dwarf-shrub abundance (as reported here), may therefore be expected to also impact *Eriophorum*, and thus graminoid, abundance.

Overall, we discovered contrasting effects of experimental warming and vegetation composition on the growth of different peatland plant functional types. Specifically, we found that growth of *Calluna*, the dominant dwarf-shrub, was greater under experimental warming, potentially reflecting a direct response to increased air temperature. In contrast, *Sphagnum*, a dominant bryophyte, grew better in the presence of dwarf-shrubs, which may be linked to a reduction in soil temperature caused by dwarf-shrub presence. Finally, growth of *Eriophorum*, the dominant graminoid, was greatest in the presence of bryophytes, but this was not associated with changes in air or soil microclimate. We recognise that our results are from a single growing season, and that we did not measure root responses to experimental warming and vegetation composition, which could be significant and have implications for ecosystem C dynamics (Bardgett et al. 2014). Nevertheless, our findings do reveal a mismatch in the growth responses of different plant functional types to simultaneous climate and vegetation change, which is currently occurring in this ecosystem (Moore 2002; Dise 2009). Our results therefore suggest that dwarf-shrub responses to warming could have longer-term effects on bryophyte abundance, and, through this, graminoid abundance. Given the importance of peatlands as a global C sink (Dise 2009), and the contrasting effects of different plant functional types on peatland greenhouse gas emissions (Dorrepaal 2007; Trinder et al. 2008; Ward et al. 2009, 2013; Gray et al. 2013), these findings could ultimately feedback to future climate by changing the relative contribution of dwarf-shrubs, graminoids and bryophytes to the C balance of peatland ecosystems.

Author contribution statement RB and NO originally conceived and designed the long-term field experiment, with contributions from SW. TW conceived and designed the study, with contributions from RB, NO, and SW, and TW performed the study. TW analysed the data and wrote the manuscript with contributions from all other authors.

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