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# Experimental warming interacts with soil moisture to discriminate plant responses in an ombrotrophic peatland

**Running head: Experimental warming and plant responses**

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Keywords: climate change; vegetation, *Sphagnum*; OTC; temperature; drought; NDVI; point-intercept survey.

## ABSTRACT

Question: A better understanding of the response of *Sphagnum* mosses and associated vascular plants to climate warming is relevant for predicting the carbon balance of peatlands in a warmer world. In peatland studies, open-top chambers (OTCs) have been used to investigate the effect on soil biogeochemical processes, but little information is available on the effects of OTCs on microclimate conditions and the associated response of plant community. We aimed to understand how simulated warming and differences in soil moisture affect overall vascular plant cover and individual plant species.

Methods and location: We used OTCs to measure the effect of a near-ground temperature increase (+ 1.5 °C on average) on vegetation dynamics in a peatland over 5 years (2008-2012). We performed this experiment in a *Sphagnum*-dominated peatland in the French Jura Mountains, in two adjacent areas (blocks) with different hydrological conditions – wet and dry. Microclimatic conditions and plant species abundance were monitored at peak biomass in years 1, 2, 3 and 5 and monthly during the plant-growing season in year 5.

Results: The response of plants to warming differed between vascular plants and bryophytes as well as among species within these groups and also varied in relation to soil moisture. *Andromeda polifolia* abundance responded positively to warming, while *Vaccinium oxycoccus* responded negatively and *Eriophorum vaginatum* showed a high resistance.

Conclusion: Depth of rooting of vascular plants appeared to control the response in plant abundance, while moss abundance depended on various other interacting factors, such as shading by the vascular plant community, precipitation and soil moisture.

## INTRODUCTION

Peatlands are long-term sinks of atmospheric carbon (C) due to the accumulation of peat (Smith et al. 2004; Yu 2011). These ecosystems develop in areas that are hydrologically and climatically characterized by a net surplus of water, *i.e.* where precipitation exceeds evapotranspiration. As a consequence, prevailing soil anoxic conditions hamper microbial decomposition of organic matter (Holden 2005).

In ombrotrophic (= rain fed) peatlands of northern hemisphere, bryophytes of the genus *Sphagnum* (peat mosses) are generally the dominant plant species (Rydin & Jeglum 2006). Peat mosses produce litter with antimicrobial properties, which hampers microbial decomposition (Turetsky 2003; Hajek et al. 2011), leading to the build up of peat. Further, *Sphagnum* mosses can affect the abundance and the performance of associated vascular plants (van Breemen 1995; Dorrepaal et al. 2006) by regulating soil moisture, energy balance, soil temperature, and nutrient availability (Turetsky et al. 2012). Ultimately, the inter-specific competition between *Sphagnum* mosses and vascular plants controls peat accumulation because an increase of vascular plant abundance and in particular their shading effect can reduce *Sphagnum* growth (Heijmans et al. 2002; Bragazza et al. 2013). Changes in the competitive balance between plant species of different growth forms has been shown to alter the C balance in peatlands (Kuiper et al. 2014), potentially by changes in the litter quality, which ultimately affects microbial decomposition (Bragazza et al. 2007; Dorrepaal et al. 2007; Gogo et al. 2011).

Climate warming and associated extreme climatic events can be detrimental to *Sphagnum* mosses as, like all bryophytes, these plants cannot actively control their water balance and therefore rely on atmospheric precipitation to maintain suitable hydrological conditions (Robroek et al. 2007, Bragazza 2008; Nijp et al. 2014). Increased air temperature can increase evapotranspiration with direct negative effects on *Sphagnum* productivity (Skre & Oechel 1981; Gerdol 1995; Weltzin et al. 2001), but with positive effects on vascular plant growth by drying out the top soil and enhancing soil oxygenation (Weltzin et al. 2000; Bragazza et al. 2013), to which plants of different functional types might respond differently (Kuiper et al. 2014). A better understanding of the response of *Sphagnum* mosses and associated vascular plants to climate warming is then relevant for predicting the C balance of peatlands in a warmer world. Indeed, a warmer climate has been reported to alter plant species abundance in peatlands, in particular favoring ericaceous dwarf shrubs (Weltzin et al. 2003, Breeuver et al. 2009), which will affect soil biogeochemical processes (Bragazza et al. 2013).

Under field conditions, simulation of climate warming can be obtained by using passive warming open-top chambers (OTCs) (Marion 1997). Although OTCs are recognized to increase temperature consistent with general circulation models, they also affect a set of microclimatological variables such as moisture, light, snow accumulation and wind speed (Bokhorst et al. 2013). In peatland studies, OTCs have been reliably used to investigate the effect on soil biogeochemical processes (Dorrepaal et al. 2009, Huguet et al. 2013), but little information is available on the effects of OTCs on microclimate conditions and the associated response of plant species (Weltzin et al. 2003, Keuper et al. 2011; Delarue et al. 2013; Jassey et al. 2013).

In the present study we used OTCs to simulate an increase of soil and air temperature and we monitored changes in vegetation cover in a *Sphagnum*-dominated peatland over 5 years of experimental warming. We aimed to understand how species abundance and plant community composition responded to simulated warming and associated changes in soil moisture, We hypothesized that the responses of plant will vary among functional types, more specifically that 1) vascular plants will respond to warming in accordance with their rooting depth, and 2) *Sphagnum* mosses will have a more complex response depending on the interaction between micrometeorological conditions and abundance of vascular plants.

## MATERIAL AND METHODS

### *Study site*

The study was performed on an undisturbed, ombrotrophic *Sphagnum*-dominated peatland situated in the Jura Mountains (The Forbonnet peatland, France, 46°49’35’’N, 6°10’20’’E, 840 m a.s.l). Climate is characterized by relatively cold winters (average temperature -1.4°C) and mild summers (average temperature 14.6°C), with annual mean temperature of 7.5°C and annual mean precipitation between 1300 and 1500 mm (Laggoun-Défarge et al. 2008).

Two areas (blocks) were selected based on their hydrological conditions. The first block (hereafter called ‘wet’) was a *Sphagnum*-dominated relatively flat area bordering a transitional poor fen, characterized by a moss cover dominated by *Sphagnum fallax*. Vascular plants such as *Eriophorum vaginatum* and *Andromeda polifolia* were recorded with low abundance, together with *Scheuchzeria palustris, Drosera rotundifolia and Vaccinium oxycoccus*. The second block (hereafter called ‘dry’) was directly adjacent to the first block in a slightly drier area and was characterized by a pattern of hummocks dominated by *Sphagnum magellanicum, V. oxycoccos, E. vaginatum and Calluna vulgaris*, and lawns with *S. fallax, Carex rostrata* and *A. polifolia*. Tree (*Pinus rotondata*) encroachment happens also in this dry block.

### *Experimental design*

In April 2008, in both the dry and the wet block, six representative plots (3 × 3 m) were selected, which were then randomly allocated to either the control or the warming treatment (Laggoun-Défarge et al., 2008). Warming treatments were obtained by using open-top chambers (OTCs) (Aronson & McNulty, 2009). OTCs (transparent polycarbonate hexagonal chambers; 50 cm high, 1.7 m top-width, 2.4 m base-width) allow quasi-natural transmittance of visible wavelengths, and minimize the transmittance of re-radiated infrared wavelengths (Marion et al., 1997). All OTCs were raised 10 cm above the peat surface to allow air circulation. The minimal (adjacent plots) and maximal (distant plots) distance between plots were *c.* 5 and 30 m, respectively.

### *Environmental monitoring*

From November 2008 to November 2012, peat temperature (7 cm below the moss carpet) and air temperature (at 10 cm above the moss carpet) were monitored at 30–minute intervals using thermocouple probes connected to a data logger (CR-1000 Campbell). Sensors were repositioned as necessary to keep height and depth of measurement constant despite moss carpet accumulation. In 2012, these measurements were augmented with combined soil temperature/moisture sensors. In each block (wet/dry) and treatment (OTC/control) a randomly chosen plot was equipped with soil temperature-moisture probes (Decagon 5TM) at 3 cm and 5 cm depth. Furthermore, precipitation at the study site and water table depth in randomly chosen plot were continuously monitored by a meteorological station and sensors connected to the CR-1000 data logger.

### *Plant species abundance*

At peak biomass (July or August, depending on the year) in 2008, 2009, 2010 and 2012, plant species abundance was measured using the point-intercept frequency method (Jonasson 1988, Buttler 1992) in 50 × 50 cm subplots located in flat lawns. 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 living vegetation and litter was recorded by species until the pin reached the *Sphagnum* surface. This field technique could account for three-dimensional biomass distribution because, at each point, each plant that was intercepted was recorded. The relative frequency of each species was then calculated.

To allow analyses on seasonal dynamics of plant species cover, during the growing season 2012 (April - September), monthly pictures were taken from aforementioned subplots. In order to obtain high-resolution images, the subplots were divided into four 25 × 25 cm quadrats. For the digital image analysis, a grid of 100 points was laid on each 25 × 25 cm picture, after which the four grids were merged into a single 400 points grid-picture. Species overlaying the grid intersects were identified at 200% digital magnification. The relative frequency of each species was then calculated for each sampling date, as for the point-intercept method. Because we could not reliably distinguish *S. fallax* and *S. rubellum* in our point-intercept field measures and in the frequency analysis on photographs, we pooled these two species.

### Sphagnum *height growth*

The cranked wire method (Clymo 1970) was used to measure *Sphagnum* growth. At the start of the 2011 and 2012 growing seasons (early April, after snow melt) cranked wires (5-10) were placed in each subplot. At the beginning of November, before snowfall, the length of the cranked wire above the moss surface was measured with a graduated pipe sliding down along the cranked wire and the average height of the *Sphagnum* capitula around the wire was calculated.

### *Seasonality of plant community*

The normalized difference vegetation index (NDVI) was used as a phenological proxy and measured every fortnight between March and November 2012 using a portable spectroradiometer sensor. This measure is also used as an indirect measure of bulk biomass (Soudani et al. 2012). The sensor was maintained at 50 cm above the moss carpet, which allowed obtaining a NDVI signal of the whole plant community, including the highest plants, while covering only the subplot surface. In each 50 × 50 cm subplot and for each campaign of sampling, 10 consecutive measures were taken according to a grid sampling design and then averaged to have a single NDVI value per plot. The NDVI measurements were performed under direct sunlight and with an umbrella to shadow the subplot.

### *Statistical analysis*

Differences in vegetation between years (i.e. 2008, 2009, 2010, 2012) were analyzed using relative species frequency data obtained from the point-intercept method in the field, whereas seasonal trend of plant species cover during the 2012 growing season was analyzed with species relative frequency data obtained from the photographic image analysis. Analysis at species level was done with Linear Mixed Models, with treatment (OTC vs. control) and years (or months for the seasonal data set in 2012) as fixed factors, and years (or months) nested in plots and block as random factors. The same model was also used to test the block effect. *Sphagnum* growth was analyzed with Linear Mixed Models, with treatment and block as fixed factors, and location of growth measures within plots given as random nested factors. The model was also tested for each block separately. NDVI was also analyzed with Linear Mixed Model, with treatment and block as fixed factors, and dates nested in plots as random factors. Random effects on the intercept were used to correct the inflation of the residual degrees of freedom that would occur if repeated measurements within sites would have been used as true replicates (Pinheiro & Bates 2000). In addition, for NDVI, separate ANOVA’s were performed for each block and date. Pearson’s correlation coefficients were calculated and tested between NDVI signals and species frequencies. Differences in monthly means of differences in daily mean air and soil temperature were assessed by ANOVA's. Comparisons of mean water level depth between blocks were done with Student t-tests. Data were log transformed prior to analysis. All statistical analyses were performed in R (R Core Team, 2014).

## Results

### *Micrometeorology*

In general, over the period 2009-2012, monthly air temperature in the OTCs was 0.2-1.5 °C higher than in the control plots ($p$<0.05). Interestingly, OTCs rarely affected significantly soil temperature, and when they did ($p$<0.05), the pattern was less clear, varying between a warming effect up to 0.3 °C in some cases, and a cooling effect up to -1 °C in some others (see also Delarue et al. 2011, 2014, 2015, Jassey et al. 2011). These effects of OTC on soil temperature were not related to the season, neither to block. Soil moisture and temperature measured in 2012 with Decagon sensors in a subset of 4 plots (dry control, dry OTC, wet control and wet OTC) indicate that soil temperature was slightly higher in OTCs this particular year (mean daily differences between OTC and control plots for soil temperature was +0.6 deg C in both blocks), and that moisture was slightly lower in OTC plots (mean daily differences between OTC and control plots for soil moisture were -0.011 and -0.067 (VWC) in dry and wet blocks, respectively).

Monthly cumulative rainfall during the period of *Sphagnum* growth measurements was higher in 2012 (2108 mm) than in 2011 (1376 mm). Depth of water level fluctuated over time, but highest water levels were recorded during spring 2012. Mean water level during the measurement period of *Sphagnum* growth was significantly higher in 2012 than in 2011 (Student t-test; $p$=0.002 in dry, $p$=0.004 in wet). Mean water level was also higher in the wet block than the dry block ($p$=0.004).

### *Annual change in species abundance*

Considering all vascular plants, abundance (relative frequency) increased significantly with the OTC treatment (Figure 1). At species level, it appeared that with warming *A. polifolia* increased its abundance consistently in wet and dry blocks, whereas the abundance of *V. oxycoccus* decreased. *D. rotundifolia* abundance responded marginally to the OTC treatment whereas *E. vaginatum* did not respond significantly. Some other species responded contrastingly to the OTC treatment in the two blocks, for example *P. strictum* and *S. fallax+rubellum* increased their abundance in the dry block, whereas their abundance decreased or did not change in the wet block (treatment x block $p$=0.0367 and 0.0767, respectively). Litter increased in the wet block, and decreased in the dry block (treatment x block $p$=0.0001). Significant changes occurred also over time, with a decrease of abundance for *V. oxycoccus* and *S. fallax+rubellum*, and an increase for *E. vaginatum* and litter.

There was also a strong block effect related to the dry and wet situations in the bog ($p<0.05$), except for *Drosera rotundifolia* for which the block effect was marginally significant, and for *Carex rostrata*, *C. limosa*, *Calluna vulgaris* and *Pinus rotundata* for which there was no significant block effect. *Vaccinium oxycoccus, D. rotundifolia*, *Scheuchzeria palustris*, and *Sphagnum fallax+rubellum* were more abundant in the wet block, whereas species such as *Andromeda polifolia*, *Eriophorum vaginatum* and *Polytrichum strictum* were more frequent in the dry block, or exclusively found in the latter one (*S. magellanicum).*

*Monthly change in species abundance*

During the 2012 study season, total vascular plant abundance and, more specifically *Andromeda polifolia* frequency increased significantly in the OTCs (Figure 2). *Vaccinium oxycoccus* abundance decreased in the wet block (treatment x block $p$=0.0034) whereas that of *Sphagnum fallax+rubellum* declined in the wet block, but increased in the dry block (treatment x block $p$=0.008). Litter increased in the wet block and decreased in the dry block (treatment x block $p$=0,0001). Significant changes occurred also over the seasons, with a decrease in abundance for *S.*

*magellanicum* (present only in the dry block) and litter, and an increase for *V. oxycoccus* and total vascular plants.

## Sphagnum growth

The length increment of *Sphagnum* species differed between years, being higher in 2012 as compared to 2011 (Figure 3). In 2011, *Sphagnum* growth was significantly lower in the wet block, but warming did not affect length increment. In 2012, there were significant block and treatment effects as well as a cross effect, with increased moss growth in the warmed plots of the dry block ($p$=0.017), whereas no-significant changes were observed in the wet block.

## Normalized Difference Vegetation Index

The values of the NDVI taken under direct sunlight and in the shade were strongly correlated ($R^2$=0.83), yet measurements at the start of the season (early May) were less correlated ($R^2$=0.49) than measurements close to the peak of biomass (mid-June; $R^2$=0.82). The precision of the measurements was calculated as the mean difference between each pairwise measurement. It gives an error of 1.6% under sun and 2.0% in the shade. As such, we only used NDVI data from sun measurements in further analyses.

Throughout the season, OTCs increased the vegetation's NDVI signal ($p$=0.001), yet the effect of OTCs differed between wet and dry blocks (block x treatment $p$=0.002). In the dry block, the NDVI signal in the OTC exceeded the signal in control plots throughout the season (Figure 4a). Such difference was mainly significant at the beginning of the growing season, and marginally different in summer. In the wet block, however, the difference between OTC and control plots was less obvious, and occurred during a more limited time in summer (Figure 4b). NDVI was positively correlated to vascular plant abundance (r=0.85, $p<0.001$), and negatively with litter (r=-0.60, $p<0.001$). The correlation between NDVI and *Sphagnum* cover was negative (r=-0.24, $p<0.045$).

## Discussion

### *Effect of OTC on microclimate*

The observed OTC warming effect on near-ground air temperature was in the range of those found in other studies (e.g., Marion et al., 1997; Hollister & Webber, 2000; Dorrepaal et al. 2003; Sullivan et al., 2005). Yet, in accordance with Dabros et al. (2010), we observed OTCs to sometimes reduce soil temperature, which potentially results from increased evapotranspiration (Delarue et al. 2011).

Daily temperature fluctuations, minimum and maximum values and day or night means have all been shown to be affected by OTC warming (e.g. Marion et al. 1997; Dabros et al. 2010). A previous study at the same site revealed that daily soil temperature amplitudes were small but often significantly different between OTC's and control plots in winter months (Delarue et al. 2011). In summer months, amplitudes were larger, and even more so in OTCs as compared to control plots in April, May and June in the dry block (but differences were marginally or not significant), whereas an opposite trend appeared in the wet block. The additional sensors Decagon 5TM installed in 2012 which integrate more soil volume might be more adapted to the very porous moss carpet than tiny thermocouples. Despite the absence of replication, it is reasonable to recognize that our OTCs had a slight warming effect on soils for the largest part of time, yet this effect has coincided with a slight reduction in soil volumetric water content. Indeed, Jassey et al. (2011) showed, in the same plots, that OTC treatment induced a significant decrease of *Sphagnum* water content in summer months.

### *Effect of OTCs on vegetation*

We showed that warming differently influenced plant abundance (or frequency) depending of the microclimatic conditions. Several species were found to respond either positively or negatively to warming. *A. polifolia* increased in abundance while *V. oxycoccus* decreased, and both *S. fallax+rubellum* and *P. strictum* responded positively to the OTC treatment in the dry block, and decreased or remained constant in the wet block. Among these species, the response of *A. polifolia* is key. This species has been shown to be sensitive to changes in environmental conditions such as snow cover and spring/summer warming (Aerts et al. 2006; Jassey et al. 2013; Robroek et al. 2013). This species allocates about 98% of the total biomass belowground, concentrated in the 0-15 cm peat layer, with the bulk at 2.5-7.5 cm, and a continuous rooting system from recent vegetation down into the peat (Wallén 1986)**.** Roots of *A. polifolia* may reach a depth of 45 cm (Flower-Ellis 1980 in: Jaquemard 1998) and fine roots form up to 24% of the total below ground biomass (Wallen 1986). *A. polifolia* might therefore be expected to have a somewhat deeper root system as compared to several other species in the bog and thus to be able to sustain growth when soil dries out at the surface. Differently, *V. oxycoccos* has a shallow root system hardly penetrating more than a few centimeters below the living parts of the moss layer (Jacquemart 1998). With its shallow roots, this species relies on the water-conducting capacity of the *Sphagnum* mosses for its water supply (Malmer et al. 1994), and indeed, a decrease of *Sphagnum* water content in the OTC treatment has been demonstrated by Jassey et al. (2011). A subsequent lowering of water table will also reduce the growth rate of *V. oxycoccos* through water stress (Malmer et al. 1994, Jacquemart 1998). Consequently, water table drawdown can hamper *V. oxycoccos* growth (Rodwell 1991), which seems to be optimal at water table depths of about 25-30 cm (Gronskis & Snickovskis 1989 in: Jacquemart 1998).

Coriaceous leaves of *A. polifolia*, their silvery-glaucous lower surface and their revolute margins could indicate drought resistance (Barvaux 1958). But anatomical features of *V. oxycoccos* such as thick epicuticular waxes and stomata – present on the abaxial surface only (Warming 1908, 1912; Vander Kloet 1983) – are considered similar to those of desert plant characteristic to a high ability to avoid drought (Jacquemart 1997). Drier soil might also promote ericoid mycorrhizal infection (Cullings 1996) and thus better access to nutrients in the soil, but this might equally apply to other Ericaceous present in the bog, such as *V. oxycoccus*.

An alternative explanation for the decrease of *V. oxycoccus* with OTC warming may come from direct nutrient resource competition (Malmer et al. 1994). This would be underpinned by our observation that in the dry block under OTC treatment, *S. fallax+rubellum* and *P. strictum* increased in abundance, and as such potentially cause nutrient limitation for *V. oxycoccus.* As, however, OTC warming coincided with a decrease in moisture content, a direct effect of moisture limitation on the shallow rooting *V. oxycoccus* cannot be ruled out.

The evidence of moisture limitation is supported by the lack of response to the OTC by *E. vaginatum*. This species is known to root deeply into the peat, up to 1.5 meters (Boggie et al 1958, Wein 1968), with roots having highest elongation rates at low soil temperatures (Shaver & Billings 1977). Contrary to *A. polifolia* and *V. oxycoccus*, no vesicular-arbuscular mycorhizas have been reported on *E. vaginatum* (Wein 1968). In warming experiment, no significant differences were reported for *E. vaginatum* root production between OTC's and control plots, albeit a tendency to higher production was observed (Sullivan & Welker 2005). We believe that the resistance of *E. vaginatum* is higher as compared to more shallow rooted species and that warming effect has to be expected on a longer term, as soil warms up at lower depth. Weltzin et al. (2003) found that within bog and fen communities, different life forms and species can respond differently to warming and water table manipulation. They showed that warming may lead to an increase in abundance of woody plants, as does lowering water table as a result of changes in rates of evapotranspiration (Gorham 1991). In the mires studied by Weltzin et al. (2003), in northeastern Minnesota, *Andromeda glaucophylla* responded mostly to the heat treatment, while other dominant shrubs (such as *Vaccinium oxycoccus*) did not, whereas graminoids decreased their cover. As observed by Weltzin et al. (2000), change in belowground biomass can be even more important. Our wet and dry sites showed similar trends for vascular plants, but not for mosses. The better growth of some mosses in warmed plots might be transient since, on the long run, mosses will be out-competed by the concomitant increase of *Andromeda* shrubs. Overall, these observations could point to a different evolution of such contrasted dry and wet situations, as for "bog" and "fen" like facies (Weltzin et al. 2003), which ultimately is also conditioned by neighboring species (Sonesson et al. 2002).

The increase of litter in the wet block and its decrease in the dry block under the OTC treatment does not follow the pattern of the abundance of total vascular plants, which could indicate that litter abundance is mainly driven by the differential decomposition rate in the dry and wet blocks. Nevertheless, this relationship between warming and decomposition is not straightforward (Aerts 2006) and would deserve a proper litter decomposition experiment.

Moss length increment was also higher in the dry block in 2011, and was promoted by OTC warming in 2012 (Figure 3). In the dryer 2011 year, the higher cover of vascular plants, i.e. *Eriophorum* leaves in the dry block is the determinant factor for moss growth and might have had a facilitating effect on *S. fallax+rubellum* in limiting the drying out of the moss carpet (Grosvernier et al. 1994, Buttler et al. 1998). Instead, in the wetter year 2012, when water limitation was not critical and engendered an overall higher length increment, the warming effect by OTC's could promote further the moss growth in the dry block. Adaptive seasonal acclimation has been shown for *S. fallax*, as reflected by the maintenance of relatively high net photosynthetic rates to lower water contents and no response differences when plants were collected from different heights above the water table (Titus et al. 1983). In our study, we pooled *S. fallax* and *S. rubellum*, because we could not reliably distinguish these two species in our point-intercept field measures and in the frequency analysis on photographs. Nevertheless, some field sampling in the plots showed that *S. fallax* is by far the most frequent species and that *S. rubellum* occurs only on some very limited patches. Similarly to *S. fallax*, *S. rubellum* has been shown to adapt and maintain similar height increment at different experimental water table depths (Robroek et al. 2007). Therefore, shading may be critical for the development of these mosses, mediating soil moisture and near ground temperature, which both are direct drivers of growth. Our results show that shading can facilitate growth in dry years, but when wetter years are combined with warmer conditions, in our case the OTC effect, this shading effect on growth is out-ruled by temperature. Nevertheless, a better length increment of *Sphagnum* might also, on the long run, change the structure of the moss carpet and consequently its moisture holding and transport capacity (Dorrepaal et al. 2003). Therefore, when analyzing long term-effect of global change, not only the change in species composition should be considered (Heijmans et al. 2008), but also the change of vegetation structure might be critical. The evolution of aboveground biomass over the seasons was well reflected in the NDVI, whose signal was also higher in OTC plots. Interestingly, it is also better correlated to vascular plants than to mosses, which explains the more obvious difference in the dry plot, where vascular plants are more abundant. Indeed, when mosses dry out temporarily in dry periods, which can be observed in the wet block where the moss carpet is less protected from wind, reflectance is lowered. Differentiating mosses from higher plants is critical in studying the carbon cycle of the boreal biome when using airborne remote sensing (Yan et al. 2014) since these plants play an important role in the soil energy balance (Beringer et al. 2001).

## Conclusion

Our study on the response of plant cover to experimental warming in two contrasting hydrological peatland habitats – wet and dry – shows that experimental warming by OTC interacts with soil wetness, resulting in divergent responses of vascular plants and bryophytes. For vascular plants, the depth of rooting seems the key in determining the response of plant cover, whereas for mosses, the growth is under the dependence of various other interacting factors, such as shading, which contributes further to regulate the microclimate conditions in the moss carpet.

## Acknowledgments

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## Captions to figures

*Figure 1:* Changes of the relative frequencies of dominant plant species from 2008 to 2012 (no records in 2011) in the Forbonnet peatland (French Jura). Mean values (n=3) and standard error bars are given for dry (solid line) and wet (broken line) blocks, and for control (black line) and OTC (grey lines) plots. Significance of Linear Mixed Model is given for treatment effect (T) and for year effect (Y). Species that are not illustrated: *Carex pauciflora* (appeared in 2009 and then was only seen in one plot the years after), *Carex limosa* (appeared only in 3 plots in 2009), *Calluna vulgaris* (only in 2 different plots in different years), *Pinus rotundata* (only in one plot in one year).

*Figure 2:* Changes of the relative frequencies of species from April to September 2012 in the Forbonnet peatland (French Jura). Mean values (n=3) and standard error bars are given for dry (solid line) and wet (broken line) blocks, and for control (black line) and OTC (grey lines) plots. Significance of Linear Mixed Model is given for treatment (T) and month effect (M). Species that are not illustrated; with no significant differences: *Scheuchzeria palustris*, *Eriophorum vaginatum*, *Carex pauciflora*, *Carex rostrata*, *Drosera rotundifolia*, *Polytrichum strictum*; present only in one plot: *Calluna vulgaris*, *Carex pauciflora* and *Polytrichum strictum*.

*Figure 3:* Length increment (mm) of *Sphagnum* mosses in the different treatments (OTC vs control) and blocks (dry vs wet) in 2011 (a: May 13 – November 27, n=60) and 2012 (b: March 30 – November 6, n=120) in the Forbonnet peatland (French Jura). Vertical bars represent standard errors. Scales of both graphs are different. Significance levels of Linear Mixed Model are given for block (B) and treatment effect (T), and for their interaction (B x T).

*Figure 4:* Normalised Difference Vegetation Index (NDVI) at plot scale in the dry (a) and wet (b) blocks in year 2012 in the Forbonnet peatland (French Jura). Curves represent mean values (n=3) for control (black) and OTC (grey) plots. Significance codes for ANOVA's are (***) p<0.001 ; (**) p<0.01 ; (*) p<0.05 ; (.) p<0.1.

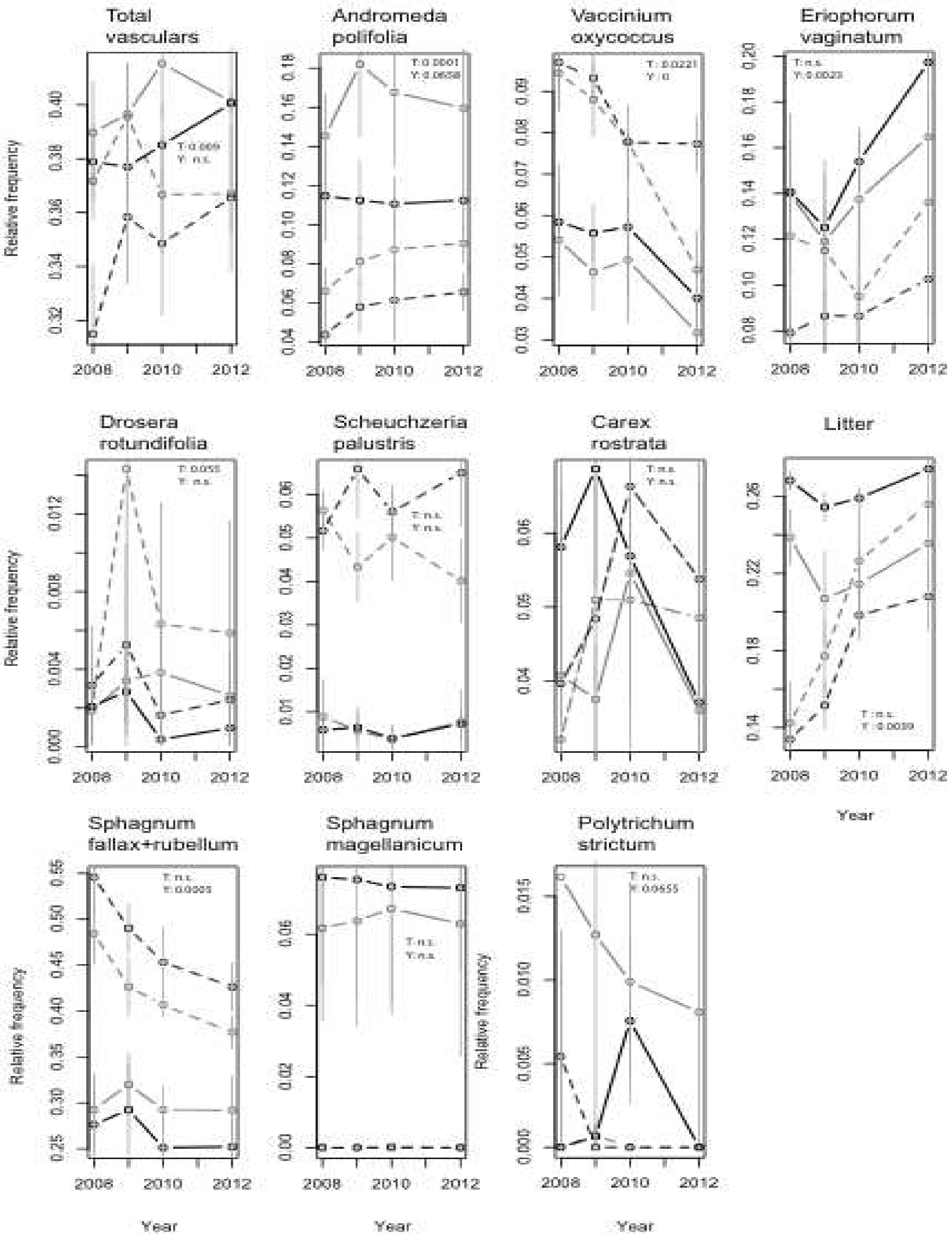

Total vasculars
T: 0.009
Y: n.s.
Andromeda polifolia
T: 0.0001
Y: 0.0658
Vaccinium oxycoccus
T: 0.0221
Y: 0
Eriophorum vaginatum
T: n.s.
Y: 0.0023
Drosera rotundifolia
T: 0.055
T: n.s.
Scheuchzeria palustris
T: n.s.
Y: n.s.
Carex rostrata
T: n.s.
Y: n.s.
Litter
T: n.s.
Y: 0.0039
Sphagnum fallax+rubellum
T: n.s.
Y: 0.0005
Sphagnum magellanicum
T: n.s.
Y: n.s.
Polytrichum strictum
T: n.s.
Y: 0.0655
Relative frequency
Year
2008
2010
2012

*Figure 1*

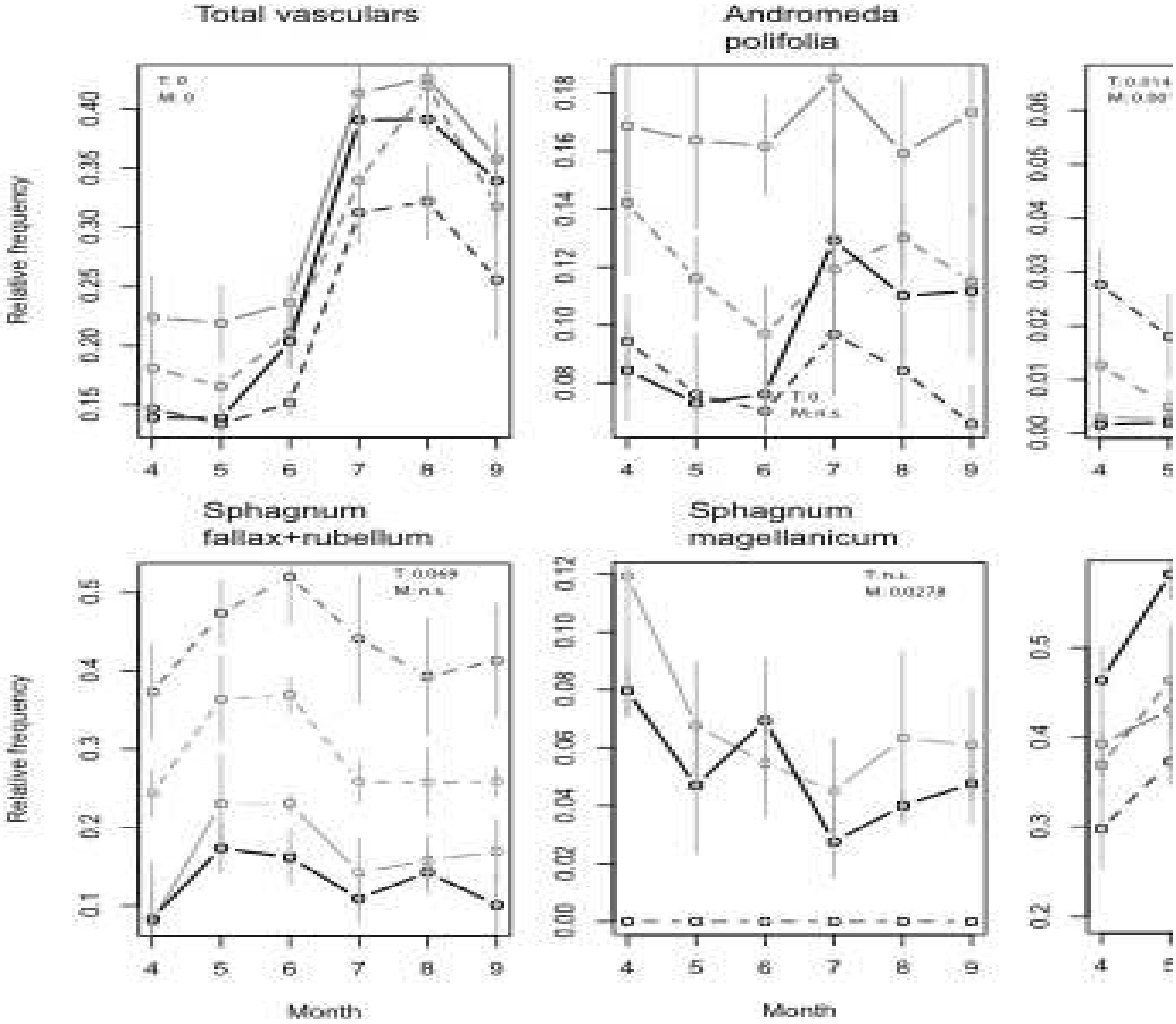

Total vasculars
T: 0
M: 0
Andromeda polifolia
T: 0
M: n.s.
T: 0.014
M: 0.00
Sphagnum fallax+rubellum
T: 0.069
M: n.s.
Sphagnum magellanicum
T: n.s.
M: 0.0278
Relative frequency
Month
4
5
6
7
8
9

*Figure 2*

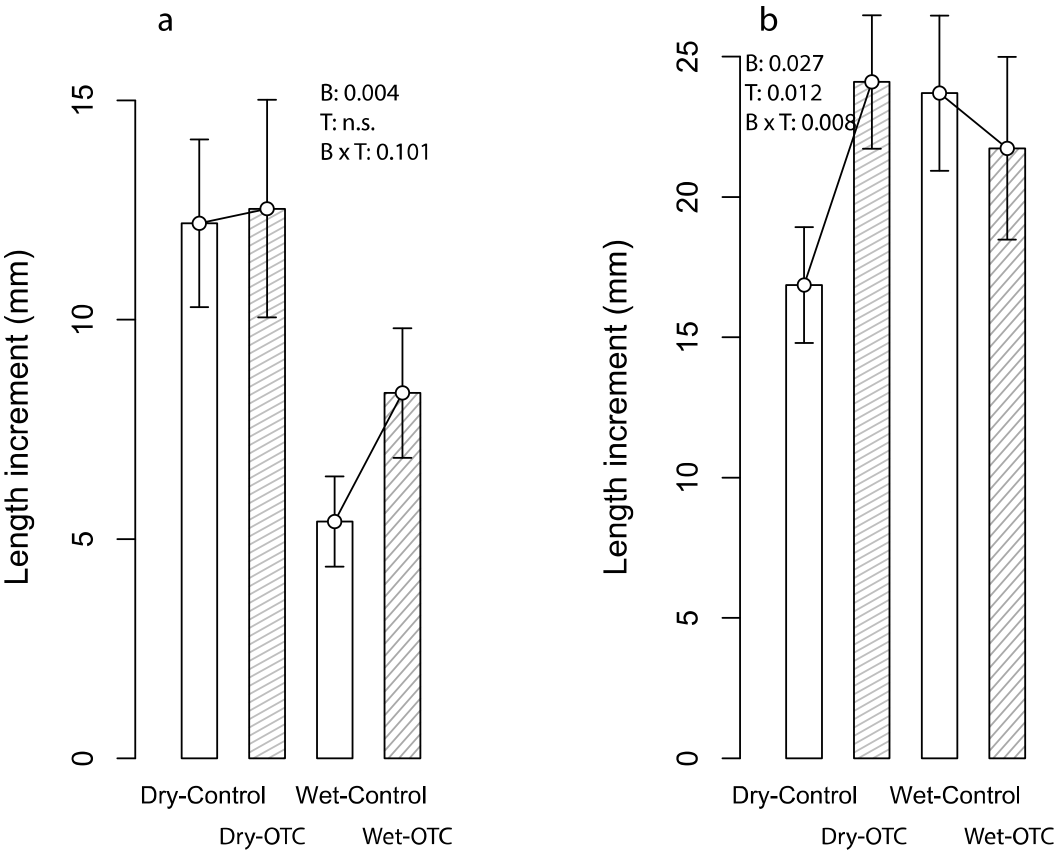

a
b
Length increment (mm)
0
5
10
15
20
25
B: 0.004
T: n.s.
B x T: 0.101
B: 0.027
T: 0.012
B x T: 0.008
Dry-Control
Dry-OTC
Wet-Control
Wet-OTC

*Figure 3*

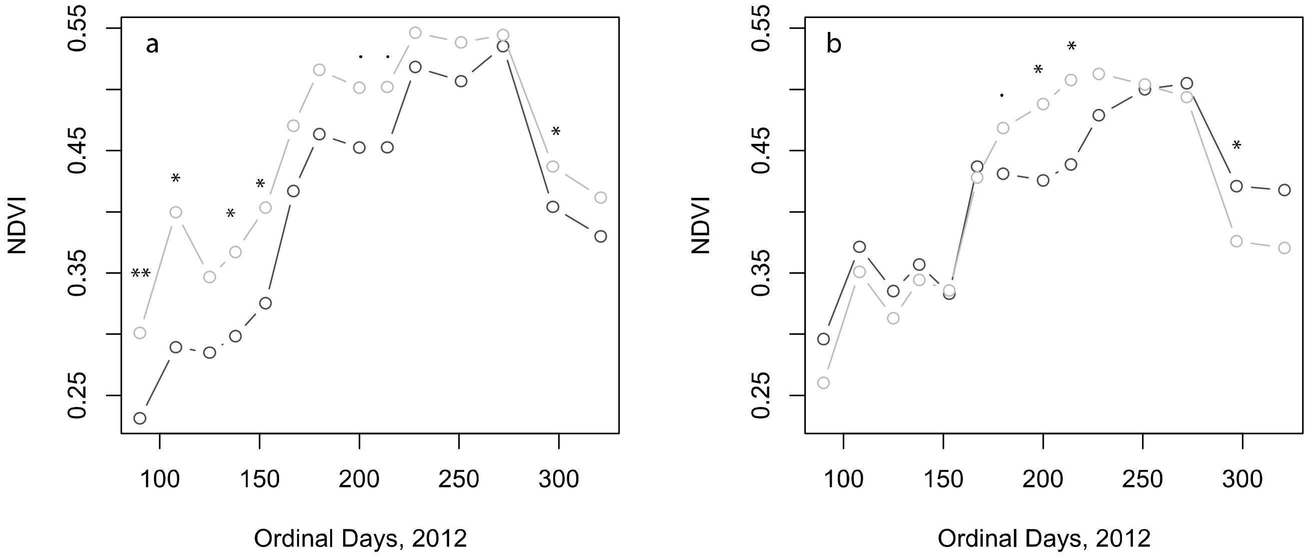
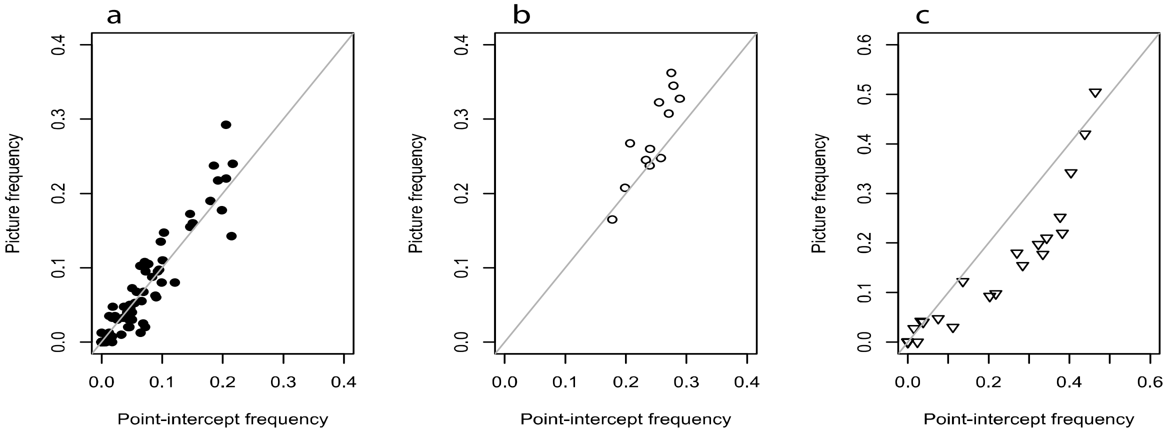

a
b
NDVI
NDVI
0.25
0.35
0.45
0.55
**
*
*
*
*
100
150
200
250
300
Ordinal Days, 2012
Ordinal Days, 2012

*Figure 4*

Electronic appendices

Supporting Information to the paper Buttler et al. 2015. Experimental warming interacts with soil moisture to discriminate plant responses in an ombrotrophic peatland. *Journal of Vegetation Science.* Appendix S1. Relationship between point-intercept frequency measures of vegetation and picture frequency analysis from the Forbonnet peatland (French Jura) for a: total vascular plants (Pearson r: 0.733, p<0.01), b: litter (Pearson r=0.873, p<0.001) and c: total Sphagnum and *Polytrichum strictum* (Pearson r=0.942, p<0.001).

The correlation between frequencies obtained by means of field point-intercepts and photographic analyses gives a good linear relation with vascular plants but shows an underestimation of mosses with the picture analysis. This is because leaves of vascular plants might hide the understory of mosses which than cannot be recorded in the one-layer photographic method, whereas in the field, the needle can hit more than one species or individual. This underestimation is mostly noticeable at intermediate moss cover, when vascular plants are most abundant. Conversely, the picture analysis overestimates litter when it is dense.


a
b
c
Picture frequency
Point-intercept frequency
0.0
0.1
0.2
0.3
0.4
0.5
0.6