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Fire temperatures and *Sphagnum* damage during prescribed burning on peatlands

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Abstract

Prescribed burning affects plant community composition including the abundance of peat-forming *Sphagnum* mosses. Understanding the processes by which fire impacts occur and the variability of impacts according to fire severity is important when making fire management decisions. We monitored fire temperatures and their impact on *Sphagnum capillifolium* in 16 experimental fires in the field. Cell damage in response to high temperature exposure in the laboratory was also quantified for five different *Sphagnum* species (*S. capillifolium*, *S. papillosum*, *S. magellanicum*, *S. austinii* and *S. angustifolium*). Maximum temperatures recorded at the moss surface during fire ranged from 33 ^{o}C to 538 ^{o}C and were higher in plots with greater dwarf shrub cover. Higher temperatures were associated with a greater proportion of cell damage in *S. capillifolium*, with 93-100% cell damage observed 10 weeks after burning in the upper parts of plants exposed to temperatures over 400 ^{o}C. All five species tested in the laboratory experiment also showed more damage at higher temperatures, with damage occurring immediately after heat exposure. These results indicate that hotter fires are likely to have a greater impact on *Sphagnum* survival and growth, and could slow the rate at which the peatland moss layer sequesters carbon.

Keywords: *Sphagnum*, moss; fire, peatland, burning, heat damage.

1. Introduction

Peatlands are important ecosystems which cover 2.84 % of the world's land surface (Xu et al. 2018b), store over 600 Gt of carbon (Yu et al. 2010; Leifeld & Menichetti 2018) and have a significant role in water supply in several key regions (Xu et al. 2018a). *Sphagnum* is the most important peat forming genus globally (Clymo & Hayward 1982), is considered a significant ecosystem engineer in arctic, temperate and boreal peatlands (Bacon et al. 2017) and can have a beneficial impact on water quality (Ritson et al. 2016). Understanding how *Sphagnum* responds to abiotic influences such as fire is therefore vital to inform predictions of changing peatland function. Comparisons between different *Sphagnum* species are also valuable, as some species form peat to a greater extent than others (Gunnarsson 2005).

Vegetation fires, in the form of both wildfires and prescribed burns, are common on peatlands worldwide. Fire has the potential to impact ecosystem function via vegetation change, including changes to *Sphagnum* abundance (Noble et al. 2018a), but impacts are likely to be variable depending on fire severity. In the UK, the most common type of peatland fire is prescribed rotational burning for grouse moor management (Douglas et al. 2015), where patches of vegetation are burned to facilitate dwarf shrub regeneration. Prescribed burns are usually controlled with the intention of burning vegetation without consuming the moss layer or igniting the underlying peat, but temperatures may vary according to fuel structure and moisture, burning technique and weather conditions (Hobbs & Gimingham 1984). Increased knowledge of how the range of temperatures experienced during prescribed burns affects *Sphagnum* would improve understanding of the processes via which fire impacts occur and inform future decisions about the use of burning in vegetation management.

Fire temperatures in the field can be measured using thermocouple sensors (Kenworthy 1963; Hamilton 2000; Davies 2005; Grau-Andrés et al. 2018) or 'pyrometers' consisting of materials (commonly lacquers) which undergo irreversible changes in appearance at specific temperatures (Whittaker 1961; Hobbs et al. 1984; Cawson et al. 2016). Past studies of prescribed burning for grouse moor management have reported maximum fire temperatures in the range of 600 – 980^{o}C (Whittaker 1961; Kenworthy 1963; Hobbs et al. 1984; Davies 2005; Harris et al. 2011). These studies were carried out on sites with a range of soil and vegetation types, including heathlands, which may have drier soils and vegetation than peatlands. At a peatland site, Hamilton (2000) recorded average maximum temperatures of around 250°C at the moss surface and around 500°C at the midpoint of total vegetation height. Grau-Andrés et al. (2018) recorded temperatures below the moss/litter layer during fire in both peatland and heathland sites, and found lower temperatures in the peatland, which could be due to lower fire temperatures in the above-ground canopy or greater insulation by the peatland moss layer, which likely had a higher moisture content and was less likely to ignite.

Previous studies investigating the impact of high temperatures have employed a range of measures to assess *Sphagnum* health, including visible physical damage and changes in photosynthetic capacity. The current evidence base indicates that a decline in *Sphagnum* health occurs following exposure to high temperatures, followed by recovery over a period of months or years (Hamilton 2000; Grau-Andrés et al. 2017; Taylor et al. 2017). Studies by Taylor et al. (2017) and Grau-Andrés et al. (2017) focussed on *S. capillifolium*, while Hamilton (2000) monitored a species mix dominated by *S. capillifolium* and *S. papillosum*. *S. capillifolium* is common on UK peatlands, making up a large proportion of cover on many sites, so knowledge of its response to fire is important. However, this species often occurs on burned sites (Burch 2008; Lee et al. 2013), and its response to fire may not be representative of other species including historically significant peat formers such as *S. austinii* (Swindles et al. 2015), *S. papillosum* and *S. magellanicum* (Blundell & Holden 2015). Knowledge of species other than *S. capillifolium* is therefore important where the aim is to protect or restore typical peatland vegetation types with a range of *Sphagnum* species (Averis et al. 2004).

Reduced *Sphagnum* water content has the potential to increase vulnerability to fire damage (Taylor et al. 2017). Understanding this effect is relevant as burning often takes place where peat water availability (and hence *Sphagnum* water content) may be reduced as a result of factors such as dry weather conditions, drainage (Ketcheson & Price 2011), past fire (Thompson & Waddington 2013; Holden et al. 2014) or the dominance of relatively deep rooted shrubs (McNamara et al. 2008). Climate change may also result in more frequent peatland drought in some regions (Gallego-Sala & Prentice 2013; Li et al. 2017). Additionally, seasonal fluctuations in moisture may mean that the timing of burning is important in determining the risk of damage to *Sphagnum*.

In this study, we aimed to assess how pre-fire vegetation composition and structure influence prescribed burning temperatures in peatlands, and to quantify the effects of fire occurrence and fire temperature on *Sphagnum* damage. To achieve this, we measured fire temperatures in 16 experimental prescribed burns on a blanket peatland site. Metrics of *Sphagnum* health including height change, cell damage and water content were measured at several time points after burning in burned and control plots. Cell damage was also assessed in five *Sphagnum* species subjected to two moisture treatments and exposed to a range of temperatures in the laboratory. The results have been considered in the context of peatland fire management.

2. Methods

2.1 Field study

The study was carried out at the Hard Hill burning and grazing experiment (54°43′N 2°23′W; Figure 1), which was established in 1954 on an area of blanket peatland at Moor House-Upper Teesdale National Nature Reserve (NNR) in the North Pennines, UK. The experiment consists of four blocks of six 30 m x 30 m plots subject to short-rotation (burned approximately every 10 years), long-rotation (burned approximately every 20 years) and 'no-burn' (unburned since 1954) treatments, in combination with fenced and grazed treatments. The vegetation surrounding the experimental blocks has remained unburned for at least 90 years. The design and history of the experiment are described further by Lee et al. (2013).

In April 2017, prescribed burning was carried out on the sixteen short- and long-rotation plots within the experiment. Prior to burning, measurement points were established by locating a patch of *Sphagnum capillifolium* (the most common *Sphagnum* species in the plots) near the centre of each plot and marking it with a cane. Pre-burn cover (%) and height (to the nearest cm) of dwarf shrubs and graminoids in a 50 cm x 50 cm quadrat centred on each measurement point were recorded.

Fire temperatures were recorded using two methods. First, a temperature datalogger (EL-TC-USB, Lascar, UK) with 30 cm K-type thermocouple (Omega, UK) was installed at each of the 16 measurement points. Dataloggers were placed in waterproof plastic bags and wrapped with heat-shielding aluminised glass fibre cloth, and the connected thermocouple sensors were positioned on the moss surface. These recorded the temperature at one second intervals, enabling determination of the maximum temperature during each fire and the number of seconds exceeding 50 °C, a critical threshold for plant tissue damage (Neary et al. 1999). Second, pyrometers similar to those used by Cawson et al. (2016), Hobbs et al. (1984) and Whittaker (1961) were made by painting 0.5 cm diameter dots of six temperature sensitive lacquers (Omegalaq, Omega, UK) onto aluminium forestry tags. The lacquers selected were designed to undergo irreversible changes in colour and/or texture at 79, 177, 260, 371, 454 or 593 ^{0}C, a range of temperatures chosen based on those measured during past work on heather burning (Whittaker 1961; Hobbs et al. 1984; Hamilton 2000). The painted tags were wrapped in aluminium foil and placed on the moss surface, at a distance of approximately 10 cm from the thermocouple sensors. Using both methods enabled comparison of their reliability, and the pyrometers ensured a backup measure of maximum fire temperature in the event of datalogger failure.

Immediately after burning in April 2017, the thermocouple-dataloggers and pyrometers were collected and a cranked wire similar to those used by Clymo (1970), Kim et al. (2014) and Walker et al. (2015) was installed at each of the 16 burn plot measurement point, as well as four control measurement points, located around 10 m north of each experimental block. Cranked wires comprised 3 mm galvanised steel wire with two opposing 90^{0} bends so that a 20cm vertical length was inserted into the moss layer and underlying peat, a 2cm horizontal length was level with the moss surface, and a 10cm vertical length protruded above. Follow up measurements were carried out in June and September 2017, 10 and 21 weeks after burning respectively. The change in *S. capillifolium* height between installation and subsequent surveys was determined by the distance from the horizontal wire section to the moss surface. The distance measured in June was subtracted from that measured in September to give the height change between surveys. The height change data for both surveys was then divided by the relevant number of weeks to give the rate of weekly change for April-June and June-September.

In April and June, *S. capillifolium* samples were collected from the 16 burn plot measurement points and four unburned reference measurement points. In September, these 20 plots were re-sampled and four additional samples were collected from extra unburned reference points around 10 m south of each experimental block, giving a total of

24 samples (16 burned, 8 reference). Samples were stored in plastic bags for transportation back to the laboratory and analysis took place on the following day.

For the samples taken in June and September, *S. capillifolium* cell damage was quantified using trypan blue, a dye which is excluded from healthy cells but can enter and stain those with a compromised plasma membrane, allowing visualisation of cell damage (Oldenhof et al. 2006; Duan et al. 2010). A *S. capillifolium* capitulum from each sample was incubated in a 0.4% trypan blue solution for 20 minutes before rinsing three times with de-ionised water. Three branches were removed from the outer area of each capitulum, mounted on a slide, and viewed at 400 x magnification. A leaf near the tip of each branch was selected and stained and unstained chlorophyllous cells were counted. The mean proportion of stained cells in each sample was then calculated for use in analysis.

Samples of *S. capillifolium* were taken in April, June and September. On each occasion samples were collected on a single day between 10am and 1pm, and immediately sealed in plastic bags. Capitulum water content was determined by weighing three capitula at field moisture, then drying at 30 ^{0}C to constant weight and calculating the percentage of total mass lost. Additionally, in June and September, peat samples were taken 30 cm from each measurement point by pushing a 6.8 cm diameter, 6 cm high plastic tube into the peat below the moss layer. The water content of peat samples was calculated by drying the samples at 105 ^{0}C to constant weight and calculating the percentage of total mass lost, and bulk density was calculated by dividing the mass remaining after drying by the volume of the sample.

2.2 Laboratory study

Sphagnum cell damage after exposure to high temperatures was further tested in a series of laboratory experiments. Samples of five *Sphagnum* species (*S. capillifolium*, *S. papillosum*, *S. magellanicum*, *S. austinii* and *S. angustifolium*) were collected from Moor House-Upper Teesdale NNR between October 2017 and March 2018. For each species, 30 crucibles (2 cm diameter x 3 cm height) were filled with the top 3 cm of *Sphagnum* stems at field density. 15 crucibles were kept wet with de-ionised water while the other 15 were allowed to dry out at room temperature for 24 hours until around 20% of the original water content remained.

Six samples (three wet and three dry) were left as unheated controls, and a further six were exposed to each of four temperature treatments (125, 250, 375 and 500 ^{o}C). Heating was achieved by using a thermocouple and datalogger with LCD display (EL-TC-USB-LCD, Lascar, UK) to measure the temperature next to a Meker burner flame, and upon reaching the desired temperature, samples were held with tongs so that the *Sphagnum* capitula were level with the thermocouple tip for 5 seconds. This was intended to provide high temperature exposure comparable to that experienced in a prescribed burn, where flames from burning canopy vegetation heat the *Sphagnum* surface, and the duration of the temperature peak at the moss layer level is typically short (Davies 2005). After heating, all samples were re-wetted with de-ionised water before trypan blue staining was carried out on one capitulum from each sample as described above. For *S. capillifolium*, the samples were then kept in natural light at a temperature of 15-18^{o}C for 11 days before trypan blue staining was carried out a second time on another capitulum from each sample.

2.3 Analysis

All statistical analyses were carried out using R 3.4.1 (R Development Core Team 2010) with the packages car (Fox & Weisberg 2011), nlme (Pinheiro et al. 2016), and ggplot2 (Wickham 2009). Of the 16 thermocouple-dataloggers deployed, 14 successfully recorded fire temperatures, and all 16 pyrometers provided temperature readings. The impacts of pre-burn vegetation (graminoid and dwarf shrub cover and height) on maximum fire temperature were assessed using linear models, and R^2 values were compared to determine the best predictor. Spearman's correlation was used to test the relationship between maximum temperatures detected by thermocouples and pyrometers, as well as the relationship between maximum temperature and time above 50 ^{o}C detected by the thermocouples.

Two approaches were used to analyse fire temperature impacts on *Sphagnum* and peat properties. In both cases, linear mixed models with temperature and survey month as fixed factors and measurement point as a random factor were used to account for the repeat surveys, and dependent variables measured on the percentage scale were logit transformed to increase compliance with model assumptions of normality. Maximum fire temperature detected by thermocouples in burned plots was used as a continuous predictor variable in one set of models. For the second set of models, the measurement points were placed in three groups to enable comparison of high (324 – 538 ^{o}C) and low (33 – 137 ^{o}C) maximum temperature exposures with the unburned control group. For the two burn plots where dataloggers failed, pyrometer readings were used to categorise fire temperature into the high or low groups.

3. Results

Maximum temperatures detected by the thermocouples during fire ranged from 33 ^{o}C to 538 ^{o}C, with a mean of 259 ^{o}C. These maximum temperatures were correlated with both length of time 50 ^{o}C was exceeded (Spearman rho = 0.89, $p < 0.001$) and the maximum temperatures detected by the pyrometers (Spearman rho = 0.75, $p = 0.002$). Of the vegetation attributes tested, dwarf shrub cover was the best predictor of maximum fire temperature ($R^2 = 0.46$, p = 0.008). The relationship between maximum temperature and *S. capillifolium* cell damage indicated by trypan blue staining (Figure 2) was significantly positive for samples collected in June, 10 weeks after burning (t = 4.67, $p < 0.001$), though marginally less positive (t = -2.08, $p = 0.059$) for samples collected in September, 21 weeks after burning (Table 1). The proportion of cell damage recorded in June ranged from 2-100% and was lowest (2-38 %) for temperatures under 100 ^{o}C and consistently high (93-100 %) for temperatures over 400 ^{o}C. There was no significant relationship between maximum temperature and *S. capillifolium* height change and water content, nor peat bulk density and water content (Table 1).

When high and low temperature groups were compared to the control group, *S. capillifolium* cell damage was found to be greater in the high temperature group than the control group, with no significant effect of month or interaction between month and temperature group (Table 2, Figure 3). Damage in the control group was consistently low in both June and September, with mean values of 13 % and 9 % respectively, and a relatively small range (Figure 3). The mean proportion of damage was intermediate in the low temperature group (25 % June, 37 % September) and greatest in the high temperature group (74 % June, 55 % September), which also had the greatest range in values. *S. capillifolium* water content did not differ significantly between temperature groups but was higher in April and September than in June. *S. capillifolium* height change was more positive in the control group than the high and low temperature groups, and showed no significant effect of month or interactive effects (Table 2, Figure 3). Peat bulk density was greater in the high temperature group than in the control group, and greater in June than in September, while peat water content was greater in the control group than in the high and low temperature groups, and greater in September than in June (Table 2).

In the laboratory experiments, exposure to higher temperatures was associated with a greater amount of cell damage in all five *Sphagnum* species tested. The slope of this relationship did not differ significantly between species (Table 3, Figure 4). The amount of cell damage did not differ between wet and dry treatments for any species. In the second survey of *S. capillifolium* (11 days after heating) there was a greater proportion of cell damage overall, but the slope of the relationship between temperature and cell damage did not differ between the two time points (Table 4).

4. Discussion

The range of fire temperatures recorded was similar to those reported by Hamilton (2000) and Davies (2005), but lower than those reported by Whittaker (1961) and Kenworthy (1963). These differences are likely to reflect differences in fuel structure and moisture between study sites, with Hobbs et al. (1984) suggesting that fuel moisture content is particularly important in determining ground surface temperatures. The cold, wet climate at Moor House (Holden & Rose 2011) means that vegetation regrowth between burns is slow, so the Hard Hill plots are likely to have a relatively low fuel load. The burn plots are also relatively small compared to burn patches measured on grouse moors (Yallop et al. 2006), potentially resulting in lower than typical fire temperatures (Tucker 2003). Dwarf shrub cover was the main driver of fire temperature, as would be expected due to the greater quantity of woody fuel in dwarf shrub dominated plots. The use of burning as a restoration tool on peatlands to reduce dwarf shrub dominance has been suggested (Uplands Management Group 2017), but our results suggest that caution is necessary with this approach because burning on sites with high dwarf shrub cover is likely to result in high fire temperatures with a potentially greater risk of damage to the moss layer and underlying peat.

The significant relationship between temperature exposure and cell damage indicates that a negative impact on *Sphagnum* can occur even when it is not visibly consumed or burned during fire. Damage to *Sphagnum* cells is likely to result in reduced photosynthetic capacity (Grau-Andrés et al. 2017) and growth for the duration of the recovery period. This could potentially result in a decreased rate of carbon uptake after fire, while decomposition of damaged tissue could lead to increased losses of carbon via respiration. Taylor et al. (2017) and Grau-Andrés et al. (2017) showed that *Sphagnum* recovery is often possible following fire, though in some cases the damaged capitula themselves do not recover and are replaced by new side shoots.

The extent of short term damage and subsequent consequences, as well as timescales for recovery is likely to depend on amount of damage sustained. For example, plants which were exposed to temperatures over 400 ^{o}C and which showed near-complete cell damage in our samples, may be less able to regenerate from the upper stem tissue. However, it is not clear whether samples exposed to lower temperatures, many of which showed 20-50 % damage, would be able to regenerate more easily. Past work on the Hard Hill experiment has found less abundant *Sphagnum* in long-rotation plots than in short-rotation plots (Lee et al. 2013; Milligan et al. 2018). Our data showed that long-rotation plots had higher mean pre-fire dwarf shrub cover (69 %) than short-rotation plots (38 %) and also experienced higher mean burn temperatures (332 ^{o}C compared to 104 ^{o}C) and *Sphagnum* damage (57 % compared to 36 %). This could indicate that lower *Sphagnum* abundance in the long-rotation plots is related to greater *Sphagnum* cell damage, though it is difficult to separate potentially confounding effects such as fire-induced changes to peat physical properties. Further work could help to establish thresholds beyond which an ecologically significant impact on *Sphagnum* recovery occurs.

Sphagnum cell damage was the only variable which had a significant relationship with maximum temperature, suggesting that this metric is a relatively sensitive indicator of fire impacts. Several other *Sphagnum* and peat related variables differed between the burned and control groups. However, it is not possible to fully attribute these differences to the most recent burn, as the burn plots have been subject to repeated burning since in 1954, while the control points have remained unburned for over 90 years. The greater peat bulk density and lower peat water content in the burn plots may therefore be a legacy of previous burns, with similar impacts on peat properties observed several years after burning in past work (Holden et al. 2014; Holden et al. 2015).

Sphagnum water content, peat water content and peat bulk density all showed changes over the course of the study, which is likely to be due to seasonal variation in the water table driven by rainfall and evaporative water losses. Seasonal changes in wetness can cause increases in peat volume and water storage capacity, leading to surface elevation changes known as mire breathing (Price & Schlotzhauer 1999; Howie & Hebda 2018). The fact that bulk density was highest and peat and *Sphagnum* water content were lowest in June, following a period of warm and dry weather, supports this explanation. It should be noted that the moisture content of *Sphagnum* capitula can vary over short timescales due to overnight dewfall, precipitation events and daytime evaporation, which is a potential source of error associated with this method.

Sphagnum height generally increased during the study in the unburned control group, suggesting growth during the summer half year, but decreased at many of the burn plot measurement points. This decrease could be due to shrinkage of the *Sphagnum* layer due to moisture loss, structural collapse or decomposition, or alternatively surface height changes in the underlying peat for similar reasons. Overall, it was difficult to separate the effects of *Sphagnum* growth, height loss and peat surface change using the cranked wire method in this context. Of the methods we used to measure fire impacts, cell damage quantification using trypan blue staining was the most closely associated with maximum temperatures and proved to be a useful method to provide a snapshot of *Sphagnum* damage.

Of the two temperature recording methods used, thermocouples provided the most detailed and accurate information on fire temperature, but readings from the pyrometers were well correlated with those from the thermocouples. This shows that pyrometers can provide a valuable means of ensuring backup maximum temperature measurements (as was the case here where two dataloggers failed) and/or greater spatial coverage more cost effectively. Additionally, the strong correlation between maximum temperatures and time exceeding 50 °C indicates that these values may serve as useful proxies for each other in peatland prescribed burns.

Cell damage observed in the laboratory experiments followed a similar pattern to the field study. This supports the conclusion that fire temperature is a key driver of *Sphagnum* damage, regardless of potentially confounding factors such as the cover of vascular plants in the field. The proportion of cells damaged by heating in the laboratory was generally lower than at similar temperatures in the field, probably due to shorter exposure times. Re-testing of *S. capillifolium* samples eleven days after temperature exposure revealed a greater level of overall damage, probably due to sub-optimal survival conditions in the laboratory. However, the slope of the relationship between temperature and cell damage did not differ, indicating that temperature damage occurs immediately, or very soon after burning.

There were no significant differences in temperature damage slopes between species, suggesting that the species tested here did not differ in their sensitivity to high temperatures. However, it is possible that secondary impacts of fire such as changes to peat physical and chemical properties (Brown et al. 2014; Holden et al. 2014; Brown et al. 2015) impact species in different ways (Sagot & Rochefort 1996; Noble et al. 2017), causing changes in relative abundance in the longer term. No significant difference in the proportion of cell damage was observed between the wet and dry treatments for any species. However, we only tested leaves from the top of capitulum branches, and it is possible that heat damage penetrated further into the *Sphagnum* capitula of dry samples due to lower heat capacity. Future work investigating cell damage in different areas of the plant could indicate whether this is the case, and whether critical zones, such as the apical meristem, are more at risk as a result.

5. Conclusion

Our results show that greater dwarf shrub cover prior to burning produces hotter fires which are potentially more damaging to peatland ecosystems. *Sphagnum* samples had a greater proportion of cell damage after exposure to higher temperatures in both the field and the laboratory. The impact of cell damage on the subsequent growth, respiration and recovery of *Sphagnum* is likely to relate to both the proportion of cells damaged and the areas of the plant affected. The implications of these impacts for peatland ecosystem services could include a reduced rate of carbon sequestration by *Sphagnum* following burning, resulting in slower peat accumulation. If less damaged *Sphagnum* is able to recover more quickly, cooler burns may have a less negative impact on *Sphagnum*. However, fire can impact vegetation in various ways in addition to heat-induced cell damage, so more work is needed to establish long-term effects of varying fire temperatures *in situ*.

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Tables

Table 1: Results from linear mixed models investigating the impact of maximum fire temperatures from 14 burn plots with *Sphagnum* and peat related variables measured during fieldwork in April and/or June and September. Intercept = reference temperature and time point; max temp = effect of increasing maximum temperature at the reference time point; June/September = effect of time point at reference temperature; max temp: June/September = difference in the slope of maximum temperature relationship between reference and subsequent time points.

		Estimate	Std error	DF	t-value	*p*-value
S. capillifolium cell damage logit %	Intercept	-2.070	0.651	12	-3.177	0.008
	Max temp	0.010	0.002	12	4.673	0.001
	September	1.198	0.921	12	1.300	0.218
	Max temp: September	-0.006	0.003	12	-2.086	0.059
S. capillifolium water content logit %	Intercept	1.404	0.393	24	3.578	0.002
	Max temp	-0.001	0.001	12	-0.546	0.595
	June	-1.208	0.555	24	-2.177	0.040
	September	0.942	0.555	24	1.697	0.103
	Max temp: June	-0.001	0.002	24	-0.418	0.680
	Max temp: September	0.001	0.002	24	0.612	0.546
S. capillifolium Height change mm wk^{-1}	Intercept	0.139	0.149	12	0.930	0.371
	Max temp	-0.001	<0.001	12	-2.131	0.054
	September	-0.107	0.194	12	-0.550	0.592
	Max temp: September	0.001	0.001	12	1.028	0.324
Peat bulk density g cm^{-3}	Intercept	0.101	0.006	12	16.419	0.000
	Max temp	0.000	0.000	12	1.214	0.248
	September	-0.012	0.007	12	-1.726	0.110
	Max temp: September	0.000	0.000	12	-1.277	0.226
Peat water content logit %	Intercept	1.758	0.039	12	45.453	<0.001
	Max temp	<0.001	<0.001	12	-1.694	0.116
	September	0.308	0.046	12	6.652	<0.001
	Max temp: September	<0.001	<0.001	12	0.574	0.576

Table 2: Results from linear mixed models investigating the impact of control, high and low temperature groups with *Sphagnum* and peat related variables measured during fieldwork in April (n=20) and/or June (n=20) and September (n=24). Intercept = reference temperature group and time point; low/high temp = effect of different temperature group at reference time point; June/September = effect of subsequent time points at reference temperature group; low/high temp: June/Sep = interactions between the categorical variables.

		Estimate	Std error	DF	t-value	*p*-value
S. capillifolium cell damage logit %	Intercept	-2.137	0.759	21	-2.814	0.010
	Low temp	0.873	0.933	21	0.935	0.360
	High temp	3.707	0.933	21	3.972	0.001
	September	-0.360	0.867	17	-0.415	0.683
	Low temp: Sep	0.957	1.105	17	0.866	0.399
	High temp: Sep	-1.010	1.105	17	-0.914	0.374
S. capillifolium water content logit %	Intercept	90.750	7.717	34	11.760	<0.001
	Low temp	-16.625	9.451	21	-1.759	0.093
	High temp	-16.125	9.451	21	-1.706	0.103
	June	-22.250	10.913	34	-2.039	0.049
	September	-1.250	9.451	34	-0.132	0.896
	Low temp: June	-2.500	13.366	34	-0.187	0.853
	High temp: June	-9.375	13.366	34	-0.701	0.488
	Low temp: Sep	18.625	12.201	34	1.527	0.136
	High temp: Sep	17.000	12.201	34	1.393	0.173
S. capillifolium Height change mm wk^{-1}	Intercept	0.011	0.122	17	0.093	0.927
	Low temp	-0.159	0.173	17	-0.922	0.370
	High temp	0.466	0.211	17	2.204	0.042
	September	0.039	0.139	17	0.278	0.785
	Low temp: Sep	-0.191	0.197	17	-0.970	0.346
	High temp: Sep	0.034	0.241	17	0.141	0.889
Peat bulk density g cm^{-3}	Intercept	0.086	0.008	21	11.095	<0.001
	Low temp	0.020	0.010	21	2.036	0.055
	High temp	0.023	0.010	21	2.412	0.025
	September	-0.023	0.008	17	-2.945	0.009
	Low temp: Sep	0.006	0.010	17	0.576	0.572
	High temp: Sep	0.002	0.010	17	0.189	0.852
Peat water content logit %	Intercept	2.014	0.100	21	20.195	<0.001
	Low temp	-0.296	0.126	21	-2.347	0.029
	High temp	-0.325	0.126	21	-2.577	0.018
	September	0.397	0.095	17	4.164	0.001
	Low temp: Sep	0.058	0.119	17	0.485	0.634
	High temp: Sep	0.055	0.119	17	0.460	0.651

Table 3: Results from linear model investigating impacts of temperature exposure (ambient – 500 ^{o}C), moisture treatment (wet or dry) and *Sphagnum* species identity on proportion of cell damage (logit transformed %).

	Estimate	Std error	t-value	p-value
(Intercept)	-3.330	0.547	-6.090	<0.001
Temperature	0.007	0.002	3.994	<0.001
Dry	0.697	0.773	0.902	0.369
S. papillosum	0.320	0.773	0.414	0.680
S. austinii	-0.513	0.773	-0.663	0.509
S. angustifolium	1.051	0.773	1.359	0.176
S. magellanicum	1.028	0.773	1.329	0.186
Temp: dry	-0.001	0.003	-0.339	0.735
Temp: *S. papillosum*	-0.002	0.003	-0.622	0.535
Temp: *S. austini*	0.000	0.003	0.134	0.894
Temp: *S. angustifolium*	0.002	0.003	0.858	0.393
Temp: *S. magellanicum*	0.000	0.003	-0.172	0.863
Dry: S. papillosum	0.550	1.094	0.503	0.616
Dry: *S. austinii*	1.218	1.094	1.114	0.267
Dry: *S. angustifolium*	0.549	1.094	0.502	0.617
Dry: *S. magellanicum*	-1.146	1.094	-1.048	0.296
Temp: dry: *S. papillosum*	-0.003	0.004	-0.877	0.382
Temp: dry: *S. austinii*	-0.003	0.004	-0.958	0.340
Temp: dry: *S. angustifolium*	-0.002	0.004	-0.632	0.528
Temp: dry: *S. magellanicum*	0.002	0.004	0.540	0.590

Table 4: Results from linear mixed model investigating impacts of temperature exposure (ambient – 500 ^{o}C), moisture treatment (wet or dry) and time (immediately after heating or 11 days later) on proportion of *S. capillifolium* cell damage (logit transformed %).

	Estimate	Std.Error	DF	t-value	p-value
(Intercept)	-3.010	0.583	26	-5.164	<0.001
Temperature	0.006	0.002	26	2.922	0.007
Dry	1.248	0.824	26	1.514	0.142
Time	0.717	0.824	26	0.870	0.392
Temp: dry	-0.004	0.003	26	-1.482	0.150
Temp: time	0.000	0.003	26	0.033	0.974
Dry: time	-0.620	1.166	26	-0.532	0.599
Temp: dry: time	0.001	0.004	26	0.315	0.756

Figures

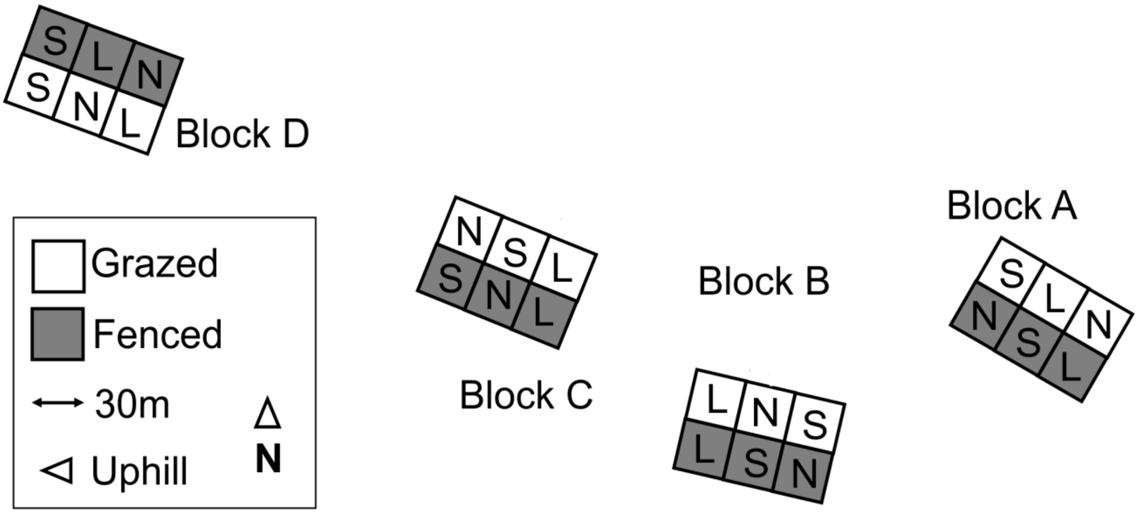

Figure 1: Map of the of the Hard Hill experimental plots (N = no-burn since 1954, L = long (20-year) rotation, S = short (10-year) rotation. Figure adapted from Noble et al (2018b)

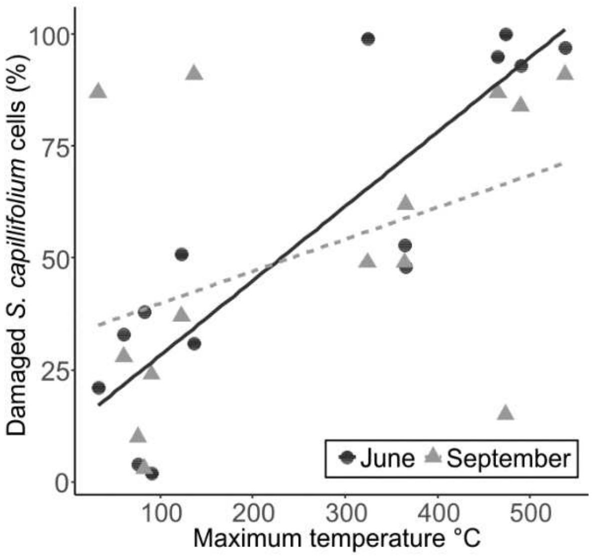

Figure 2: Relationships between maximum temperature exposure and cell damage in *Sphagnum capillifolium* samples taken from 14 experimental burn plots, 10 (June) and 21 (September) weeks after burning.

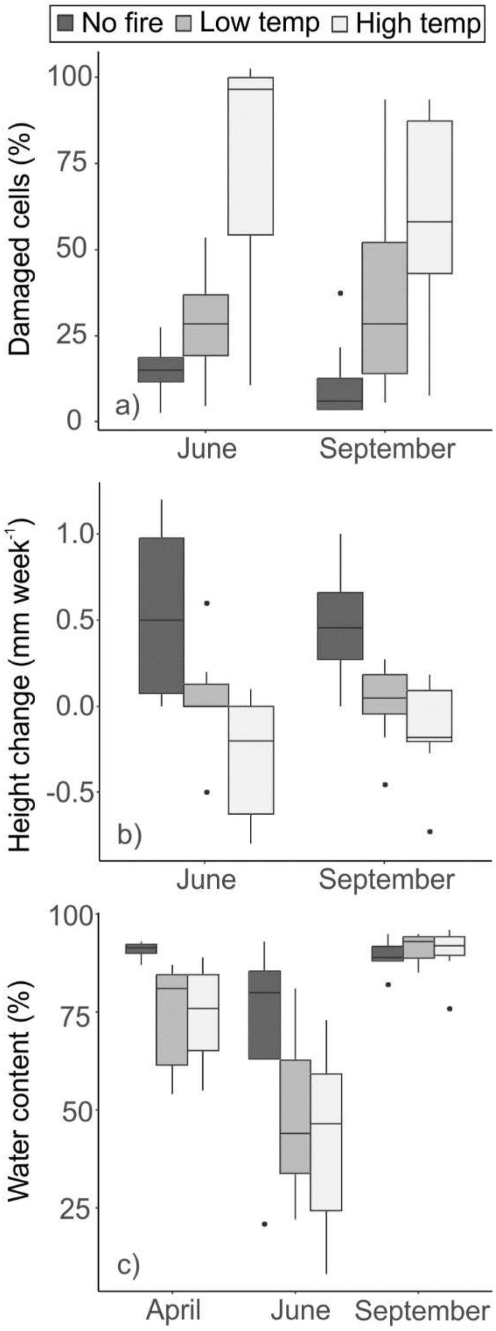

Figure 3: Boxplots showing comparisons between no fire, low temperature and high temperature groups for a) proportion of damaged *Sphagnum capillifolium* cells, b) *S. capillifolium* mean weekly height change and c) *S. capillifolium* water content as a percentage of wet weight. Measurement times were immediately (April), 10 (June) and 21 (September) weeks after fire.

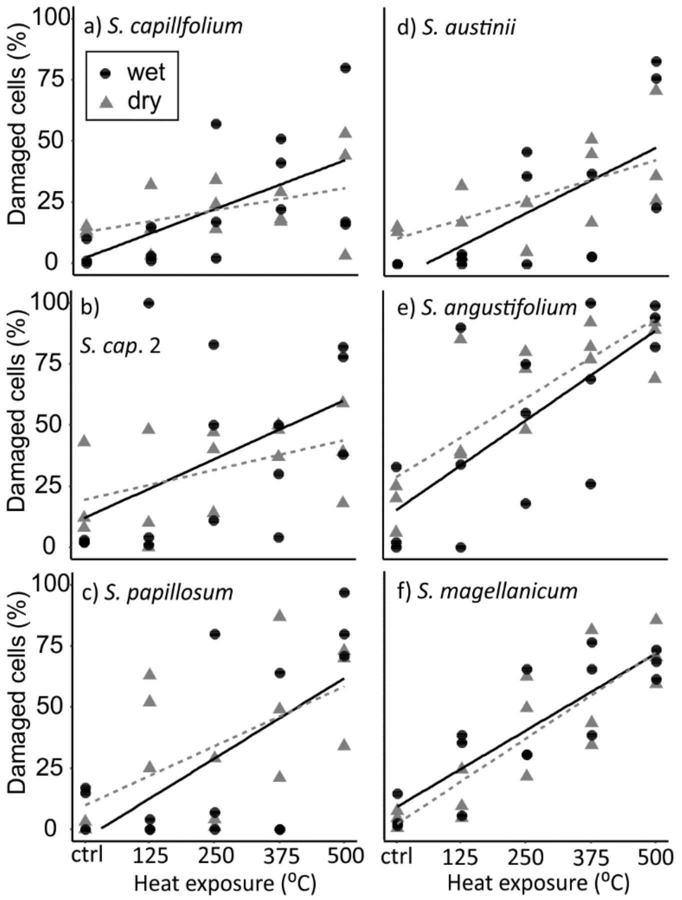

Figure 4: Proportion of damaged cells in wet and dry *Sphagnum* samples in the control (ctrl) group, or exposed to 125, 250, 375 or 500 ^{o}C for 5 seconds by heating with a Meker burner flame in the laboratory. Damage was measured within 24 hours of temperature exposure, except in b) where damage was measured 11 days after temperature exposure.