The impacts of prescribed burning on blanket peatland vegetation

Alice Kathryn Noble

Submitted in accordance with the requirements for the degree of

Doctor of Philosophy

The University of Leeds

School of Geography

September 2018

Declaration and author contributions

The candidate confirms that the work submitted is her own, except where work which has formed part of jointly authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

Chapter 2 has appeared in publication as:

Noble A, Palmer SM, Glaves DJ, Crowle A, Brown LE, Holden J. (2017) Prescribed burning, atmospheric pollution and grazing effects on peatland vegetation composition. *Journal of Applied Ecology* 00:1–11. https://doi.org/10.1111/1365-2664.12994

Contributions: LB, JH and SP were investigators on the EMBER project which supported some earlier data collection. AC and DG were investigators and supervised the botanical data collection from the EMBER and CM sites. DG, AC, JH, SP and AN conceived the ideas for this paper. AN analysed the data and led the writing of the manuscript. All authors contributed to methodology and interpretation of the analysis, critically assessed the drafts and approved the final version.

Chapter 3 has appeared in publication as:

Noble A, Palmer SM, Glaves DJ, Crowle A, Holden J (2017) Impacts of peat bulk density, ash deposition and rainwater chemistry on establishment of peatland mosses. *Plant and Soil* 419: 41. https://doi.org/10.1007/s11104-017-3325-7

Contributions: All authors contributed to the conception and planning of the study. AN led the study conception, carried out the experiment, analysed the data and drafted the manuscript. All authors critically assessed the manuscript and approved the final version.

Chapter 4 has appeared in publication as:

Noble A, O'Reilly J, Glaves DJ, Crowle A, Palmer SM, Holden J (2018) Impacts of prescribed burning on *Sphagnum* mosses in a long-term peatland field experiment. *PLoS ONE 13(11): e0206320. https:// doi.org/10.1371/journal.pone.020632*

Contributions: AN led analysis of all of the historical and recent field survey data, the interpretation of results and the writing of the manuscript. DG, AC and JO designed the 2015/16 field survey, which was undertaken by JO with assistance from AN. All authors critically assessed the drafts and gave final approval for submission.

Chapter 5 is under consideration for publication, following an initial round of peer review and a request for revisions:

Noble A, Palmer SM, Glaves DJ, Crowle A, Holden J (2018) Peatland vegetation change and establishment of re-introduced *Sphagnum* moss after prescribed burning. *Manuscript in review*

Contributions: AN planned the study with support from all authors, carried out all fieldwork and analysis, and led the writing of the manuscript. All authors critically assessed the drafts and approved the final version.

Chapter 6 is under consideration for publication, following an initial round of peer review and a request for revisions:

Noble A, Crowle A, Palmer SM, Glaves DJ, Holden J (2018) Fire temperatures and *Sphagnum* damage during prescribed burning on peatlands. *Manuscript in review*

Contributions: AN planned the study with support from all authors, and undertook all fieldwork, laboratory work and analysis. AN led the writing of the manuscript and all authors critically assessed the drafts.

Thesis by alternative format rationale

This thesis follows the University of Leeds Faculty of Environment protocol for the format and presentation of an alternative style of doctoral thesis including published material. The research questions of the project were investigated using a range of approaches, which made the presentation of the data chapters as five individual manuscripts appropriate. Three of the manuscripts have now been published, and the final two manuscripts are under review. The main body of the thesis therefore consists of the published and submitted manuscripts. This is preceded by an introduction, which provides background information, reviews relevant literature, and outlines the aims and objectives of the work. A synthesis chapter, bringing together the findings of the five manuscripts and discussing them in the context of the research questions, concludes the thesis.

Copyright declaration

Acknowledgements

While writing this thesis I was lucky to receive support from many people. First and foremost, I am grateful to my supervisors Joseph Holden, Sheila Palmer, Alistair Crowle and David Glaves. All four have been generous with their time, advice and expertise. They have also given me the encouragement and freedom to develop as a researcher. Thanks also to Lee Brown and Andrew Baird at the University of Leeds who provided useful feedback throughout the project.

Many people at the University of Leeds, Natural England and other organisations kindly offered support with the planning and delivery of this project, as well as company in the field, laboratory and office. Thanks to Martin Furness for welcoming me at Moor House and John O’Reilly for sharing his extraordinary botanical skills. Thanks also to everybody in the University of Leeds Peat Club for sharing their knowledge, advice and friendship. It has been a real pleasure to be part of the School of Geography for the past four years thanks to the wonderful people in the department, and the many occasions for tea, cake and beer.

Sue and Deb have been a welcome family presence in Leeds. Tim and Rebecca also helped me to feel at home when I moved here. My friends and family in Newcastle and further afield are consistently amazing, and I’d like to thank all of them, especially my brother Leon. Extra special thanks to Jack who provided endless encouragement and also helped out in the field without complaining once. Finally, thanks to my mum Jude and dad Tom (another fieldwork victim) for their unwavering belief and support, without which I would never have embarked on this journey.

Abstract

Peatlands are internationally important ecosystems, and play a vital role in carbon sequestration, water provision and global biodiversity. Fire occurs on peatlands worldwide and includes prescribed burning for purposes including agriculture and wildfire control. Many UK blanket peatlands are subject to prescribed burning to encourage production of the game bird red grouse (*Lagopus lagopus scotica*), but such burning may not be compatible with environmental outcomes related to carbon, water and biodiversity. Vegetation plays a key role in peatland ecosystem services, so evidence of how fire affects vegetation is needed to inform decisions about the future of prescribed burning. The work in this thesis considers vegetation change in the years following prescribed burning, with a focus on peat-forming *Sphagnum* mosses. A range of approaches including field monitoring and laboratory experiments were used to investigate the key plant taxa affected, timescales of change, and processes responsible for fire impacts.

Important findings include differences in vegetation composition between burned and unburned plots on national and regional scales. Evidence of negative impacts of burning on *Sphagnum* mosses was found, with lower cover on recently burned plots on a national scale, reduced growth in response to fire-induced changes to peat properties, and increased cell damage after high temperature exposure, although ash addition increased growth. Data from a long-running field experiment revealed that fire impacts on *Sphagnum* can persist for several decades. Timescales of vegetation change were observed to vary between sites, but in general bare peat and acrocarpous mosses were likely to increase temporarily following burning, and a high abundance of graminoids a few years after fire was followed by dwarf shrub dominance in the longer term. These changes are likely to have consequences for peatland ecosystem services.

Initialisms, acronyms and abbreviations used in this thesis

ANOVA	Analysis of variance
Bx (B1, B5, *etc.*)	Burned x years before study commenced
CM	Condition monitoring [dataset]
CO_2	Carbon dioxide
Defra	Department for Environment, Food & Rural Affairs
DOC	Dissolved organic carbon
ECN	Environmental Change Network
EMBER	Effects of Moorland Burning on the Ecohydrology of River basins [research project and dataset]
GLM	Generalised linear model
GLMM	Generalised linear mixed model
HSD	Honest significant difference
ICP-OES	Inductively coupled plasma optical emission spectrometry
IUCN	International Union for Conservation of Nature
JNCC	Joint Nature Conservation Committee
LED	Light-emitting diode
LM	Linear model
LMM	Linear mixed model
NE	Natural England
NERC	Natural Environment Research Council
NMDS	Non-metric multidimensional scaling
NNR	National Nature Reserve
PERMANOVA	Permutational multivariate analysis of variance
UK	United Kingdom

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Chapter 1: Introduction

This introductory chapter seeks to place the thesis in context by providing background information and reviewing the relevant literature. First, it is necessary to explain the characteristics of peatlands and their importance to ecosystem services on a global scale. The typical vegetation of blanket peatlands is then discussed, with specific attention paid to *Sphagnum* mosses because of their importance as ecosystem engineers. This is followed by some background information about prescribed burning, a review of the existing evidence of fire impacts on blanket peatlands, and consideration of the likely pathways for fire impacts on vegetation communities. Finally, the aims, objectives and methods used to address the key research questions are described and the overall structure of the rest of the thesis is defined.

1.1 Peatlands

Peatlands are areas where plant remains have accumulated due to incomplete decomposition in wet, anaerobic conditions, forming a layer of highly organic soil known as peat (Rydin and Jeglum, 2006; Clymo, 1984). These ecosystems exist across a range of latitudes, but a large proportion occur at mid to high latitudes in the northern hemisphere (Xu et al., 2018b). The plant groups responsible for peat formation vary geographically (Bacon et al., 2017) but include woody plants, graminoids and mosses. *Sphagnum* mosses are particularly important for peat formation in northern peatlands, and may store more carbon than any other plant genus worldwide (Clymo and Hayward, 1982; Rydin and Jeglum, 2006).

Although peatlands account for less than 3% of the land surface globally (Xu et al., 2018b), they store in the region of one-third of global soil carbon (Page et al., 2011; Dargie et al., 2017). In addition, peatlands play a significant role in global water and biogeochemical cycles (Rezanezhad et al., 2016), and are vital for the provision of potable water in several key regions (Xu et al., 2018a). Peatland condition can also influence the quality of water draining from catchments (Martin-Ortega et al., 2014), and the magnitude and frequency of flooding events downstream (Holden, 2005). Furthermore, they contribute to regional and global biodiversity, hosting a range of plants, animals and microorganisms, many of which are specialised to peatland habitats (Minayeva and Sirin, 2012; Littlewood et al., 2010).

A broad classification of two peatland types can be made based on their hydrology. Minerotrophic peatlands (fens) are fed mainly by ground and surface water which supply a greater quantity of nutrients, whereas ombrotrophic peatlands (bogs) receive water dominantly from atmospheric deposition and tend to be nutrient poor. Further classifications can be made based on characteristics such as landform and vegetation type but terminology varies between countries and classification systems (Rydin and Jeglum, 2006). The minimum peat depth required to classify a site as a peatland also varies, though 30 cm is a commonly used value internationally (Joosten and Clarke, 2002; Lindsay, 2010; Bain et al., 2011).

Blanket peatlands are a type of ombrotrophic bog found in Europe, North America, South America, Asia and Australasia (Gallego-Sala and Prentice, 2013). They occur when peat deposits cover (‘blanket’) large areas of land, including sloping terrain (Gorham, 1957; Charman, 2002). Blanket peatland vegetation is treeless and characterised by dwarf shrubs, graminoids and mosses, with *Sphagnum* the most important peat forming group (Gallego-Sala and Prentice, 2013; Moore, 2002). In the UK, blanket peatlands represent the largest remaining semi-natural terrestrial habitat type (Bain et al., 2011) and they are a priority habitat for conservation in the UK and Europe (JNCC, 2014; JNCC, 2008).

1.2 *Sphagnum*

The ability of *Sphagnum* moss to form peat is a result of traits which enable it to retain large volumes of water (Hayward and Clymo, 1982) and acidify the local environment (Andrus, 1986), slowing decomposition. The wet and acidic conditions created by *Sphagnum* can also impede the root function of vascular plants, reducing competition (Hemond, 1980; van Breemen, 1995). *Sphagnum* plants grow from the apex, where branches form a compact head called the capitulum. As new branches are produced, the stem segments between older branches elongate. Individual stems are unable to remain vertical independently, instead forming carpets of capitula beneath which the lower stems eventually die and undergo partial decomposition, forming peat (Clymo and Hayward, 1982).

The genus *Sphagnum* consists of an estimated 300-500 species globally (Clymo and Hayward, 1982; Shaw et al., 2010) with a range of environmental tolerances in terms of moisture, nutrients, temperature and light (Hill et al., 2007). However, some general principles apply across the genus. As *Sphagnum* lacks vascular tissue, water is supplied to the capitulum via capillary transport (McCarter and Price, 2014), so it requires a relatively high water availability and can exhibit a decreased growth rate under drought (Bu et al., 2013; Clymo, 1973). The efficiency of capillary transport varies, with hummock forming species generally able to maintain capitulum moisture at a greater height above the water table than hollow dwelling species (Hayward and Clymo, 1982). Nonetheless, work by Gignac et al. (2000) and Gunnarsson (2005) suggested that local and climatic factors relating to water availability are key predictors of *Sphagnum* occurrence globally.

Many *Sphagnum* species thrive in nutrient poor conditions (Rydin and Jeglum, 2006), capturing small nutrient inputs efficiently (van Breemen, 1995), and can be sensitive to nutrient enrichment. For example, sulphur pollution (Ferguson et al., 1978) was a major factor in the widespread loss of *Sphagnum* near industrial centres in the South Pennines (UK) during the 20th century (Carroll et al., 2009; Tallis, 1964). Elevated nitrogen inputs can increase competition from vascular plants (Limpens et al., 2011) and may even have a direct negative impact on some *Sphagnum* species (Granath et al., 2012; Gunnarsson and Rydin, 2000). There is also evidence that ozone exposure may have direct physiological effects on some *Sphagnum* species (Mörsky et al., 2011; Niemi et al., 2002; Potter et al., 1996b; Potter et al., 1996a).

The response of *Sphagnum* to ambient temperature appears to be variable, with work by Walker et al. (2015) and Breeuwer et al. (2009) suggesting that higher temperatures can restrict growth, whereas Robroek et al. (2007), Gunnarsson et al. (2004) and Gerdol et al. (1998) observed a positive response to higher temperatures in some species. This variation may reflect different temperature optima in species with different distributions (Robroek et al., 2007). Increasing light availability has been observed to have a positive impact on *Sphagnum* growth in some studies (Bonnett et al., 2010; Clymo, 1973), but photoinhibition and reductions in growth can occur at higher light intensities (Murray et al., 1993).

In the field, moisture, nutrients, temperature and light levels are often confounded with each other, and their effects can interact (Manninen et al., 2011; Clymo, 1973). These factors are also frequently associated with the presence of other species and can play a role in interspecific interactions. For example, shading of *Sphagnum* by a vascular plant canopy can influence light availability, temperature and humidity (Pouliot et al., 2011; Walker et al., 2015; Malmer et al., 2003). Vascular species can also influence *Sphagnum* growth positively by stabilising peat surfaces (Laberge et al., 2013) and providing structural support (Malmer et al., 1994). Pouliot et al. (2011) found that a low density of vascular plants facilitated *Sphagnum* hummock formation, but a high density caused etiolation of *Sphagnum* stems and reduced biomass. Competition for resources such as space, light and water can also occur between bryophytes, including different *Sphagnum* species (Bu et al., 2013; Rydin 1993).

1.3 Blanket peatland vegetation

1.2.1 Vegetation composition

A range of plant groups including dwarf shrubs, graminoids and non-*Sphagnum* mosses commonly occur alongside *Sphagnum* on blanket peatlands. The species present and their relative abundance vary spatially (JNCC, 2008), but communities are generally likely to be made up of functionally similar species (Robroek et al., 2017). On UK blanket peatlands, *Calluna vulgaris* is often the dominant species in the dwarf shrub canopy with *Erica* spp., *Empetrum nigrum* and *Vaccinium* spp. also common in some regions. Common graminoid species include the sedges *Eriophorum vaginatum, Eriophorum angustifolium* and *Trichophorum germanicum*. Non-*Sphagnum* mosses can be divided into pleurocarpous (prostrate, branching) mosses such as *Hypnum* spp. and *Plagiothecium undulatum*, and acrocarpous (upright, cushion forming) mosses such as *Dicranum* spp. and *Campylopus introflexus*.

1.3.2 Vegetation and ecosystem function

The abundance of different species and groups of plants can influence peatland function and associated ecosystem services. For example, Kivimaki et al. (2008) found that while peatland plots without vegetation acted as carbon sources, sedge-dominated plots were carbon sinks, and plots with *Sphagnum* had an even greater sink function. Paleoecological evidence also suggests that *Sphagnum* dominance can be associated with more rapid carbon accumulation than sedge dominance (Nichols et al., 2014). Work by Dixon et al. (2015) on blanket peatlands in the South Pennines, UK, found that plots dominated by *C. vulgaris* were likely to be carbon dioxide (CO_2) sources, and that taller *C. vulgaris* canopies were larger sources of CO_2.

Overland flow has been observed to be fastest over areas of bare peat, intermediate over areas of sedge cover, and slowest over areas of *Sphagnum* cover (Holden et al., 2008) with slower flows potentially resulting in reduced river flow peaks (Gao et al., 2015; Grayson et al., 2010). Peatland vegetation composition can also affect the quality of water draining the catchment, which can impact the likelihood of meeting statutory requirements such as those outlined in the Water Frameworks Directive (JNCC, 2010), as well as the costs of water treatment where peatlands supply potable water (Ritson et al., 2016). For example, dissolved organic carbon (DOC) released from peat causes colouration of water which requires treatment with coagulants (Worrall and Burt, 2009). A study by Armstrong et al. (2012) found that *C. vulgaris* dominated areas were associated with higher DOC concentrations than areas dominated by *Sphagnum* or the grass *Molinia caerulea*, with sedge dominated areas intermediate. DOC derived from *Sphagnum* may also be easier to treat than that derived from vascular plants (Ritson et al., 2016).

Vegetation composition contributes to and influences the biodiversity supported within peatland habitats, which include a number of species of conservation importance (Littlewood et al., 2010). Peatland vegetation composition can impact a range of taxa including microbes (Opelt et al., 2007; Bragina et al., 2012; Andersen et al., 2013; Andersen et al., 2010), macroinvertebrates (Savage et al., 2011; Hannigan and Kelly-Quinn, 2012) and birds (Smith et al., 2001; Pearce-Higgins and Grant, 2006). Although increased environmental heterogeneity is likely to support a greater diversity of species at the habitat scale (Anke et al., 2014), the extent to which communities differ between habitats contributes to the overall biodiversity of a geographic area (Whittaker, 1972). Therefore, species which are specialised or restricted to peatland habitats are particularly significant when considering peatland biodiversity (Littlewood et al., 2010), and their abundance may be more important than overall species richness.

1.3.3 Vegetation change

Climate and nutrient supply can be large-scale drivers of peatland vegetation change, with climate change predicted to cause a shift from *Sphagnum* to vascular plants globally (Bu et al., 2011). In the UK, continuing increases in upland temperature (Pepin, 1995; Holden and Adamson, 2012) and changing patterns of precipitation (Werritty, 2002; Burt et al., 1998) are likely to increase the frequency of drought (Worrall et al., 2006) and could potentially result in migration or local extinction of some species

(Holden et al., 2007) and a decline in the distribution of actively growing blanket peatlands (Clark et al., 2010). Although atmospheric deposition of sulphur has decreased in the UK, recovery of affected *Sphagnum* has been slow (Carroll et al., 2009; Evans et al., 2016). Nitrogen availability has not declined to the same extent in the UK (Evans et al., 2016), and climate warming may increase mineralisation of both nitrogen and phosphorus (Nadelhoffer et al., 1991), potentially benefiting dwarf shrubs over *Sphagnum* (Berendse et al., 2001) and graminoids (Kool and Heijmans, 2009).

Land management also impacts vegetation communities, and many blanket peatland sites have been subject to grazing, drainage, afforestation, or a combination of these practices. Grazing has been linked to graminoid dominance and the loss of dwarf shrubs (Bragg and Tallis, 2001; Anderson and Yalden, 1981), though the extent of impacts depends on the stocking rate (Lee et al., 2013a). During the latter half of the 20th century, many UK blanket peatlands were drained by cutting open ditches. Coulson et al. (1990) observed that this ditching led to a reduction in dwarf shrubs and increase in graminoid abundance. However, variation in drainage intensity, slope and precipitation between sites make the generalisation of effects difficult (Ramchunder et al., 2009). Afforestation of some UK blanket peatlands also occurred in the 20th century, with commercial conifer species replacing typical peatland vegetation and requiring deep drainage with the potential to impact surrounding non-forested areas of peat (Pyatt, 1993).

1.4 Prescribed burning

1.4.1 Background

Fire is a common occurrence on peatlands globally and can take the form of wildfires and prescribed burns. Wildfires may occur naturally in some peat-rich biomes, but can also occur as a result of human ignition. Prescribed burning is commonly practiced for purposes such as land clearance, agricultural improvement and habitat management. Both wildfires and prescribed burns can vary in severity, but prescribed burns are generally smaller, and can be controlled to burn only aboveground vegetation, whereas wildfires often cover extensive areas and can burn into the underlying peat. For this reason, the results of studies on wildfires may not be directly applicable to prescribed burning.

Prescribed burning in the UK occurs in a range of habitats including shrub and graminoid dominated peatlands, heathlands and grasslands, and is particularly common in upland areas dominated by *C. vulgaris* and managed for shooting of the game bird red grouse (*Lagopus lagopus scotica*). Patches up to around 4000 m^2 are burned sequentially on an annual basis. This creates a mosaic of vegetation stand ages (Yallop et al., 2006) which provide suitable habitat for grouse to nest and feed. This type of burning became widespread during the first half of the 20th century (Yallop et al., 2006; Holden et al., 2007), at which time Pearsall (1941) described the use of extensive burning and drainage to convert *Sphagnum* dominated bog to grouse moor.

Paleoecological evidence suggests that fire occurred periodically on UK blanket peatlands prior to the onset of prescribed burning, and tended to cause a change in vegetation followed by recovery over decades (Blundell and Holden, 2015). Burning has also been used to improve grazing in upland areas for several centuries, with large areas burned on an irregular basis. Prescribed patch burning may produce less severe fires than large scale burning, but is also likely to occur more frequently and extensively and hence may differ in its impacts.

In the UK, the burning season is restricted to avoid peat ignition and other damage in the drier summer months and risk to breeding birds in the spring. The Heather and Grass Burning Code (Defra, 2007) provides guidance on perceived good practice, which includes avoiding sensitive areas (e.g. adjacent to watercourses or on eroding soils) and implementing ‘cool’ burns which leave the bryophyte layer intact. Rotation lengths may vary between 7-25 years depending on the perceived requirement for different vegetation types. Yallop et al. (2006) found a median burn return time of 20 years, but noted a trend of increasing burn frequency in recent decades up to the point of their study.

Recent estimations suggest that around 18% of UK peatlands, and 40% of moorland in England have been subjected to burning (Defra, 2010). Guidance states that there should be a strong presumption against burning on blanket peatland (Defra, 2007), and the habitat is considered to be a climax community which should not require burning for maintenance (Fielding and Haworth, 2002). However, remote sensing suggests that increases in the area of blanket bog burned have occurred recently (Douglas et al., 2015; Thacker et al., 2015; Yallop et al., 2006). It has been suggested that burning may be a useful tool to reduce dominant dwarf shrub cover and restore *Sphagnum* cover on degraded peatlands (Uplands Management Group, 2017), but more evidence is needed to establish whether this is the case (IUCN, 2017; Thacker et al., 2015).

1.4.2 Impacts on blanket peatlands

Prescribed burning has been shown to impact physical, chemical and biological properties of peatlands and associated watercourses (Brown et al., 2014; Glaves et al., 2013; Worrall et al., 2010; Brown et al., 2015), with consequences for ecosystem services. Burned peatlands are likely to lose carbon via fuel consumption (Clay and Worrall, 2011; Allen et al., 2013) and can experience increased gross CO_2 exports (Ward et al., 2007), DOC exports (Yallop et al., 2010; Grayson et al., 2012) and erosion (Kinako and Gimingham, 1980) after burning. However, it is not clear whether there is a consistent net effect of burning on peatland carbon budgets (Glaves et al., 2013; Gray and Levy, 2009).

Altered water chemistry and changes in the composition of aquatic invertebrate communities in watercourses draining peatland catchments have also been associated with burning (Brown et al., 2013; Ramchunder et al., 2013). Some work suggests that burning could lead to shallower water tables due to decreased dwarf shrub transpiration (Clay et al., 2009; Worrall et al., 2013); however, in a study of 10 peatland catchments, Holden et al. (2015) found that water tables were deeper and more variable on recently burned plots, potentially due to higher peat surface temperatures enhancing evaporation (Brown et al., 2015). In addition, peat bulk density can be greater and hydraulic conductivity lower on recently burned sites (Holden et al., 2014), and rivers draining burned peatlands can experience intensified flow peaks during large storm events (Holden et al., 2015). Many of these impacts are likely to interact with vegetation-related variables (Figure 1.1), so increased understanding of vegetation change after burning may help to clarify the processes and feedbacks involved.

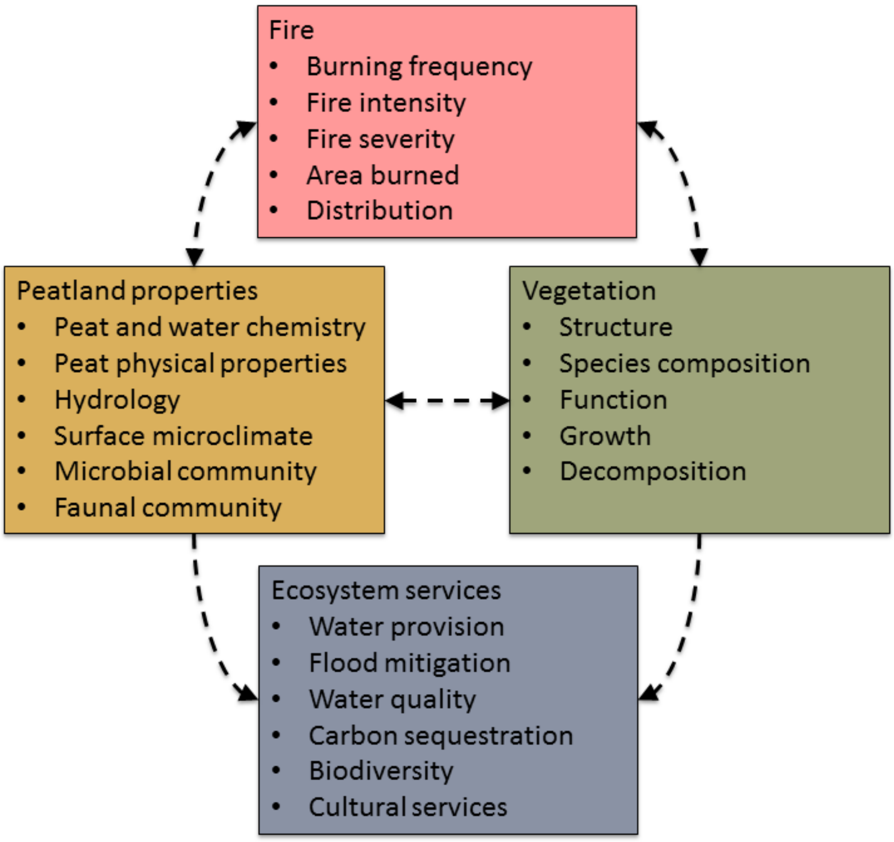

Figure 1.1: Variables related to fire, vegetation, peatland properties and ecosystem services, with arrows representing the direction(s) of potential impacts from each category.

The existing evidence base on burning impacts on blanket peatland vegetation is largely drawn from local-scale work, including several studies on the long-term burning experiment at Hard Hill, Moor House-Upper Teesdale NNR, UK (Alday et al., 2015; Lee et al., 2013a; Milligan et al., 2018; Hobbs, 1984; Rawes and Hobbs, 1979). This experiment has provided a valuable source of data on different burning rotations, but due to the relatively small (30 x 30 m) experimental burns, high altitude of the site, and regular trampling of the plots by researchers, it may not be typical of UK peatlands and caution should be used when generalising results (Gray and Levy, 2009; Lindsay, 2010).

Several reviews have considered prescribed burning impacts on vegetation, and their broad conclusions have generally agreed (Tucker, 2003; Glaves et al., 2013; Stewart et al., 2004; Worrall et al., 2010; Shaw et al., 1996; Harper et al., 2018; Mowforth and Sydes, 1989; Coulson et al., 1992; Glaves et al., 2005). The available evidence suggests that burning on blanket peatlands is often followed by a period of graminoid dominance lasting several years, before replacement by dwarf shrubs as the dominant group. A decline in the overall abundance of bryophytes and an increase in bare ground have also been reported (Glaves et al., 2013). *Sphagnum* is often regarded as fire-sensitive, but past work has reached mixed conclusions, with both increases and decreases over varying timescales after fire reported (Hamilton, 2000; Milligan et al., 2018; Grau-Andrés et al., 2017). Lower *Sphagnum* propagule abundance has also been observed on burned sites, even when area cover shows the opposite pattern (Lee et al., 2013a; Lee et al., 2013b). Overall there is no clear consensus on how burning affects *Sphagnum*, perhaps indicating that factors such as species identity and burn severity modify impacts. The suitability of burning as a management tool on UK peatlands is a contentious subject (Harper et al., 2018), so further evidence of burning impacts on vegetation (particularly *Sphagnum*) and function is important to guide policy and management decisions to ensure the continuing provision of ecosystem services.

1.5 Pathways for fire impacts on vegetation

Fire has the capacity to impact blanket peatland vegetation via multiple processes. These include direct impacts such as combustion, which is likely to affect plants with low pre-fire moisture content to a greater extent (Davies, 2005). Physiological damage due to high temperature exposure can also occur, and has been observed in *Sphagnum* (Taylor et al., 2017; Grau-Andrés et al., 2017). Meanwhile, regeneration and seed germination of fire-adapted species such as *C. vulgaris* may be stimulated by burning (Måren et al., 2010), potentially increasing their abundance.

Fire can also impact vegetation indirectly. For example, bare ground created by burning may facilitate colonisation by new species or expansion of existing species, particularly those which are fast-growing and tolerant of post-burning conditions (Duncan and Dalton, 1982; Thomas et al., 1994; Buttler et al., 1998; Chirino et al., 2006; Campeau and Rochefort, 1996). Such conditions include changes in peat and water chemistry, with the potential for ash deposition to increase nutrient availability immediately after burning (Allen et al., 1964; Allen et al., 1969). This may be followed by depletion of some nutrients in following years (Brown et al., 2014), which could lead to a change in plant species composition over time. Meanwhile, fire-induced changes to peat physical properties such as increased bulk density can decrease water availability at the peat surface (Holden et al., 2014). This, along with deeper water tables (Holden et al., 2015), may limit the growth of *Sphagnum* to a greater extent than vascular plants (which can access and transport water more easily) and other bryophytes with lower water requirements (Thompson and Waddington, 2013; Price and Whitehead, 2001).

Removal of the vascular plant canopy by burning can alter the microclimate at the peat surface, including the thermal regime, with more extreme temperature minima and maxima observed after burning by Brown et al. (2015). This has the potential to increase or decrease growth rates depending on species tolerance and phenology, but it has been suggested that the stable temperatures and humidity promoted by an intact canopy are favourable to *Sphagnum* growth (Pouliot et al., 2011). Greater light availability may increase productivity of understory species such as *Sphagnum* (Clymo, 1973; Bonnett et al., 2010), up to the point of photoinhibition (Murray et al., 1993). The net effects of canopy removal by burning are therefore likely to vary according to factors such as climate.

Other drivers of vegetation change may interact with burning to mitigate or intensify impacts. For example, preferential grazing of regenerating shoots can supress recovery of some species, including *C. vulgaris*, after burning (Palmer, 1997), and high atmospheric pollution may limit the availability of *Sphagnum* propagules (Lee et al., 2013b) and favour colonisation of bare ground by more pollution tolerant species. These potential interactions add to the complexity of interpreting the impacts of fire, which may influence vegetation communities via multiple and conflicting pathways.

1.6 Synthesis

In summary, past work has shown that fire has the capacity to impact important ecosystem services provided by peatlands. These ecosystem services can often be linked to vegetation community composition and therefore there is a need to understand how prescribed burning impacts peatland vegetation communities, including key species which play a significant role in ecosystem function. Knowledge of the timescales of vegetation change after burning may allow inference of ecosystem recovery timescales, and inform guidance on suitable burning intervals. Finally, information about the specific processes (direct and indirect) by which fire impacts vegetation is likely to improve understanding of the responses of individual species with reference to their specific ecology, and communities as a whole.

1.7 Aims and objectives

This project aims to evaluate the impact of burning on blanket peatland vegetation in the context of ecosystem services outcomes and conservation goals. The work has a particular focus on *Sphagnum* mosses because of their importance to blanket peatland function, and is targeted to address three overarching research questions:

a) What are the impacts of burning on blanket peatland vegetation composition?

b) Over what timescales do these impacts occur?

c) Which processes play an important role in driving impacts?

A variety of techniques were applied at a range of spatial scales to aid in developing a broad understanding of vegetation change after burning, underpinned by an investigation of the mechanisms responsible. The rest of this thesis consists of the results of this research, organised with respect to the five manuscripts arising from the work, and ending with a discussion chapter which considers the work as a whole. The methods used in each chapter are described below.

- **Chapter 2: Prescribed burning, atmospheric pollution and grazing effects on peatland vegetation composition.**
  Existing large vegetation datasets were supplemented with additional environmental data and satellite imagery, to observe how drivers including burning, grazing and atmospheric pollution are associated with blanket peatland vegetation composition.
- **Chapter 3: Impacts of peat bulk density, ash deposition and rainwater chemistry on establishment of peatland mosses.**
  An environmentally controlled growth experiment was used to quantify how indirect fire impacts including changes to physical and chemical peat properties affect growth of three key moss species.
- **Chapter 4: Impacts of prescribed burning on *Sphagnum* mosses in a long-term peatland field experiment.**
  New and historical data from a long-term burning and grazing field experiment were analysed to investigate the impacts of different burning regimes on *Sphagnum* and aid interpretation of past results from this experiment.

- **Chapter 5: Peatland vegetation change and establishment of re-introduced *Sphagnum* moss after prescribed burning.**
  Vegetation change and *Sphagnum* introduction success were monitored over time since burning at three blanket peatland sites.
- **Chapter 6: Fire temperatures and *Sphagnum* damage during prescribed burning on peatlands.**
  Direct fire impacts on different *Sphagnum* species were investigated by quantifying damage after exposure to high temperatures in the field and laboratory.
- **Chapter 7: Conclusion**
  The results obtained were considered in the context of biodiversity conservation, ecosystem services, land management and policy with a view to informing future research directions and decisions on the sustainable management of blanket peatlands.

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Chapter 2: Alteration of peatland vegetation linked to prescribed burning, atmospheric pollution and grazing

Alice Noble[a], Sheila M. Palmer[a], David J. Glaves[b], Alistair Crowle[b], Lee E. Brown[a], and Joseph Holden[a]

[a]water@leeds, School of Geography, University of Leeds, Leeds, UK

[b]Natural England, Foss House, Kings Pool, Peasholme Green, York, UK

Abstract

1. Peatlands are valued for ecosystem services including carbon storage, water provision and biodiversity. However, there are concerns about the impacts of land management and pollution on peatland vegetation and function.
2. We investigated how prescribed vegetation burning, atmospheric pollution and grazing are related to vegetation communities and cover of four key taxa (*Sphagnum* spp., *Calluna vulgaris, Eriophorum vaginatum* and *Campylopus introflexus*) using two datasets from a total of 2,013 plots across 95 peatland sites in the UK.
3. NMDS and PERMANOVA showed differences in vegetation community composition between burned and unburned plots at regional and national scales.
4. Analysis of key taxa using GLMMs showed that burned sites had less *Sphagnum* and greater *C. vulgaris* cover on a national scale. On a regional scale, plots burned between two and ten years ago had greater cover of invasive moss *C. introflexus* and less *E. vaginatum* than unburned sites.
5. Livestock presence was associated with less *Sphagnum* and *C. vulgaris*, whilst atmospheric pollution was associated with less *Sphagnum*, but greater *C. introflexus* cover, and appeared to have more impact on burned sites.
6. **Synthesis and applications**: We suggest that to promote cover of peat-forming species, peatlands should not be routinely burned or heavily grazed. Current or historical atmospheric pollution may hinder peat forming species, particularly on burned sites.

2.1 Introduction

Peatlands cover an estimated 4 million km^2 of the Earth's surface, and are important globally for carbon storage, hydrological function and biodiversity (Evans et al., 2014). Plant community composition on peatlands impacts these functions (Kivimaki et al., 2008; Kuiper et al., 2014; Ward et al., 2013), and therefore knowledge of how species and communities respond to environmental change is important when making management decisions. Arguably the most important genus for peatland function globally is *Sphagnum*, a genus of mosses which retain large volumes of water and acidify their local environment, slowing decomposition and enabling peat accumulation (Clymo and Hayward, 1982). On sloping blanket peatlands, *Sphagnum*-dominated surfaces experience slower overland flow velocities than sedge dominated or bare peat surfaces (Holden et al., 2008), which may lead to reduced peak flows in rivers (Gao et al., 2015).

Due to the carbon storage and hydrological functions of *Sphagnum*, its re-establishment has been a focus in many peatland restoration programmes globally (Evans et al., 2014; Parry et al., 2014; Rochefort, 2000). Sedges such as *Eriophorum vaginatum* also form peat, and can colonise and stabilise eroding peat (Evans and Warburton, 2008). Dwarf shrubs such *Calluna vulgaris* occur naturally on blanket peatlands, often as a short canopy (Averis et al., 2004), but dominance by *C. vulgaris* is associated with impacts on peatland soil ecosystem functions such as net carbon storage (Dixon et al., 2015), water storage and routing (Holden, 2005) and dissolved organic carbon production in soils (Armstrong et al., 2012). Invasive species such as *Campylopus introflexus*, an acrocarpous moss native to the southern hemisphere which is now widely distributed in several European countries (Equihua and Usher, 1993), may also threaten ecosystem function by competing with native species.

Fire is common in peat rich biomes and can threaten carbon stocks depending on peatland vulnerability and the type of fire regime (Turetsky et al., 2015). Prescribed burning occurs on many peatlands globally for purposes including wildfire prevention, forestry, land clearance and habitat management (Brown et al., 2015; Buytaert et al., 2006). Unlike wildfires, prescribed burns are usually controlled to ignite vegetation, but not the underlying peat. In the UK uplands for example, patches of up to 4000 m^2 are burned in rotations of around 5-20 years to create a mosaic of *C. vulgaris* ages to improve forage and nesting habitat for the game bird red grouse (*Lagopus lagopus* *scotica*). Despite guidance that there should be a strong presumption against burning on deep peat in the UK (Defra, 2007; Scottish Government, 2011), there is evidence that burns have increasingly encroached onto these areas (Douglas et al., 2015; Thacker et al., 2015; Yallop et al., 2006). In recent years there has been considerable debate over burning practice (Brown et al., 2016; Dougill et al., 2006), and further evidence of how burning affects vegetation is vital to inform management and policy decisions.

Fire can alter vegetation directly by combustion, depending on water content and other factors affecting flammability, and indirectly by alteration of local environmental conditions. For example, greater peat bulk density (Holden et al., 2015) and lower near-surface hydraulic conductivity (Holden et al., 2014) in recently burned areas may reduce water availability to *Sphagnum*, which relies on passive capillary transport (Thompson and Waddington, 2008). Burning vegetation can also cause higher maximum and lower minimum near-surface soil temperatures in the years following a fire (Brown et al., 2015), which may impact *Sphagnum* growth negatively (Walker et al., 2015). The interaction between vegetation properties, fire severity and local soil conditions is likely to explain why evaluations of the effects of prescribed burning on *Sphagnum* in the field have yielded mixed conclusions (Glaves et al., 2013; Worrall et al., 2010). *C. vulgaris* shows evidence of fire adaptation and may increase after burning unless suppressed by grazing. Burning may also allow new species to colonise. *C. introflexus* can carpet bare soil rapidly (Southon et al., 2012) but whether this occurs to an ecologically significant extent after burning is unknown. One issue that prevents generalisations from being made is that the current evidence base on the effects of burning on peatland vegetation draws mainly from localised case studies, and the applicability of these findings to larger scale (e.g. national) patterns remains unestablished.

When considering peatland vegetation patterns at large-scales (i.e. national-global), atmospheric pollution, particularly deposition of sulphur and nitrogen, becomes an important consideration (Payne, 2014; van Dijk et al., 2012; Wieder et al., 2010). In the UK, *Sphagnum* die back near industrial centres has been attributed to sulphur deposition (Ferguson et al., 1978). Nitrogen additions can limit *Sphagnum* growth directly (Granath et al., 2012) or by increasing competition (Malmer et al., 2003), but can favour *C. introflexus* (Field et al., 2014; Southon et al., 2012). Grazing is also widespread on many peatlands and experimental work has shown that different species groups can respond to grazing in varying ways (Milligan et al., 2016). Further knowledge of the relationship between grazing and peatland vegetation on a national scale may help when weighing up economic, cultural and conservation concerns.

Sloping peatlands such as blanket bogs are common in hyperoceanic areas such as Atlantic northwest Europe, western Canada, southern Alaska, eastern Russia and southern South America (Gallego-Sala and Prentice, 2013). The UK has approximately 1.5 M ha of blanket peatland (Bain et al., 2011); around 13% of the global total. This represents the most important terrestrial carbon store and the largest remaining semi-natural habitat in the UK (Bain et al., 2011), and is a designated conservation priority under the EU Habitats Directive (JNCC, 2014) In recent decades restoration of biodiversity and ecosystem functions has increasingly been a focus for blanket peatlands (Cris et al., 2011; Parry et al., 2014). However, the extent to which blanket peatland vegetation is affected by interactions amongst widespread management practices (burning and grazing) and atmospheric pollution is not clear. In the UK, prescribed vegetation burning and atmospheric pollution both intensified during the 20th century, therefore it is important to try and understand the extent to which they may have interactive effects.

In this paper we present the first synthesis of national scale vegetation survey data from 1893 plots across 85 peatland sites in England, alongside a regional dataset with 123 plots across 10 peatland sites. The study aims to evaluate the relationships between environmental drivers (including prescribed burning, atmospheric pollution and grazing) and blanket peatland vegetation community composition as a whole, as well as four key taxa (*Sphagnum spp.*, *C. vulgaris*, *E. vaginatum* and *C. introflexus*). The findings are discussed in the context of peatland restoration and management.

2.2 Methods

2.2.1 Data sources

Two datasets were analysed (Figure 2.1). The first comprised vegetation survey data produced as part of the UK NERC-funded EMBER (Effects of Moorland Burning on the Ecohydrology of River basins) project, which established 12-15 sampling plots in each of five unburned and five burned catchments in the English Pennines (Table 2.1; Brown et al., 2014). Within each burned site, plots were distributed between four age classes; patches burned <2 years (B2), 3-4 years (B4), 5-7 years (B7) and >10 years

(B10+) prior to the study. The abundance of all vascular plants, bryophytes and terricolous lichens within a 2 m x 2 m quadrat in each plot was recorded using the Domin scale and transformed to an approximation of percentage cover using the Domin 2.6 transformation (Currall, 1987). Peat depth was measured up to a 118 cm probe length limit. National Vegetation Classification (NVC) types (Rodwell, 1991) present at each site were also determined.

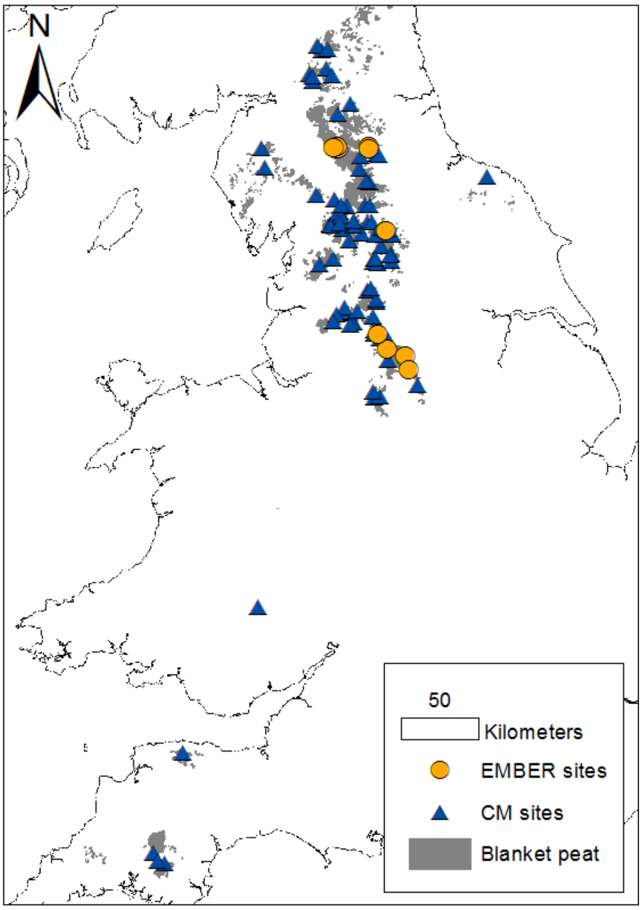

Figure 2.1: Map indicating distribution of study sites and extent of blanket peatland mapped as part of Natural England's Priority Habitat Inventory © Natural England copyright with Ordnance Survey data © Crown copyright 2017.

Table 2.1: Locations and dominant National Vegetation Classification types of EMBER sites. All sites occur on blanket peatland.

Site	Region	NVC type(s)
Burned		
Bull Clough	Peak District	**H9b** (*Calluna vulgaris – Deschampsia flexuosa* heath), **M6** (*Carex echinata – Sphagnum recurvum/auriculatum* mire)
Eggleshope Beck	North Pennines	**M19a** (*Calluna vulgaris – Eriophorum vaginatum* blanket mire)
Lodgegill Sike	North Pennines	**M6**, **H12a** (*Calluna vulgaris – Vaccinium myrtillus* heath), **M19a**
Rising Clough	Peak District	**H9b**
Woo Gill	Yorkshire Dales	**M19a**, **M20b** (*Eriophorum vaginatum* blanket & raised mire)
Unburned		
Green Burn	North Pennines	**M19b** (*Calluna vulgaris – Eriophorum vaginatum* blanket mire)
Moss Burn	North Pennines	**M19b**
Trout Beck	North Pennines	**M19b**
Crowden Little Brook	South Pennines	**M20b**
Oakner Clough	South Pennines	**M20b**

The second source was a habitat condition monitoring dataset (henceforth CM data). This was derived from a representative sample of mapped habitat polygons in Natural England's Blanket Bog Priority Habitat Inventory. Percentage cover values for indicator species (Table A1.1) were recorded using 2 m x 2 m quadrats. Peat depth was measured up to a 150 cm probe length limit and the presence of livestock droppings was recorded. Data from 1, 893 plots (from 85 sites) with peat depth ≥ 30 cm were used in this analysis; 30 cm being regarded as the minimum depth on which blanket peatland vegetation normally occurs (Lindsay 2010). Satellite imagery from Google Earth™ and Bing Maps™ was used to determine whether plots had been subject to recent prescribed burning (788, 41.6%) or not (1105) based on the visibility of characteristic burn patches. This is an effective method for determining the burn status of areas of peatland (Allen et al., 2016; Yallop et al., 2006). However, in this instance it was not possible to determine the age of individual burn patches with confidence, so the 'burned' category encompassed a range of burn ages and severities. The time taken for full visual recovery after burning varies according to the speed of vegetation regeneration, but is likely to be at least 25 years where dwarf shrubs are abundant (Yallop et al., 2006). However, detection of burning on grass dominated moorland from imagery is problematic due to a short lived burn signature (Yallop et al., 2006), so plots comprising grassland vegetation types were excluded from the analysis.

Atmospheric pollution data (deposition of acid, nitrogen, ammonia, nitrogen oxides, sulphur dioxide and ozone) were sourced from the Air Pollution Information Service online database (APIS, 2014), which provides 5 km resolution modelled values for pollutants, averaged over 3-5 years (ozone 2007-2012, all other pollutants 2012-2014). Elevation and slope values for individual plots were extracted from the Ordnance Survey Terrain 50 digital elevation model using ESRI ArcGIS 10.2.2.

2.2.2 Data analysis

All statistical analyses were carried out in R 3.1.1 (R Development Core Team, 2010) with the packages ggplot2 (Wickham, 2009), lme4 (Bates et al., 2015), MASS (Venables and Ripley, 2002) and vegan (Oksanen et al., 2013). To explore how vegetation community composition differs according to the application of prescribed burning, Non Metric Multidimensional Scaling (NMDS), an ordination method which projects multivariate data into a space with fewer dimensions, was performed on each dataset separately using Bray-Curtis dissimilarities and the best 2D fit was retained. This enabled visual inspection of differences between vegetation communities in burned and unburned plots, with more similar vegetation communities appearing closer together. Permutational Multivariate Analysis of Variance (PERMANOVA) was used to test for significant differences between vegetation communities in plots with different burn ages. The envfit function in R was used to fit linear relationships between environmental variables and NMDS axes to enable exploration of their associations with vegetation community composition.

Relationships between cover of key taxa (*Sphagnum* spp., *C. vulgaris, E. vaginatum* and *C. introflexus*) and environmental variables were investigated using generalised linear mixed models (GLMMs) for each dataset separately, with Poisson error distributions as the percentage cover data were bounded at zero. Site was included in all models as a random effect to account for grouping of plots within sites in both datasets. Species cover data from both datasets were overdispersed, which was accounted for by including an observation level random effect in the models (Harrison, 2014). Continuous variables were tested for correlation with each other and where a significant ($p < 0.05$) relationship with a Pearson correlation coefficient > 0.2 occurred between two variables, one was excluded (Tables A2 and A3) according to which was considered most ecologically relevant to the study. The remaining continuous variables were scaled and centred before analysis with GLMMs.

Two sets of GLMM analyses were performed on each dataset. First, models with all non-correlated predictor variables identified as significant in the envfit analysis, along with burn status (and livestock presence status in the CM data) were fitted. Second, models with burn status, atmospheric pollution (total deposition of nitrogen) and their interaction were fitted. The interaction models investigated the effect of atmospheric pollution on vegetation cover within and between burn groups. R^2 values for each model were calculated using the methods described by Nakagawa and Schielzeth (2013).

2.3 Results

2.3.1 Vegetation community composition

NMDS of the EMBER data (stress = 0.23) showed separation of burned and unburned plots (Figure 2.2), but there was no clear pattern within burned plots related to time since burning. PERMANOVA indicated significant effects of both site (R^2=0.40, p<0.001) and burn status (R^2=0.14, p<0.001) on species composition of plots. When only burned plots were compared, the effect of burn age was not significant (p=0.06). The distribution of sites in the NMDS plot reflects both geographic location and NVC type (Table 2.1). Within the unburned sites two groups are apparent; North Pennine sites with NVC type M19b *C. vulgaris* and *E. vaginatum* mire (Green Burn, Moss Burn and Trout Beck) and South Pennine sites with M20b *E. vaginatum* mire (Oakner and Crowden). Associations for the burned sites were less clearly distributed; Eggleshope Beck (North Pennine, M19a) is similar to the unburned North Pennine sites whereas Lodgegill Sike (North Pennine M6, H12a, M19a) has more in common with Rising Clough and Bull Clough, both Peak District sites with H9b vegetation, a *Calluna* dominated dry heath type characteristic of frequent burning (Elkington et al. 2001). Woo Gill (Yorkshire Dales, M19a, M20b) lacks obvious similarity to other sites.

In the NMDS ordination of the CM data (stress = 0.24) unburned and burned plots occupy overlapping areas in the ordination space (Figure 2.3), but with a greater concentration of unburned and burned sites in negative and positive regions of axis 1 respectively. PERMANOVA indicated a significant difference between burned and unburned plots (R^2=0.05, p<0.001). Geographic location (northing and easting), atmospheric pollution and physical site attributes (elevation and peat depth) were all associated with species composition.

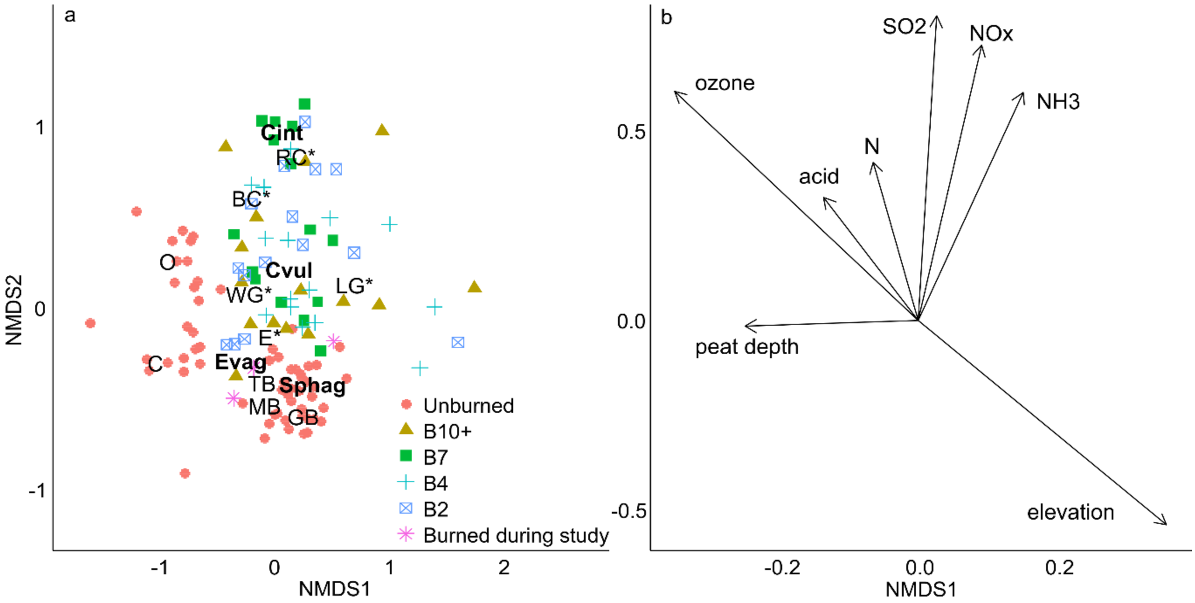

Figure 2.2: NMDS ordination (stress = 0.23) of EMBER vegetation data showing (a) unburned plots and plots burned 2, 4, 7 or 10+ years prior to survey with centroids for site (BC = Bull Clough, E = Eggleshope Beck, LG = Lodgegill Sike, RC = Rising Clough, WG = Woo Gill, GB = Green Burn, MB = Moss Burn, TB = Trout Beck, C = Crowden, O = Oakner; sites with * are burned) and species of interest (Cint = *C. introflexus*, Cvul = *C. vulgaris*, Evag = *E. vaginatum*, Sphag = *Sphagnum* spp.), (b) linear Envfit vectors for environmental variables which were significantly correlated with the NMDS ordination (direction of arrow = increasing value of variable).

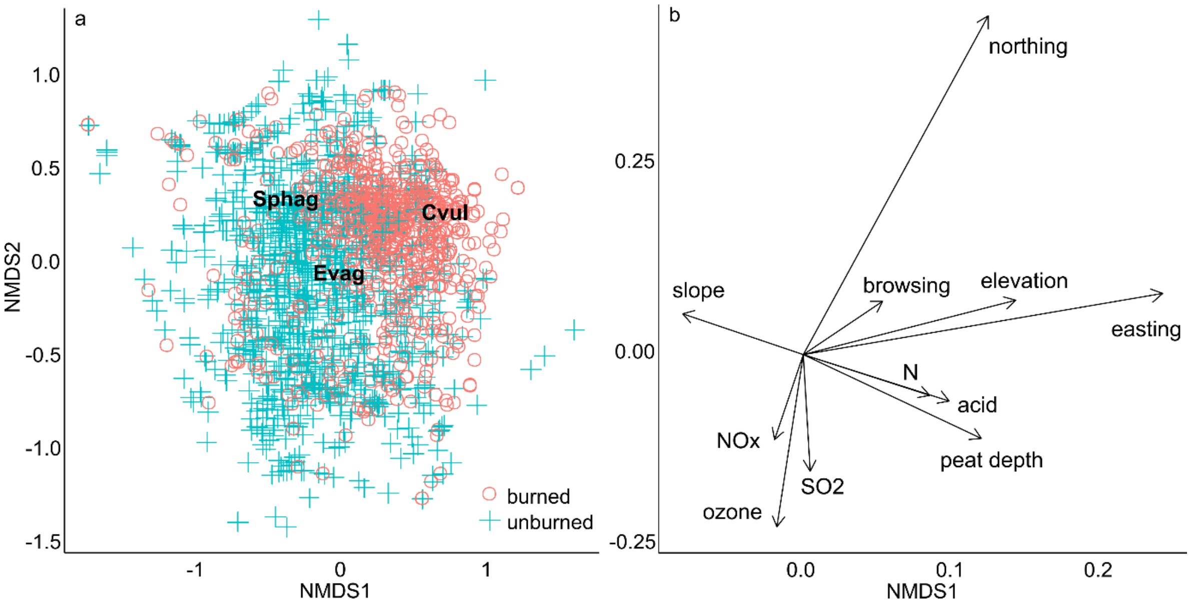

Figure 2.3: NMDS ordination (stress = 0.24) of Condition Monitoring (CM) vegetation data showing (a) unburned and burned plots and centroids for species of interest (Cvul = *C. vulgaris*, Evag = *E. vaginatum*, Sphag = *Sphagnum* spp.) and (b) linear Envfit vectors for environmental variables which were significantly correlated with the NMDS ordination (direction of arrow = increasing value of variable).

2.3.2 Relationships between key taxa and environmental variables

Results from the GLMM models revealed that several environmental and management variables were correlated with cover of one or more of the taxa of interest (Figure 2.4, Table A1.4). At EMBER sites there was less *E. vaginatum* on B2 ($Z = -2.41$, $p = 0.016$) and B7 ($Z = -2.63$, $p = 0.009$) plots than unburned plots. Mean cover values were 11.8% and 4.9% for B7 and B2 plots compared to 18.1% on unburned plots. Conversely, there was more *C. introflexus* on B2 ($Z = 5.38$, $p < 0.001$), B4 ($Z = 4.92$, $p < 0.001$) and B7 ($Z = 4.47$, $p < 0.001$) plots with mean cover values of 23.9%, 21.9% and 18.3%, respectively, compared to 0.5% on unburned plots. Differences in *Sphagnum* cover between unburned plots and plots of different burn ages were not significant in the EMBER dataset (Table A1.4).

Nitrogen deposition in the EMBER dataset was negatively correlated with *Sphagnum* ($Z = -2.42$, p=0.016) and positively correlated with *C. introflexus* ($Z = 2.91$, $p = 0.004$). Increasing elevation was associated with more *Sphagnum* ($Z = 4.68$, $p < 0.001$), but less *C. introflexus* ($Z = -3.60$, $p < 0.001$) cover, whilst increasing peat depth was associated with more *E. vaginatum* cover ($Z = 2.88$, $p = 0.004$).

The CM data indicated less *Sphagnum* on burned plots ($Z = -2.33$, $p = 0.02$) with a mean cover of 8.2% compared to 10.5% on unburned plots, and also on plots with livestock droppings ($Z = -2.88$, $p = 0.004$) with a mean cover of 6.7% compared to 10.7% on those without (Figure 2.5, Table A1.4). There was more *C. vulgaris* ($Z = 9.05$, $p < 0.001$) on burned plots with 37.5% mean cover compared to 10.7% on those without, and less *C. vulgaris* on plots with livestock droppings ($Z = -3.28$, $p = 0.001$) with a mean of 12.3% cover compared to 24.4% on plots without droppings.

Plots further north were associated with more *Sphagnum* ($Z = 3.81$, $p < 0.001$), *C. vulgaris* ($Z = 2.48$, $p = 0.013$), and *E. vaginatum* ($Z = 2.99$, $p = 0.003$), whilst elevation was positively correlated with *C. vulgaris* ($Z = 4.24$, $p < 0.001$) and *E. vaginatum* ($Z = 5.91$, $p < 0.001$) but negatively correlated with *Sphagnum* ($Z = -3.35$, $p = 0.001$). Nitrogen deposition had a negative relationship with *Sphagnum* ($Z = -2.51$, $p = 0.012$).

2.3.3 Interactions between burning and atmospheric pollution

At EMBER sites, an interaction between burn age and nitrogen deposition impacted cover of *E. vaginatum*, with a significantly more negative relationship ($Z = -2.26$, $p = 0.024$,) on B2 plots than unburned plots (Figure 2.6, Table A1.5). In the CM data, nitrogen deposition had a significantly more negative relationship ($Z = -3.26$, $p = 0.001$) with *Sphagnum* cover on burned plots than unburned plots (Figure 2.7, Table A1.5).

2.4 Discussion

Analysis of the two datasets in this study revealed that blanket peat vegetation community composition is associated with burning status, grazing, atmospheric pollution and site physical attributes including northing and elevation. The four taxa of interest in this study were associated with several of these variables. Although effect size and the significance of associations differed between the two datasets, the direction of effects was generally consistent. These results suggest that burning and grazing practices, along with atmospheric pollution, have the capacity to shift vegetation community composition on peatlands, and that burning and atmospheric pollution have an interactive effect on the abundance of some species.

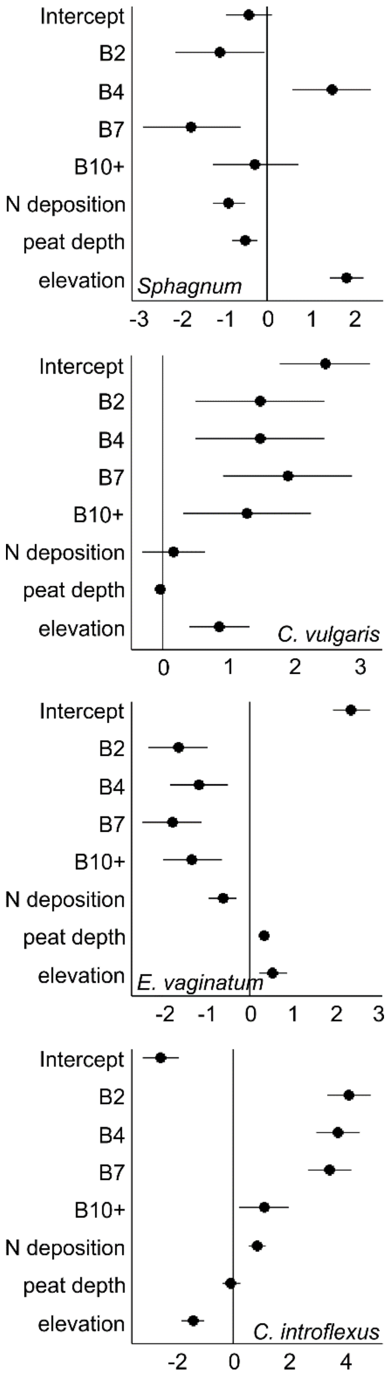

Figure 2.4: Coefficient plots of EMBER GLMMs showing standardised coefficient estimates and standard error for comparison of cover of *Sphagnum*, *C. vulgaris*, *E. vaginatum* and *C. introflexus* on B2, B4, B7 and B10+ plots to unburned plots and the relationships of cover with nitrogen deposition, peat depth and elevation. Marginal R^2 = 0.47, 0.30, 0.50 and 0.66 respectively; Conditional R^2 = 0.50, 0.90, 0.75 and 0.69 respectively.

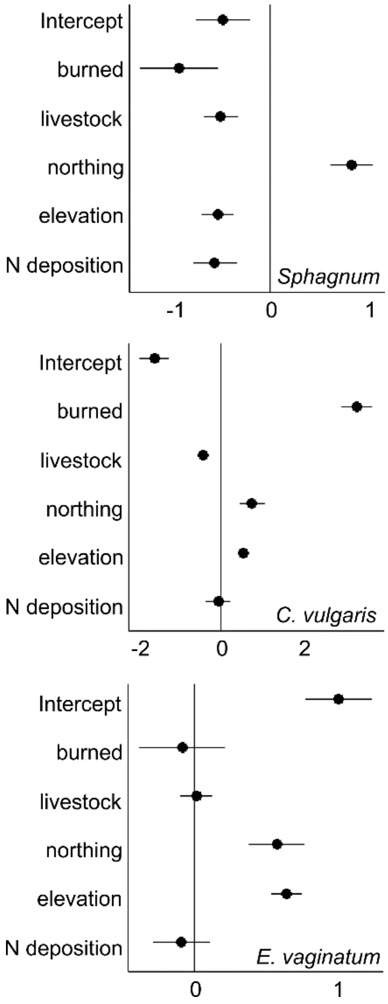

Figure 2.5: Coefficient plots of CM GLMMs showing standardised coefficient estimates and standard error for the comparison of cover of *Sphagnum*, *C. vulgaris*, and *E. vaginatum* on burned plots to unburned plots; plots with livestock droppings to those without livestock droppings; and the relationships of cover with northing, elevation and nitrogen deposition. Marginal R^2 = 0.13, 0.25 and 0.09 respectively; Conditional R^2 = 0.42, 0.73 and 0.50 respectively.

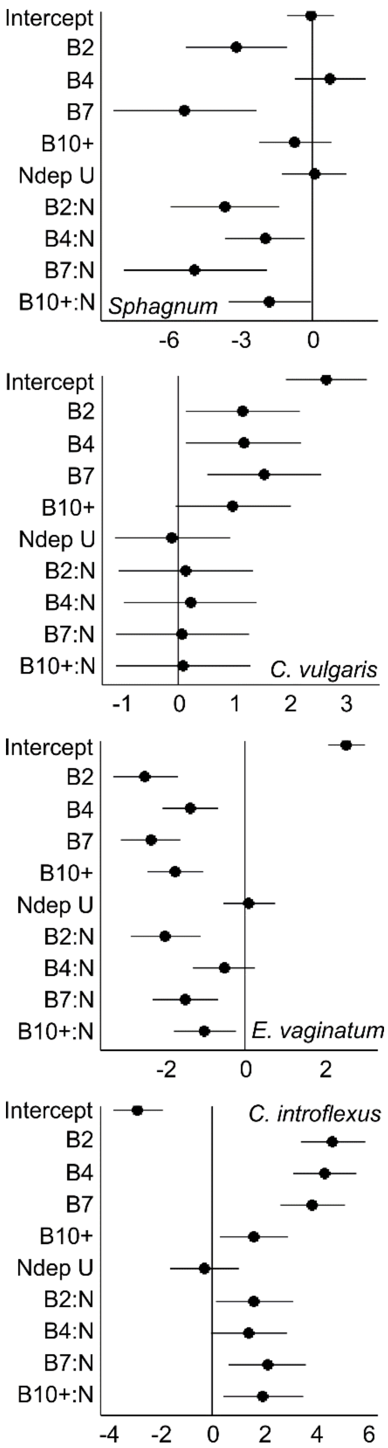

Figure 2.6: Coefficient plots of EMBER GLMMs showing standardised coefficient estimates and standard error for the comparison of cover of *Sphagnum*, *C. vulgaris*, *E. vaginatum* and *C. introflexus* cover on B2, B4, B7 and B10+ plots to unburned plots; the relationship of cover with nitrogen deposition on unburned plots; and comparison of the relationship of cover with nitrogen deposition on B2, B4, B7 and B10+ plots to unburned plots. Marginal R^2 = 0.54, 0.12, 0.57 and 0.51 respectively; Conditional R^2 = 0.72, 0.88, 0.79 and 0.70 respectively.

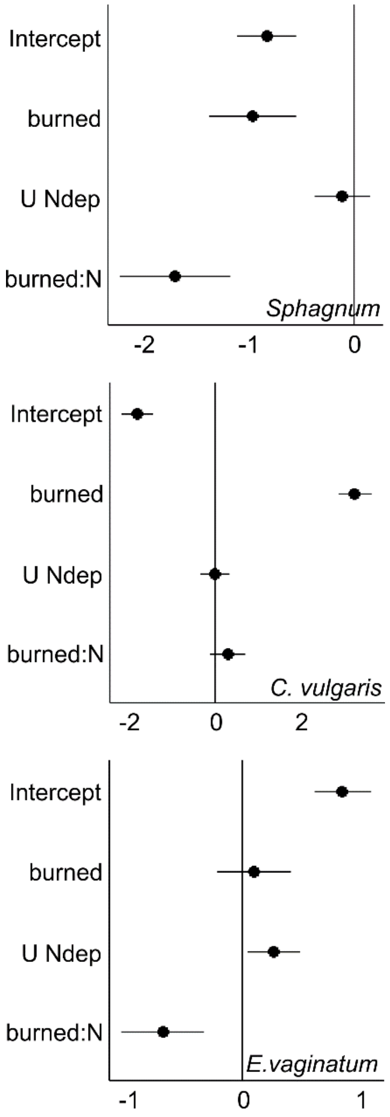

Figure 2.7: Coefficient plots of CM GLMMs showing standardised coefficient estimates and standard error for the comparison of cover of *Sphagnum*, *C. vulgaris*, *E. vaginatum* and *C. introflexus* cover on burned plots to unburned plots; the relationship of cover with nitrogen deposition on unburned plots; and comparison of the relationship of cover with nitrogen deposition on burned plots to unburned plots. Marginal R^2 = 0.09, 0.17 and 0.01 respectively; Conditional R^2 = 0.39, 0.71 and 0.49 respectively.

2.4.1 Drivers of community composition

Analyses spanning regional to national scales both suggested that burning is associated with differences in vegetation community composition, as previously observed in local (Hobbs, 1984; Lee et al., 2013a) and regional (Harris et al., 2011) studies. The similar envfit relationships of different atmospheric pollutants observed in both datasets may be due to comparable effects on vegetation or spatial correlation in deposition and thus it is difficult to evaluate pollutants individually. Blanket peatlands are oligotrophic, nutrient poor habitats so it is likely that input of nutrients via pollution impacts species composition by enhancing the competitive ability of vascular plants as well as via toxic effects on pollution sensitive species (Berendse et al., 2001).

The NMDS and PERMANOVA analysis of the EMBER data indicated that burned plots of different ages were more similar to each other than to unburned plots, suggesting that vegetation was still distinct from unburned sites 10+ years after burning. Full recovery may depend on re-establishment of features such as microtopography, thermal regime and hydrological function and this can take several years after burning (Brown et al., 2015; Holden et al., 2015). The vegetation of the unburned sites shows a clear divide between North and South Pennine sites in the EMBER NMDS ordination (Figure 2.2) in line with the two mire NVC types they supported (Table 2.1). However, this north-south divide is not apparent in the burned plots, and three of the five burned sites supported heath vegetation types associated with burning, grazing and atmospheric pollution (Elkington et al., 2001). This suggests that geographically variable vegetation community characteristics can be overridden by the effects of burning.

Although there was less clear separation of burned and unburned plots in the CM NMDS, clustering was still evident, indicating that many burned sites have similarities in vegetation composition on a national scale. The overlap between burned and unburned plots in the ordination space is unsurprising considering the range of burn ages and severities represented in the burned plots. It should also be noted that the CM NMDS was based on cover of 26 indicator taxa (Table A1.1). These taxa represent the majority of cover and the most ecologically important species on UK blanket peatland sites (Averis et al., 2004); however, it is possible that further differences between plots would be observed with the inclusion of rarer species.

2.4.2 Variation in *Sphagnum* cover

Analysis of the CM data, compiled from 1893 plots at 85 sites across England, indicated lower *Sphagnum* cover on average where burning was identified. The finding is contrary to observations of *Sphagnum* cover at a single experimental burn site in northern England (Hard Hill, Moor House-Upper Teesdale NNR) where *Sphagnum* cover was greatest on plots burned every 10 years (Lee et al., 2013a). A reduced *Sphagnum* propagule bank was observed on burned plots at Hard Hill (Lee et al., 2013b), but this may have had a limited effect on cover because the experimental plots are surrounded by intact peatland vegetation which could have contributed to *Sphagnum* recruitment within the burned plots. In contrast, the CM sites represent a range of intact and degraded vegetation types and management strategies. Our results suggest that current burning practices may leave *Sphagnum* vulnerable to decline in some cases. This could reflect fire damage to *Sphagnum* similar to that described by Lindsay and Ross (1994), competitive effects, or an indirect impact via peat physical and hydrological properties (Brown et al., 2015; Clay et al., 2009; Holden et al., 2014; Holden et al., 2015).

Data from the ten EMBER catchments showed that differences in *Sphagnum* cover between unburned plots and burned plots of any age were not significant, although effect directions were negative with the exception of B4 plots. These findings contrast with the larger CM dataset which shows burning is negatively associated with *Sphagnum* cover, as well as local scale studies showing *Sphagnum* cover to be highest in plots that are burned on a ten-year rotation (Lee et al., 2013a). It is possible that changes in *Sphagnum* abundance after burning were asynchronous across sites, or that the smaller number of EMBER vegetation samples (3 samples per burn age x 5 sites) did not control adequately for factors affecting *Sphagnum* abundance (e.g. burn severity, microtopography and livestock access) but which the larger CM study captured across 788 burned plots.

Nitrogen deposition had a negative relationship with *Sphagnum* cover in both datasets. Both nitrogen and sulphur (deposition of which was correlated with nitrogen) can have direct physiological impacts on *Sphagnum* (Ferguson et al., 1978; Granath et al., 2012), as well as nitrogen increasing competition from vascular plants (Limpens et al., 2011) and promoting graminoid cover (Field et al., 2014). Sulphur deposition has declined faster than nitrogen deposition in recent decades (Battarbee et al., 2014; Curtis and Simpson, 2014), but a legacy impact of reduced *Sphagnum* cover and propagules due to higher historic levels is possible.

The significantly more negative relationship between nitrogen deposition and *Sphagnum* cover on burned plots compared to unburned plots in the CM data may indicate that atmospheric pollution affects *Sphagnum* re-establishment by limiting growth or propagule availability after burning. *Sphagnum* peatlands are vulnerable to N deposition (Granath et al., 2014), and this interaction suggests that vulnerability may be enhanced if burning continues to increase. The positive relationship between *Sphagnum* and northing is difficult to attribute to a single influence, but may be associated with geographic variation in rainfall (Nijp et al., 2014), temperature (and hence evapotranspiration), geology or land management. The lower *Sphagnum* cover on plots with livestock droppings may be due to nutrient inputs, physical damage or hydrological impacts of trampling such as peat compaction leading to less water availability (Meyles et al., 2006).

2.4.3 Variation in *Calluna vulgaris* cover

The greater *C. vulgaris* cover on burned sites in the CM data was expected, as burning is often practiced to regenerate heather. It could be suggested that dwarf shrub dominated vegetation is more likely to be selected for burning, but all plots were on deep peat (>30 cm), which suggests that this vegetation type is itself a legacy of management. On intact, *Sphagnum*-dominated blanket peatland, *C. vulgaris* is thought to regenerate naturally through layering of branches as *Sphagnum* grows up through the stems (Forrest, 1971; Macdonald et al., 1995). Burning may disrupt this process and enhance *C. vulgaris* regeneration from seeds and roots (Forrest and Smith, 1975). The processes behind the increase in *C. vulgaris* may also be hydrological, as burning can result in deeper water tables and less water availability (Holden et al., 2015), and *C. vulgaris* is primarily a heath species which can tolerate drier conditions than many other peatland species.

The CM data also indicated a positive correlation between *C. vulgaris* cover and both elevation and northing value, which could be due to geographic variation of multiple influences as discussed for *Sphagnum*. Plots with livestock droppings had less *C. vulgaris* cover than those without, perhaps indicating a negative impact of grazing in accordance with the findings of Hulme et al. (2002). However, it is also possible that dense heather limits livestock access or other areas are grazed preferentially.

2.4.4 Variation in *Eriophorum vaginatum* cover

The lower cover of *E. vaginatum* on plots burned 2, 7 and 10+ years ago compared to plots at unburned EMBER sites was unexpected given the dominance after fire observed in past studies (Hobbs, 1984). However, in the CM data, there was no significant difference in *E. vaginatum* cover between burned and unburned plots. The ability of *E. vaginatum* to survive burning may be dependent on fire intensity, which was not quantifiable in this study, and the extent to which fire penetrates tussocks, damaging growing buds. Rapid regeneration of *C. vulgaris* after fire may also limit the opportunity for *E. vaginatum* to proliferate.

The positive relationship between *E. vaginatum* and both northing and elevation in the CM data may indicate enhanced competitive ability in cooler, wetter conditions. The interactive relationship of burning and nitrogen deposition with *E.vaginatum* observed in the EMBER data could exist because species which gain a competitive advantage from nutrient inputs are more likely to out-compete young *E. vaginatum* plants recolonising after burning than established tussocks on unburned plots (Kool and Heijmans, 2009; Wein and Bliss, 1973).

2.4.5 Variation in *Campylopus introflexus* cover

Results from EMBER data suggested that *C. introflexus* colonises rapidly after burning and is able to sustain increased cover for at least seven years post burn. This pattern is consistent with reports of *C.introflexus* colonising bare and disturbed peat ((Equihua and Usher, 1993) and suggests that disturbance events such as burning may have assisted the spread of this non-native species in Europe. Cover was less at higher elevations, which could indicate climatic preferences or limited dispersal. Nitrogen deposition had a positive relationship with *C. introflexus*, consistent with reports of a positive response of the species to nitrogen (Southon et al., 2012), which suggests it may be able to occupy a niche vacated by pollution sensitive native species such as *Sphagnum*.

2.5 Conclusions

Our results suggest that burning, atmospheric pollution and livestock presence are all associated with the alteration of peatland vegetation. If the trend of further encroachment of prescribed burning onto blanket peatland continues, our results suggest that a shift towards greater cover of *C. vulgaris* and *C. introflexus,* less of the peat formers *E. vaginatum* and *Sphagnum,* and greater vulnerability to nitrogen impacts are possible. Livestock presence was also associated negatively with *Sphagnum* cover and we suggest that the use of burning and grazing as management tools on peatlands should be approached with caution where restoration or maintenance of active, peat forming vegetation is an aim.

2.6 Acknowledgements

This analysis was funded by a NERC-CASE studentship [NE/L008572/1] supported by Natural England, awarded to JH, SMP, DG and AC in open competition. Natural England are thanked for data provision. Stuart Hedley and ADAS are thanked for vegetation surveys on the EMBER and CM sites respectively. NERC are acknowledged for funding the EMBER project NE/G00224X/1). We thank Dave Stone (Natural England) and Andy Baird (University of Leeds) for comments on earlier drafts.

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Chapter 3: Impacts of peat bulk density, ash deposition and rainwater chemistry on establishment of peatland mosses

Alice Noble[a], Sheila M. Palmer[a], David J. Glaves[b], Alistair Crowle[b] and Joseph Holden[a]

[a]water@leeds, School of Geography, University of Leeds, Leeds, UK

[b]Natural England, Foss House, Kings Pool, Peasholme Green, York, UK

Abstract

Background and Aims: Peatland moss communities play an important role in ecosystem function. Drivers such as fire and atmospheric pollution have the capacity to influence mosses via multiple pathways. Here, we investigate physical and chemical processes which may influence establishment and growth of three key moss species in peatlands.

Methods: A controlled factorial experiment investigated the effects of different peat bulk density, ash deposition and rainwater chemistry treatments on the growth of *Sphagnum capillifolium*, *S. fallax* and *Campylopus introflexus*.

Results: Higher peat bulk density limited growth of both *Sphagnum* species. *S. capillifolium* and *C. introflexus* responded positively to ash deposition. Less polluted rain limited growth of *C. introflexus*. Biomass was well correlated with percentage cover in all three species.

Conclusions: Peat bulk density increases caused by fire or drainage can limit *Sphagnum* establishment and growth, potentially threatening peatland function. Ash inputs may have direct benefits for some *Sphagnum* species, but are also likely to increase competition from other bryophytes and vascular plants which may offset positive effects. Rainwater pollution may similarly increase competition to *Sphagnum*, and could enhance positive effects of ash addition on *C. introflexus* growth. Finally, cover can provide a useful approximation of biomass where destructive sampling is undesirable.

3.1 Introduction

Peatlands are a globally important provider of ecosystem services including carbon storage, biodiversity and water quality maintenance. However, many peatlands have been degraded by human influences including atmospheric pollution and fire (Evans et al., 2014; Holden et al., 2007). In northern hemisphere peatlands *Sphagnum* spp. often play a key role in peat formation, so re-establishing or increasing *Sphagnum* cover is an important focus of restoration (Parry et al., 2014). A range of other bryophytes occur on peatlands, but dominance of less characteristic species at the expense of *Sphagnum* may threaten ecosystem function. One such species is *Campylopus introflexus*, an invasive species native to the southern hemisphere which has shown an expanded range and increased abundance on some northern hemisphere peatlands in recent decades (Equihua and Usher, 1993).

Peatland vegetation is frequently influenced by multiple environmental drivers including grazing, cutting, prescribed burning, wildfire and atmospheric pollution (Holden et al., 2007). Each driver may influence vegetation via multiple pathways; alteration of the hydrological, thermal, chemical and biological properties of peat all have the potential to impact mosses (e.g. Bu et al., 2013; Lukenbach et al., 2015; Price and Whitehead, 2001), potentially in conflicting ways. Knowledge of which processes exert the greatest control on important peatland moss species has the potential to inform the adaptation of management tools to support ecosystem function.

Fire is a common disturbance on peatlands globally and can take the form of wildfire or prescribed burning. Fire regimes are subject to change over time according to environmental conditions, human activity and policy. For example, Kasischke and Turetsky (2006) found that the incidence of fire increased across the North American boreal region from 1959-99. In the UK around 15% of land cover is peat and an estimated 18% (3150km^2) of this has been subjected to prescribed burning (Worrall et al., 2010), mainly to manage vegetation for game or livestock. Douglas et al. (2015) observed an increase in the annual number of burns in the UK from 2001 to 2011. However, the environmental impacts of burning practices have been the subject of several studies and significant debate in recent years (Brown et al., 2016; Dougill et al., 2006). An important question in the debate is the effect of burning on *Sphagnum* spp., but past studies have produced conflicting conclusions, with *Sphagnum* sometimes increasing and sometimes declining after burning, and abundance varying with time since burn (Glaves et al., 2013). Increased knowledge of the pathways via which burning affects *Sphagnum* is therefore urgently required. *C.introflexus* has been observed to colonise rapidly after fire Southon et al. (2012), including on many northern hemisphere peatlands where it is not native, but understanding of the processes controlling fire effects on mosses in general is still limited.

One way in which drivers including fire may influence mosses is by altering peat properties such as near-surface peat bulk density. Increased bulk density can reduce water availability to mosses, which are non-vascular and rely on passive capillary transport, but species may differ in their responses depending on water requirements and desiccation tolerance (Sagot and Rochefort, 1996). Holden et al. (2014) measured a mean bulk density of 0.259 (±0.013) g cm^{-3} in peatland plots where the surface vegetation had been subjected to prescribed burning 2 years previously compared to 0.110 (±0.008) g cm^{-3} in unburned plots, potentially due to drying-induced compression and collapse of the peat mass after burning. Prescribed burns are normally controlled to burn vegetation without igniting the underlying peat. However, similar bulk density effect observed in a North American peatland was attributed to the exposure of denser peat when surface layers were consumed in a wildfire (Thompson and Waddington, 2013). Near-surface bulk density may also be influenced by drivers including drainage (Ketcheson and Price, 2011) and peat harvesting (Van Seters and Price, 2002). While several studies have investigated the influence of water table on *Sphagnum* growth (Buttler et al., 1998; Grosvernier et al., 1997; Robroek et al., 2009), changes in bulk density have the potential to affect water availability to mosses even when the water-table depth is favourable by reducing soil water storage capacity, potentially increasing soil water retention, and slowing the rate at which water lost via evapotranspiration is replaced at the peat surface (Boelter, 1968). These changes can reduce the amount of water loss needed to cause soil water pressure to fall below around -100 mb (Thompson and Waddington, 2013), a point at which *Sphagnum* plants are unable to withdraw moisture from the peat (Price et al., 2003; Hayward and Clymo, 1982).

Another process which may affect mosses after fire is ash deposition. Ash deposited after fire on peatlands is often largely a product of woody species such as heather (*Calluna vulgaris*). Nearly all nitrogen is lost during burning, but ash is a source of cations including Ca^{2+}, Mg^{2+}, Na^{+} and K^{+}, which can impact soil water pH, as well as plant growth and competition (Allen, 1964; Allen et al., 1969). At high concentrations these cations can have toxic effects, but at lower levels they can enhance growth of some species, particularly in ombrotrophic peatlands which may be nutrient limited (Hoosbeek et al., 2002; Vicherova et al., 2015). Ash may also block near-surface macropores in peat and alter hydrology, potentially affecting water availability to mosses (Holden et al., 2014). Much work on the effects of ash in peatland systems has focussed on the fertilisation of forest plantations with wood ash, which can cause visible damage to *Sphagnum* (Dynesius, 2012). However, the application rate of ash for fertilisation can be around 20 times higher than the amount deposited after vegetation fire (Moilanen et al., 2002), and it is often applied in a processed form, so results from these studies may not be comparable to the effects of prescribed burning and wildfire.

In the absence of ash, rainwater is the most significant source of plant nutrients on ombrotrophic peatlands. Concentrations of nutrients including nitrogen and sulphur can vary regionally according to atmospheric pollution levels. Historically, *Sphagnum* abundance has been reduced in regions with high atmospheric pollution, including areas near industrial centres in the UK (Lee et al., 1987) where in the 20th century *Sphagnum* previously dominant on peatlands was almost completely extirpated, leading to drying and erosion of peat (Carroll et al., 2009). Negative effects of sulphur have been documented in several *Sphagnum* species (Ferguson et al., 1978), but concentrations in rainwater have fallen in the UK in recent decades. Conversely, nitrogen levels have remained high in some regions (Carroll et al., 2009). On blanket peatlands nitrogen inputs are likely to benefit faster growing vascular plants, increasing competition to mosses (Malmer et al., 2003). *C introflexus* has been shown to respond positively to nitrogen inputs (Southon et al., 2012), but negative physiological effects on some *Sphagnum* species have been observed (Granath et al., 2012). It has been suggested that current levels of nitrogen and sulphur are not likely to prevent *Sphagnum* growth in the UK (Carroll et al., 2009), but individual species may respond differently. Furthermore, it is possible that rainwater chemistry interacts with ash deposition to influence nutrient dynamics.

In this study we use a controlled factorial experiment to isolate and quantify the effects of three variables related to fire and atmospheric pollution (peat bulk density, ash deposition and rainwater chemistry) on the establishment of *Sphagnum capillifolium*, *Sphagnum fallax* and *C. introflexus*. These species were chosen as they are common on blanket peatlands in the UK, and are thought to have varying preferences for moisture and nutrients (Table 3.1) which may influence their ability to establish on degraded peat. Based on existing knowledge of these species, we hypothesise that increased bulk density will affect *S. fallax* most negatively, followed by *S. capillifolium*, with little or no impact on *C. introflexus*. More polluted rainwater is expected to impact the two *Sphagnum* species, particularly *S. capillifolium*, negatively, but benefit *C. introflexus*. We would also expect ash to benefit *C. introflexus*, a species associated with burned areas, but to have a negative effect on both *Sphagnum* species, and for leached ash to have less impact than unleached ash.

Table 3.1: Ellenberg habitat indicator values for moisture and nitrogen (scale of 1-10, higher values indicate wetter conditions for moisture and more fertile conditions for nitrogen) for *S. capillifolium*, *S. fallax* and *C. introflexus,* adapted from Hill et al. (2007).

Species	*S. capillifolium*	*S. fallax*	*C. introflexus*
Moisture	Moist substrates (7)	Waterlogged substrates (9)	Moderately moist substrates (5)
Nitrogen	Extremely infertile sites (1)	Moderately infertile sites (3)	Infertile sites (2)

3.2 Methods

3.2.1 Substrate preparation

To collect peat as a substrate for the experiment with minimal disturbance to its structure, straight sided, bottomless pots were created using 6 cm lengths of 68 mm diameter PVC pipe. Peat was collected from an area of bare blanket peat, exposed by erosion, at Moor House-Upper Teesdale National Nature Reserve (henceforth Moor House) in the north of England. The site had not been burned for at least 60 years at the time of collection. For the pots with normal bulk density, 6 cm pots were pushed into the peat until level with the peat surface, taking care not to compress the peat, and removed. Pots with increased bulk density were prepared by inserting 10 cm lengths of pipe and then compressing the 10 cm peat core into 6 cm pots. Three sample pots from each treatment were dried to constant weight and mean bulk density was calculated to be 0.131 (±0.004) g cm^{-3} for normal pots and 0.169 (±0.030) g cm^{-3} for compressed pots. Pots were stored at 4°C for two days prior to the start of the growth experiment.

3.2.2 Rainwater preparation

Two types of artificial rainwater were produced to represent precipitation chemistry at UK upland sites with relatively low and high atmospheric pollution levels (Table 3.2). Chemical composition was based on ECN data (Rennie et al., 2015a) averaged over 5 years (2007-2012) for two sites: Allt a'Mharcaidh in the Cairngorms, Scotland (less polluted) and Wardlow Hay Cop in the Peak District, England (more polluted). Concentrated solutions were made every four weeks by dissolving compounds (NaCl, $MgSO_4$, $CaSO_4.2H_2O$ and NH_4NO_3) in a 250 mL volumetric flask of deionised water at 100 times the required strength. The concentrated solutions were stored at 4°C in 50 mL plastic vials and diluted with deionised water as required. HCl (0.1 M) was then added dropwise as necessary to give a pH between 5.2 and 5.8 for both rainwater types.

Table 3.2: Composition of the two artificial rainwater types produced for the experiment.

Component	Cairngorm water meq L^{-1}	Peak District water meq L^{-1}
Ca^{2+}	0.002	0.022
Cl-	0.075	0.073
Mg^{2+}	0.016	0.015
Na+	0.074	0.067
NH_4^+	0.011	0.028
NO_3^-	0.011	0.028
SO_4^{2-}	0.018	0.036

3.2.3 Ash preparation

To make the ash, vegetation consisting almost entirely of *C. vulgaris* was harvested at Moor House by cutting stems close to the ground. In the lab, vegetation was cut into 5 cm lengths, oven dried for 24 hours at 105°C, weighed, and then ignited in a muffle furnace at 450°C. This temperature was chosen as it is comparable to temperatures recorded during prescribed burning in the field (Whittaker, 1961). One third of the 108 pots used in the experiment had no ash added, while ash was scattered on the surface of the remaining two thirds at a rate of 10 g m^{-2} to correspond to a dry weight of 672 g m^{-2}, the average *C.vulgaris* biomass 16 years after burning recorded by Alday et al. (2015) at Moor House. Half of the ash added was subject to leaching with artificial rainwater (corresponding with the type to be supplied during the experiment) before adding to pots at a rate of 413 L m^{-2} (1.5 L per pot), which approximates a mean value for total spring (March, April and May) rainfall at Moor House (Rennie et al., 2015b). In the UK, burning is restricted to the winter half year (October-April), so this amount is comparable to the rain a site might receive between burning and the growing season. For the growth experiment (section 2.4), ash was leached on filter paper rather than *in situ* on the pots as this was quicker and avoided confounding effects of the leaching process (e.g. differential drying of leached and unleached pots) on moss growth. However, for the chemical impacts on peat experiment (section 2.5), ash was added to the peat surface before the start of the leaching process.

3.2.4 Growth experiment

Bryophyte material was collected from Moor House (*S. capillifolium* and *S. fallax*) and Leek Moors in the Peak District (*C. introflexus*). Diaspores comprising individual capitula for both *Sphagnum* species and individual stems for *C. introflexus* were prepared and ten diaspores of an individual species were added to each pot. Diaspores were initially watered in from above with 50 mL of artificial rainwater, equivalent to 13.77 mm or around 3 days spring rainfall at Moor House (Rennie et al., 2015b), per pot. Pots were arranged in 18 plastic trays, each of which contained six pots representing the six bulk density-species combinations. Ash and rainwater treatments were the same within individual trays to avoid nutrient contamination. Each species x bulk density x ash x rainwater combination was replicated three times, giving 108 pots in total.

The growth experiment took place in a controlled environment room with two LED light units (Heliospectra AB, Sweden), which were on between 5am and 9pm to simulate spring/summer daylight hours in the UK. The temperature in the environment room was 9°C at night (9pm to 9am) and 14°C during the day. These temperatures are comparable to mean summer temperatures at UK upland sites (Rennie et al., 2015b).

The experiment was run for 152 days, during which the two rainwater types were supplied to pots by filling the trays as required to maintain a water-table depth between 2 cm and 5 cm. The following variables were recorded for each pot every 14 days: survival (proportion of diaspores which had not dried out), proportion of diaspores which had produced new material, cover (percentage of the peat surface covered by moss) and maximum height of moss. At the end of the experiment, all moss was harvested from the peat surface of each pot using tweezers, air dried to constant weight, and the final dry biomass was recorded as a measure of growth.

3.2.5 Chemical impacts of ash addition and leaching

Separately from the growth experiment, the impact of ash addition and leaching on peat chemistry was investigated using 18 samples. At the start of the leaching process, 18 pots of peat were wetted with 250 mL of artificial rainwater and allowed to drain. Ash was then added to half of the pots as described in section 2.3. Twelve of the cores were subjected to leaching at the rate described in section 2.3; six with each rainwater type. Water was added to all pots at the rate it drained from the slowest draining pots; approximately 200 mL a day, and pots were covered with plastic sheeting to reduce evaporation.

After the leaching process, surface peat samples were taken from all 18 pots and $BaCl_2$ extractions were performed using 5 g of fresh peat and 45 mL of 0.1M $BaCl_2$ per sample. The resulting mixture was shaken for 2 hours at 15 rpm, centrifuged for 15 minutes at 2115 rpm and filtered through Whatman No 41 filter paper before analysis of exchangeable Ca^{2+}, Mg^{2+}, Na^+ and K^+ by ICP-OES. Concentrations measured were converted from mg L^{-1} to $cmol_c$ kg^{-1} dry weight for reporting.

3.2.6 Data analysis

All statistical analyses were carried out using R 3.2.3 (R Development Core Team, 2010) with the packages car (Fox and Weisberg, 2011), nlme (Pinheiro et al., 2016), lsmeans (Lenth, 2016) and ggplot2 (Wickham, 2009).

Correlations between the different measurements of moss establishment (biomass and final measurements of survival, height and cover) were assessed using Pearson's product-moment correlation. Mixed ANOVA, accounting for the split-plot experimental design, was used to test effects of bulk density, ash and rainwater type and their interactions on dry biomass of each species separately. The Tukey HSD test was used to test for pairwise differences. Normality of residuals and homogeneity of variances were inspected graphically for all models.

Natural logarithm transformation was applied to the cation concentration data from the peat samples to reduce heteroscedasticity. Factorial ANOVA and Tukey HSD tests were then carried out to investigate the effects of ash and rainwater type on concentrations of Ca^{2+}, Mg^{2+}, Na^+ and K^+ in peat samples.

3.3 Results

3.3.1 Moss biomass

Air dried moss biomass was used as the dependent variable in the analyses as it represented the most objective measure of establishment success and was strongly correlated with final measurements of cover, survival, growth and height in both *Sphagnum* species (Table 3.3). Survival of the original diaspores of *C. introflexus* was uniformly low, as was height in this species, but biomass was well correlated with cover and the proportion of diaspores which gave rise to new growth.

Table 3.3: Pearson's product moment correlation of biomass (g dry weight) with proportion of pot covered by moss, number of moss fragments surviving, number of fragments showing signs of growth and moss height. P values for all correlations shown are < 0.001. N/A = not tested.

Species	Cover %	Survival proportion	Growth proportion	Height (mm)
Sphagnum capillifolium	0.78	0.66	0.70	0.66
Sphagnum fallax	0.84	0.68	0.68	0.70
Campylopus introflexus	0.82	N/A	0.51	N/A

ANOVAs carried out on the biomass data indicated that the effects of the three treatments manipulated in the experiment varied depending on moss species (Table 3.4). Pots with normal bulk density produced greater biomass of both *S. capillifolium* (F = 16.55, p = 0.002) and *S. fallax* (F =18.33, p = 0.001) compared to those with high peat bulk density (Figure 3.1). There was no significant effect of bulk density on *C. introflexus* (F < 0.01, p = 0.950). Ash addition impacted *S. capillifolium* (F = 15.28, p = 0.001) and Tukey HSD tests indicated significantly higher biomass in pots with unleached ash than those with leached ash or no ash, and likewise in pots with leached ash compared to those with no ash (Figure 3.2). In *S. fallax*, no significant impact of ash on biomass was observed (F = 1.76, p = 0.213).

Ash (F = 16.61, p < 0.001), rainwater chemistry (F = 20.67, p = 0.001) and the interaction between the two (F = 10.26, p = 0.003) impacted *C. introflexus* biomass. Pots watered with Peak District rainwater overall produced higher *C. introflexus* biomass than those watered with Cairngorm rainwater. The impact of ash was nonsignificant in pots watered with Cairngorm water, but pots watered with Peak District rainwater had lower biomass when no ash was added compared to unleached and leached ash (Figure 3.3). Rainwater chemistry did not significantly impact biomass of either *S. capillifolium* (F = 1.51, p = 0.242) or *S. fallax* (F = 0.71, p = 0.417).

Table 3.4: Results of mixed ANOVA of final biomass (g dry weight) of *S. capillifolium*, *S. fallax* and *C. introflexus* according to water chemistry, ash treatment and peat bulk density.

Species	Variable	Degrees of freedom	Sum of Squares	Mean Square	F value	Pr(>F)
S. capillifolium	Ash	2	0.113	0.057	15.281	0.001
	Rainwater	1	0.006	0.006	1.513	0.242
	Ash:rainwater	2	0.006	0.003	0.805	0.470
	Residuals	12	0.044	0.004		
	Bulk density	1	0.042	0.042	16.551	0.002
	Ash:bulk	2	0.002	0.001	0.456	0.644
	Rainwater:bulk	1	0.001	0.001	0.328	0.577
	Ash:rainwater:bulk	2	0.003	0.002	0.643	0.543
	Residuals	12	0.031	0.003		
S. fallax	Ash	2	0.033	0.017	1.764	0.213
	Rainwater	1	0.007	0.007	0.708	0.417
	Ash:rainwater	2	0.015	0.008	0.800	0.472
	Residuals	12	0.113	0.009		
	Bulk density	1	0.237	0.237	18.334	0.001
	Ash:bulk	2	0.035	0.018	1.374	0.290
	Rainwater:bulk	1	0.002	0.002	0.189	0.671
	Ash:rainwater:bulk	2	0.002	0.001	0.065	0.937
	Residuals	12	0.155	0.013		
C. introflexus	Ash	2	0.005	0.003	16.610	<0.001
	Rainwater	1	0.003	0.003	20.670	0.001
	Ash:rainwater	2	0.003	0.002	10.260	0.003
	Residuals	12	0.002	0.000		
	Bulk density	1	0.000	0.000	0.004	0.950
	Ash:bulk	2	0.000	0.000	0.160	0.854
	Rainwater:bulk	1	0.000	0.000	0.010	0.921
	Ash:rainwater:bulk	2	0.000	0.000	0.037	0.964
	Residuals	12	0.008	0.001		

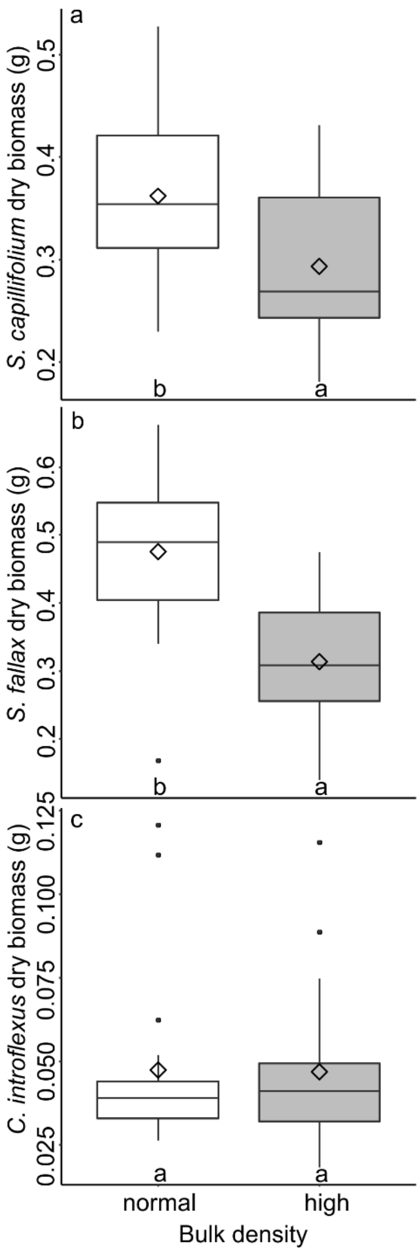

Figure 3.1: Boxplot showing dry biomass of a) *S. capillifolium* and b) *S. fallax* grown in pots with normal or high peat bulk density (n=54). The horizontal line, box, whiskers, dots and ◊ indicate the median, upper and lower quartiles, minimum and maximum excluding outliers, outliers and mean respectively. Treatments which do not share a letter are significantly different ($p<0.05$).

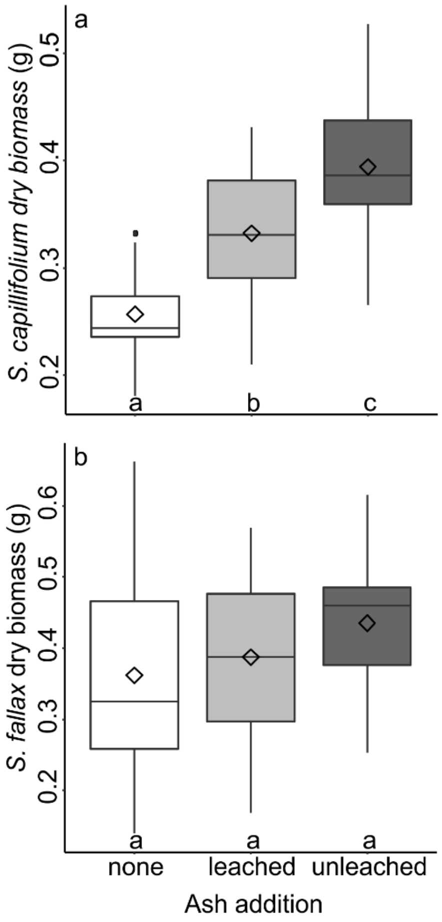

Figure 3.2: Boxplot showing dry biomass of *S. capillifolium* grown in pots with no ash, leached ash or unleached ash (n=36). The horizontal line, box, whiskers, dots and ◊ indicate the median, upper and lower quartiles, minimum and maximum excluding outliers, outliers and mean respectively. Treatments which do not share a letter are significantly different (p<0.05).

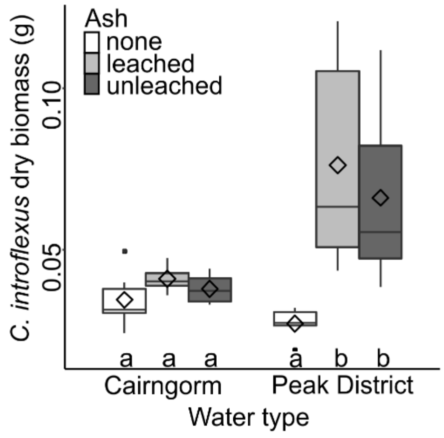

Figure 3.3: Boxplot showing dry biomass of *C. introflexus* grown in pots with no ash, leached ash or unleached ash and Cairngorm or Peak District water chemistry (n=18). The horizontal line, box, whiskers, dots and ◊ indicate the median, upper and lower quartiles, minimum and maximum excluding outliers, outliers and mean respectively. Treatments which do not share a letter are significantly different (p<0.05).

3.3.2 Impacts of ash addition and leaching on peat chemistry

Factorial ANOVA and Tukey HSD tests revealed significantly greater concentrations of Ca^{2+}, Mg^{2+}, Na^{+} and K^{+} in unleached peat samples with ash added compared to unleached samples without ash (p = 0.002; 0.004; <0.001; <0.001 respectively). However, differences in the concentrations of Ca^{2+}, Mg^{2+}, Na^{+} and K^{+} between samples with and without ash were not significant after leaching with either Cairngorm (p = 0.465; 0.634; 0.786; 0.574) or Peak District (p = 0.650; 0.964; 0.327; 0.054) rainwater (Figure 3.4).

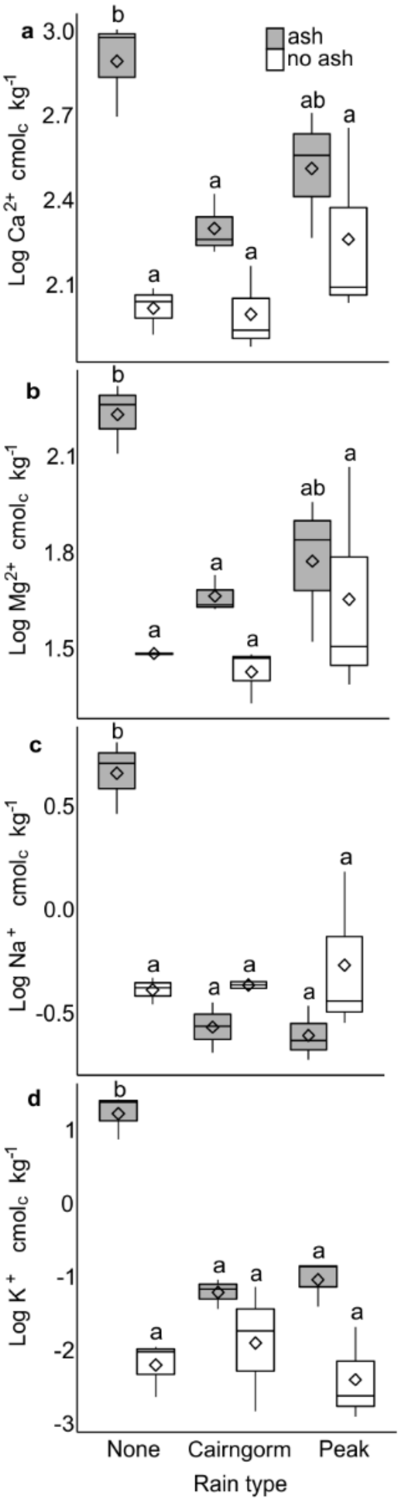

Figure 3.4: Concentrations (natural log cmol$_c$ kg^{-1} dry weight) of Ca^{2+}, Mg^{2+}, Na^+ and K^+ in surface peat samples taken from pots with and without ash additions and either left unleached or leached with 1.5 L of either Cairngorm or Peak District recipe artificial rainwater (n=3). The horizontal line, box, whiskers, dots and ◊ indicate the median, upper and lower quartiles, minimum and maximum excluding outliers, outliers and mean respectively. Treatments which do not share a letter are significantly different ($p<0.05$).

3.4 Discussion

The results of this study showed that growth of all three moss species responded differently to the experimental treatments. Both *Sphagnum* species were affected by bulk density and *S. capillifolium* was affected by ash addition, whilst *C. introflexus* was affected by both ash addition and rainwater chemistry. This highlights the importance of considering species individually and indicates that even species with a similar functional niche may respond differently to environmental change. Of the variables measured, cover was best correlated with biomass in all three species (Table 3.3), suggesting that recording percentage cover would be an appropriate alternative to biomass measurements in experiments where destructive sampling is not possible. Comparison of mean values for biomass and cover indicate that the differences in biomass observed within treatments represented ecologically significant differences in percentage cover (Table 3.5).

Table 3.5: Mean and standard error values for final biomass (g dry weight) and percentage cover of *S. capillifolium*, *S. fallax* and *C. introflexus* according to water chemistry, ash treatment and peat bulk density.

		Sphagnum capillifolium		*Sphagnum fallax*		*Campylopus introflexus*	
Factor	**Level**	Biomass (g)	Cover %	Biomass (g)	Cover %	Biomass (g)	Cover %
Bulk density	Normal	0.36±0.08	58±14	0.48±0.12	57±18	0.05±0.03	10±6
	High	0.29±0.07	42±17	0.31±0.09	41±14	0.05±0.02	14±10
Ash addition	None	0.26±0.05	34±14	0.36±0.16	44±19	0.03±0.01	2.2±1.9
	Leached	0.33±0.07	51±12	0.39±0.13	44±17	0.06±0.03	17±7
	Unleached	0.39±0.07	65±9	0.44±0.10	59±15	0.05±0.02	16±5
Rainwater type	Cairngorm	0.34±0.10	50±18	0.38±0.11	48±15	0.04±0.01	10±6
	Peak	0.32±0.07	50±17	0.41±0.15	50±21	0.06±0.03	14±10

The negative impact of increased bulk density on both *S. capillifolium* and *S. fallax* suggests that water availability to these species was affected at higher bulk density. This could be the result of reduced water storage capacity, increased water retention, and decreased hydraulic conductivity associated with higher bulk densities. These conditions can increase the incidence of low soil water pressures (e.g. below -100mb), which would be unsuitable for *Sphagnum* (Price, 1997; Hayward and Clymo, 1982). Based on data provided by Boelter (1968) and Thompson and Waddington (2013) the difference in bulk density between the normal pots and the compacted pots may equate to a difference in volumetric water content between these treatments of ~0.1 at -100mb. Although water tables in the experiment were within a range considered favourable to *Sphagnum* (2 to 5 cm), the surfaces of many of the high bulk density pots were visibly drier than those with normal bulk density throughout the experiment, suggesting that water was less able to move through the peat matrix to replace evaporative loss at the surface. Hayward and Clymo (1982) identified this as a key potential issue for *Sphagnum*, even when there are relatively shallow water table conditions. In future work, measuring water pressure and/or water content at the peat surface could help to quantify this effect and develop our understanding of critical thresholds for *Sphagnum*. The fact that *C. introflexus* was unaffected reflects the species' lower Ellenberg indicator value for moisture (Table 3.1) and could indicate a risk of a shift to species which can tolerate lower water availability at high bulk density. Holden et al. (2014) found that peat bulk densities decreased with time since burning, so leaving sites unburned for longer may create more favourable conditions for *Sphagnum* establishment. However, the high bulk density treatment in this experiment was actually lower than many of the bulk densities measured on burned plots by Holden et al. (2014), suggesting that greater limitations to *Sphagnum* establishment may occur in the field. On the other hand, the bulk density - water retention plots presented by Thompson and Waddington (2013) for soil water pressures of -100mb flatten out considerably for bulk densities > 0.17 g cm-3 and so the effects on water retention, at -100mb, of enhanced bulk density beyond the range we tested may not be substantially greater in the field for fire affected sites. The normal bulk density treatment was similar to bulk densities measured by Holden et al. (2014) on unburned plots. As water was supplied from below throughout the experiment, water intercepted from precipitation was not accounted for, but past work has shown that dependence on precipitation can increase susceptibility to drought and reduce carbon uptake in *Sphagnum* (Nijp et al., 2014).

The positive impact of ash on *S. capillifolium* was unexpected given previous reports of damage to *Sphagnum* by ash (Dynesius, 2012). This may be due to inputs of limiting nutrients since pots with unleached ash produced greater *S. capillifolium* biomass than pots with leached ash. Although concentrations of Ca^{2+}, Mg^{2+}, Na^{+} and K^{+} in peat with leached ash were not significantly different to those without ash, it is possible that small residual quantities of these or other nutrients had an effect, or that another nutrient was less easily leached. An increase in pH as a result of ash addition could also have affected *Sphagnum* growth. *Sphagnum* usually prefers acidic habitats (Clymo, 1963), but tolerance ranges and optima can vary between species (Haraguchi, 1996). The fact that rainwater chemistry had no impact on either *Sphagnum* species may suggest that the effect was down to a nutrient supplied by the ash and lacking in the rainwater. Phosphorus has been observed to affect *Sphagnum* both positively and negatively depending on the species and concentrations of other nutrients (Carfrae et al., 2007; Li et al., 1993; Sottocornola et al., 2007), but was found by Allen (1964) to leach from ash at a similar rate to magnesium. It is possible that ash addition from burning may facilitate establishment of *S. capillifolium* under some circumstances, but the benefit may be decreased if burning is shortly followed by a heavy rainfall event that leaches deposited ash. Furthermore, positive effects may be offset by the negative impacts of increased bulk density as well as increased competition from vascular plants and other mosses (including *C. introflexus*) benefiting from ash inputs. The fact that a similar pattern was not observed in *S. fallax* indicates that *Sphagnum* species vary in their responses to ash addition. Work by Brown et al. (2014) suggests that repeated prescribed burning may reduce peat cation exchange capacity, so in the field initial cation enrichment may be followed by depletion in the longer term.

C. introflexus was the only species which showed a response to rainwater chemistry, which is consistent with reports of a positive response to nitrogen increases (Southon et al., 2012). The interaction of rainwater chemistry with ash addition suggests that *C. introflexus* is limited by more than one nutrient, as biomass was greatest under nutrient inputs from both ash and Peak District rain. Neither of the *Sphagnum* species showed a response to rainwater chemistry, which suggests that current atmospheric pollution deposition is not directly limiting to these species. However, there is potential for competitive effects from other species including *C. introflexus* in the field. Given that the Ellenberg value for *S. fallax* indicated a higher nitrogen tolerance than *C. introflexus* (Table 3.1), a positive response to increased rainwater nutrients may have been expected. However, previous experimental work has shown a negative physiological response of the species to nitrogen increases, and it is suggested that local environmental conditions and supply of other nutrients may play a role in determining net impacts (Granath et al., 2012).

Overall, the results of this study show that anthropogenic influences including fire and atmospheric pollution can impact mosses via both physical and chemical processes.

Effects were not consistent across the three species studied and in the case of *S. capillifolium*, ash addition and bulk density increase had opposing effects. The positive effect of ash addition on *S. capillifolium* may indicate that in some instances, ash can facilitate colonisation. However, increased competition from other mosses and vascular plants is likely to be a significant factor in the field. The negative impact of increased bulk density on both *Sphagnum* species indicates that peat physical properties governing water availability are an important factor to consider alongside water table depth in restoration efforts. Species specific responses highlight the importance of differentiating between moss species to ensure appropriate management and considering both species identity and local environmental conditions when planning *Sphagnum* re-introductions.

3.5 Acknowledgements

This research was funded by a Natural Environment Research Council studentship [NE/L008572/1] supported by Natural England, awarded to JH, SMP, DG and AC in open competition. We thank Dr Catherine Moody (University of Leeds) for comments on an earlier version of the manuscript.

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Chapter 4: Impacts of prescribed burning on *Sphagnum* mosses in a long-term peatland field experiment

Alice Noble[a], John O'Reilly[b], David J Glaves[c], Alistair Crowle[c], Sheila M Palmer[a], Joseph Holden[a].

[a]water@leeds, School of Geography, University of Leeds, UK

[b]Ptyxis Ecology, Lambley, Brampton, UK

[c]Natural England, Foss House, Kings Pool, Peasholme Green, York, UK

Abstract

Understanding fire impacts on peatland vegetation can inform management to support function and prevent degradation of these important ecosystems. However, time since burn, interval between burns and number of past burns all have the potential to modify impacts. Grazing regime may also affect vegetation directly or via an interaction with burning. We used new, comprehensive survey data from a hillslope-scale field experiment initiated in 1954 to investigate the effects of burning and grazing treatments on *Sphagnum*. Historical data were consulted to aid interpretation of the results.

The unburned reference and the most frequently burned (10-year rotation) treatments had greater *Sphagnum* abundance and hummock height than intermediate treatments (20-year rotation and no-burn since 1954). Abundance of the most common individual species (*S. capillifolium*, *S. subnitens* and *S. papillosum*) followed similar patterns. Light grazing had no impact on *Sphagnum*-related variables, nor did it interact with the burning treatments.

These results suggest that in some cases fire has a negative impact on *Sphagnum*, and this can persist for several decades. However, fire return interval and other factors such as atmospheric pollution may alter effects, and in some cases *Sphagnum* abundance may

recover. Fire severity and site specific conditions may also influence effects, so we advise consideration of these factors, and caution when using fire as a management tool on peatlands where *Sphagnum* is considered desirable.

4.1 Introduction

Peatlands, which cover around 4.23 million km^2 globally (Xu et al., 2018), are important landscapes for biodiversity, carbon storage and hydrological functions (Evans et al., 2014). On many peatlands, particularly at high latitudes, *Sphagnum* mosses are central to ecosystem function, influencing hydrology (Hayward and Clymo, 1982), chemistry (Clymo, 1984), temperature (van Breemen, 1995) and microtopography (Eppinga et al., 2009), as well as sequestering carbon (Clymo and Hayward, 1982). Fire is common on peatlands worldwide and includes both wildfire and prescribed burning for purposes including wildfire prevention, land clearance, agricultural grazing and game management (Kasischke and Turetsky, 2006; Yallop et al., 2006; Turetsky et al., 2015). Knowledge of the impacts of fire on *Sphagnum* is therefore vital to inform fire-impact predictions and nature conservation management decisions.

Prescribed burning occurs in many peatland ecosystems worldwide including areas of North America (Geron and Hays, 2013) and Europe (Hochkirch and Adorf, 2007; Renard et al., 2016). Fires are often controlled to burn vegetation without igniting the underlying peat, so results from studies of wildfire, where moss and surface peat layers can be consumed, may not be directly applicable. In the UK, prescribed burning is commonly carried out on patches of up to c.4000 m^2 (0.4ha) in rotations of around 7-25 years. The canopy layer, which on UK peatlands is usually dominated by dwarf shrubs (including *Calluna vulgaris*) and sedges (commonly *Eriophorum vaginatum* and *E. angustifolium*) is burned to create a range of vegetation ages suitable for nesting and foraging of the game bird red grouse (*Lagopus lagopus scotica*). Official guidance advocates a strong presumption against burning on deep peat (Defra, 2007), but there is evidence that burning has increased on UK peatlands in recent decades (Yallop et al., 2006; Thacker et al., 2015; Douglas et al., 2015).

While national-scale work has shown that there is less *Sphagnum* cover on peatlands subject to prescribed burning in England (Noble et al., 2018), results from local and regional scale studies suggest that effects can vary depending on fire severity and return interval (Hamilton, 2000; Lee et al., 2013a). Burning may influence *Sphagnum* by heat damage or combustion with varying recovery prospects (Hamilton, 2000; Grau-Andrés et al., 2017; Taylor, E.S. et al., 2017), and changes in substrate properties can also have an effect. For example, higher near-surface peat bulk densities and lower soil water availability on recently burned sites (Holden et al., 2014) can limit *Sphagnum* growth (Noble et al., 2017), and more extreme peat surface temperatures in the years after burning (Brown et al., 2015b) may also have a negative impact (Walker et al., 2015). Ash deposition from burning may cause short term cation enrichment (Allen, 1964) with potentially positive effects for some *Sphagnum* species (Noble et al., 2017), but this may also increase competition, and some cations may be depleted in the longer term (2+ years after burning) (Brown et al., 2014). Previous field studies have reported *Sphagnum* abundance (Noble et al., 2018; Lee et al., 2013a), but hummock height, which may also be affected by burning representing a change in biomass, is seldom reported. Understanding burning effects on both abundance and hummock height would contribute to a more complete knowledge of impacts on carbon sequestration and other ecosystem services.

The Hard Hill vegetation burning and grazing experiment at Moor House National Nature Reserve in the North Pennines, UK was established in 1954. The main experiment includes three burning treatments with plots burned on either short (10-year) or long (20-year) rotations, or burned once in 1954/55 and left unburned since (S, L and N plots; Table 4.1). Reference (R) plots were established adjacent to the main experiment plots, outside of the 1954 burn area. Studies of the vegetation of the main experiment plots were published in the 1970s (Rawes and Hobbs, 1979) and 1980s (Hobbs, 1984). More recent work has shown greater *Sphagnum* abundance (Lee et al., 2013a) and lower *Sphagnum* propagule availability (Lee et al., 2013b) on the 10-year (S) rotation plots compared to 20-year (L) and no-burn since 1954 (N) plots. However, a direct comparison of *Sphagnum* abundance between the experiment and reference (R) plots has not previously been carried out, so it is not known how the experimental treatments compare to surrounding vegetation. Furthermore, previous surveys may not have captured rarer or less evenly distributed *Sphagnum* species (Glaves et al., 2013).

Table 4.1: Burning treatments in the Hard Hill experiment.

Code	Treatment
R	Reference, unburned for 90+ years
N	No-burn since 1954/55, unburned for 60+ years
L	Long (20-year) rotation
S	Short (10-year) rotation

Here we present the results of a comprehensive survey of the main experiment and reference plots, including hummock height data and mapping of all *Sphagnum* patches in every plot at species level, with the aim of investigating the effect of burning treatments. This represents the most complete survey of *Sphagnum* in a burning experiment to date and the first time the Hard Hill experimental treatments have been compared to a reference. Changes over time are also considered with reference to data from past surveys. The results are discussed in the context of the potential processes responsible for burning impacts on *Sphagnum* and implications for future burn management and policy.

4.2 Methods

4.2.1 Experimental design

The Hard Hill experiment consists of four 90m x 60m blocks, each made up of six 30m x 30m plots. At the start of the experiment in 1954, half of each block (three plots) was fenced to exclude grazing, and within each half three burning treatments (S, L and N) were allocated at random. All of the main experiment plots were burned at the start of the experiment and the S and L plots have been burned on approximately 10- and 20-year rotations respectively since then (subject to suitable weather conditions). Unfenced reference plots which had remained unburned for at least 30 years prior to 1954 (28) were established alongside each block outside of the initial burn areas (Figure 4.1). The burning and survey schedule of the experiment is described in Lee et al. (19), which also provides information on the overall vegetation composition. Briefly, the plots comprise *Calluna vulgaris- Eriophorum vaginatum* blanket mire which is characteristic of much of the blanket bog in the English Pennines which has been modified to a greater or lesser extent by grazing and burning management and other impacts.

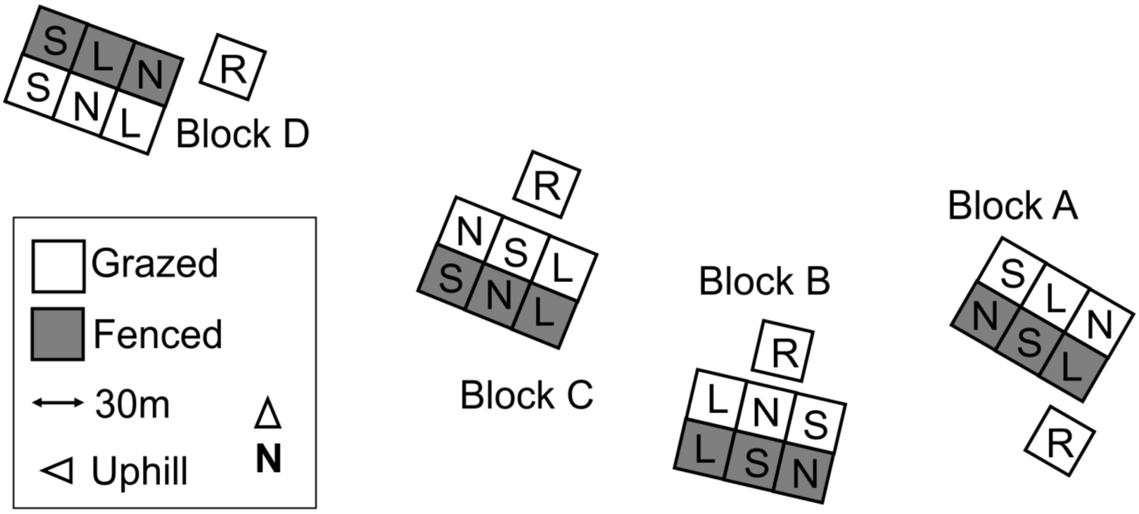

Figure 4.1: Layout of the Hard Hill experimental plots (R=reference, N=no-burn since 1954, L=long (20-year) rotation, S=short (10-year) rotation.

4.2.2 *Sphagnum* surveys

The 24 main experiment plots and four reference plots were surveyed between August 2015 and April 2016. Within each plot 10 transects were laid out at evenly spaced intervals. Transects were located at least 1.5 m away from the plot edges to avoid heavily trampled areas and edge effects and hence were between 22.5 and 27 m long. Survey data were recorded at 10 evenly spaced pin points along each transect (100 points total per plot). *Sphagnum* presence or absence was recorded at each pin point, and where *Sphagnum* was present the species was identified. *S. capillifolium* ssp. *capillifolium* (Ehrh.) Hedw. and *S. capillifolium* ssp. *rubellum* (Wilson) M.O.Hill were initially recorded separately, but the two subspecies could not always be differentiated with certainty so analysis was undertaken at species level. *Sphagnum* patch length and width were measured to the nearest cm at the widest points parallel and perpendicular to the transect, and patch area was calculated using the formula $area = \pi\left(\frac{length + width}{4}\right)^2$. *Sphagnum* patch height was measured to the nearest cm by inserting a cane vertically into the patch at the pin point until it met resistance from the underlying peat. For the 24 main experiment plots the height data were recorded approximately 6 months later than the frequency, species identity and length/width data, so it was not possible to replicate precisely the original pin points.

Alongside the transect survey, a mapping survey was conducted to record the location, species and approximate area of every *Sphagnum* patch in all 24 plots. This was carried out by walking along the nine 2.5-3 m wide strips between transects in each plot and drawing each *Sphagnum* patch encountered as a polygon on a corresponding map. Transects were marked with tape measures to provide a reference for patch position. To calculate *Sphagnum* frequency from the resulting maps, a transparent overlay with 1296 regular grid squares for each plot was used. The number of squares partly or entirely occupied was counted for each *Sphagnum* species, and *Sphagnum* as a genus.

4.2.3 Past surveys

Vegetation surveys which recorded *Sphagnum* and other species in some or all of the Hard Hill plots were carried out in 1961, 1965, 1972/3, 1982, 1991, 2001 and 2011 using various recording methods (Table 4.2). Analysis of the 1972 – 2001 data from the S, L and N plots and investigation of change between 1965 and 2011 in the R plots was carried out by Lee et al. (19). Rawes and Hobbs (28) presented results from the 1961 survey, but differences in *Sphagnum* between treatments were not discussed. No comparison of the N and R plot data from the 1965 data has been published to date. Therefore, to support the interpretation of the 2015/16 data, we analysed *Sphagnum* abundance from the plots surveyed in 1961 (all main experiment plots) and 1965 (grazed N and R plots).

Table 4.2: Summary of past surveys of Hard Hill plots. Burn treatments are short rotation (S), long rotation (L), no-burn since 1954 (N) and unburned reference (R).

Year(s)	Treatments	Survey type	Samples per plot
1961	S, L, N	Domin	25 x 1 m^2 quadrats
1965	N, R	Domin	5 (R) or 10 (N) 1 m^2 quadrats
1972/3, 1982, 1991, 2001	S, L, N	Point quadrats	20 x 1 m^2 quadrats x 5 pins
2011	R	Domin	25 quadrats
2015/6	S, L, N, R	Transect/mapping	10 transects, 100 pin points

4.2.4 Data analysis

All statistical analyses were carried out using R 3.1.0 (R Development Core Team, 2010). Data from the main experiment plots were analysed using split plot ANOVA with split plot nested within block as the error term and burning, grazing and their interaction as factors. Second, data from the grazed main experiment plots and reference plots were compared using ANOVA with burn status and block as factors. The two types of analysis both represent balanced experimental designs, and were carried out separately to account for the absence of a fenced reference treatment.

Dependent variables in the 2015-2016 data included transect hits, patch size, hummock height, and proportion of map squares occupied for *Sphagnum* as a genus. The proportion of transect hits and map squares occupied were calculated for individual species and where species were present in more than one percent of samples these variables were analysed in the same way.

Analysis of the 1961 and 1965 historical data used similar methods, with split plot ANOVA for the 1961 main experiment data and ANOVA with burn status and block as factors for the 1965 N and R plot data. Domin scores were transformed using the Domin 2.4 transformation (Currall 1987) to give an approximation of percentage cover. To account for potential effects of unequal sampling effort between treatments only the first five quadrats from each grazed N plot in 1965 were used in the analysis.

For each ANOVA model homogeneity of variances and normality of residuals were inspected graphically, and where appropriate data were transformed to reduce skew and/or heteroscedasticity. Tukey's Honest Significant Difference (HSD) pairwise test was used to investigate differences between treatment combinations.

4.3 Results

4.3.1 Comparison of main experiment plots in 2015-16

For *Sphagnum* spp. (hereafter *Sphagnum*), both transect hits and map frequency were significantly associated with burn treatment (Table 4.3), with more frequent occurrence in S plots than in L and N plots and more frequently in L plots than in N plots (Figure 4. 2). However, neither median patch area nor hummock height were significantly associated with burn status (Table 4.3). The only species present at more than 1 % of transect pin points was *S. capillifolium*, which was also significantly associated with burn treatment (Table 4.3), occurring more frequently in S plots than in L and N plots. *S. capillifolium*, *S. subnitens* and *S. papillosum* all occurred in more than 1% of the map squares and all three were significantly associated with burn treatment (Table 4.3). *S. capillifolium* occurred more frequently in S plots than in L and N plots and more frequently in L plots than in N plots, while *S. subnitens* and *S. papillosum* occurred more frequently in S plots than in N plots. Neither grazing treatment nor its interaction with burn treatment were significantly associated with any of the *Sphagnum*-related variables tested.

Table 4.3: Results of split plot ANOVAs for *Sphagnum*-related variables (transformations in brackets), recorded in the main experiment plots (grazed and fenced S, L and N) in 2015-16.

Dependent variable	Error	Factor	Df	Sum sq	Mean sq	F value	Pr(>F)
Sphagnum spp. Transect frequency (square root)	Block	Residuals	3	0.2161	0.0720		
	Grazing	Grazing	1	0.0005	0.0005	0.04	0.861
		Residuals	3	0.0396	0.0132		
	Within	Burn	2	0.4167	0.2084	48.07	<0.001
		Grazing:Burn	2	0.0152	0.0076	1.75	0.215
		Residuals	12	0.0520	0.0043		
Sphagnum spp. Map frequency	Block	Residuals	3	0.4740	0.1580		
	Grazing	Grazing	1	0.0312	0.0312	0.78	0.443
		Residuals	3	0.1209	0.0403		
	Within	Burn	2	0.9110	0.4555	45.25	<0.001
		Grazing:Burn	2	0.0111	0.0055	0.55	0.591
		Residuals	12	0.1208	0.0101		
Sphagnum spp. Patch area (m^2)	Block	Residuals	3	0.1440	0.0480		
	Grazing	Grazing	1	0.0115	0.0115	0.24	0.656
		Residuals	3	0.1426	0.0475		
	Within	Burn	2	0.0886	0.0443	1.29	0.310
		Grazing:Burn	2	0.0985	0.0493	1.44	0.276
		Residuals	12	0.4113	0.0343		
Sphagnum spp. Hummock height (cm)	Block	Residuals	3	40.37	13.46		
	Grazing	Grazing	1	19.26	19.26	0.57	0.505
		Residuals	3	101.54	33.85		
	Within	Burn	2	9.33	4.66	0.31	0.702
		Grazing:Burn	2	36.58	18.29	1.20	0.340
		Residuals	10	151.92	15.19		
S. capillifolium Transect frequency (square root)	Block	Residuals	3	0.2348	0.0783		
	Grazing	Grazing	1	0.0032	0.0032	0.27	0.640
		Residuals	3	0.0358	0.0119		
	Within	Burn	2	0.3408	0.1704	37.29	<0.001
		Grazing:Burn	2	0.0251	0.0126	2.75	0.104
		Residuals	12	0.0548	0.0046		
S. capillifolium Map frequency (square root)	Block	Residuals	3	0.4931	0.1644		
	Grazing	Grazing	1	0.0359	0.0359	1.07	0.376
		Residuals	3	0.1003	0.0334		
	Within	Burn	2	0.5407	0.2703	46.26	<0.001
		Grazing:Burn	2	0.0042	0.0021	0.36	0.704
		Residuals	12	0.0701	0.0058		
S. subnitens Map frequency (square root)	Block	Residuals	3	0.0148	0.0049		
	Grazing	Grazing	1	0.0018	0.0018	0.34	0.602
		Residuals	3	0.0164	0.0055		
	Within	Burn	2	0.1027	0.0513	8.29	0.005
		Grazing:Burn	2	0.0013	0.0007	0.11	0.898
		Residuals	12	0.0743	0.0062		
S. papillosum Map frequency (square root)	Block	Residuals	3	0.0089	0.0030		
	Grazing	Grazing	1	0.0036	0.0036	0.62	0.487
		Residuals	3	0.0173	0.0058		
	Within	Burn	2	0.0767	0.0384	9.56	0.003
		Grazing:Burn	2	0.0040	0.0020	0.50	0.616
		Residuals	12	0.0481	0.0040		

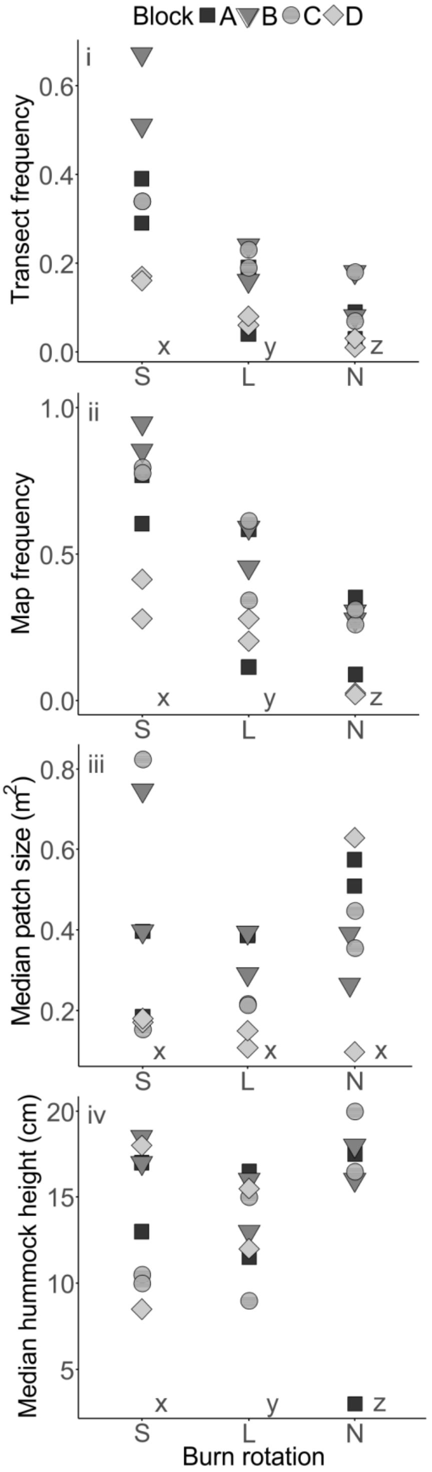

Figure 4.2: Values for i) transect frequency (0-1), ii) map frequency (0-1), iii) median patch size (m^2) and iv) median hummock height (cm) of *Sphagnum* for all plots (grazed and fenced) within the main experiment in 2015-16. Burn treatments are short rotation (S), long rotation (L) and no-burn (N). Treatments which do not share an x, y, z letter coding are significantly different ($p < 0.05$) according to Tukey HSD tests.

4.3.2 Comparison of reference and grazed main experiment plots in 2015-16

Sphagnum was significantly associated with burn status (Table 4.4), occurring more frequently in R and S plots than in L and N plots according to both the transect and map data (Figure 4.3). Patch area was not significantly associated with burning status, but hummock height was (Table 4.4), with higher values in R plots than in L or N plots (Figure 4.3). In both the transect and map data, *S. capillifolium* occurred more frequently in R and S plots than in L and N plots (Table 4.4). *S. subnitens* and *S. papillosum* were both significantly associated with burning status in the map data (Table 4.4) and were more frequent in S than in N plots, with *S. papillosum* also more frequent in S than in R plots.

Table 4.4: Results of ANOVAs for *Sphagnum*-related variables recorded in the 2015-16 survey in the grazed main experiment (S, L and N) and reference (R) plots. Transformations of the dependent variables are noted in brackets.

Spp.	Dependent variable	Factor	Df	Sum sq	Mean sq	F value	Pr(>F)
Sphagnum spp.	Transect frequency	Burn	3	0.1389	0.0463	11.24	0.002
		Block	3	0.1772	0.0591		
		Residuals	9	0.0371	0.0041		
	Map frequency	Burn	3	0.5790	0.1930	32.17	<0.001
		Block	3	0.3696	0.1232		
		Residuals	9	0.0540	0.0060		
	Patch area (m^2)	Burn	3	0.4467	0.1489	1.25	0.348
		Block	3	0.9077	0.3026		
		Residuals	9	1.0705	0.1190		
	Hummock height (cm)	Burn	3	283.30	94.44	6.58	0.015
		Block	3	145.90	48.62		
		Residuals	8	114.80	14.35		
S. *capillifolium*	Transect frequency	Burn	3	0.1012	0.0337	8.94	0.005
		Block	3	0.1857	0.0619		
		Residuals	9	0.0340	0.0038		
	Map frequency (square root)	Burn	3	0.3693	0.1231	23.04	<0.001
		Block	3	0.3555	0.1185		
		Residuals	9	0.0481	0.0053		
S. *subnitens*	Map frequency (square root)	Burn	3	0.3693	0.1231	23.04	<0.001
		Block	3	0.3555	0.1185		
		Residuals	9	0.0481	0.0053		
S. *papillosum*	Map frequency (square root)	Burn	3	0.0713	0.0238	5.42	0.021
		Block	3	0.0136	0.0045		
		Residuals	9	0.0395	0.0044		

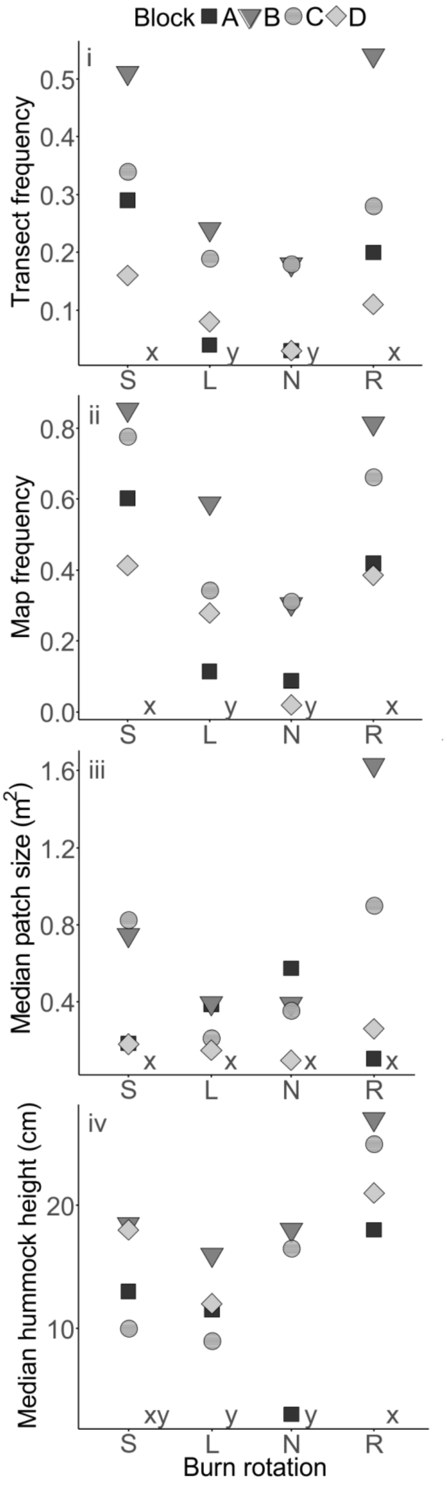

Figure 4.3: Values for i) transect frequency (0-1), ii) map frequency (0-1), iii) median patch size (m^2) and iv) median hummock height (cm) of *Sphagnum* for grazed plots within the main experiment, and reference plots in 2015-16. Burn treatments are short rotation (S), long rotation (L), no-burn (N) and reference (R). Treatments which do not share an x, y, z letter coding are significantly different ($p < 0.05$) according to Tukey HSD tests.

4.3.3 Past surveys

Analysis of the 1961 data from the main experiment plots showed no significant difference in cover of *Sphagnum* according to burn treatment, grazing or their interaction (Table 4.5, Figure 4.4) seven years after the initial burn. Analysis of the data from N and R plots in 1965 found that the reference plots had significantly greater *Sphagnum* cover (Table 4.6, Figure 4.5).

Table 4.5: Results of ANOVA for *Sphagnum* cover (%; square root transformed) in the main experiment plots (grazed and fenced S, L and N) in 1961.

Error	Factor	Df	Sum sq	Mean sq	F value	Pr(>F)
Block	Residuals	3	258.9	86.29		
Block:Grazing	Grazing	1	136.19	136.19	5.28	0.105
	Residuals	3	77.43	25.81		
Block:Grazing:Burn	Burn	2	130.77	65.38	2.85	0.097
	Grazing:Burn	2	54.63	27.31	1.19	0.338
	Residuals	12	275.25	22.94		
Within	Residuals	576	1845	3.203		

Table 4.6: Results of ANOVA for *Sphagnum* cover (%; square root transformed) in the grazed no-burn (N) plots and reference (R) plots in 1965.

Factor	Df	Sum sq	Mean sq	F value	Pr(>F)
Burn	1	9.09	9.09	7.63	0.009
Block	3	20.04	6.68		
Residuals	35	41.72	1.19		

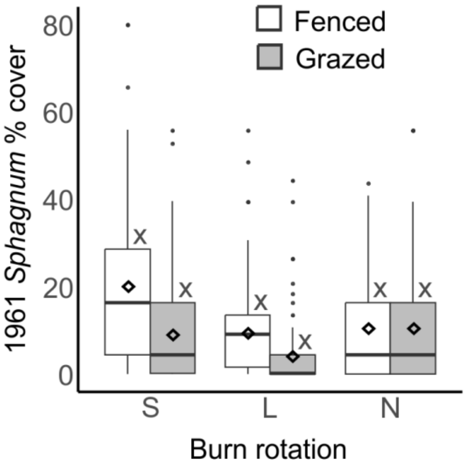

Figure 4.4: Boxplots showing Sphagnum % cover (transformed from Domin scale values) in grazed and fenced plots within the main experiment in 1961 (data from 25 quadrats in each of 4 plots per treatment; n = 100). Burn treatments are short rotation (S), long rotation (L) and no-burn (N). The horizontal line, box, whiskers, dots and ◊ indicate the median, upper and lower quartiles, minimum and maximum excluding outliers, outliers and mean respectively. Treatments sharing the letter x coding are not significantly different (p > 0.05) according to Tukey HSD tests.

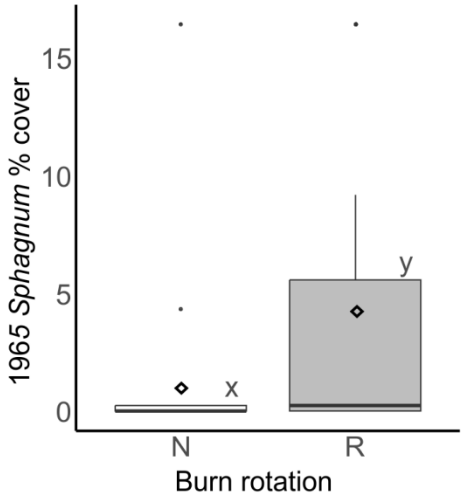

Figure 4.5: Boxplots showing *Sphagnum* cover (recorded on the Domin scale and transformed to %) in reference (R) and grazed no-burn (N) plots (data from 5 quadrats in each of 4 plots per treatment; n =20). The horizontal line, box, whiskers, dots and ◊ indicate the median, upper and lower quartiles, minimum and maximum excluding outliers, outliers and mean respectively. Treatments which do not share an x, y, z letter coding are significantly different (p < 0.05).

4.4 Discussion

4.4.1 Recording methods and *Sphagnum* occurrence

The mapping survey provided the most comprehensive measure of *Sphagnum* frequency, with a greater number of species recorded than in the transect survey. *Sphagnum* frequency recorded in the transect survey was systematically lower than in the map survey, but the pattern of results was similar (Table A2.1, Figures 4.2 and 4.3). This indicates that on the scale of this experiment, transect sampling is an acceptable way to evaluate treatment effects on more common species, but mapping surveys may be a more appropriate method to record less frequent species.

Sphagnum as a genus, and the individual species which were common enough to analyse separately, appeared to respond to burning treatments similarly. However, it is possible that some of the species occurring in less than one percent of plots, which were not analysed separately, responded differently. For example, *S. angustifolium* did not occur in the main experiment plots but was the second most common species in the reference plots, and conversely *S. russowii* occurred only in the main experiment plots (Table A2.1), but the relative rarity of these species within the Hard Hill plots means that it is difficult to confidently attribute these differences to burning effects. A greater number of species occurred in the 24 main experiment plots compared to the four reference plots (Table A2.1), which was expected due to the greater area covered.

4.4.2 *Sphagnum* frequency in the main experiment plots

The results of the 2015-16 survey indicate that *Sphagnum* is most frequent in S plots (10-year rotation), followed by L plots (20-year rotation), and least frequent in the N plots (unburned since 1954). Previous work by Lee et al. (2013a) using data from point quadrat surveys in 1972/3, 1982, 1991, and 2001 showed that *Sphagnum* abundance was greatest in S plots, but did not report any significant difference between N and L plots.

We found no significant differences in *Sphagnum* patch area or hummock height between treatments, which suggests that the difference in frequency could be due to more numerous patches in the more frequently burned treatments. The cause of this difference could be a more open canopy or increased bare ground after burning providing a release from competition and an opportunity for *Sphagnum* to establish (Lee et al., 2013a). Alternatively, ash produced by fire can release limiting nutrients such as phosphorus, which can promote moss spore germination (Pouliot et al., 2015) and growth of some *Sphagnum* species (Noble et al., 2017). As the S plots have been burned most frequently (five times since 1954 compared to twice in L plots), there have been more potential establishment opportunities in this treatment. Furthermore, the shorter rotation in S compared to L plots means less biomass accumulation between burns (Alday et al., 2015) and therefore less fuel, potentially resulting in lower fire temperatures (Davies, 2005). This may have reduced the chance of heat-related damage to existing *Sphagnum* (Taylor, E.S. et al., 2017), contributing to the greater abundance than in the L treatment.

It is also possible that atmospheric pollution at the time of burning is relevant. After the UK clean air act of 1956, levels of sulphur pollutants peaked around 1960 and subsequently declined (Ayres, 1997; RoTAP, 2012; Curtis and Simpson, 2014). High atmospheric pollution levels in the 1950s may therefore have inhibited *Sphagnum* regeneration after burning, resulting in vegetation dominated by other species, as observed in N plots which were last burned in 1954. However, in S and L plots, subsequent burns which occurred under reduced atmospheric pollution levels may have facilitated *Sphagnum* growth by reducing competition as discussed above. Though different sampling methods were used, the data from the 2015 transect survey and the point quadrats used by Lee et al. (2013a) both provide an estimate of percentage cover and comparison suggests that this may have increased recently, e.g., from 7% in the S grazed treatment in 2001 (Lee et al., 2013a) to 33% in 2015. *Sphagnum* is known to be affected by atmospheric pollutants (Ferguson et al., 1978; Granath et al., 2009) and Noble et al. (2018) observed that an interaction between burning and atmospheric pollution was associated with *Sphagnum* abundance. Further study could help to clarify the processes behind such interactions.

Grazing treatment had no impact on any of the *Sphagnum*-related variables. Similarly Lee et al. (2013a) found no effect of burning on *Sphagnum* or overall vegetation composition, which they suggested may be due to the low density, summer only grazing regime at Hard Hill. Past work has found some evidence of higher density grazing impacting *Sphagnum* (Rawes and Hobbs, 1979), and Noble et al. (2018) found that plots with livestock droppings had less *Sphagnum* cover, suggesting that there could be a negative effect at some stocking levels.

4.4.3 *Sphagnum* frequency in the grazed main experiment and reference plots

The results of the comparison between the grazed main experiment and reference plots, in particular the three times greater *Sphagnum* map frequency in R plots compared to N plots, suggest that the 1954 burns had a negative impact on *Sphagnum* which has persisted for over 60 years. This indicates the importance of considering and critically evaluating ‘control’ treatments when interpreting results from long term experiments. Although the R plots at Hard Hill may have been burned historically prior to the experiment, they are likely to provide a more representative baseline than the N plots. The severity of the 1954 burns is unknown (and could have varied between blocks), and therefore the difference in *Sphagnum* abundance between N and R plots could be a result of combustion, temperature related damage Taylor, E.S. et al. (2017), or indirect effects via changes to peat properties (Kettridge et al., 2014; Brown et al., 2015a; Holden et al., 2015) after the 1954 fires.

The R plots also had more *Sphagnum* than L plots, but a similar amount to S plots, suggesting that the 10-year burning rotation in these plots has mitigated the impact of the initial 1954 burn. The greater hummock height in R plots than in L and N plots (Figure 4.3) could indicate that hummocks in the R plots are generally older, or have grown at a faster rate over the course of the experiment, whilst the hummock height in S plots (which had no significant difference with any other group) could be due to an intermediate growth rate. NMDS analysis (Figure A2.1) showed that R plots were distinct from, and occupied a smaller area of the ordination space than the grazed experimental plots, suggesting that they were more consistent in terms of *Sphagnum* species composition than the S, L and N plots. Apart from burning treatments, the only consistent difference between the main experiment and reference plots is likely to be greater trampling by humans, as the main experiment plots have been surveyed more frequently (Lindsay, 2010).

4.4.4 *Sphagnum* frequency in past surveys

Analysis of the data from the 1961 survey showed no significant difference in *Sphagnum* abundance between the main experiment treatments at this time (Figure 4.4). This was expected, as in 1961 all of the main experiment plots had been subject to the same treatment (burned once in 1954). Comparison of the N and R plots in 1965 showed that there was significantly more *Sphagnum* in R plots at this point. This shows that the negative effect of the 1954 burn on *Sphagnum*, observed in the 2015-16 survey, was apparent 11 years after burning.

Although the 1961 and 1965 surveys used the same Domin abundance survey methodology, the *Sphagnum* abundance recorded in the N plots in 1965 was lower than in 1961 (Figures 4.4 and 4.5). This could be an artefact of the variation in sample sizes or differing interpretations of the nonlinear Domin scale by surveyors on the two occasions. Alternatively a decrease in *Sphagnum* abundance in N plots between 1961 and 1965 could have been caused by the unusually cold winter of 1962-63 (Met Office, 2017), the relatively high levels of atmospheric pollutants such as SO_2 at this time (Ayres, 1997; RoTAP, 2012), or an interaction between one of these factors and burning. As R plots were not surveyed in 1961 and S and L plots were not surveyed in 1965, it is not possible to determine whether this difference was specific to the N plots. The difference highlights some of the potential problems with comparing data collected by different surveyors and at different times and makes it difficult to interpret how *Sphagnum* abundance in R plots compared to S and L plots in the early years of the experiment.

4.4.5 Caveats

The Hard Hill experiment has provided a significant amount of published knowledge on prescribed burning impacts (Lee et al., 2013a; Hobbs, 1984; Rawes and Hobbs, 1979; Lee et al., 2013b; Alday et al., 2015; Garnett et al., 2000; Ward et al., 2007; Clay et al., 2009; Clay et al., 2010; Worrall et al., 2007). However, caution is required when extrapolating results to peatland or moorland in general. For example, it has been suggested that local conditions at Moor House including high altitude and high annual rainfall may cause a delay in regeneration of *C. vulgaris* compared to other sites (Taylor, P. and Rawes, 1974), which may give other plants, including *Sphagnum*, more opportunity to establish and grow after burning.

The burning carried out for the Hard Hill experiment is likely to have been carefully controlled, and does not represent the full range of burning methods and severities which occur on peatlands. The experiment also represents a relatively small area of a hillslope otherwise dominated by vegetation that has remained unburned for over 90 years, which may influence the hydrology of the plots and provide a source of *Sphagnum* propagules. On sites managed for grouse shooting, a much larger proportion of the site may be burned and fire effects on water availability (Holden et al., 2014; Holden et al., 2015) and the *Sphagnum* propagule bank (Lee et al., 2013b) may be compounded.

4.5 Conclusions

Our results suggest that, as in the case of the 1954 burn, a single fire event can lead to reduced *Sphagnum* over 60 years later. This provides evidence against burning previously unburned (or long-unburned) areas of blanket peatland where *Sphagnum* is present. Thus the recent trend in some parts of the UK for burning encroachment onto areas of peat that have not been burned for at least several decades (Yallop et al., 2006; Thacker et al., 2015; Douglas et al., 2015) could reduce *Sphagnum* cover with potentially deleterious impacts on ecosystem function (Holden et al., 2015; Holden et al., 2008). Shorter rotations may lead to greater *Sphagnum* abundance compared to longer rotations in some cases, though environmental conditions including atmospheric pollution may influence this effect. We would caution against burning on a shorter rotation as a method of encouraging *Sphagnum* because of the potential for other negative effects on peatland function (Glaves et al., 2013; Brown et al., 2015a; Worrall et al., 2010). The longevity and scale of the Hard Hill experiment make it a valuable source of information, but care should be taken when generalising results from any single site, and in particular the specific management history and climate of Moor

House should be considered. Furthermore, interpreting historical data can be challenging, particularly where surveyors, methods or sample sizes are inconsistent, and apparent changes over time should be treated with caution.

4.6 Acknowledgements

Daniel Madden, Julia Quinonez and Kath Tonge are thanked for fieldwork assistance.

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Chapter 5: Peatland vegetation change and establishment of re-introduced *Sphagnum* moss after prescribed burning

Alice Noble[a], Sheila M Palmer[a], David J Glaves[b], Alistair Crowle[b], Joseph Holden[a]

[a]water@leeds, School of Geography, University of Leeds, Leeds, UK

[b]Natural England, Foss House, Kings Pool, Peasholme Green, York, UK

Abstract

Fire, including prescribed burning, is common on peatlands globally and can impact vegetation, including peat-forming *Sphagnum* mosses, and affect ecosystem services. We monitored vegetation in different burn age categories at three UK peatland sites over a 19 month period. Half of the plots had *Sphagnum* added and survival was assessed. Community composition associations with site and burn age category and changes in vegetation over time were investigated.

Plots in the most recently burned category were likely to have more bare peat, a thinner moss layer and shorter vegetation. Graminoid cover initially increased after burning but was low after 10+ years. Dwarf shrub cover increased after burning and remained high after 10+ years. At the most *Sphagnum*-rich site, a high proportion of existing *Sphagnum* cover was bleached one year after burning, but recovery occurred during the study period. *Sphagnum* re-introduction success decreased over the study period in the most recent and intermediate burn-age categories at the most *Sphagnum*-poor site.

These results show that burning rotation length is an important factor in determining site-level vegetation community composition on burned sites. More frequent burning will result in a greater proportion of land in the early post-burning stages, potentially resulting in a thinner moss layer, more bare peat and less healthy *Sphagnum*, with

potential consequences for carbon balance. No evidence was found to support the use of burning as a tool to increase existing *Sphagnum* or promote *Sphagnum* re-establishment success.

5.1 Introduction

Peatlands are important carbon stores (Yu et al., 2010), covering around 423 million ha globally (Xu et al., 2018). In a healthy state, peatland ecosystems have the potential to accumulate carbon (Clymo et al., 1998), support biodiversity (Littlewood et al., 2010) and regulate hydrological processes (Labadz et al., 2010). However, degradation due to anthropogenic influences can threaten peatland function (Evans et al., 2014). In particular, changes to vegetation community composition have the potential to harm the provision of ecosystem services (Grayson et al., 2010; Holden et al., 2008; Nichols et al., 2014; Ritson et al., 2016).

On northern hemisphere blanket peatlands, vegetation often largely consists of mosses, graminoids and dwarf shrubs. Vegetation community composition plays a central role in ecosystem function, and although a range of species occur naturally on blanket peatlands, some may have a detrimental impact when dominant. Mosses can make up a significant component of the vegetation and include *Sphagnum* mosses which are of central importance for peat formation (van Breemen, 1995) and water quality (Armstrong et al., 2012; Ritson et al., 2016), but require relatively wet conditions (Price and Whitehead, 2001) and can be pollution sensitive (Ferguson et al., 1978; Gunnarsson, U. and Rydin, 2000). A variety of pleurocarpous and acrocarpous moss species are also found on peatlands, particularly where local conditions are drier, but differences in water storage capacity (Elumeeva et al., 2011) as well as net ecosystem exchange and decomposition rates (Orwin and Ostle, 2012) mean that these groups do not support peat accumulation to the same extent as *Sphagnum*. Vascular plants including graminoids and dwarf shrubs contribute to the structural diversity of peatland habitats (Malmer et al., 1994) and can provide food and shelter for livestock and wildlife (Garnett et al., 2000; Robertson et al., 2017). Some graminoid species, such as the sedge *Eriophorum vaginatum,* can also contribute to peat formation (Kalnina et al., 2015; McClymont et al., 2011). However, dominance of some vascular plants, such as *Calluna vulgaris*, may increase the amount of carbon lost as dissolved organic carbon (DOC) and CO_2 (Armstrong et al., 2012; Dixon et al., 2015).

Prescribed vegetation burning occurs on many peatlands worldwide for purposes including agricultural production and wildfire risk management. In the UK, it is often used as a vegetation management tool on blanket peatlands, particularly to improve habitat for the game bird red grouse (*Lagopus lagopus scotica*) on sport shooting estates (Douglas et al., 2015). Patches of up to around 4000 m^2 are burned on a rotation of c.7-25 years to produce a mosaic of vegetation ages suitable for foraging and nesting. Burn severity varies, but good practice guidelines recommend 'cool' burns which remove the canopy layer of vegetation without consuming the moss or litter layer or igniting underlying peat (Defra, 2007; Scottish Government, 2011). The area of UK peatlands managed by burning has increased in recent decades (Douglas et al., 2015; Thacker et al., 2015; Yallop et al., 2006), causing concern about potential impacts on peatland function and debate about the sustainability of current practice (Allen et al., 2016; Brown et al., 2016; Harper et al., 2018).

Past research has shown that burning is associated with altered vegetation communities and that the abundance of key species can fluctuate in the years following burning (Noble et al., 2018). However, timescales of change after burning, and variation in the process between sites, remain poorly understood. For *Sphagnum*, understanding post-burning change is complicated by the fact that water deficiency or temperature damage can cause visible bleaching and reduced photosynthetic efficiency (Harris, 2008; Taylor et al., 2017), but recovery or regeneration from this state may be possible (Taylor et al., 2017). Knowledge of when important vegetation changes occur in the post burning trajectory will aid our ability to place past research into context and help to inform monitoring and land management decisions.

Sphagnum re-introduction via deliberate human intervention can be used as a tool to reinstate peat forming vegetation as part of peatland restoration projects (Chirino et al., 2006; Ferland and Rochefort, 1997; Gunnarsson, Urban and Söderström, 2007; Robroek et al., 2009). *Sphagnum* re-introductions have taken place on some degraded UK peatlands, where historically abundant *Sphagnum* has been reduced by drivers including pollution and drainage (Carroll et al., 2009). *Sphagnum* can be added in the form of vegetative diaspores (Campeau and Rochefort, 1996), plugs, or contained within manufactured products including beads and gel (Hinde et al., 2010). Past work has investigated influences on *Sphagnum* establishment success, including water availability (Noble et al., 2017; Robroek et al., 2009), nutrient status (Noble et al., 2017), propagule size (Gunnarsson, Urban and Söderström, 2007) and climatic conditions (Chirino et al., 2006). However, it is not known how time since burning impacts establishment success of added *Sphagnum*. Increased knowledge in this area would be helpful when planning re-introductions on previously burned sites. Additionally, it has been suggested that burning may be useful as a restoration tool to remove dominant dwarf shrub canopies and facilitate *Sphagnum* establishment (Uplands Management Group, 2017), but more evidence is needed to determine the effectiveness of such an approach (Lunt et al., 2011; IUCN, 2017).

In this study, we aim to understand timescales of vegetation change and the potential for establishment of re-introduced *Sphagnum* after burning, and consider variation in these processes between sites. By monitoring existing vegetation over two years at three blanket peatland sites, using plots which had different durations since they were last burned, we were able to construct a timeline of post-burning change and infer potential impacts on peatland ecosystem services. Measuring survival and growth of *Sphagnum* added to duplicate plots enabled assessment of how re-introduction for peatland restoration might interact with current burning regimes and burning undertaken for restoration purposes.

5.2 Methods

Three blanket peatland sites were chosen to represent key regions for this habitat in England; the Cheviot Hills, the North Pennine Hills, and the Peak District (Table 5.1). All three sites were managed for grouse shooting and burned on a rotational basis. Their vegetation principally consisted of dwarf shrubs (mainly *Calluna vulgaris*), graminoids (including *Eriophorum vaginatum* and *Eriophorum angustfolium*) and mosses (a mix of pleurocarps, acrocarps and *Sphagnum* spp.), which occur in varying quantities at each site (Table 5.1).

Table 5.1: Site locations, mean living cover of key vegetation groups (taken from summer 2016 surveys) and modelled values for contemporary (2014-2016) atmospheric acid deposition (APIS 2018). All sites are on deep peat (< 40cm) and managed for grouse shooting.

Site	Lat	Long	Dwarf shrub cover %	Graminoid cover %	Moss cover (*Sphagnum*) %	Acid keq ha^{-1} yr^{-1}
Cheviot	55.455	-2.112	52	19	35 (3)	1.41
North Pennine	54.864	-2.396	37	54	77 (29)	1.51
Peak District	53.233	-1.980	45	28	69 (<1)	1.98

At each site, five burn patches in each of three age categories were chosen with the help of land managers. Assessment of burn age was based on site specific knowledge and morphology of *C. vulgaris*. After burning, *C. vulgaris* regenerates mainly from root stock and produces distinct new shoots during each year’s growth season, which can be counted, enabling approximation of years since fire. The youngest burn age category (B1) comprised patches of vegetation burned approximately 12-18 months before the first survey in March 2016. The intermediate burn age category (B5) comprised patches burned approximately 5 years before the first survey, and the oldest category (B10+) comprised patches burned at least 10 years before the first survey.

Within each patch, two 1 x 1 m plots were located 5 m apart and marked using bamboo canes. These plots were surveyed either four (Cheviot) or five (North Pennine and Peak District) times between March 2016 and October 2017. On each occasion, vegetation height and moss depth were measured at five points to 1 cm accuracy and the mean was recorded. Cover of dwarf shrubs, graminoids, individual moss species, lichen, fungi, liverworts and other plants were recorded as percentages, as was cover of bare peat. For plants other than *Sphagnum*, only living cover was analysed. However, for *Sphagnum* both ‘healthy’ cover, and total cover including bleached patches, were analysed. Five plots (two pairs of B10+ plots and one B5 plot) were burned during the study at the Cheviot site and these were completely excluded from the analyses.

In July 2016, *Sphagnum* vegetative material was added to one of each pair of plots. A mix of *Sphagnum* species representative of those present was collected at each site, and 10 ‘plugs’ of approximately 4 cm diameter consisting of several *Sphagnum* stems with the capitula facing upwards were added to each plot, surrounded by the existing moss layer or vascular plants present. The survival (‘re-introduction success’) of the added *Sphagnum* was assessed during three subsequent surveys on a semi-quantitative percentage scale, where scores ranged from 0, indicating that all added *Sphagnum* was dead, dried out or absent, to 100, indicating that all added *Sphagnum* appeared alive and healthy.

All statistical analyses were carried out using R 3.1.0 (R Development Core Team, 2010) and the packages vegan (Oksanen et al., 2013), nlme (Pinheiro et al., 2016), lsmeans (Lenth, 2016) and ggplot2 (Wickham, 2009). Firstly, an exploratory Non-metric Multidimensional Scaling (NMDS) ordination was carried out on the multivariate vegetation data from all surveys on the plots without *Sphagnum* additions. This enabled visual inspection of how plots from different sites and burn age categories differed in their vegetation community composition by projecting them into a two-dimensional ordination space where plots with less similar vegetation are located further apart.

Linear mixed models were used to determine how vegetation characteristics (vegetation height, moss depth, bare ground cover), cover of plant taxonomic groups (dwarf shrubs, graminoids, pleurocarpous mosses, acrocarpous mosses, *Sphagnum* spp.) and *Sphagnum* re-introduction success varied according to site, burn age category, time during the study, and the interactions between these variables. Aggregating individual moss species into groups enabled investigation of how groups of related species responded to predictor variables, including species which were too infrequent to analyse independently or absent from one or more sites. Dependent variables recorded as percentages were logit transformed for this analysis to satisfy model assumptions and improve fit, assessed by visual inspection of residual plots. Time during the study was treated as a continuous variable and was centred so that the mid-point of the study acted as the reference value. Plot ID was included in each model as a random effect to account for the repeat surveys. Least-squares means were compared (with Tukey’s adjustment for multiple comparisons) to reveal significant differences between site and burn age combinations.

5.3 Results

The NMDS ordination results (Stress = 0.184, K = 2) suggest that vegetation communities differed according to both site and burn age category. The North Pennine site was associated with the positive region of axis 1, whereas the Peak District and Cheviot sites were more associated with the negative region (Figure 5.1a). Meanwhile, the most recently burned (B1) plots were more likely to fall in the positive region of axis 2, with the least recently burned plots (B10+) falling in the negative region, and the intermediate (B5) plots were spread around the origin in both positive and negative regions (Figure 5.1b).

Individual vegetation characteristics and taxonomic groups showed differences according to site and burn age, and change over the course of the study for some variables (Table 5.2, Table 5.3). All differences described are significant at $p < 0.05$. Bare peat was greater in B1 plots than B10+ plots at the Peak District site and greater in B1 plots than B5 and B10+ plots at the Cheviot site, with a decrease over time in the B1 plots (Figure 5.2a). Moss depth was greater in B10+ plots than B1 plots at both the North Pennine and Peak District sites (Figure 5.2b). Meanwhile, vegetation height was greater in B10+ plots than B1 plots at the Peak District and Cheviot sites and decreased over time in B1 plots at the North Pennine site (Figure 5.2c).

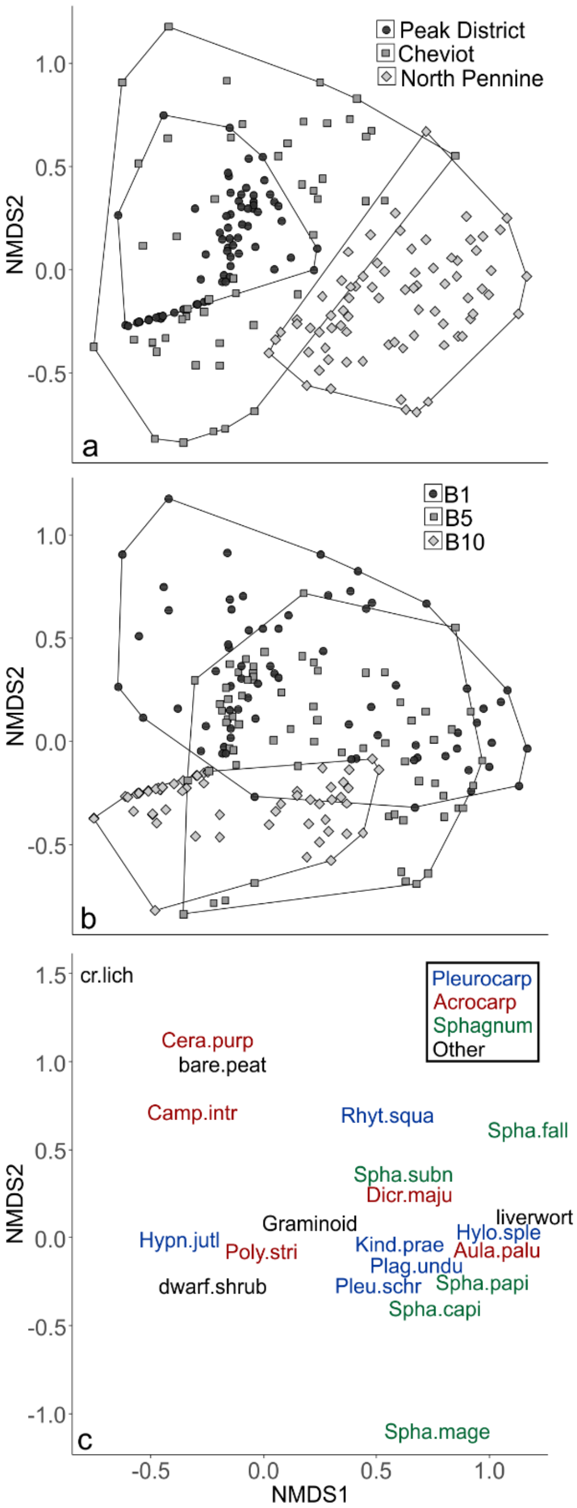

Figure 5.1: NMDS ordination of vegetation data from 201 blanket peatland plots showing a) dissimilarities between plots according to site, b) dissimilarities between plots according to burn age (B1 – burned 1 year before start of study, B5 – burned c.5 years before start of study, B10 – burned at least 10 years before start of study) and c) species associations.

Table 5.2: Results of LMM analyses of vegetation characteristics and vascular plant group cover showing least-squares means for each burn age category at each site (groups sharing a number coding are not significantly different to each other) and the slope value for change over the study period (time slope) in each category. Significance codes indicate p values which are significant at the 0.05 (*), 0.01 (**) or 0.001 (***) level.

Variable	Site	Burn age	L.S. mean	Std. error	Group	Time slope	Std. error	Significance
Bare peat cover (logit cover %)	Cheviot	B1	-0.898	0.224	3	-0.567	0.096	***
		B5	-3.160	0.250	12	-0.072	0.107	
		B10+	-3.664	0.289	12	0.000	0.124	
	North Pennine	B1	-3.391	0.216	12	0.000	0.068	
		B5	-3.664	0.216	1	0.000	0.068	
		B10+	-3.664	0.216	1	0.000	0.068	
	Peak District	B1	-2.558	0.216	2	0.065	0.068	
		B5	-2.798	0.216	12	0.069	0.068	
		B10+	-3.664	0.216	1	0.000	0.068	
Moss depth (cm)	Cheviot	B1	3.455	1.060	1	-0.210	0.487	
		B5	7.538	1.185	123	0.725	0.545	
		B10+	6.500	1.368	123	0.000	0.629	
	North Pennine	B1	7.772	1.016	123	0.100	0.344	
		B5	10.067	1.016	34	0.220	0.344	
		B10+	12.988	1.016	4	-0.100	0.344	
	Peak District	B1	3.782	1.016	1	0.180	0.344	
		B5	4.945	1.016	12	-0.120	0.344	
		B10+	9.424	1.016	234	-0.460	0.344	
Vegetation height (cm)	Cheviot	B1	22.024	2.133	12	1.520	0.880	.
		B5	23.110	2.385	12	-0.125	0.984	
		B10+	33.066	2.754	2	1.367	1.137	
	North Pennine	B1	22.381	2.062	12	-2.140	0.623	***
		B5	22.773	2.062	12	-1.540	0.623	
		B10+	30.097	2.062	2	0.140	0.623	
	Peak District	B1	13.932	2.062	1	0.100	0.623	
		B5	13.722	2.062	1	0.020	0.623	
		B10+	30.425	2.062	2	-0.120	0.623	
Dwarf shrub cover (logit %)	Cheviot	B1	-1.800	0.324	1	0.303	0.110	**
		B5	0.066	0.363	23	-0.018	0.123	
		B10+	2.831	0.419	4	0.049	0.142	
	North Pennine	B1	-2.029	0.317	1	0.229	0.078	**
		B5	-0.774	0.317	12	0.159	0.078	*
		B10+	0.714	0.317	3	-0.015	0.078	
	Peak District	B1	-1.732	0.317	1	0.005	0.078	
		B5	-1.180	0.317	12	-0.017	0.078	
		B10+	1.261	0.317	34	-0.080	0.078	
Graminoid cover (logit %)	Cheviot	B1	-1.490	0.372	12	0.506	0.115	***
		B5	-0.175	0.416	234	-0.036	0.128	
		B10+	-2.779	0.480	1	-0.172	0.148	
	North Pennine	B1	0.800	0.365	4	0.141	0.081	.
		B5	0.650	0.365	34	-0.148	0.081	.
		B10+	-0.929	0.365	123	0.035	0.081	
	Peak District	B1	-0.262	0.365	234	0.321	0.081	***
		B5	0.072	0.365	234	0.055	0.081	
		B10+	-2.450	0.365	1	0.039	0.081	

Table 5.3: Results of LMM analysis of moss group cover and *Sphagnum* re-introduction success showing least-squares means for each burn age category at each site (groups sharing a number coding are not significantly different to each other) and the slope value for change over the study period (time slope) in each category. Significance codes indicate p values which are significant at the 0.05 (*), 0.01 (**) or 0.001 (***) level.

Variable	Site	Burn age	L.S. mean	Std. error	Group	Time slope	Std. error	Significance
Pleurocarpous moss cover (logit %)	Cheviot	B1	-1.946	0.396	1	0.352	0.155	*
		B5	-1.445	0.443	123	0.298	0.174	.
		B10+	-1.446	0.511	123	-0.231	0.200	
	North Pennine	B1	-0.605	0.384	123	0.172	0.110	
		B5	-1.539	0.384	12	0.037	0.110	
		B10+	-0.273	0.384	1234	0.057	0.110	
	Peak District	B1	0.347	0.384	34	0.000	0.110	
		B5	0.145	0.384	234	-0.113	0.110	
		B10+	1.287	0.384	4	-0.108	0.110	
Acrocarpous moss cover (logit %)	Cheviot	B1	-2.132	0.356	12	0.631	0.146	***
		B5	-1.494	0.398	2	0.107	0.163	
		B10+	-3.372	0.460	12	0.192	0.188	
	North Pennine	B1	-2.677	0.345	12	-0.023	0.103	
		B5	-2.188	0.345	12	-0.239	0.103	*
		B10+	-3.229	0.345	12	-0.174	0.103	.
	Peak District	B1	-2.303	0.345	12	0.080	0.103	
		B5	-2.222	0.345	12	-0.024	0.103	
		B10+	-3.664	0.345	1	0.000	0.103	
Healthy *Sphagnum* cover (logit %)	Cheviot	B1	-3.408	0.314	1	-0.022	0.088	
		B5	-3.054	0.351	1	-0.145	0.098	
		B10+	-3.664	0.405	1	0.000	0.113	
	North Pennine	B1	-1.172	0.309	2	0.378	0.062	***
		B5	-0.492	0.309	2	0.112	0.062	.
		B10+	-0.519	0.309	2	0.110	0.062	.
	Peak District	B1	-3.664	0.309	1	0.000	0.062	
		B5	-3.206	0.309	1	0.060	0.062	
		B10+	-3.664	0.309	1	0.000	0.062	
Total *Sphagnum* cover (logit %)	Cheviot	B1	-3.065	0.345	1	-0.235	0.091	*
		B5	-3.054	0.385	1	-0.145	0.101	
		B10+	-3.664	0.445	1	0.000	0.117	
	North Pennine	B1	-0.715	0.340	2	-0.002	0.064	
		B5	-0.492	0.340	2	0.074	0.064	
		B10+	-0.519	0.340	2	0.110	0.064	.
	Peak District	B1	-3.664	0.340	1	0.000	0.064	
		B5	-3.150	0.340	1	0.039	0.064	
		B10+	-3.664	0.340	1	0.000	0.064	
Sphagnum re-introduction success (logit %)	Cheviot	B1	-0.346	0.681	123	0.619	0.410	
		B5	1.706	0.681	123	0.457	0.410	
		B10+	-1.562	0.880	12	0.116	0.530	
	North Pennine	B1	2.086	0.681	23	0.540	0.410	
		B5	1.674	0.681	123	0.027	0.410	
		B10+	2.433	0.681	3	-0.097	0.410	
	Peak District	B1	-1.328	0.681	1	-0.971	0.410	*
		B5	-0.580	0.681	123	-1.051	0.410	*
		B10+	0.582	0.681	123	0.328	0.410	

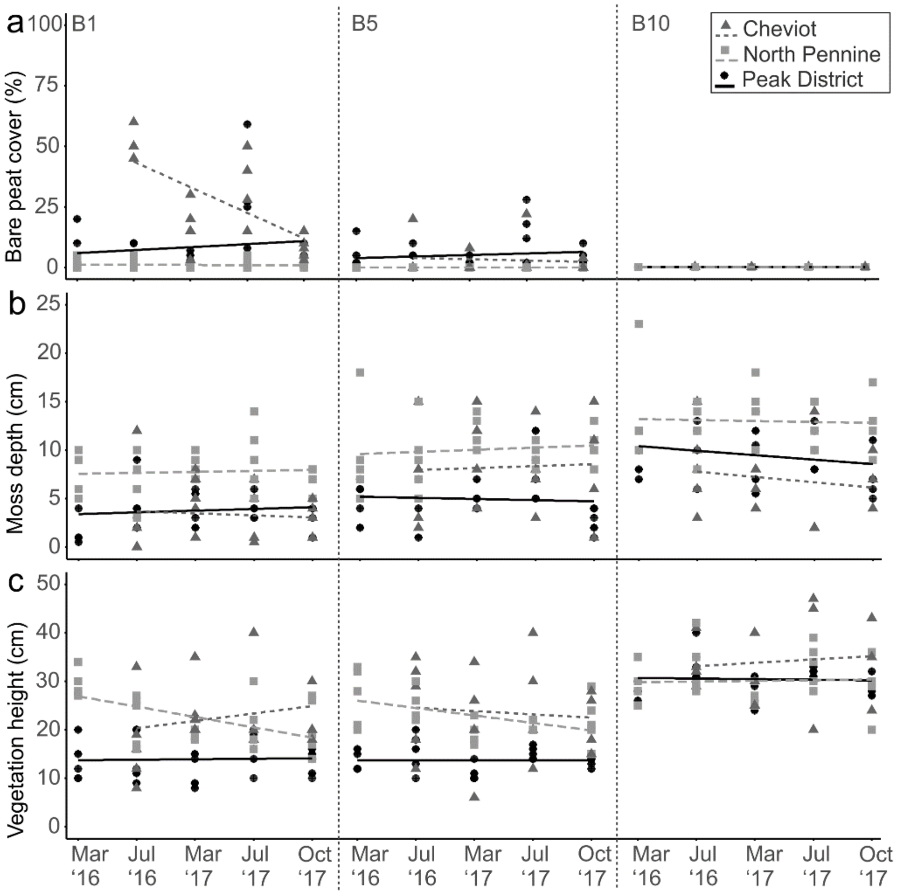

Figure 5.2: Change over time with fitted relationships for a) bare peat, b) moss depth and c) vegetation height according to site and burn age category (B1 – burned 1 year before start of study, B5 – burned c.5 years before start of study, B10 – burned at least 10 years before start of study).

Dwarf shrub cover increased over the study period in B1 plots at the Cheviot site and B1 and B5 plots at the North Pennine site. At all three sites B10+ plots had greater cover than B5 and B1 plots, and at the Cheviot site B5 plots also had greater cover than B1 plots (Figure 5.3a). Graminoid cover increased over the study period in B1 plots at all three sites, but was greater in B5 plots than B10+ plots at the Cheviot site, greater in B1 plots than B10+ plots at the North Pennine site, and greater in both B1 and B5 plots than in B10+ plots at the Peak District site (Figure 5.3b).

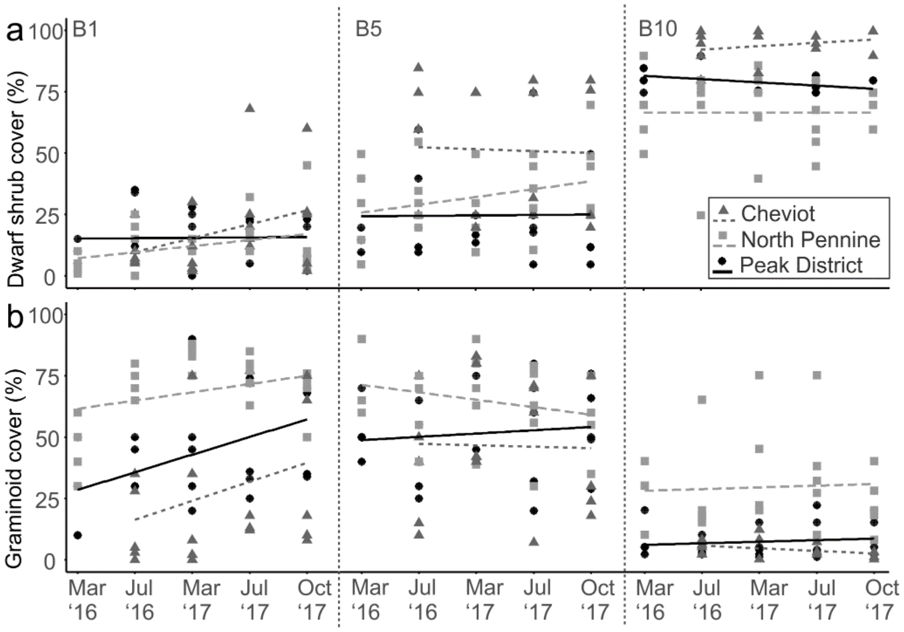

Figure 5.3: Change over time with fitted relationships for a) dwarf shrub cover and b) graminoid cover according to site and burn age category (B1 – burned 1 year before start of study, B5 – burned c.5 years before start of study, B10 – burned at least 10 years before start of study).

Pleurocarpous moss cover was greater at the Peak District site than the Cheviot site, and increased over the study period in Cheviot B1 plots, but showed no significant differences according to burn age (Figure 5.4a). Acrocarpous mosses increased over the study period in B1 plots at the Cheviot site (Figure 5.4b). For existing *Sphagnum*, healthy cover increased over time in B1 plots at the North Pennine site (Figure 5.5a), while total cover (including bleached areas) decreased over time in B1 plots at the Cheviot site (Figure 5.5b). Cover of both healthy and total existing *Sphagnum* was greater at the North Pennine site than the other two sites (Figure 5.5).

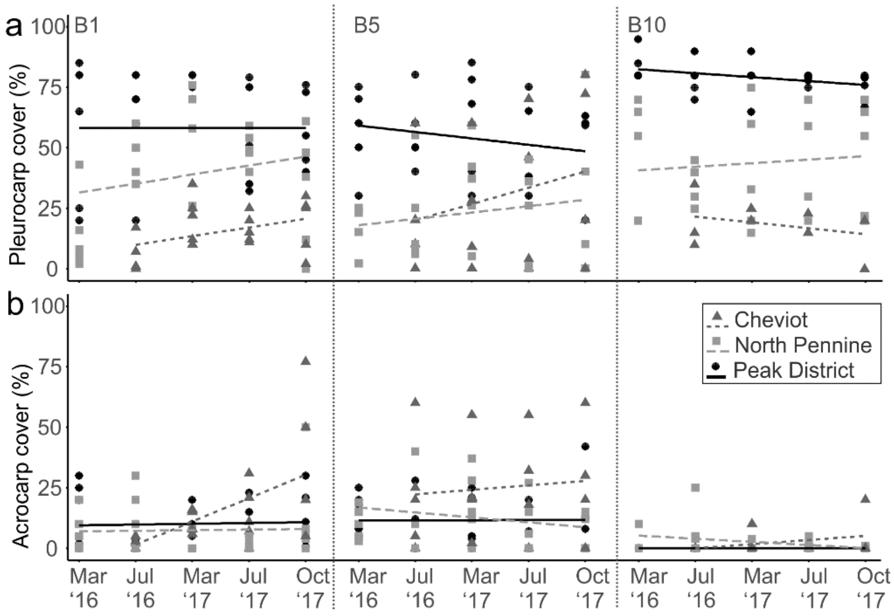

Figure 5.4: Change over time with fitted relationships for a) pleurocarpous moss cover and b) acrocarpous moss cover according to site and burn age category (B1 – burned 1 year before start of study, B5 – burned c.5 years before start of study, B10 – burned at least 10 years before start of study).

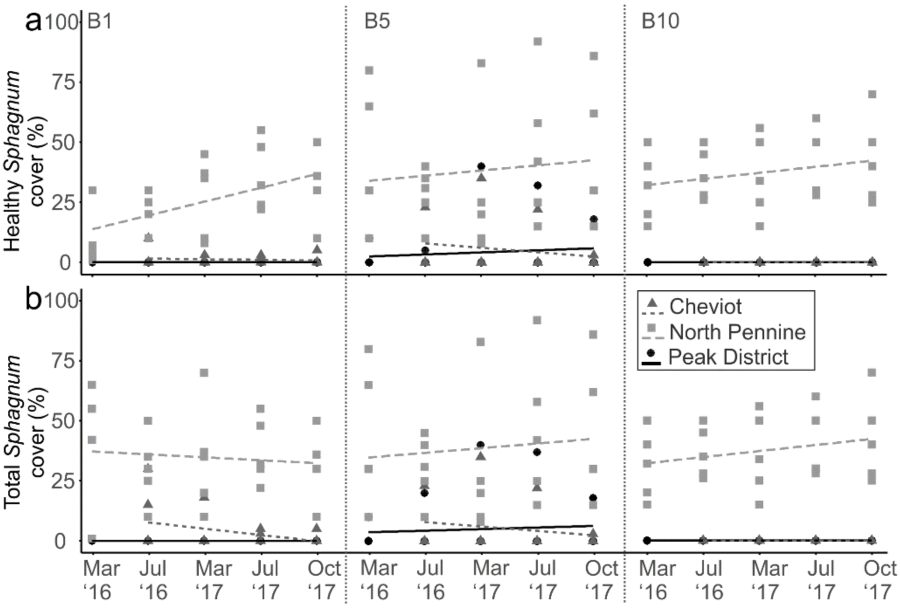

Figure 5.5: Change over time with fitted relationships for a) healthy Sphagnum cover and b) total Sphagnum cover (including bleached patches) according to site and burn age category (B1 – burned 1 year before start of study, B5 – burned c.5 years before start of study, B10 – burned at least 10 years before start of study).

In plots where *Sphagnum* was added, there was no significant difference in re-introduction success according to burn age. However, there was a decrease in success score over the recording period in B1 and B5 plots at the Peak District site. Success was greater at the North Pennine site than the Peak District site within the B1 category, and greater at the North Pennine site than the Cheviot site in the B5 category (Figure 5.6).

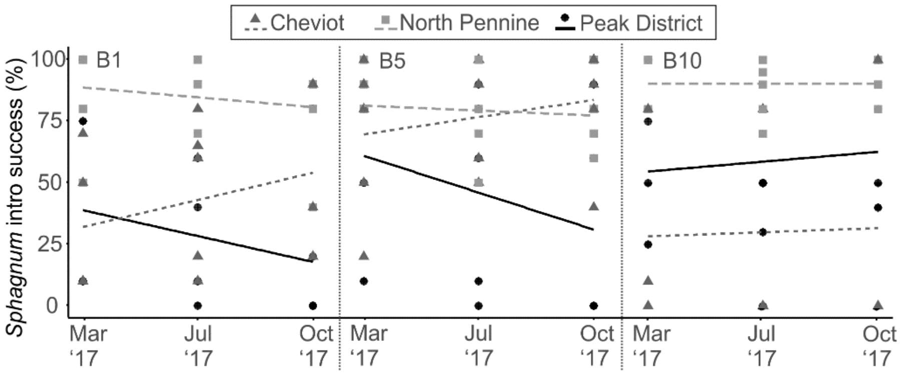

Figure 5.6: Change over time with fitted relationships for *Sphagnum* re-introduction success according to site and burn age category (B1 – burned 1 year before start of study, B5 – burned c.5 years before start of study, B10 – burned at least 10 years before start of study).

5.4 Discussion

The NMDS ordination suggested that time since burning is an important factor in determining vegetation community composition, alongside local site conditions. The B10+ plots appeared to occupy a smaller area of the NMDS ordination than B1 or B5 plots, indicating greater similarity between plots, which could be the result of a few species or groups (such as dwarf shrubs) common to all three sites dominating at this stage of the burning cycle.

The results of the univariate analyses suggest that burning can increase bare peat and cause thinning of the moss layer. This is consistent with the reduced bryophyte biomass observed in more recently burned plots by Ward et al. (2007). Such changes could potentially result in faster overland flow (Holden et al., 2008), increased vulnerability to erosion (Holden et al., 2007), increased DOC in water courses (Yallop et al., 2010), and decreased carbon storage in the moss layer (Ward et al., 2007) in the years following burning. Bare peat was absent in the B10+ plots, indicating that revegetation occurred within the rotational burning cycle at these sites.

Vegetation height was lower in the most recently burned plots at two out of three sites, which was expected due to loss of canopy layer dwarf shrubs during fire. At the North Pennine site there was no difference in vegetation height between burn age categories, but a decrease occurred over time in B1 plots. This could be due to partially burned dwarf shrubs remaining after the burn before gradually reducing due to mechanical damage from weather or trampling. The residual burned stems could indicate that burn severity was lower at the North Pennine site, a theory which is supported by the lower proportion of bare peat observed after burning compared to the other sites. Differences in burn severity can be a function of fuel structure and moisture (Davies and Legg, 2011), wind speed (Santana and Marrs, 2014) and burning technique (e.g. fuel assistance, fire direction relative to wind and patch size).

Dwarf shrub cover increased with time since burning, with greater cover in older patches, and the largest increase between the B5 and B10+ categories. Graminoid cover increased after burning before an apparent decline between the B5 and B10+ categories. These results suggest that burning on a shorter rotation may lead to graminoid dominance, while longer rotations are likely to favour greater dwarf shrub cover, and are similar to past observations of burning effects on these groups (Harper et al., 2018; Lee et al., 2013; Ward et al., 2007).

Analysis of the three moss groups indicated that pleurocarpous mosses persist throughout the burning cycle. This could suggest fire tolerance in some pleurocarpous species, as well as tolerance to changes in light, moisture availability and soil water chemistry (Brown et al., 2014) during the burning cycle. Acrocarpous mosses increased over the study period in B1 plots at the Cheviot site, possibly due to the higher proportion of bare peat at this site after burning. *Ceratodon purpureus*, an acrocarpous moss common in the Cheviot B1 plots, has previously been observed to colonise bare ground after fire (Duncan and Dalton, 1982; Thomas et al., 1994), as have other acrocarpous mosses including *Campylopus introflexus* (Equihua and Usher, 1993; Noble et al., 2018). It is possible that extensive colonisation by acrocarpous mosses after fire could negatively impact the regeneration of other vegetation (Equihua and Usher, 1993), but the ecological consequences of such an effect require further research.

Burning had no significant impact on *Sphagnum* at the Peak District site, which had low overall abundance in all burn age categories. At the North Pennine site where abundance was much higher, cover of healthy *Sphagnum* increased over time in the B1 plots. However, total *Sphagnum* cover (including bleached patches) remained constant in the same plots, suggesting that the increase in healthy *Sphagnum* represented the recovery of bleached patches which had been damaged as a result of fire. The temporary bleaching is likely to be associated with a reduction in photosynthetic efficiency (Taylor et al., 2017), potentially affecting growth rate and carbon balance during this period. In B1 plots at the Cheviot site, healthy *Sphagnum* cover remained constant, but total *Sphagnum* cover decreased over time, suggesting that some of the bleached patches did not recover and were lost. However, overall *Sphagnum* cover measured at the Cheviot site was low and the trend over time was driven by a relatively small amount of cover in a few patches so caution is needed in interpreting this result. Differences in *Sphagnum* abundance (and vegetation composition more generally) between sites could be the result of variation in current and historic atmospheric pollution (Table 5.1), grazing regimes, and/or water availability determined by rainfall, evapotranspiration, geomorphology and peat physical properties.

Sphagnum re-introduction success was consistently high at the North Pennine site, which also had the greatest existing *Sphagnum* abundance. This could indicate that *Sphagnum* abundance at the other two sites was limited by environmental factors, such as water availability, rather than propagule availability. At the Peak District site, *Sphagnum* re-introduction success declined over the study period in B1 and B5 plots. This effect could be due to *Sphagnum* plugs drying out over time, as these plots had less dwarf shrub cover and shorter vegetation so were more exposed, and potentially subject to hotter summer temperatures (Brown et al. 2015b). These results do not support the theory that removing the dwarf shrub canopy benefits *Sphagnum* growth as suggested in some current management guidance resources (Uplands Management Group, 2017).

5.5 Conclusions

The results of this work suggest that different burning frequencies will result in different vegetation community composition outcomes, with shorter rotations generally favouring graminoids and longer rotations favouring dwarf shrubs. Vegetation therefore has the potential to impact ecosystem services in different ways over the course of the burning cycle. The timescale and extent of vegetation change after burning varied between the three study sites, suggesting that some sites may be more resilient to burning. However, repeated burning, or stressors such as drainage, pollution, grazing or climate change could decrease resilience. Finally, this study found no evidence to suggest that burning is effective as a restoration tool to encourage *Sphagnum*, or that removing the canopy by burning increases *Sphagnum* re-introduction success.

5.6 Acknowledgements

This analysis was funded by Natural Environment Research Council studentship [NE/L008572/1] supported by Natural England, awarded to JH, SMP, DG and AC in open competition. We thank the gamekeepers and landowners at all three field sites for allowing access and contributing their time and expertise during the planning of the study. We are also grateful to members of Natural England and Northumberland

National Park Authority for assistance finding field sites. Tom Noble and Jack Gordon provided assistance in the field.

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Chapter 6: Fire temperatures and *Sphagnum* damage during prescribed burning on peatlands

Alice Noble[a], Alistair Crowle[b], David J Glaves[b], Sheila M Palmer[a], Joseph Holden[a]

[a]water@leeds, School of Geography, University of Leeds, Leeds, UK

[b]Natural England, Foss House, Kings Pool, Peasholme Green, York, UK

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 °C to 538 °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 °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.

6.1 Introduction

Peatlands are important ecosystems which cover around 2.84 % of the world's land surface (Xu et al., 2018b), store over 600 Gt of carbon (Leifeld and Menichetti, 2018; Yu et al., 2010) 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 and 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., 2018), 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 and 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°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 later, which likely had a higher moisture content.

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 and 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 drainage (Ketcheson and Price, 2011), past fire (Thompson and Waddington, 2013) 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 and 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.

6.2 Methods

6.2.1 Field study

The study was carried out at the Hard Hill burning and grazing experiment, 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 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, temperature dataloggers (EL-TC-USB, Lascar, UK) with 30 cm K-type thermocouples (Omega, UK) were installed. 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 at each measurement point. 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 (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 °°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 cranked wires similar to those used by Clymo (1970), Kim et al. (2014) and Walker et al. (2015) were installed at the burn plot measurement points, 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°° 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 capitulum branches were removed from each sample, 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.

The capitulum water content of *S. capillifolium* was determined for samples taken in April, June and September by weighing three capitula at field moisture, then drying at 30 °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 °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.

6.2.2 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 °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°C for 11 days before trypan blue staining was carried out a second time on another capitulum from each sample.

6.2.3 Analysis

All statistical analyses were carried out using R 3.4.1 (R Development Core Team 2010) with the packages car (Fox and 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 °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 °C) and low (33 – 137 °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.

6.3 Results

Maximum temperatures detected by the thermocouples during fire ranged from 33 °C to 538 °C, with a mean of 259 °C. These maximum temperatures were correlated with both length of time 50 °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 6.1) 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 6.1). The proportion of cell damage recorded in June ranged from 2-100% and was lowest (2-38 %) for temperatures under 100 °C and consistently high (93-100 %) for temperatures over 400 °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 6.1).

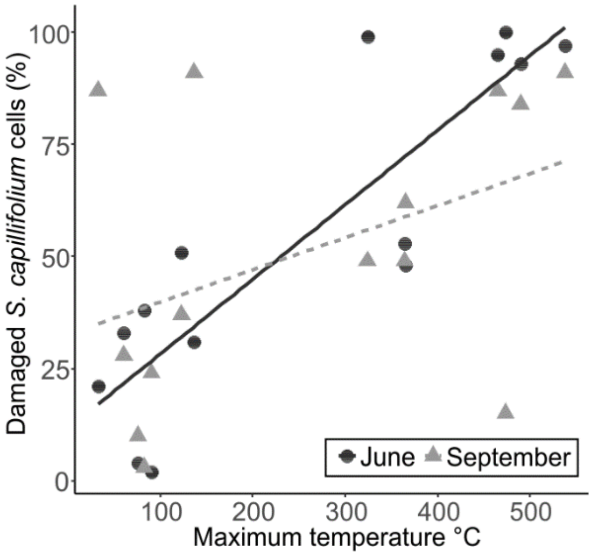

Figure 6.1: Relationships between maximum temperature exposure and cell damage in *Sphagnum capillifolium* samples taken from 14 experimental burn plots, 10 (June) and 21 (September) weeks after burning.

Table 6.1: 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	Intercept	-2.070	0.651	12	-3.177	0.008
cell damage	Max temp	0.010	0.002	12	4.673	0.001
logit %	September	1.198	0.921	12	1.300	0.218
	Max temp: September	-0.006	0.003	12	-2.086	0.059
S. capillifolium	Intercept	1.404	0.393	24	3.578	0.002
water content	Max temp	-0.001	0.001	12	-0.546	0.595
logit %	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	Intercept	0.139	0.149	12	0.930	0.371
height	Max temp	-0.001	<0.001	12	-2.131	0.054
mm wk^{-1}	September	-0.107	0.194	12	-0.550	0.592
	Max temp: September	0.001	0.001	12	1.028	0.324
Peat	Intercept	0.101	0.006	12	16.419	0.000
bulk density	Max temp	0.000	0.000	12	1.214	0.248
g cm^{-3}	September	-0.012	0.007	12	-1.726	0.110
	Max temp: September	0.000	0.000	12	-1.277	0.226
Peat	Intercept	1.758	0.039	12	45.453	<0.001
water content	Max temp	<0.001	<0.001	12	-1.694	0.116
logit %	September	0.308	0.046	12	6.652	<0.001
	Max temp: September	<0.001	<0.001	12	0.574	0.576

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 6.2, Figure 6.2). 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 6.2). 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 6.2, Figure 6.2). 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 6.2).

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 6.3, Figure 6.3). 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 6.4).

Table 6.2: 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	Intercept	-2.137	0.759	21	-2.814	0.010
cell damage	Low temp	0.873	0.933	21	0.935	0.360
logit %	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	Intercept	90.750	7.717	34	11.760	<0.001
water content	Low temp	-16.625	9.451	21	-1.759	0.093
logit %	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	Intercept	0.011	0.122	17	0.093	0.927
height	Low temp	-0.159	0.173	17	-0.922	0.370
mm wk^{-1}	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	Intercept	0.086	0.008	21	11.095	<0.001
bulk density	Low temp	0.020	0.010	21	2.036	0.055
g cm^{-3}	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	Intercept	2.014	0.100	21	20.195	<0.001
water content	Low temp	-0.296	0.126	21	-2.347	0.029
logit %	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

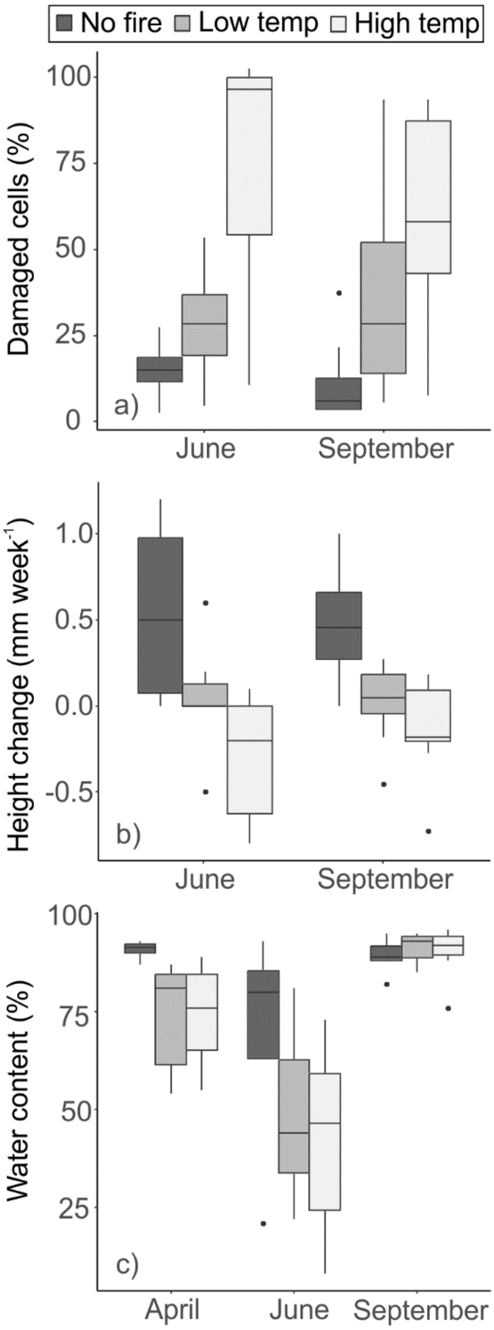

Figure 6.2: Boxplots showing comparisons between no fire, low temperature and high temperature groups for a) proportion of damaged *Sphagnum capillifolium* cells, b) *S. capillifolium* mean weekly height change and c) *S. capillifolium* water content as a percentage of wet weight. Measurement times were immediately (April), 10 (June) and 21 (September) weeks after fire.

Table 6.3: Results from linear model investigating impacts of temperature exposure (ambient – 500 °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

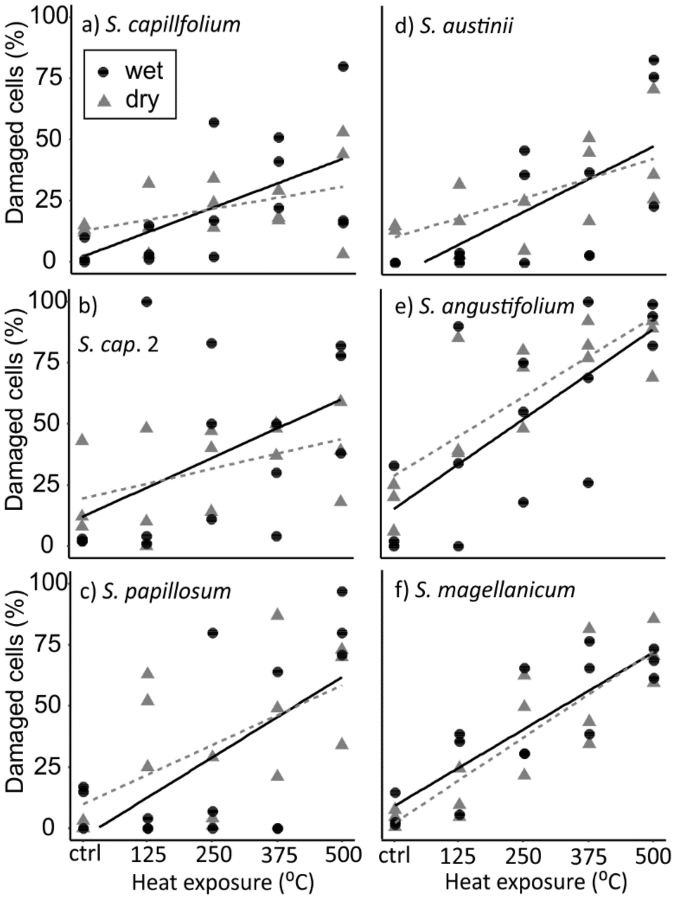

Figure 6.3: Proportion of damaged cells in wet and dry *Sphagnum* samples in the control (ctrl) group, or exposed to 125, 250, 375 or 500 °C for 5 seconds by heating with a Meker burner flame in the laboratory. Damage was measured within 24 hours of temperature exposure, except in b) where damage was measured 11 days after temperature exposure.

Table 6.4: Results from linear mixed model investigating impacts of temperature exposure (ambient – 500 °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

6.4 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 and 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 °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 °C compared to 104 °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., 2015; Holden et al., 2014).

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 and Schlotzhauer, 1999; Howie and 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.

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 this type of fire.

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) may impact species in different ways (Sagot and 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 may have 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, could be more at risk as a result.

6.5 Conclusion

Our results indicate that greater dwarf shrub cover prior to burning is likely to produce 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 in the longer term. 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*.

6.6 Acknowledgements

This analysis was funded by Natural Environment Research Council studentship [NE/L008572/1] supported by Natural England, awarded to JH, SMP, DG and AC in open competition. We thank John O’Reilly at Ptyxis Ecology for help locating and identifying different *Sphagnum* species and colleagues in the Faculty of Biological Sciences, University of Leeds for support with the *Sphagnum* damage assessment methodology.

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Chapter 7: Discussion

7.1 Section outline

Further to the individual discussion and conclusion sections in each of the preceding chapters, this chapter seeks to summarise the project as a whole, and discuss how the work contributed to answering the three overarching research questions:

a) What are the impacts of burning on blanket peatland vegetation composition?

b) Over what timescales do these impacts occur?

c) Which processes play an important role in driving impacts?

The project findings are therefore discussed in the context of these questions and subsequent implications for ecosystem services outcomes and conservation goals. Areas in which the understanding or interpretation of past work has been extended or challenged are also considered. The relevance of the work to the wider international context and some of the project limitations are reflected upon. Finally, overall conclusions and resulting recommendations for peatland management, policy and future research directions are outlined.

7.2 Impacts of prescribed burning on blanket peatland vegetation and their timescales

7.2.1 Vegetation community composition and structure

The results of the project provide strong evidence that peatland vegetation community composition is impacted by prescribed burning. National and regional data indicated that vegetation composition differed between burned and unburned sites at both scales (Chapter 2). In the regional dataset, plots with a range of durations (2-10+ years) since burning were all distinct from unburned comparisons. The vegetation of unburned sites in this dataset showed an association with geographic location, but this was not apparent in the burned sites, suggesting that burning can override geographically variable vegetation community characteristics.

The results in Chapter 5 showed that after burning, vegetation change can take place in a succession-like process whereby different species or groups peak in abundance at different stages in the trajectory of vegetation development (Figure 7.1). Referring back to the regional dataset results in Chapter 2, it is possible to infer that the vegetation community may be unlikely to return to a state comparable to an unburned peatland within typical burning rotation timescales (c. 8-25 years). Instead, the length of the burn rotation is likely to determine the end point of the trajectory and thus influence the relative abundance of species within a site. Species composition and vegetation structure in a patch are in turn likely to affect the temperature and severity of subsequent burns (Figure 7.1), as observed in Chapter 6.

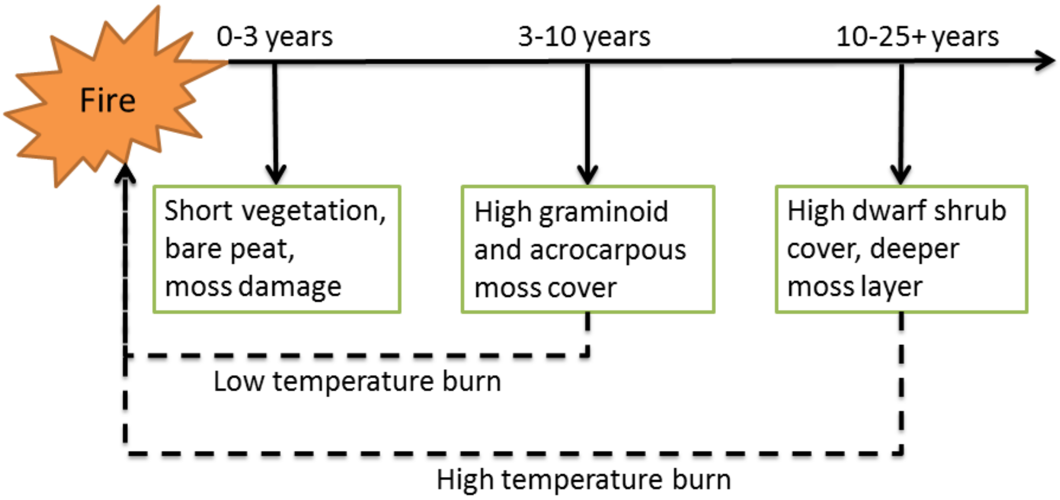

Figure 7.1: Conceptual diagram summarising approximate timescales of change for key vegetation attributes after prescribed burning. Dashed lines indicate the likely fire temperatures produced by burning at each point in the trajectory.

An expected result of vegetation burning is the combustion of the canopy layer, resulting in a low vegetation height in the early post-burning stages, which then increases over time as observed in Chapter 5. This effect is important as it is likely to cause changes to the peat surface microclimate during the post-burning trajectory, influencing the survival and growth of understorey species (Walker et al., 2015). Burning can also expose bare peat (Chapter 5), which may promote species which colonise effectively. Changes to the moss layer can also occur during the post burning trajectory. In Chapter 5 more recently burned plots were generally observed to have a thinner moss layer, and *Sphagnum* hummock height varied between burning treatments in Chapter 4. The fact that *Sphagnum* hummock height was lower in plots burned 60+

years ago than in plots burned 90+ years ago (Chapter 4) suggests that a fire event can continue to influence this aspect of vegetation structure for many decades, with potential consequences for peatland carbon sequestration (Kivimaki et al., 2008).

7.2.2 *Sphagnum*

Analysis of national-scale vegetation data yielded the important finding that burned plots had less *Sphagnum* cover on average than unburned plots (Chapter 2). In the past, local-scale studies of *Sphagnum* and burning have observed both increases and decreases after fire (Hamilton, 2000; Milligan et al., 2018; Grau-Andrés et al., 2017), but this result provides evidence from a large and representative sample of blanket peatlands in England to suggest that the net effect of prescribed burning on *Sphagnum* is negative. The relationship between *Sphagnum* cover and atmospheric nitrogen pollution was also observed to be significantly more negative on burned sites. Past work has shown that pollutants including nitrogen can impact *Sphagnum* negatively (Gunnarsson and Rydin, 2000; Ferguson et al., 1978; Tallis, 1964), but this finding provides new evidence that an interaction with burning can occur, potentially leaving *Sphagnum* more vulnerable to decline where burning and high pollution levels coincide.

No significant difference in *Sphagnum* cover between burned and unburned plots was found at the regional scale (Chapter 2), but the results did show fluctuations in cover over time after burning. The vegetation survey work described in Chapter 5 showed that bleached *Sphagnum* patches were present for 1-3 years after burning, similarly suggesting that the abundance of healthy *Sphagnum* can vary over time on burned plots. Such variations may reflect the impacts of multiple, potentially conflicting processes (see section 7.3), as well as differences in the responses of individual *Sphagnum* species. When the survival of introduced *Sphagnum* was assessed, success was high regardless of time since burning at the most *Sphagnum* rich site, but declined over the study period in recently burned plots at the most *Sphagnum* poor site, suggesting that these plots had sub-optimal conditions for *Sphagnum* survival.

Sphagnum abundance also differed significantly between burning treatments in the Hard Hill experiment at Moor House-Upper Teesdale NNR (Chapter 4). Past studies of this experiment have compared three treatments (10-year and 20-year burn rotations and no-burn since 1954) and concluded that burning on short rotations is more beneficial to

Sphagnum than no burning (Milligan et al., 2018; Lee et al., 2013). However, a comparison between these treatments and long-unburned reference plots (Chapter 4) produced new results which facilitate further interpretation of treatment effects. The fact that there was less *Sphagnum* in the no-burn plots (burned in 1954) than the reference plots (unburned for 90+ years) suggests that the 1954 burn had a long-lasting negative impact. Relatively high *Sphagnum* cover in the 10-year rotation plots suggest that some recovery has taken place due to subsequent burning. This could be due to lower atmospheric pollution at the time of subsequent burns, perhaps reflecting an interaction between burning and atmospheric pollution as observed in Chapter 2. A large proportion of published material on peatland prescribed burning impacts is drawn from the Hard Hill experiment (Glaves et al., 2013), so these new results provide important context to the existing evidence base.

7.2.3 Other key plant groups

Work in Chapters 2 and 5 showed that vascular plant groups can undergo large changes in abundance as a result of burning. On a national scale, mean cover of the dwarf shrub *C. vulgaris* on burned blanket peatland sites is 3.5 times greater than their unburned equivalent (Chapter 2). This may be expected, as the regeneration of *C. vulgaris* is a key aim of prescribed burning (Pearsall, 1941). The results in Chapter 5 showed that dwarf shrub cover was low soon after burning but increased with time, and in plots burned 10+ years ago, cover was commonly 50-100 %. Such a high cover of dwarf shrubs over a large proportion of a site could potentially have a negative impact on water quality and carbon sequestration (Armstrong et al., 2012; Dixon et al., 2015) and lead to the failure to meet statutory conservation targets (JNCC, 2009).

Graminoid cover generally increased in the first 1-5+ years after burning, but was lowest in plots burned 10+ years ago, in which it had largely been replaced by dwarf shrub cover. These results back up past findings which suggest that in peatlands, short rotations are likely to lead to graminoid dominance and long rotations to dwarf shrub dominance (Glaves et al., 2013; Lee et al., 2013). However, results from the EMBER data in Chapter 2 found that there was less of the sedge *E. vaginatum* where burning had recently occurred. This may indicate that this species does not always follow the pattern typical of graminoids as a group, and as *E. vaginatum* can contribute to peat formation (Kalnina et al., 2015; McClymont et al., 2011), it may be useful to consider this species separately when making fire impact predictions. A more negative relationship between nitrogen deposition and *E. vaginatum* cover was also observed on recently burned plots in the regional data (Chapter 2), which could be the result of increased competition from dwarf shrubs at high nutrient supply (Kool and Heijmans, 2009).

Regarding non-*Sphagnum* mosses, the results of Chapter 5 showed that acrocarpous species can increase in cover in the short term after burning. In Chapter 2, cover of the non-native acrocarp *C. introflexus* was found to be much higher on plots burned 2-7 years ago than unburned plots. This is consistent with past accounts of acrocarpous mosses rapidly colonising after disturbance including fire (Southon et al., 2012; Duncan and Dalton, 1982; Thomas et al., 1994; Equihua and Usher, 1993), though the ecological implications of this process are not fully understood. It is possible that acrocarpous moss cover is preferable to bare peat, which could be vulnerable to erosion, but widespread cover may hinder the establishment of other peatland species (Equihua and Usher, 1993). The fact that *C. introflexus* cover was low in plots burned 10+ years ago in the EMBER data, as were acrocarpous species in the 10+ burn age category plots surveyed in Chapter 5, suggests that these mosses are eventually out-competed, potentially due to shading by dwarf shrubs.

7.3 Processes by which burning impacts vegetation

As well as characterising typical patterns of vegetation change after fire, this project aimed to investigate the processes responsible for those patterns of change. These processes can include the direct impacts of fire on vegetation as well as indirect impacts resulting from fire-induced changes to the local environment (Figure 7.2). Work in Chapter 6 revealed that high temperature exposure during fire causes cell damage in *Sphagnum*, and that the higher the temperature, the greater the damage. These results suggest that the reduced photosynthetic efficiency observed in *S. capillifolium* after high temperature exposure in past work (Grau-Andrés et al., 2017; Taylor et al., 2017) may be a result of cell damage. Taylor et al. (2017) recommended investigation of multiple *Sphagnum* species to see if temperature impacts can be generalised across species, and the results in Chapter 6 suggest that generalisation is possible, as five *Sphagnum* species with a range of environmental tolerances all sustained greater cell damage at higher temperatures. The relationship between fire temperature and damage may also go some way towards explaining the pattern of *Sphagnum* abundance observed at the Hard Hill experiment, as fire temperatures and damage were lower in the 10-year rotation plots, which had greater *Sphagnum* cover than in the 20-year rotation plots.

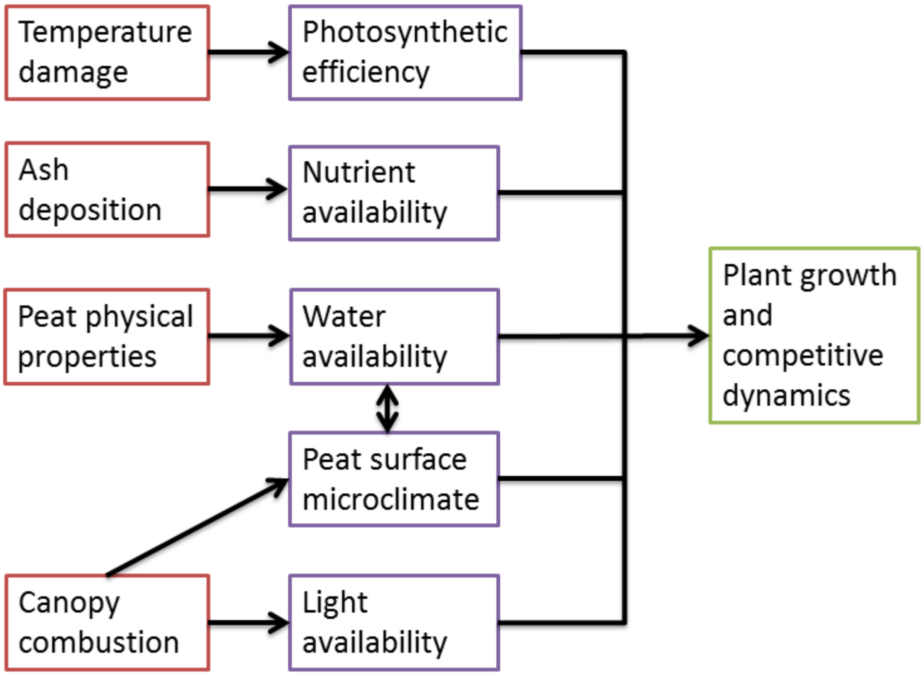

Figure 7.2: Pathways by which prescribed burning is likely to impact blanket peatland vegetation.

In Chapter 3, changes to water availability as a result of fire were shown to have the potential to impact vegetation. Prescribed burning can impact peat properties including near surface bulk density (Holden et al., 2015; Holden et al., 2014) which can restrict the amount of water accessible to mosses (Price et al., 2003; Clymo and Hayward, 1982; Thompson and Waddington, 2013a). The work in Chapter 3 showed that high bulk density restricted growth of *Sphagnum*, but not *C. introflexus*. This may partly explain the high cover of acrocarpous mosses such as *C. introflexus* observed after burning in Chapters 2 and 5.

Ash addition as a result of burning was found to have various impacts on different moss species (Chapter 3). *S. capillifolium* and *C. introflexus* benefitted from ash inputs, while *S. fallax* showed no significant response. These results indicate that ash inputs may influence the relative abundance of moss species after fire. Past work suggests that nutrients in peat may become depleted in the longer term (2+ years) after burning

(Brown et al., 2014), which could cause vegetation change over time. The positive impact of ash on *S. capillifolium* contrasts with the negative impacts of high temperature exposure and reduced water availability, and it is possible that the extent and timescales of these effects and associated changes in competitive dynamics may be responsible for the fluctuations in *Sphagnum* cover after burning observed in Chapter 2.

Finally, the results of this project suggest that the growth rate of different species will lead to changing conditions and competitive dynamics over time after burning, which are likely to influence overall community composition. For example, if a more open canopy produced by burning is followed by high graminoid cover and eventual dwarf shrub dominance (Chapter 5), this will cause changes in peat surface microclimate, light availability and the quantity and quality of litter inputs, all of which have the potential to impact understorey species including bryophytes (Walker et al., 2015; Malmer et al., 2003).

7.4 Wider implications and limitations of the project

The work in this project focussed on the type of prescribed rotational burning often carried out for grouse moor management in the UK uplands. However, some of the findings are likely to be applicable in a wider context. Prescribed burning carried out internationally for purposes such as grazing improvement (Tubbs, 1974), nature conservation management (Hochkirch and Adorf, 2007) and forestry (Renard et al., 2016; Geron and Hays, 2013) may be similar in intensity, and therefore have similar effects to grouse moor burning. Burning is also common in non-peatland ecosystems including grassland and heathland, where species composition and soil properties differ from those of peatlands. While the specific dynamics of vegetation change may not be comparable, some of the findings from this project may contribute to a wider body of evidence on burning impacts which can be generalised across ecosystems. For example, interactive effects of burning and atmospheric pollution on vegetation (as observed in Chapter 2) have been also found in heathland (Britton and Fisher, 2007).

Wildfires are common on peatlands worldwide, and are predicted to increase as a result of climate change (Turetsky et al., 2015; Kelly et al., 2018; Leng et al., 2018; Tarnocai, 2006). They are often more severe than prescribed burns, resulting in greater vegetation loss and peat combustion. However, many of the processes occurring after wildfire are similar to those discussed in section 7.3, and therefore the impacts on vegetation may be similar in some instances, particularly where fire severity is low. For example, wildfire can increase peat bulk density (Sherwood et al., 2013), which may contribute to preferential colonisation by acrocarpous mosses as observed after prescribed burning in chapters 2, 3 and 5. Similarly, where *Sphagnum* remains after wildfire (Thompson and Waddington, 2013b), it is likely to have sustained cell damage as observed in Chapter 6.

A key limitation of this project was the difficulty encountered in ascertaining fire impacts on less frequent species, including some potentially important peat-forming *Sphagnum* species. Existing data on such species can be scarce as it is often more resource efficient to focus on indicator species or groups, as was the case in the national dataset in Chapter 2. Where field data for less common species was collected as part of this project, they often occurred too infrequently to be able to confidently attribute patterns of abundance to fire effects rather than random variation, as was the case in Chapter 4. Additionally, when comparing vegetation between sites with differing species compositions it can be more meaningful and practical to aggregate similar species into groups, which was the approach in Chapter 5. A useful way to assess the responses of less common species is through the use of controlled experiments such as the temperature exposure work in Chapter 6. Future work could make use of this approach to further investigate fire impacts on such species.

Another limitation of this work was the challenge associated with selecting a suitable control to compare burned vegetation with. Much, if not all of the UK’s vegetation has been modified by anthropogenic drivers, and for many blanket peatlands this includes the occurrence of fire at some point in history, often in addition to grazing, atmospheric pollution and/or drainage (Holden et al., 2007; Harper et al., 2018). The importance of this consideration was highlighted in Chapter 4 where there were significant differences between two ‘control’ treatments (one unburned for 60+ years, and one unburned for 90+ years). The work in Chapter 2 of this project sought to address this limitation through the use of large multi-site datasets where confounding variables could be controlled for, to give a broad-scale comparison between sites with and without a recent history of burning.

There are also limitations associated with the use of space-for-time substitution (chronosequence) to infer vegetation change (Pickett, 1989; Johnson and Miyanishi, 2008). Although this method is useful where the timescales of vegetation change are too long to measure the full process, the assumption that the only difference between chronosequence plots is their age (in this case time since burning) requires careful consideration when interpreting results. Space-for time substitution formed aspects of Chapters 2, 4 and 5 of this project and it should be noted that factors such as atmospheric pollution, climate, grazing pressure and burn severity may have varied temporally, influencing the trajectory of vegetation change in different burn age categories. Additionally, where space-for-time substitution occurs at a coarse scale, short-term and transient aspects of vegetation change may not be captured. For these reasons, work in Chapter 5 included monitoring of vegetation in fixed plots over time as well as space-for-time substitution with the aim of capturing short and long-term dynamics of vegetation change, and increasing confidence in the directional changes inferred.

7.5 Conclusions and recommendations

Overall, the results of this project show that prescribed burning on blanket peatlands affects multiple plant species by both direct and indirect pathways, with probable consequences for ecosystem services outcomes and conservation goals. Importantly, burning can cause damage to *Sphagnum* mosses, which play a vital role in peatland carbon sequestration, hydrological function and biodiversity. Other impacts can include the exposure of bare peat and/or colonisation by acrocarpous mosses after fire, and a short term peak in graminoid abundance followed by dwarf shrub dominance. Each of these impacts may lead to a failure to meet statutory conservation objectives (JNCC, 2009) and past research suggests that they have the capacity to negatively affect ecosystem services. For these reasons it is recommended that prescribed burning on blanket peatlands should generally be avoided. Burning has been proposed as a method to restore dwarf shrub-dominated areas (Uplands Management Group, 2017), but this project found that greater dwarf shrub cover resulted in hotter fires which were more damaging to *Sphagnum*, so this approach may not be advisable where *Sphagnum* is present.

The results of this project also suggest that vegetation may remain modified for several decades after burning. Therefore, useful directions for future research may include the investigation of blanket peatland vegetation recovery after cessation of burning.

Evaluation of the suitability of conservation interventions such as vegetation cutting, rewetting and species introductions could provide valuable knowledge of how best to encourage the formation of typical, active blanket peatland vegetation communities on previously burned sites. It would also be worthwhile for such work to take into account spatially and temporally variable environmental influences including atmospheric pollution and climate, with the aim of safeguarding peatland function and ecosystem services and promoting resilience to future environmental change.

7.6 References

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Appendices

A1 Supporting information for Chapter 2

Table A1.1: Indictor species in the CM dataset and their occurrence as a percentage of unburned (UB), burned (B) and all plots.

Species	**Plant Type**	**UB**	**B**	**All**
Andromeda polifolia	dwarf shrub	2	1	2
Betula nana	dwarf shrub	<1	<1	<1
Carex spp.	sedge	11	7	9
Cornus suecica	herb	<1	0	<1
Calluna vulgaris	dwarf shrub	34	80	53
Drosera spp.	herb	<1	0	<1
Eriophorum angustifolium	sedge	51	49	50
Erica cinerea	dwarf shrub	5	11	8
Empetrum nigrum	dwarf shrub	11	16	13
Erica spp.	dwarf shrub	<1	<1	<1
Erica tetralix	dwarf shrub	16	17	16
Eriophorum vaginatum	sedge	63	65	64
Juncus sp.	rush	30	15	24
Molinia caerulea	grass	42	17	32
Myrica gale	dwarf shrub	<1	<1	<1
Non-crustose lichens	lichen	6	11	8
Narthecium ossifragum	herb	9	2	6
Pleurocarpous mosses	pleurocarpous moss	63	74	68
Rubus chamaemorus	herb	1	4	2
Racomitrium lanuginosum	acrocarpous moss	1	<1	1
Saxifraga spp.	herb	<1	<1	<1
Sphagnum spp.	*Sphagnum*	46	39	43
Trichophorum cespitosum	sedge	17	9	14
Vaccinium myrtillus	dwarf shrub	38	40	39
Vaccinium oxycoccus	dwarf shrub	6	4	5
Vaccinium vitis-idaea	dwarf shrub	1	3	2

Table A1.2: Summary statistics and correlation (Pearson's *r*) between variables in the EMBER dataset. Correlation values in bold are statistically significant ($p<0.05$).

	Acid	Ammonia	Elevation	Nitrogen	Nitrogen oxides	Ozone	Peat Depth	Sulphur dioxide
Units	keq ha^{-1} yr^{-1}	µg m^{-3}	m	Kg ha^{-1} yr^{-1}	µg m^{-3}	ppb hours	m	µg m^{-3}
Mean	1.95	1.41	503	24.3	6.56	781	164	1.38
Median	1.95	1.13	525	23.52	5.59	776	200	1.24
Minimum	1.38	0.55	349	17.36	4.30	357	45	0.90
Maximum	2.38	3.63	632	33.6	13.90	1053	200	2.26
NMDS envfit R^2	0.13	0.33	0.44	0.18	0.50	0.50	0.07	0.65
Ammonia	**0.56**							
Elevation	0.05	**-0.33**						
Nitrogen	**0.98**	**0.71**	0.00					
Nitrogen oxides	**0.54**	**0.92**	**-0.46**	**0.66**				
Ozone	0.10	0.15	**-0.45**	0.12	**0.38**			
Peat depth	0.01	0.09	-0.07	0.04	-0.02	-0.01		
Sulphur dioxide	**0.55**	**0.85**	**-0.46**	**0.66**	**0.95**	**0.56**	-0.07	

Table A1.3: Summary statistics and correlation (Pearson's *r*) between variables in the CM dataset. Correlation values in bold are statistically significant ($p<0.05$).

	Acid	Browsing	Easting	Elevation	Nitrogen	Northing	Nitrogen oxides	Ozone	Peat depth	Slope	Sulphur dioxide
units	keq ha^{-1} yr^{-1}	%	co-ord	m a.s.l.	Kg ha^{-1} yr^{-1}	co-ord	µg m^{-3}	ppb hours	cm	degrees	µg m^{-3}
mean	2.04	9	381858	431	24.99	460583	8.86	815	70	7.65	1.89
median	2.05	0	386591	423	24.92	479179	7.70	792	60	6.50	1.63
minimum	1.32	0	256509	192	16.52	70624	3.82	296	30	0.05	0.50
maximum	2.93	100	472033	702	34.44	598096	25.47	2078	150	39.51	4.37
NMDS envfit R^2	0.01	0.01	0.06	0.03	0.01	0.21	0.01	0.05	0.03	0.01	0.02
Browsing	**0.07**										
Easting	**0.21**	**0.06**									
Elevation	**0.17**	**0.15**	**-0.11**								
Nitrogen	**0.99**	**0.08**	**0.17**	**0.19**							
Northing	**0.10**	**0.05**	**0.52**	**-0.08**	**0.07**						
Nitrogen oxides	**0.18**	0.01	**0.27**	**0.05**	**0.20**	**-0.07**					
Ozone	**-0.27**	**-0.11**	**-0.09**	**-0.07**	**-0.26**	**-0.60**	**0.11**				
Peat depth	**0.11**	0.01	**0.10**	**0.21**	**0.10**	**-0.11**	**0.06**	0.01			
Slope	**0.15**	**0.12**	-0.01	**0.22**	**0.15**	0.04	**0.10**	**-0.12**	**-0.14**		
Sulphur dioxide	**0.24**	0.00	**0.41**	-0.01	**0.24**	-0.02	**0.94**	**0.14**	**0.07**	**0.08**	

Table A1.4: Results of GLMM analysis of species % cover according to management and environmental variables. EMBER each burn age n=15, unburned n=60; CM burned=788, unburned=1105

		Sphagnum				***C. vulgaris***				***E. vaginatum***				***C. introflexus***			
	Variable	Estimate	Std. Error	z value	Pr (>|t|)	Estimate	Std. Error	z value	Pr (>|t|)	Estimate	Std. Error	z value	Pr (>|t|)	Estimate	Std. Error	z value	Pr (>|t|)
EMBER	Intercept	-0.432	0.540	-0.799	0.424	2.485	0.690	3.602	0.000	2.382	0.444	5.366	0.000	-2.536	0.643	-3.941	0.000
	B2 v U	-1.091	1.037	-1.052	0.293	1.485	0.984	1.509	0.131	-1.674	0.696	-2.406	0.016	4.126	0.767	5.380	0.000
	B4 v U	1.487	0.909	1.637	0.102	1.483	0.984	1.507	0.132	-1.190	0.680	-1.748	0.080	3.746	0.761	4.921	0.000
	B7 v U	-1.755	1.130	-1.553	0.120	1.909	0.988	1.932	0.053	-1.816	0.691	-2.628	0.009	3.443	0.771	4.465	0.000
	B10+ v U	-0.281	0.986	-0.285	0.776	1.287	0.988	1.303	0.192	-1.344	0.692	-1.940	0.052	1.111	0.863	1.286	0.198
	Nitrogen	-0.897	0.371	-2.415	0.016	0.163	0.482	0.338	0.735	-0.625	0.323	-1.934	0.053	0.870	0.299	2.907	0.004
	Peat depth	-0.524	0.297	-1.767	0.077	-0.041	0.076	-0.545	0.586	0.331	0.115	2.883	0.004	-0.054	0.312	-0.173	0.862
	Elevation	1.843	0.394	4.678	0.000	0.862	0.462	1.864	0.062	0.545	0.325	1.675	0.094	-1.409	0.391	-3.603	0.000
	Model AIC	624				1100				796				468			
CM	Intercept	-0.492	0.281	-1.749	0.080	-1.620	0.357	-4.539	0.000	1.012	0.233	4.340	0.000				
	B v U	-0.933	0.400	-2.333	0.020	3.280	0.362	9.049	0.000	-0.082	0.303	-0.269	0.788				
	Livestock present	-0.509	0.177	-2.883	0.004	-0.443	0.135	-3.283	0.001	0.015	0.115	0.129	0.897				
	Northing	0.831	0.218	3.812	0.000	0.736	0.296	2.482	0.013	0.580	0.194	2.985	0.003				
	Elevation	-0.542	0.162	-3.354	0.001	0.538	0.127	4.240	0.000	0.650	0.110	5.911	0.000				
	Nitrogen	-0.570	0.227	-2.512	0.012	-0.084	0.307	-0.274	0.784	-0.092	0.200	-0.460	0.645				
	Model AIC	8898				11282				13064							

Table A1.5: Results of GLMM analysis of species % cover according to burn status, nitrogen (N) deposition (Kg ha^{-1} year^{-1}), and their interaction. EMBER each burn age n=15, unburned n=60; CM burned=788, unburned=1105

		Sphagnum				***C. vulgaris***				***E. vaginatum***				***C. introflexus***			
	Variable	Esti-mate	Std. Error	z value	Pr (>|t|)	Esti-mate	Std. Error	z value	Pr (>|t|)	Esti-mate	Std. Error	z value	Pr (>|t|)	Esti-mate	Std. Error	z value	Pr (>|t|)
EMBER	(Intercept)	-0.100	0.969	-0.103	0.918	2.647	0.723	3.664	0.000	2.563	0.451	5.682	0.000	-2.875	0.971	-2.961	0.003
	B2 v U	-3.153	2.084	-1.513	0.130	1.164	1.024	1.137	0.255	-2.508	0.821	-3.057	0.002	4.651	1.232	3.777	0.000
	B4 v U	0.700	1.450	0.483	0.629	1.178	1.024	1.151	0.250	-1.370	0.689	-1.988	0.047	4.339	1.234	3.517	0.000
	B7 v U	-5.279	2.966	-1.780	0.075	1.546	1.024	1.510	0.131	-2.369	0.749	-3.162	0.002	3.855	1.246	3.095	0.002
	B10+ v U	-0.730	1.504	-0.486	0.627	0.991	1.024	0.968	0.333	-1.763	0.704	-2.503	0.012	1.599	1.334	1.199	0.231
	Nitrogen U	0.054	1.332	0.041	0.968	-0.095	1.036	-0.092	0.927	0.105	0.655	0.160	0.873	-0.310	1.337	-0.232	0.816
	N B2 v U	-3.625	2.232	-1.624	0.104	0.148	1.192	0.124	0.901	-1.993	0.884	-2.255	0.024	1.625	1.482	1.097	0.273
	N B4 v U	-1.957	1.643	-1.191	0.234	0.229	1.192	0.192	0.848	-0.517	0.775	-0.668	0.504	1.407	1.481	0.950	0.342
	N B7 v U	-4.856	2.928	-1.659	0.097	0.084	1.192	0.071	0.944	-1.490	0.827	-1.801	0.072	2.125	1.497	1.419	0.156
	N B10+ v U	-1.791	1.695	-1.056	0.291	0.099	1.192	0.083	0.934	-1.011	0.785	-1.287	0.198	1.947	1.538	1.265	0.206
	Model AIC	637				1107				795				480			
CM	(Intercept)	-0.815	0.278	-2.931	0.003	-1.790	0.371	-4.827	0.000	0.863	0.244	3.532	0.000				
	B v U	-0.945	0.404	-2.338	0.019	3.250	0.387	8.398	0.000	0.104	0.315	0.330	0.742				
	Nitrogen U	-0.111	0.259	-0.428	0.668	0.000	0.341	-0.001	0.999	0.271	0.230	1.179	0.239				
	N B v U	-1.669	0.511	-3.264	0.001	0.294	0.423	0.694	0.488	-0.683	0.356	-1.921	0.055				
	Model AIC	9019				11315				13097							

A2 Supporting information for Chapter 4

A2.1 *Sphagnum* occurrence in 2015-16

The transect survey recorded seven *Sphagnum* species in the experiment and reference plots while the mapping survey recorded 12 (Table A). The most common species, representing around 90% of *Sphagnum* recorded, was *S. capillifolium*. Four species (*S. tenellum*, *S. cuspidatum*, *S. rusowii* and *S. girgensohnii*) were present in the main experiment plots and absent from the reference plots, while two species (*S. angustifolium* and *S. palustre*) were present in the reference plots and absent from the main experiment plots.

Table A2.1: Frequencies of *Sphagnum* as a genus and all individual species (names and botanical authorities from the UK Species Inventory) observed in the 2015-16 transect and mapping surveys. One species was recorded for each transect hit, but multiple species could occur in each map square. Experiment (fenced and grazed) n = 24 plots, reference (grazed) n = 4 plots.

		Transect hits %		Map squares %	
Species	Botanical authority	Experiment	Reference	Experiment	Reference
Sphagnum spp.	L.	19.71	28.25	42.71	57.02
S. capillifolium	(Ehrh.) Hedw.	17.50	26.50	39.57	52.53
S. subnitens	Russow & Warnst.	0.88	1.00	2.91	1.74
S. papillosum	Lindb.	0.50	0.25	1.49	0.27
S. fallax	(H.Klinggr.) H.Klinggr.	0.38	0.25	0.77	1.64
S. angustifolium	(C.E.O.Jensen ex Russow) C.E.O.Jensen	0.00	0.25	0.00	2.84
S. tenellum	(Brid.) Bory	0.42	0.00	0.39	0.00
S. fimbriatum	Wilson	0.00	0.00	0.13	0.02
S. cuspidatum	Ehrh. ex Hoffm.	0.00	0.00	0.05	0.00
S. palustre	L.	0.00	0.00	0.00	0.21
S. magellanicum	Brid.	0.00	0.00	0.02	0.14
S. russowii	Warnst.	0.04	0.00	0.03	0.00
S. girgensohnii	Russow	0.00	0.00	0.02	0.00

A2.2 NMDS analysis of *Sphagnum* species abundance in the grazed experimental treatments and reference plots in 2015-16

Non-metric Multidimensional Scaling (NMDS) ordination analysis was carried out using the map frequency data for all *Sphagnum* species occurring in the grazed experimental plots and reference plots to enable visualisation of how the treatments differed in terms of their overall *Sphagnum* species composition.

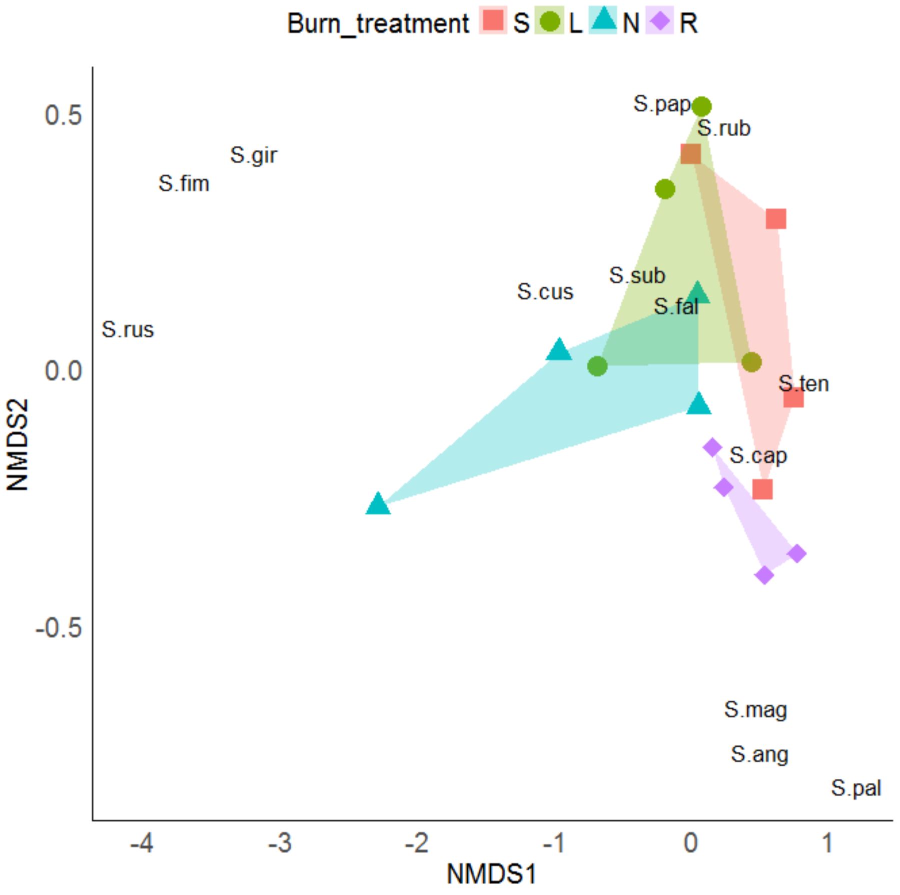

Figure A2.1: NMDS ordination of *Sphagnum* abundance in the grazed experimental treatments and reference plots in 2015-16