The Impact of Fire on Blanket Bogs: Implications for Vegetation and the Carbon Cycle

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Declaration of Authorship

I confirm that this work is my own and this thesis has been written by me unless otherwise stated. No part of this work has been submitted for any other degree or professional qualification.

Emily S Taylor

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Lay Summary

Peat is produced by the slow decomposition of plant material so is rich in carbon. In the UK peat soils are a bigger carbon store than all the vegetation growing above ground making them very important in the context of carbon cycling and greenhouse gas emissions from land use and climate change. Blanket bogs are a special type of peatland, with deep peat soils and waterlogged conditions, globally recognised for their carbon storage capacity and their wildlife. In the UK they are also important to a number of industries and managed for forestry, farming and game such as red grouse and deer. Fire has been used by land managers for over a century as a way of improving grazing and habitat for livestock and game and, although of concern, the impacts of burning on the ecology and carbon cycle of blanket bogs is relatively understudied. The objective of this research was to assess the effect of fire on *Sphagnum*, important bog mosses, and greenhouse gas emissions from blanket bogs.

Methane emissions and the release of carbon dioxide by plants and bacteria (respiration) were measured at three sites in Scotland which had recently been burnt. The response of *Sphagnum* to different fire conditions was also assessed at the field sites and in a unique laboratory experiment. The effect of fire on methanotrophic bacteria, bacteria which use methane as food turning it into carbon dioxide and found in *Sphagnum*, was studied in the laboratory to see if the high temperatures caused by fire would kill the bacteria and thus, be a mechanism for fire increasing methane emissions to the atmosphere. The results show that fire did not increase methane emissions or respiration over the study period and that *Sphagnum* had the capacity to respond to fire by growing new stems. Methane removal by bacteria in samples of *Sphagnum* was found to be difficult to detect, with no affect of fire observed. Despite these results suggesting that low severity fires, which leave the moss layer and peat intact, have no impact on the elements of the carbon cycle studied here and can be survived by *Sphagnum*, they reiterate that burning legislation and guidelines must continue to strive to ensure that burning is only carried out on blanket bogs when conditions are conducive to low severity fires.

Abstract

Peatlands are multiservice ecosystems: they are the largest terrestrial store of carbon in the UK, unique habitats which provide a home for internationally important species and managed for forestry, farming and game management and shooting. This makes understanding the impact of management practices on their ecology important if they are to be sustainably managed for multi-benefits. Fire has long been used to manage peatlands in the UK to improve grazing and habitat provision for livestock and game. The effect of fire on carbon cycling in blanket bogs is of increasing concern as greenhouse gas emissions from land use is now an important management as well as political issue. Gaps however, still exist in our understanding of the controls on greenhouse emissions from blanket bogs and the impact fire may have on them both directly and indirectly by modifying vegetation composition and environmental conditions.

The main objective of this research was to assess the effect of fire on greenhouse gas emissions by measuring methane and ecosystem respiration after burning at blanket bog sites across Scotland for a period of up to 3 years and relating changes in fluxes with changes in vegetation composition and abiotic conditions. In addition, the response of the *Sphagnum* layer to burning was assessed by looking at the recovery of *Sphagnum capillifolium* in the field and in a novel laboratory experiment. The indirect effects of fire on methane emissions were further investigated by a laboratory experiment devised to test if high temperatures would be fatal to methanotrophic bacteria in the *Sphagnum* layer, reducing methanotrophy, and thus a mechanism for fire to increase methane emissions in the short term.

The results showed that methane emissions and ecosystem respiration were not significantly different in burnt plots when compared to adjacent unburnt plots at each of the three sites studies. Methane emissions were only weakly correlated to the position of the water table and neither methane fluxes or ecosystem respiration correlated with measures of vegetation composition and above ground biomass. Methanotrophy in *Sphagnum* was found to be difficult to detect, with a high temperature treatment having no significant effect on rates of methane oxidation.

S. capillifolium was found to respond to fire by growing new auxiliary stems if the capitulum was consumed or irreversible damaged physiologically by temperatures experienced at the moss surface, with surface temperatures around 400^{o}C with a temperature residency time of 30 seconds on artificially dried samples the most damaging, but not lethal, treatment.

These results suggest that low severity fires which only consume the canopy vegetation, not penetrating the peat and leaving the moss layer mostly intact, do not have significant effects on methane emissions and ecosystem respiration in the short and medium term. In addition, it suggests that *S.capillifolium* can, under certain circumstances, survive a fire with the characteristics of those studied here. These findings reiterate that best practice burning guidelines must continue to ensure that burning is only carried out on blanket bog when conditions are conducive to fires with the characteristics studied here, which had little effect on important components of the carbon cycle and are survivable by at least one of the most common species of *Sphagnum*.

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Dedication

To my Grandad

Douglas Ward Beasley

1925-2014

Contents

List of Figures

List of Tables

1. Introduction

1.1 Peatlands: Globally Important Ecosystems

Peatlands can be found across the world and cover around 3.8 million km^2, 3% of the earth's surface (Joosten, 2010). The term peatland describes systems where the accumulation of peat, formed from organic matter due to slow rates of decay, is the common feature. Most peatlands are found in the cold boreal and sub-arctic regions or in the tropics where the cold or wet and humid climates facilitate anoxic conditions and slow rates of decay (Parish *et al.*, 2008). Peatlands can be divided into four main ecosystems; marshes, which are permanently flooded, swamps, characterised by a lower water table, fens which are minerotrophic with a water table close to the surface, and bogs which also have a water table close to the surface but receive their nutrients and water solely from precipitation, making them ombrotrophic (Rydin and Jeglum, 2006). These unique conditions not only vary between these ecosystems but also considerably within a system. In bogs areas can be characterised as lawns, pools, hollows and hummocks depending on *Sphagnum* moss growth and moisture regimes, all of which support unique assemblages of organisms adapted to life in the different conditions. Traditionally the importance of peatlands has been valued in relation to the unique habitats they provide and the specialised organisms they support, but increasingly their global significance is emphasised in relation to their role in the terrestrial carbon cycle.

Acting as a long term carbon sink, it is estimated that peatlands store 30% of the world's soil carbon (Parish *et al.*, 2008) and so within the context of greenhouse gas emissions and climate change they act to sequester CO_2 and lock away carbon from the atmosphere. The observed rise in the atmospheric concentrations of greenhouse gases such as CO_2 and CH_4, both gases naturally emitted from peatlands, is now understood to drive global warming and changes in our climate (IPCC, 2013). This makes managing peatlands to help mitigate climate change of higher priority politically and has given rise to international incentives to promote the restoration and sustainable management of peatlands through initiatives such as the Clean Development Mechanism under the Kyoto Protocol and Nationally Appropriate Mitigation Actions (NAMAs) aimed at developing countries (FAO and Wetlands International, 2012) and more locally the Peatland Action fund for peatland restoration in Scotland. However, peatlands are valued as “multi-service” ecosystems and are managed across the world for agriculture and forestry and provide a host of other services such as water regulation and nutrient cycling (Millenium Ecosystem Assessment, 2005). Conflict inevitably arises between different management objectives and utilisation of services, with management practices having the potential to be detrimental to the ecology of a peatland. Understanding the full impacts of management practices and disturbance events on a peatland system is therefore important in informing sustainable management and ensuring peatlands still provide their vital services.

1.2 Fire in Northern Peatlands

Fire, a naturally occurring form of disturbance caused by lightning strikes, can affect extensive areas of a peatland and evidence suggests that the frequency and severity of fires in the future will increase with global warming (Schneider *et al.*, 2007). Fires are also started deliberately, used as a management tool to regenerate vegetation and clear land for farming and forestry. This makes fire important to understand if we are to mitigate the risk of both wild and management fires which are detrimental to the ecology and carbon cycle of a system.

Fires regularly occur on open and forested peatlands across the world (NASA Earth Observations, 2014). Russia, which has the greatest peatland cover of any country, and the second largest peat carbon stock after Canada (Joosten, 2010), has seen significant wildfires in recent years. One estimate suggests that 8.23 million ha (±9%) burns annually in the territories of Russia (Shvidenko *et al.*, 2011). In Canada it is estimated that an average 9000 fires occur annually which can burn up to 2 million ha (Natural Resources Canada, 2012) and in Alaska 613 fires occurred in 2013 alone, covering an area over 500,000 ha (Alaska Interagency Coordination Centre, 2013). Fires can vary not only in their geographical extent but also their severity, which is usually defined by how much organic matter gets consumed during a fire (Keeley, 2009). Of concern is the growing evidence that climate change and the associated increases in air temperatures and changes in precipitation patterns is driving an increase in both fire frequency and severity (Gillett *et al.*, 2004). North America for example is now seeing double the number of peatland fires than it did in the 1950’s, which is linked to a lower watertable and associated drying (Kasischke and Turetsky, 2006).

1.3 Peatland in the UK

Under the UK soil classification system peatland soils can be classed as soils with peaty pockets, shallow peat soils and deeper peaty soils with a peat depth greater than 50cm and include fens, blanket bog and raised bogs, the majority being blanket bog (Joint Nature Conservation Committee, 2011). Although in global terms the UK holds less than 0.5% of the global peatland area (Joosten, 2010), at the country scale around one third of the UK is covered by peat soils, the vast majority found in Scotland (JNCC 2011). This makes it a substantial part of the UK's land resource and significant carbon store, estimated to contain 3000 Mt of carbon (Smith *et al.*, 2007). Peatlands are however, also valued for their habitat and the species assemblages which they support.

Under the EC Habitats Directive many peatland habitats types are Annex 1 Habitats and in the UK are recognised as Biodiversity Action Plan Priority Habitats with many designated Sites of Special Scientific Interest or Specials Areas of Conservation for their fauna and flora. They support, although often not exclusively, species of conservation concern, designated both in the UK and internationally (Joint Nature Conservation Committee, 2014) and internationally blanket bogs are particularly recognised for their breeding bird assemblage (Littlewood *et al.*, 2010). Although species are not always exclusive to certain peatland habitats they are often highly specialised for living in the wet and acidic conditions. Species groups may be particularly important for ecosystem functions, such as the peat forming *Sphagnum* mosses and invertebrate and bacterial groups associated with the processing of plant litter in the decay process (Coulson and Butterfield, 1978). Populations of grazing mammals supported by peatlands such as red deer (*Cervus elaphus*) and ferral goats may also have important implications for vegetation and peatland condition (LINK Deer Task Force, 2013). Most peatlands in the UK have, however, been modified in some way by man, with significant areas of blanket, basin and lowland peats eroded, drained and managed for agriculture and forestry (Joint Nature Conservation Committee, 2011).

Peatlands in the UK are important for farming and game management which, particularly in the last 100 years, has led to the extensive drainage of both upland blanket bog and lowland raised bog to improve grazing. Drains are cut to lower the water table, which can have pronounced long term effects on the hydrology over large areas and subsequently vegetation composition, biodiversity and carbon cycling. Lowering the water table will cause the upper layers of peat to dry out, increasing oxidation of the peat and carbon loss (Bussell *et al.*, 2010). Drains can also directly export carbon from a system as dissolved and particulate carbon as well as cause significant erosion of the peat mass (Holden *et al.*, 2004). Peat forming function may also be lost due to drier conditions and a reduction in peat forming species such as the *Sphagnum* mosses (Lindsay, 2010). In recent years this had lead to funding being made available through agri-environment schemes and Government funded initiatives, such as the Peatland Action fund in Scotland (Scottish Natural Heritage, 2015), to block drains and increase the height of the water table to improve conditions for peat formation, reduce carbon loss and improve bog habitat. Peatlands are also drained and ploughed for commercial forestry which can have long term implications for their ecology (Lindsay *et al.*, 2014a). Lowland raised bogs in particular have also been extensively drained for agriculture, forestry and commercial extraction for peat for the horticulture industry. In England for example two fifths of raised bogs have been reclaimed for agriculture, with another sixth under forestry (Joint Nature Conservation Committee, 2011). Peat has also been cut commercially for use as a fuel and domestic peat cutting has long been vital to areas where wood fuel was not available such as the Shetland and Western Isles (Lindsay *et al.*, 2014b). The less direct impacts of grazing, burning and pollution from sulphur dioxide from fossil fuel use and the atmospheric deposition of nitrogen has led to significant changes in vegetation and in some areas has caused significant erosion (Yeloff *et al.*, 2006, Holden *et al.*, 2007, Sheppard *et al.*, 2014). This has led to many of the UK's peatlands being deemed to be in a degraded state, no longer in "favourable condition", a term used to describe an active bog with semi natural vegetation cover and a near permanently waterlogged catotelm (Lindsay and Immirzi, 1996). In 2010 it was estimated that within designated sites in Scotland 72% of upland bog bogs were in unfavourable or unfavourable recovering condition (Scottish Natural Heritage, 2010). This makes understanding the impact of management practices such as burning on the ecology of a peatland vital if policy and best practice guidance is well informed and able to mitigate the potential degradation of peatlands.

1.4 Fire in the UK

Management for livestock and grouse traditionally involves the use of fire, in Scotland called muirburn, to encourage new plant growth for more nutritious grazing and to maintain suitable habitat and the right grazing for grouse. Managed burns already have to adhere to strict legislation and guidelines set out in the Muirburn Code in Scotland and the Heather and Grass burning code in England. The aim of these codes is to reduce the risk of the potentially detrimental effects fire can have on peatland ecosystems, restricting burning to times and sites which are least likely to cause damaging fires (Table 1. 1). Although these codes of practice have helped manage the use of fire in the UK there have been calls to re-examine their content to take into consideration the wider impacts of burning and future climate change (EnviroCentre Ltd and CAG Consultants, 2010).

Fire has been used widely as a management tool in the uplands across the UK for at least 200 years (MacDonald, 1999). Although the increase in the use of fire has been associated with the expansion of game management during the last century (Stevenson *et al.*, 1996), burning is used today to manage heather and grass to increase fodder for livestock and deer and provide grazing and habitat for grouse (Tucker, 2003). Fires on peatlands in the UK may also occur in the form of wildfires, which are started accidently or maliciously, and are of growing concern as it is envisaged wildfire events will increase in response to climate change and changes in land management (Cavan and McMorrow, 2009). It is already evident anecdotally that periods of drought have been associated with significantly more wildfires, which may be exacerbated by the build-up combustible biomass due to a decline in grazing (Legg *et al.*, 2005) and prescribed burning due to cost (Hudson, 1992). Currently the full extent of wildfires is difficult to assess as many may go un-reported, particularly those out-with areas where there are more established burning regimes and systems of recording (Legg et al. 2005). How much land is burned for management purposes is also difficult to determine due to the opportunistic use of fire when conditions are right and the limited management records in some areas. Estimates based on interpretation of Landsat Thematic Imagery (TM) satellite imagery from 1984 suggest that in areas where heather constitutes more than 50% of the species present 87,000ha in Scotland and 110,601ha in England were managed by burning (Burnhill *et al.*, 1991). This represent only 1.1 and 0.8% of the total heather cover respectively. The figure estimated for England is similar to that estimated by Natural England (2010), however, in Scotland there were significant gaps in the satellite images due to snow or cloud cover which may have resulted in significant underestimates of the heather coverage and amount of burning in a number of Scottish regions. More recently DEFRA (Merrington *et al.*, 2010) estimated that 18% of the UK's peatlands are being burnt, which based on Joosten (2010) estimate of 17,113km^2 of peatland in the UK suggests that 3150 km^2 (315,000ha) of UK peatland is subjected to burning. Satellite imagery has also demonstrated the differences in burning patterns between areas and over time. The amount of heather burning in the Scottish Borders and Grampian regions for example has stayed about the same between the 1940's and 1980's, although significantly more is burnt in the grouse moor dominated Grampians (Hester and Sydes, 1992). Burning has however, increased significantly in some regions such as in the uplands of England within National Park boundaries

Table 1. 1 Summary of key management restrictions and guidance for prescribed burning in Scotland and England set out in the Muirburn Code (Scotland) and the Heather and Grass Burning Code (England). * Burning can be granted up to the 30th of April, and extended through the year under license for conservation, restoration, research of public safety objectives. **Burning can occur out-with the burning season under license from Natural England if the burning is for the conservation, enhancement or management of the natural environment for the benefit of present and future generations, or for the essential management of railway land.

Code of Practice	**Principal Governing Legislation**	**Burning Season**	**Key Restrictions**	**Key Recommendations**
Muirburn Code (Scotland)	Hill Farming Act (1946) as amended by the Wildlife and Natural Environment (Scotland) Act 2011 and the Climate Change (Scotland) Act 2009	1st October to 15th April*	No Night Burning Consent required by SNH for burning on SSSI's Sufficient people/equipment required Notice of intention to burn given to landowners and occupiers of land within 1km or proposed burn 7 days prior to burning	Mosaic of burnt/unburnt habitat should be retained Burnt with the direction of wind into fire break Blanket bog should only be burnt if heather constitutes >75% vegetation Avoidance of areas of steep hillside, exposed scree and rock and eroded peat
Heather and Grass Burning Code 2007 (England)	The Heather ad Grass etc. Burning (England) Regulations 2007	1st October to 15th April (Uplands only)** 1st November to 31st March (elsewhere)**	No night burning Sufficient people/equipment required License needed if burning on: slopes >45°, areas with >50% coverage of scree/expose rock, areas >10ha	Avoidance of sensitive areas such as woodland, areas of erosion, very thin soil, steep hillsides and gullies and mountain habitat Peatbogs and wet heath should only be burned in line with management plan agreed with Natural England and must not damage the moss layer

where habitat management perhaps may be more targeted to maintain habitat structure for grouse as well as other species (Yallop *et al.*, 2006). Such increases in burning have also been associated with an increase in the take up of agri-environment grant aid such as the Environmental Sensitive Areas scheme (Penny Anderson Associates Ltd., 2006).

1.5 Characteristics of Prescribed Fires

It has long been noted that there is a lack of quality information regarding fire behaviour and its effect on vegetation and the subsequent implications this may have for management regimes (eg. McArthur and Cheney, 1966, Worrall *et al.*, 2010). The vast majority of research into the characteristics and behaviour of fire on peatlands has come from studying management fires on *Calluna vulgaris* (L.) Hull (from here expressed as *Calluna*) dominated heaths, which has shown that fire behaviour can vary in relation to a number of ecological and meteorological factors. The temperatures within a fire have been shown to exhibit a strong gradient vertically through the vegetation stand, with temperatures within the canopy usually exceeding those experienced at ground level (eg. Hobbs and Gimingham, 1984a, Hamilton, 2000, Davies, 2005). Fire temperatures have also been associated with vegetation structure, demonstrated in *Calluna* fires, where temperatures increase and become more variable with stand age (Hobbs and Gimingham, 1984a). *Calluna* has long been recognised as varying in structure with age which has led to age classes being referred to as pioneer, building, mature and degenerate (Gimingham, 1972). Historically this has been used by land managers as a way of determining fire rotation times (Watt, 1955), usually resulting in burning regimes that will target heather before reaching the degenerate stage. Comparatively little work has been carried out on grass dominated heaths, which are more typical of management fires aiming to increase grazing availability for sheep and cattle (Tucker, 2003). *Molinia caerulea* (L.), with its propensity to produce a build-up of dead leaves and to grow in tussocks will potentially create large but patchy fuel loads which could lead to fires different in behaviour to those in *Calluna* stands. Lloyd (1968) for instance found that although temperatures within fires on *Festuca-Helictotichon* grass plots were comparable to those recorded on *Calluna* dominated heaths there was significant temperature variation due to the distribution of tussocks and areas of open soil.

Categorising fires by temperature increase alone may therefore not be the most effective indicator of the potential ecological impacts of a fire, as high temperatures may be reached but only for varying periods of time (Hobbs and Gimingham, 1984a, Hamilton, 2000, Davies, 2005). This is demonstrated by observations of fires where the peat ignites and smoulders, which although at comparatively low temperatures compared to the canopy (Ashton *et al.*, 2007), may burn for substantial lengths of time (Rein *et al.*, 2008) and have very severe impacts on a peatland ecosystem (Maltby *et al.*, 1990). This has led to the use of measurements of fire intensity, to describe time averaged energy flux, and fire line intensity, the rate of heat transfer per unit length of the fire edge and fire severity, defined as the immediate impact of burning on an ecosystem due to the direct transformation of organic matter (Keeley, 2009). It is important to note that other studies may use different interpretations of these terms such as such as Yallop *et al.*, (2006) who uses the term fire severity to infer fire frequency. These parameters have been found to correlate well with vegetation structure and fuel distribution as well as fuel moisture content and wind speed (eg. Kayll, 1966, Hamilton, 2000, Molina and Llinares, 2001, Hobbs and Gimingham, 1984a, Davies, 2005, Davies *et al.*, 2009, Davies *et al.*, 2010). However, they still may not necessarily indicate the ecological impact of a fire. For example, post fire recovery has been found to be most adversely affected in older *Calluna* stands (Hobbs and Gimingham, 1984b, Davies *et al.*, 2010). This highlights the variability in fire behaviour, pre and post-fire ecological and physical conditions, and variable impact this may have on vegetation recovery both within and between fires making categorising and predicting the impacts of fire difficult. This will consequently hamper the formulation of national best practice policy and guidelines, particularly when considering most research has focussed on *Calluna* heaths, with little work on the impact of fire on blanket bogs or grass dominated systems.

1.6 Aims of this Research

The primary objective of this research was to identify and quantify some of the impacts of management burning on areas of deep peat blanket bog, a wetter habitat than the historically better studied *Calluna* dominated wet and dry heaths. A potentially significant difference between these habitats is the dominance of the peat forming mosses, *Sphagnum*. *Sphagnum spp.* are vital to a healthy bog system, maintaining the wet and acidic conditions needed for an active bog. As burning on blanket bog is permitted in certain circumstances (Table 1. 1) it is important to expand the research into the impact of fire on this habitat to better inform best practice burning policies and guidance. Using field based measurements and novel lab based experiments the following chapters address some of the questions surrounding the impact of burning on blanket bog both in regards to impacts on carbon cycling and the *Sphagnum* layer. More specifically this study set out to answer the following research questions:

1. Does fire increase methane emissions from blanket bogs? Is a reduction in methanotrophy in the *Sphagnum* layer a potential mechanism for this?

2. Does ecosystem respiration change due to the changes in vegetation and abiotic conditions after a fire that does not penetrate the peat?

3. How does *Sphagnum* respond to burning? Is there a critical temperature at which *Sphagnum* cannot recover?

4. What short-term changes in blanket bog vegetation composition does fire bring about? Do changes have wider implications for carbon cycling?

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2. The Impact of Burning on CH_4 Fluxes and Ecosystem Respiration of Blanket Bogs

2.1 Abstract

Peatlands are the largest terrestrial carbon store in the UK and so it is important to understand the impacts of management practices such as burning, carried out deliberately in the UK to improve grazing and habitat provision for livestock and game, on peatland carbon cycling. Field studies have shown that fire increases both methane emissions from blanket bog as well as changing net ecosystem respiration, leading to the concern that fire has repercussions for the overall carbon budget of a bog, making them a net source rather than a net sink of carbon while increasing greenhouse gas emissions to the atmosphere. Here the results of a field based study using static chambers to measure methane fluxes and ecosystem respiration at three blanket bog sites in Scotland which had been subjected to fire are presented. The results show that fire had no significant effect on methane or ecosystem respiration when comparing burnt plots to adjacent unburnt plots sampled up to 2.5 years from time of burning. This indicates that quick moving “best practice” fires, which leave the moss layer largely intact and do not penetrate the peat at sites burnt infrequently (>20 year rotations) as per the fires studied here, do not significantly change methane fluxes and ecosystem respiration in the medium term. This shows that the impact of fire on methane and ecosystem respiration is variable as this contradicts previous findings. It is suggested that this is due to differences in fire behaviour and severity, making it important not to consider fire a uniform treatment.

2.2 Introduction

Peatlands are recognised as being globally important carbon stores holding as much as one third of soil carbon (Gorham, 1991) despite covering just 3% of the global surface (Kaat and Joosten, 2009). In the UK, peat soils are estimated to contain 3000 Mt of carbon (Smith *et al.*, 2007) making them the primary carbon store, with above ground vegetation in England, Scotland and Wales estimated to comprise just 114 million tonnes of carbon (Milne and Brown, 1997). The concern regarding fire on peatlands is that large amounts of carbon may be lost directly through the combustion of biomass, and indirectly by changing the physical environment, peat and vegetation (Turetsky *et al.*, 2002, Lindsay, 2010). Peatlands naturally sequester CO_2 from the atmosphere through primary production with plant biomass ultimately forming peat and effectively “locking up” carbon from the atmosphere. Peatlands, particularly those degraded by management and erosion, can be net emitters of CO_2 and CH_4 (Lindsay, 2010), important greenhouse gases which have increased in global atmospheric concentrations since the industrial revolution and now associated with driving observed and predicted global warming (IPCC, 2007). This makes it necessary to understand the impacts of management practices such as fire on peatlands as they could potentially affect the exchange of both CO_2 and CH_4 in the short and long term, changing the carbon dynamics of a peatland and ultimately their carbon storage potential.

2.2.1 Fire and the Peatland Carbon Cycle

The carbon which accumulates and ultimately gets stored in peat soils is sequestered from the atmosphere in the form of CO_2 through the process of photosynthesis (Figure 2. 1). In an active peat forming bog the build up of plant biomass is then either decomposed in the aerobic layers of the acrotelm or compressed and retained as organic carbon eventually reaching the more biologically inactive catotelm (Clymo 1984). *Sphagnum* spp. are recognised as the primary peat forming vegetation group, with the unique attributes of inhibiting decay through their ability to maintain acidic conditions by the production of phenols and uronic acids at cation exchange sites (Clymo and Hayward, 1982), and their ability to take up ammonia making it unavailable to microorganisms and the decay process (Painter, 1998). Primary productivity varies between vegetation groups and peatland type, with productivity on bogs greatest in bryophytes and shrubs while graminoids have greatest rates of productivity on poor fens (Moore *et al.*, 2002). Primary productivity is offset by autotrophic and heterotrophic respiration with the balance between primary productivity and ecosystem respiration (ER) important for making peatlands a net carbon sink or source. Abiotic factors such as height of the water table, and thus the extent of the aerobic zone, and soil temperature are important controls on heterotrophic respiration (Silvola *et al.*, 1996) and ER (Lafleur *et al.*, 2005) and ER has been found to be higher on some burnt peatlands (Ward *et al.*, 2007). However, whether a peatland is a long term sink or source of carbon does not simply equate to the net ecosystem exchange (NEE) of a system as carbon can also be lost naturally in the form of CH_4. The impact of burning on CH_4 emissions is particularly important to consider as CH_4 has a global warming potential 34 times that of CO_2 over a 100 year time horizon (IPCC, 2013).

The complex mechanisms controlling natural CH_4 fluxes in peatlands have been associated with both the physical conditions of a system and vegetation composition, with release to the atmosphere through various pathways (Figure 2. 1). CH_4 is produced from the breakdown of organic matter in the anaerobic waterlogged layer of the peat by a series of processes carried out by a consortium of micro-organisms. Firstly, organic polymers have to be hydrolysed by hydrolytic micro-organisms before being fermented by bacteria in a process known as acidogenesis. Homoacetogenic or syntrophic bacteria then produce acetates through acetogenesis of the fermented metabolites which go on to be consumed by methanogenic bacteria together with H_2 and CO_2, alcohols or methylated compounds, producing CH_4 (Garcia *et al.*, 2000). Methanogenic archaea are highly sensitive to oxygen and will only live in the anaerobic waterlogged layers of the peat making the hydrology of a peatland system critical for CH_4 production with the position of the water table having been demonstrated to correlate well with CH_4 fluxes (eg. Moore and Knowles, 1990, Shannon and White, 1991, Funk *et al.*, 1994, Whalen and Reeburgh, 2000). However, the position of the water table not only determines the extent of the anaerobic zone but also the aerobic zone above, the site of CH_4 oxidation by methanotrophic bacteria.

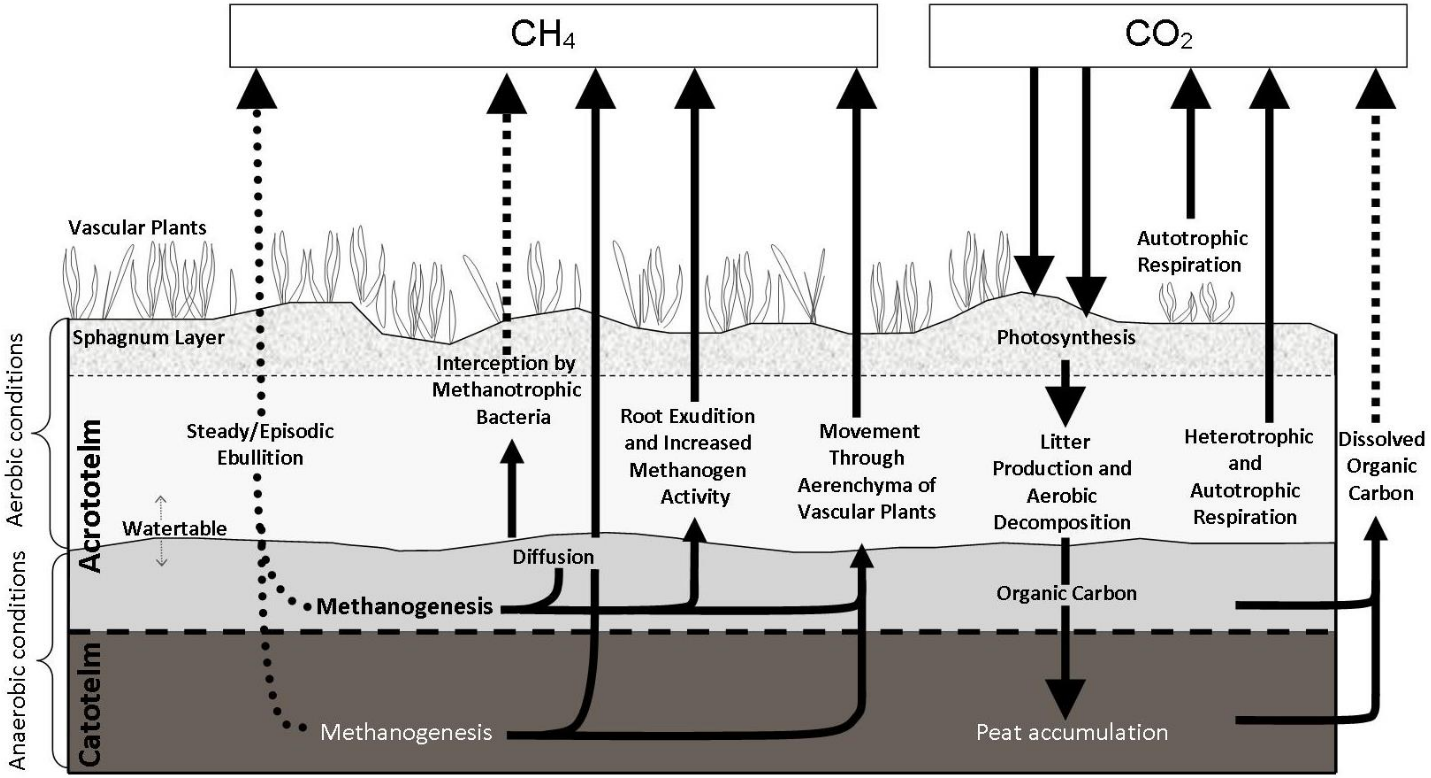

Figure 2. 1 The mechanisms for surface exchange of CO_2 and CH_4 in a peatland system.

Various controls on methanotrophic and methanogenic activity such as soil temperature, pH, osmotic pressure and substrate composition (Dunfield *et al.*, 1993, Garcia *et al.*, 2000, Bergman *et al.*, 1998) have been demonstrated and fire has the potential to change these conditions thus influencing CH_4 production and oxidation. For example, above ground biomass removal due to burning may increase soil temperatures, which can increase methogenesis (Rydin and Jeglum, 2006), by exposing the soil surface to solar radiation (Jury and Horton, 2004). Any loss of the *Sphagnum* layer could also potentially reduce the amount of CH_4 oxidised by the methanotrophs which reside there. The understanding of the effect of fire on the *Sphagnum* layer is limited but some studies have shown that the *Sphagnum* layer may experience biologically lethal temperatures (Davies, 2005, Glime, 2007) and can be consumed by a fire (Hamilton 2000). There is also limited research into the effect of fire on the bacterial community of peat soils, particularly the impact on methanogenic bacteria (Andersen *et al.*, 2013) but a general reduction in methanotroph population size together with an increase in the dominance of type II methanotrophs has been demonstrated on a burned *Calluna vulgaris* (L.) Hull (from herein referred to as *Calluna*) dominated peatland (Chen *et al.*, 2008). CH_4 can however also naturally bypass oxidation by methanotrophs in both the acrotelm and the *Sphagnum* layer, by travelling through much more direct pathways between the site of production and the atmosphere.

The most direct pathway for CH_4 loss to the atmosphere is through steady or episodic ebullition, where CH_4 rises through the acrotelm getting released as bubbles at the surface (Figure 2. 1). For CH_4 bubbles to be produced the partial pressure of all the gases in solution has to exceed the hydrostatic pressure of the peat (Chanton *et al.*, 1995) and grow in size (Kellner *et al.*, 2005) to create areas of over pressurised peat which release the bubbles to the surface by ejection or soil pore enlargement (Kellner *et al.*, 2004). Ebullition can be a significant pathway for the loss of CH_4 over short time scales from a system (Glaser *et al.*, 2004) and in some instances may be the most dominant pathway for CH_4 loss from a peatland (Coulthard *et al.*, 2009). The direct loss of CH_4 to the surface may also be facilitated by the movement of CH_4 through gas conduits in vegetation.

Some plants which have their roots in waterlogged anoxic soils have developed larger aerenchyma, internal chambers allowing the movement of gasses between the root and shoot (Jackson and Armstrong, 1999). Although facilitating the flow of oxygen to roots and rhizomes, the outward diffusion of oxygen from aerenchyma to the rhizosphere induces the intake of CH_4, thus acting as a conduit for CH_4 to travel through the plant to the atmosphere along a diffusion gradient (Jackson and Armstrong, 1999). A number of studies have shown how common blanket bog species which possess aerenchyma such as *Eriophorum* spp. can dramatically increase CH_4 emissions from the soil (eg. Schimel, 1995, Green and Baird, 2011). Fire can induce a change in the dominant vegetation from *Calluna* to *Eriophorum* spp. (Jackson and Armstrong, 1999, Stewart *et al.*, 2004, Ward *et al.*, 2007) which could increase direct movement of CH_4 to the surface. Wetland plants can also facilitate CH_4 transport when an internal/external pressure gradient exists resulting in the drawing up of CH_4 through the plant with release to the atmosphere through stomata or cuticle (Morrissey *et al.*, 1992, Jackson and Armstrong, 1999). This pressurised ventilation is commonly caused by thermo-osmosis, when gas flows from young tissue, which internally has a smaller pore diameter, to old tissue and rhizomes as a result of differences in internal and external temperatures (Grosse *et al.*, 1991, Whalen, 2005) and a humidity induced diffusion (Jackson and Armstrong, 1999). The role of vascular plants in the efflux of CH_4 from peatlands is also complicated by their ability to change the soil substrate and oxygen levels in the rhizosphere and influencing bacterial activity and CH_4 production and oxidation in the soil. Radial oxygen loss (ROL) increases oxygen levels in soil and thus may inhibit methanogenisis (Jackson and Armstrong, 1999). This can also favour methanotrophy which can only occur in the presence of oxygen (Chanton, 2005). However, vascular plants may also increase bacterial activity, including methanogenesis, in peatlands by increasing the availability of organic carbon through root exudation (Öquist and Svensson, 2002). This complex relationship between vascular plants and CH_4 production, oxidation and CH_4 release means understanding how fire may bring about changes in vegetation is not only important for the surface exchange of CO_2.

2.3 Aims

The aim of this study was to measure short term (<3 years) CH_4 fluxes and Ecosystem Respiration (ER) from areas of burnt blanket bog while concurrently measuring fluxes on adjacent unburnt control plots. Specifically, the study aimed to establish sampling sites in areas where fires had characteristics akin to those of management fires which follow the best practice guidance, namely being quick moving consuming mostly just the upper vegetation canopy and leaving the moss layer intact. In addition, vegetation composition, soil temperature, soil moisture and position of the water table were measured to see how well these measurements could explain observed fluxes and if any differences in these potential controls on carbon cycling could be found between burnt and unburnt blanket bog. It was intended that CH_4 fluxes be measured as soon as possible after a fire to determine if there was a short term increase in CH_4 emissions as has been found previously (Gray 2006). It was hypothesised that [1] CH_4 emissions would be significantly higher at burnt plots when compared to unburnt plots immediately after the fire, as seen by Gray (2006), when changes in the vegetation and abiotic conditions could be most different between treatments and [2] ER would be significantly different between burnt and unburnt plots due to the change in vegetation composition and abiotic factors brought about by fire. These assumptions led to hypothesis [3] that CH_4 and Ecosystem Respiration would be related to vegetation, water table position soil temperature and soil moisture conditions.

2.4 Methodology

2.4.1 Site descriptions

Three study sites were established across Scotland, in Caithness, the Eastern Grampians and in the Pentlands (Table 2. 1). First to be established in April 2011 was a wildfire site situated within the Flow Country, Caithness, Northern Scotland, 2km south of Forsinard (Appendix 2.1). Study plots were located within an area of *Sphagnum papillosum*/*Eriophorum vaginatum* dominated blanket bog, most closely attributed to the JNCC UK National Vegetation Classification (NVC) M17a *Scirpus cespitosus – Eriophorum vaginatum* blanket mire Drosera – Sphagnum sub community (further details on NVC classifications are given in Chapter 5). The site had been burnt by a wildfire most likely originating from a passing steam train on the nearby railway tracks. Although no information was available on the specific characteristics of the fire it was quick moving and consumed canopy vegetation and small discrete patches of the *Sphagnum* lawn and hummocks, but in the area sampled did not penetrate the peat. The climate at Forsinard can be described as cool and wet with mean annual temperatures of between 7.5-8.0°C with an annual precipitation ranging between 650-1000mm (Centre for Ecology and Hydrology, 2012). 12 plots were established at the site, on the southern edge of the fire, with 6 situated either side of the fire edge on burnt and unburnt ground.

Second to be established in March 2012 was a site situated on Eastside Farm in the Pentlands (Appendix 2.1). Dominated by *Calluna* and *Eriophorum vaginatum* the area is burned under a rotated muirburn regime primarily to maintain palatable grazing for sheep. The area sampled lies over peat between 40 and 125cm in depth with some wetter areas dominated by *Sphagnum capillifolium* (Ehrh.) Hedw. and *Sphagnum fallax* (Klinggr.) Klinggr. Historically drains have been cut in an effort to dry the area, however, over time some have become blocked resulting in a patchwork of wetter/dryer areas dominated by *Eriophorum spp.* and *Calluna* respectively. In the areas which were studied (*Calluna* dominated) the vegetation could best be described as NVC community M20b *Eriophorum vaginatum* mire: *Calluna vulgaris- Cladonia* sub community. A total of 14 randomly located plots were established at this site, 7 burnt and 7 unburnt plots. Unburnt plots were established on areas which did not naturally burn while others were located on areas where fire retardant hoods, made from fire retardant woven glass fibre material (FirePro PU28), had been placed to ensure areas remained unburnt throughout the burn area to act as controls. Annual rainfall in this region is 789mm (Ball *et al.*, 2012) with a mean soil temperature of 7.2°C during the study period.

Finally a site was established at the James Hutton Research Institute research farm and Environmental Change Network (ECN) site, Glensaugh, in the Eastern Grampians, Aberdeenshire (Appendix 2.1). Here experimental burn plots had been established for burning as part of a long term experiment to look at the impact of rotational burning on peatlands. 8 plots were situated at this site, 4 within an area burned as part of the experiment and 4 established on ground adjacent to the burnt area. The climate at the site has a mean soil temperature of 7.3°C (Levy *et al.*, 2012) and an annual rainfall of 1130mm (UK Environmental Change Network, 2012). This site differed slightly from the other two sites as at it lies on a north facing 9° slope with an NVC vegetation community best described as M20b *Eriophorum vaginatum* blanket & raised mire: *Calluna vulgaris – Cladonia spp.* sub-community.

Table 2. 1 Gas sampling site descriptions (See Appendix 2.1 for maps, images and dates of sampling)

Site Name	Location	Grid Ref	Date of Burn	Plots
Forsinard	Caithness	NX 884 408	18th April 2011	6 Burned, 6 Unburned
Eastside	Pentlands	NT 162 602	14th March 2012	7 Burned, 7 Unburned
Glensaugh	Eastern Grampians	NO 664 810	27th March 2012	4 Burned, 4 Unburned

As an indication of the difference in pre-burn fuel loads at Eastside and Forsinard unburnt plots adjacent to the burnt areas were harvested, split into the dominant plant types, dried and weighed (Table 2. 2). Glensaugh could not be harvested as it was part of a long term burning and grazing experiment. The primary difference in fuel load and structure was in the amount of woody shrubs, with Eastside having significantly more woody-shrub biomass than Forsinard, being primarily dominated by *Calluna*. Although Glensaugh could not be harvested, *Calluna* was similar in abundance to Eastside.

Table 2. 2 Dry weights of the most significant components of the vegetation from harvested plots adjacent to burned areas at Forsinard and Eastside as an indication of differences in fuel load and structure. Weights given are summed from 6 randomly sampled plots at each site covering a total area 0.9 m^2. For full details of the species making up each component see Chapter 5.

Site	**Graminoids**	**Shrubs**	**Sedges**
Forsinard	143g	12g	22g
Eastside	136g	126g	24g

2.4.2 Sampling Methodology

CH_4 fluxes were measured using closed static chambers comprising a plastic collar and metal lid, based on methodologies set out in Livingston and Hutchinson (1995). The chamber collars were made from 30 litre black polypropylene tree planting pots (SOPARCO, ScotPlant Direct, UK), 43cm in diameter (at the rim) and 23 cm in height (after the bottom 7cm sawn off to create the collar which could be sunk into the ground). Collars were situated across a range of dominant vegetation types/structures, although often limited to areas where a good seal could be made (ie.

where they could be sunk far enough into the peat, on average 11cm). A flat metal lid was clamped onto the collars using 10 x 15 cm spring ratchet clamps which compressed a ring of rubber draft excluder between collar rim and lid. Each lid had a 3 way valve (Discofix ® C 3-way Stopcock) secured and sealed within the lid and a 5cm length of flexible tubing (Bev-a-Line®) attached to the valve reaching within the chamber. Once the lid was sealed 100ml headspace samples were immediately removed (time zero) and on three more occasions thereafter at 15 to 30 minute intervals (with the time of sampling recorded accurate to within 3 seconds). The syringe was slowly pumped twice with the headspace air prior to each sample removal to aid headspace mixing within the chamber. Each sample was removed slowly to reduce the effect of the pressure change within the chamber, which could induce methane diffusion to the surface. 25ml glass vials were pre-sealed with an aluminium cap and pre-fitted silicone septa (National Scientific Company, Rockwood) and filled with the sample headspace air by using an additional needle inserted into the cap so the entire 100ml sample could be flushed through the vial, eliminating the need to pre-evacuate the vials. Both the additional needle and sample needle were removed from the cap before flushing was complete to ensure external air was not pulled into the vial. Immediately after sampling volumetric soil water content, referred to as soil moisture (SM), was measured using a Hydrosense™ 20cm probe (Hydrosense™ CS620, Campbell Scientific) and soil temperature (ST) recorded using a digital temperature sensor with 12cm probe (Digitron 2080R, Sifam Instruments Ltd.), both measurements being taken in the soil inside each chamber. Dipwells made from 4cm diameter plumbing pipe between 80cm and 120cm in length, with 6mm holes drilled on three sides every 12cm down their length, were sunk vertically into the peat adjacent to each chamber. The distance to the water table (WT) was measured as the distance from the surface of the peat/moss interface to the surface of the water in each dipwell. Headspace volume of each chamber was estimated by measuring the depth of each chamber (distance from the rim of the chamber to the ground) at 5 locations in the chamber. The ground was defined as the point a ruler could not easily be pushed down any lower so included areas of dense vegetation with little airspace, as well as the point at which the ruler hit the peat surface. Volume (m3) was calculated using equation 2.1, where A is the area of chamber and mD is the mean depth of the chamber.

$$v = A \times mD$$

Eq 2. 1

2.4.3 Gas Chromatography

Samples were analysed within 7 days from time of sampling using a Gas Chromatograph fitted with a flame ionisation detector (HP5890 Series II, Hewlett Packard, Agilent Technologies UK Ltd, Stockport, UK) and 50 sample autosampler (Genesis Headspace Sampler, Varian®). To calculate concentrations of the field samples four standard gases were used with known concentrations of CO_2 and CH_4. These standard samples were analysed at the start and end of each run of field samples and every 12 field samples throughout an analysis run to minimise the effect of any drift in the voltage signal of the gas chromatograph. The area under each output peak (in mV) of each sample was calculated using Clarity Chromatography

Software (v.3.0.6.589). A linear regression was used to calibrate the peak area with the known concentrations of the four standard samples. This allowed the calculation of the concentrations of CO_2 and CH_4 in the unknown field samples.

2.4.4 Flux Calculations

Using the calculated concentrations of each field sample and the recorded time of sampling, a flux could be calculated for each chamber using the software GCFlux V2 (Levy, 2012). To calculate a flux in µmol m^2 s^{-1} equation 2.2 was used where: dC is the initial rate of change in concentration (µmol mol^{-1}), dt is the rate of change in time (s), p is the density of air (mol m^3), V is volume of the chamber headspace (m^3) and A is the surface area of the soil or vegetation (m^2) (Levy *et al.*, 2011).

$$Flux\ (umol\ m^2\ s^{-1}) = \frac{dC}{dt} \times \frac{pV}{A}$$

Eq 2. 2

To establish if CH_4 fluxes were linear, CO_2 sample concentrations, valid in respect to errors in sampling or from the sealing efficiency of the chambers, were used as a comparison. Where CO_2 fluxes were positive and looked linear, with no drop in concentration over time, it was assumed that the chambers had sealed well and therefore the CH_4 concentrations calculated were valid. Where an unexpectedly low concentration of CO_2 was found for a sample, departing from a general increase in CO_2 over time, the sample was rejected and not used when calculating CH_4 fluxes as it was assumed there was an error when sampling. Likewise, if no steady increase in CO_2 was observed, with concentrations staying around ambient, it was assumed the chamber was not sufficiently sealed and the CH_4 flux calculated for the chamber was not valid and omitted from further analysis.

2.4.5 Vegetation Assessment

Flux measurements were repeated on the same plots at each site for a period of up to two and a half years, with harvesting of plant biomass on the final day of sampling (766 days since the site was burned at Forsinard and 439 days at Eastside). Plots at Glensuagh could not be harvested as they were within the boundary of a long-term grazing experiment so vegetation could not be disturbed on site. Vegetation at each plot was separated from the peat surface and removed. Within 2 days the vegetation was sorted into species with *Calluna* and graminoids further sorted into “green” and “woody/brown” components. To measure dry weight each sub-sample was dried in an oven at 70°C for a maximum of 12 days or until samples no longer lost weight and weighed. Prior to drying, the leaf area of 3 leaves/blades of each species (3 samples of green leaves and finer branches in the case of *Calluna*) were measured using an area meter (Licor LI3100C, Licor) and weighed once dried to allow for a calculation of leaf area (cm^3) per gram dry weight (g_{dw}). Total leaf area of each species could then be extrapolated from total dry weight per species. Percentage cover of *Sphagnum spp.* per plot was used in the analysis instead of leaf area which could not be accurately calculated.

To evaluate the relationship between vegetation composition and CH_4 fluxes and ER only fluxes measured on the final day of sampling were used. It was not deemed appropriate to compare the vegetation data to fluxes calculated across the whole sampling period due to changes in vegetation over time, particularly in the burnt plots.

2.4.6 Statistical Analysis

Paired two-sample t tests were used to compare SM, ST and WT between burned and unburned plots measured on the same day. When the data was not normally distributed, or when sample sizes were small (such as at the Glensaugh site), a Wilcoxon signed rank test was used. One-Way Analysis of Variance (ANOVA) was used to show any significant differences in ST, SM and WT between sites and CH_4 and ER between sites.

In order to evaluate any treatment effect, as well any relationship with measured abiotic factors, on CH_4 and ER, linear mixed effects models were used to allow for the dependence of the calculated fluxes, as they were repeated measurements made at the same plots over time. By allowing for random effects the models could also be used to evaluate within and between site variation in fluxes. CH_4 fluxes and ER were log transformed to meet model assumptions and modelled separately with the same fixed and random effects terms (Table 2. 3). Random effect terms were assessed first using Akaike Information Criterion (AIC) computed from Restricted Maximum Likelihood (REML) parameter estimates with the amount of variance explained by each term in the model assessed and terms discarded until a model was established which had the smallest AIC and composed of the most relevant random effect terms. As there was only one fixed effect (treatment) this was kept in all models to show its significance with a Wald test. All statistics were carried out using the statistical program R (v R i386 3.0.1) (R Core Team, 2013) with mixed effects modelling computed using the package lme4 (Bates *et al.*, 2013).

Table 2. 3 Fixed and random effects terms used in mixed effects modelling of CH_4 fluxes and ecosystem respiration (ER).

Model Term	**Abbreviation**	**Description**
Fixed Effects		
Treatment		Burnt or unburnt
Random Effects (accounting for variance within Treatment)		
Plot	P	Plot
Day	D	The day plots were sampled given as the number of days since the site had been burnt
Site	S	Site
Water table	WT	Distance from height of water within dipwell to peat surface (cm)
Soil Moisture	SM	Volumetric soil water content (%)
Soil Temperature	ST	Temperature of the soil at each plot (^oC)
Site:Plot	S:P	Plot nested within Site to specify variance between plots at the same site
Site:Day	S:D	Day nested within Site to specify variance between days at the same site

2.5 Results

2.5.1 Soil Moisture, Water table and Soil Temperature

Measurements were made across a range of conditions; soil temperature varying from 3^oC to 10^oC, soil moisture from 20 to 100% and water table position 36cm below the surface to being at the surface (Appendix 2.2). In general measurements were made in drier conditions at Glensaugh (F*(2,339)=14.74,* *p=<0.001*) while a wider range of soil temperatures were recorded at Eastside. Soil temperature, soil moisture and position of the water table varied between plots, with a strong seasonal pattern found for soil temperature with warmer temperatures seen during summer months. Greatest variation in water table position was found between plots at Eastside, with the most homogeneous conditions found in the plots at Forsinard. No significant differences in soil temperature, soil moisture or water table position were found between burnt and unburnt plots at any site.

2.5.2 CH_4 Fluxes

CH_4 fluxes ranged from 0.03 to 557.60 nmol m^2 s^{-1} and were significantly different between sites (F*(2,160)=6.3, p=0.01*) and varied considerably between plots and over time (Table 2. 4, Appendix 2.3). However, the linear mixed effects modelling showed no significant treatment effect on the measured fluxes at any site (Figure 2. 2, Table 2. 5). The random effects which best accounted for variation in fluxes were plot, day, water table and soil temperature. Plot to plot variation within site explained the most variance (Figure 2. 3) but the amount of residual variation suggests there was a lot of variation not accounted for by the model (Figure 2. 3). Despite being a component of the most appropriate model with the lowest AIC soil temperature and water table accounted for little of the variation in fluxes.

Table 2. 4 CH_4 fluxes at each site and treatment (nmol m^2 s^{-1}±StE)

Site	Plots	Min	Max	Mean
Eastside	All	0.03	557.60	30.4±11.1
	Burnt	0.03	557.60	45.1±23.3
	Unburnt	0.08	164.10	17.9±15.5
Forsinard	All	0.99	43.65	14.6±1.3
	Burnt	0.99	41.12	16.3±1.9
	Unburnt	1.25	43.65	12.8±1.8
Glensaugh	All	0.24	98.59	20.8±4.8
	Burnt	0.24	29.32	13.9±5.6
	Unburnt	0.49	98.59	26.7±7.5

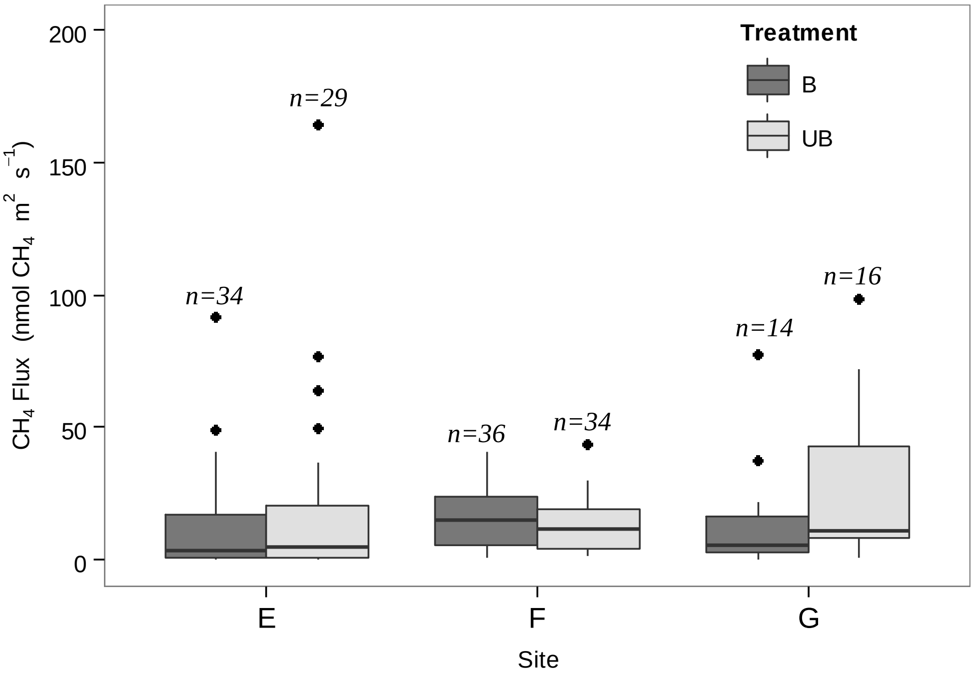

Figure 2. 2 CH_4 fluxes at each site (E=Eastside, G=Glensaugh, F=Forsinard) under each treatment where bold lines show median value, horizontal edges of boxes upper and lower quartiles, end of lines smallest and largest values and outliers circles. Only valid samples used in analysis (n). Positive numbers indicate CH_4 release to the atmosphere.

Table 2. 5 Results of linear mixed effects model of CH_4 fluxes with the optimum model selected using AIC criteria to determine random and fixed effects. Model with the lowest AIC criteria and thus largest negative delta AIC (ΔAIC) was selected.

Model	AIC	ΔAIC
Random Effects		
P+D+[S:D]+S+[S:P]+WT+ST+	582.6	–
SM	**580.6**	**-2.0**
P+D+[S:D]+S+[S:P]+WT+ST	580.9	-1.7
P+D+[S:D]+S+[S:P]+WT	581.4	-1.2
P+D+[S:D]+S+[S:P]	587.6	+5.0
P+D+[S:D]+S	585.6	+3.0
P+D+[S:D]	583.6	+1.0
P+D	613.9	+31.3
P		
Fixed Effects		
Treatment	580.3	–

Wald Test of Final Model

Fixed Effect Treatment *Random Effect* P+D+[S:D]+S+[S:P]+WT+ST

	Chi Sq	Df	P value
Treatment	0.4905	1	0.4837

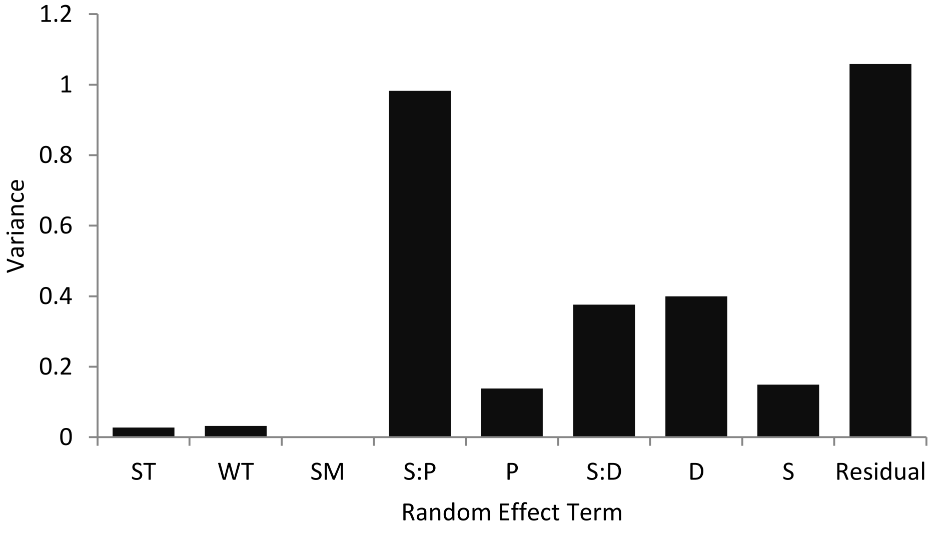

Figure 2. 3 The amount of within treatment variance explained by the different random effects terms in the largest CH_4 mixed effect model described in Table 2. 5. The only random effect to be removed from final model was soil moisture (SM).

2.5.3 Ecosystem Respiration

Ecosystem Respiration (ER) between the ranges of 0.04 and 5.96 µmol m^2 s^{-1} were recorded across the sites (Table 2. 6, Figure 2. 4). ER varied between sites and sampling days (Appendix 2.4) with Treatment not a significant fixed effect term in the linear mixed effects model (Table 2. 7), although on one occasion at Eastside and one at Glensaugh ER was significantly higher on the unburnt plots recorded at day 5 and 440 days after the fire respectively (Appendix 2.4). The most appropriate model with lowest AIC included the random effects terms describing variation between days within sites (S:D) and variation between plots within site (S:P). In contrast to the CH_4 model there was less residual variation and the abiotic conditions (ST, WT and SM) accounted for little or no variation in ER (Figure 2. 5). There was a significant difference between sites (F*(2,121)=12.54, p=0.0007*) with ER lowest at Eastside and highest at Glensaugh where there were some particularly high values recorded (Figure 2. 4).

Table 2. 6 ER at each site and treatment (µmol m^2 s^{-1})

Site	**Plots**	**Min**	**Max**	**Mean±StE**
Forsinard	All	0.04	4.57	1.68±0.21
	Burnt	0.05	3.88	1.83±0.34
	Unburnt	0.04	4.57	1.50±0.35
Eastside	All	0.07	2.62	0.89±0.09
	Burnt	0.11	2.23	0.79±0.11
	Unburnt	0.07	2.62	0.99±0.13
Glensaugh	All	0.44	5.97	1.91±0.21
	Burnt	0.44	4.72	1.63±0.30
	Unburnt	0.79	5.97	2.16±0.30

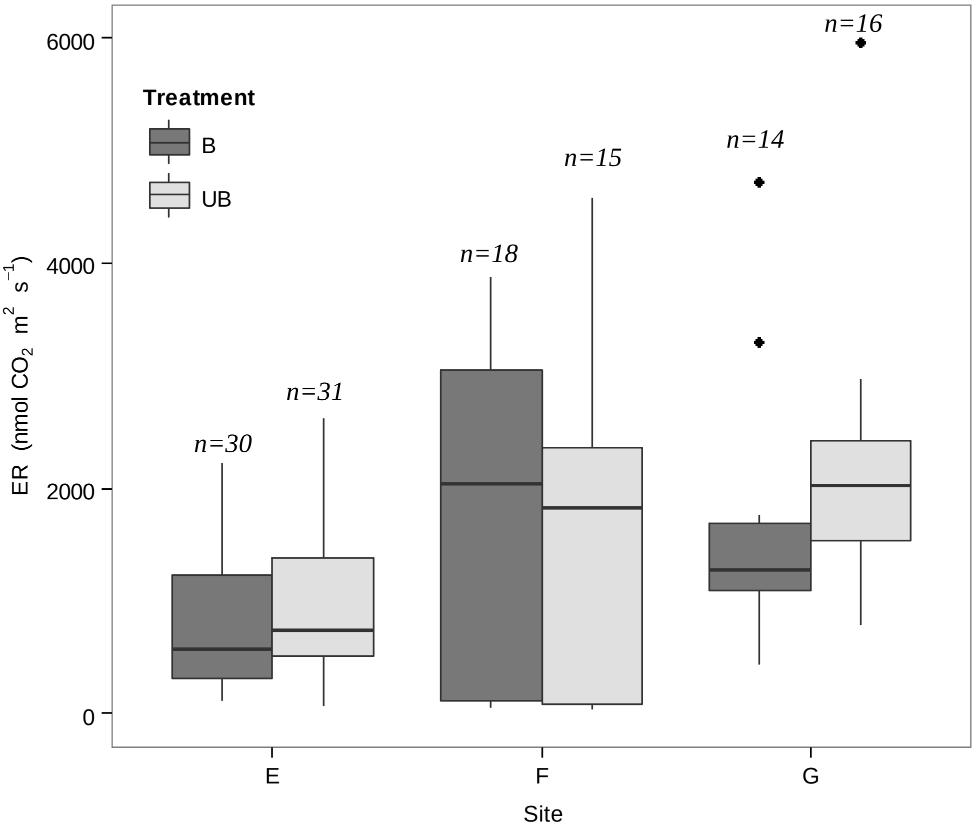

Figure 2. 4 Ecosystem Respiration (ER) at each site (E=Eastside, G=Glensaugh, F=Forsinard) under each treatment where bold lines show median value, horizontal edges of boxes upper and lower quartiles, end of lines smallest and largest values and outliers circles. Only valid samples used in analysis (n). Positive numbers indicate CO_2 release to the atmosphere.

Table 2. 7 Results of linear mixed effects model of ER with the optimum model selected using AIC criteria to determine random and fixed effects. Models with the lowest AIC criteria and thus largest negative delta AIC (ΔAIC) were selected.

Model	**AIC**	**ΔAIC**
Random Effects		
D+[S:D]+[S:P]+S+ST+P+SM+	289.2	–
WT	287.2	-2.0
D+[S:D]+[S:P]+S+ST+P+SM	285.2	-4.0
D+[S:D]+[S:P]+S+ST+P	283.5	-5.7
D+[S:D]+[S:P]+S+ST	283.9	-5.3
D+[S:D]+[S:P]+S	**282.0**	**-7.2**
D+[S:D]+[S:P]	296.3	+7.1
D+[S:D]	294.3	+5.1
D		
Fixed Effects	279.7	–
Treatment		

Wald Test of Final Model

Fixed Effect Treatment *Random Effect* D+[S:D]+[S:P]

	Chi Sq	**Df**	**P value**
Treatment	0.654	1	0.4187

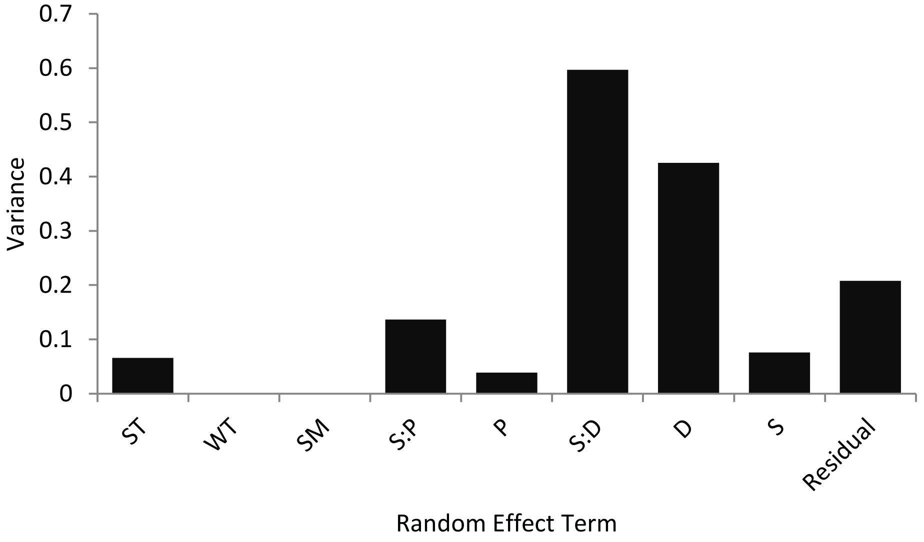

Figure 2. 5 The amount of within treatment variance explained by the different random effects terms in the largest ER mixed effect model described in Table 2. **7**.
The only random effect terms kept in the final model were D, S:D and S:P.

2.5.4 Fluxes and Vegetation

No clear relationship was found between any measure of vegetation (biomass, leaf area or species composition) and CH_4 fluxes or ER at Forsinard or Eastside (Glensaugh was not harvested) (Figure 2. 6, Figure 2. 7) even when included as random effects in the linear mixed effects models of CH_4 emissions and ER (not reported). A more detailed discussion of vegetation composition at the sites is given in Chapter 5 but in general *Sphagnum* spp. cover was greatest at Forsinard with only 3 plots at Eastside containing *Sphagnum* spp and similar ranges of total vascular plant biomass, leaf area and *Eriophorum* spp. dry weight were found at the two sites. The vegetation at the two sites did match to different National Vegetation Classification sub communities, with the greatest uniformity in vegetation found between the plots at Forsinard.

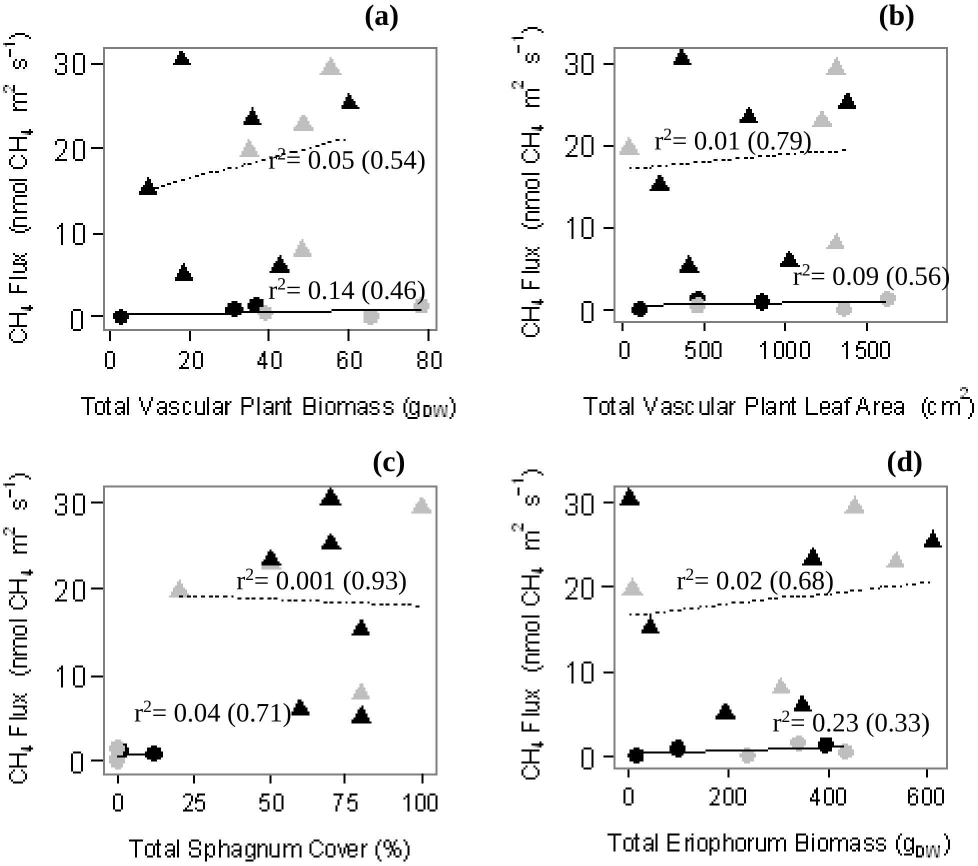

Figure 2. 6 Methane fluxes at each plot plotted against (a) total vascular plant biomass, (b) total vascular plant leaf area, (c) total percent *Sphagnum spp.* cover and (d) total *Eriophorum spp.* dry weight with r^2 values and p values (shown in brackets). Triangles represent Forsinard plots (n=10), circles Eastside (n=6), black points burnt plots and grey unburnt.

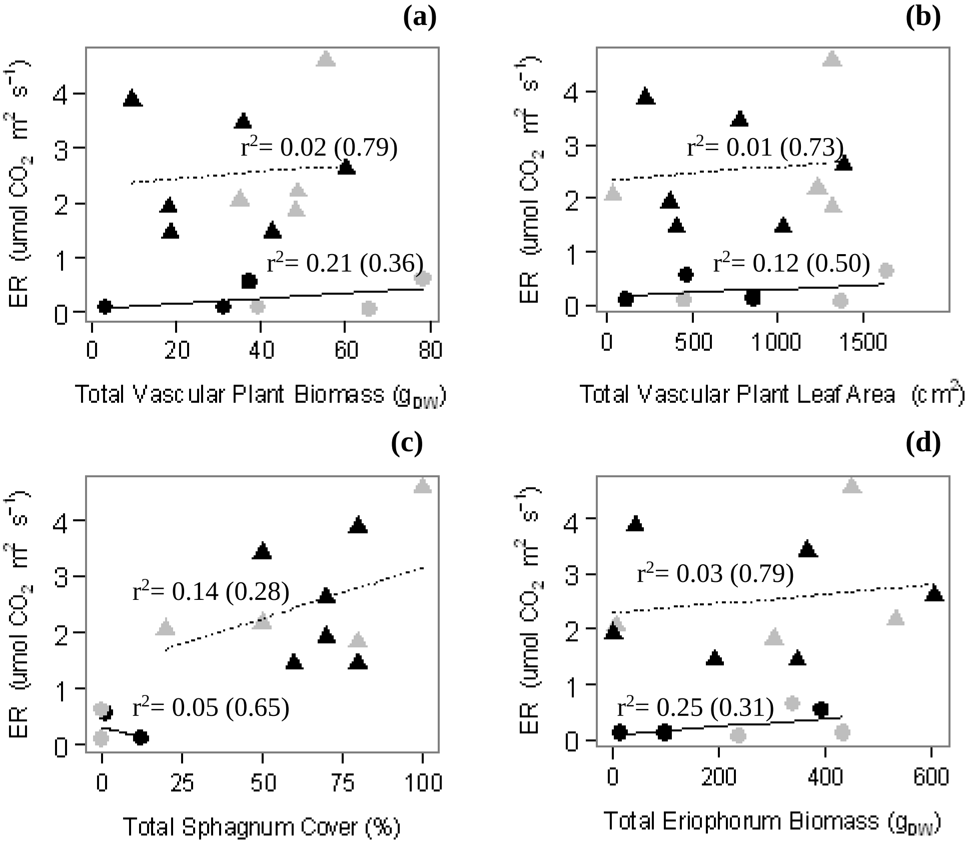

Figure 2. 7 Ecosystem Respiration (ER) at each plot plotted against (a) total vascular plant biomass, (b) total vascular plant leaf area, (c) total percent *Sphagnum spp*. cover and (d) total *Eriophorum spp*. dry weight with r^2 values and p values (shown in brackets). Triangles represent Forsinard plots (n=10), circles Eastside (n=6), black points burnt plots and grey unburnt.

2.6 Discussion

2.6.1 CH4 fluxes

There was no significant difference in CH_4 fluxes between burnt and unburnt control plots at any of the three sites studied. Fluxes recorded are consistent with those previously reported on blanket bog in the UK (eg. Hargreaves and Fowler, 1998, Ward *et al.*, 2007, Dinsmore *et al.*, 2009, Loyd, 2010, Levy *et al.*, 2012, Stockdale, 2012) and were of a similar range as those recorded by Gray (2006) at an area of blanket bog which had been burned close to the area studied here at Forsinard. Therefore hypothesis [1], CH_4 emissions would be significantly higher in burnt plots when compared to unburnt plots, has to be rejected. Previous studies which have measured CH_4 fluxes on burnt and unburnt blanket bog have been contradictory and shown that burning was both associated with an increase in CH_4 emissions immediately after burning as with Gray (2006), and a reduction in CH_4 emissions on burnt plots when compared to unburnt plots (Ward *et al.*, 2007). Taken with the results of this study the effect of burning on CH_4 fluxes therefore still seems to be inconsistent.

Determining the effect of fire on blanket bog is confounded by fire not being a standard treatment, instead one which varies in its severity (Hobbs and Gimingham, 1984) and frequency (Yallop *et al.*, 2006), both factors which may influence the impact of fire on an ecosystem (Schimmel and Granstrom, 1996, Neary *et al.*, 1999). Ecosystem response to fire may also be related to ecosystem state and vegetation structure and composition pre-burn (Davies *et al.*, 2010). This makes it necessary to put the fires studied here into context as they did not affect the peat and consumed little of the moss layer, removing just the top canopy shrubs and graminoids. Therefore, the results imply that fires which have no impact on the substrate do not affect CH_4 fluxes of blanket bogs in the medium term (less than three years as measured here). It has been widely shown that fires which do penetrate the peat cause significant carbon loss to the atmosphere (Turetsky and Wieder, 2001, Davies *et al.*, 2013) and it is important to reiterate the distinction between these types of fire and the fires studied here.

In addition to the characteristics of a fire, it may also be important when considering the long term impacts of a fire on vegetation and carbon cycling to consider fire history. The sites studied here are all likely to have seen some managed burning and wildfires in the past, but not at the frequency of the site studied by Ward *et al.* (2007). Frequent burning and its potential to induce changes in vegetation composition (Gray, 2006, Worrall *et al.*, 2007, Ward *et al.*, 2012) promoting aerenchymatous species such as *Eriophorum angustifolim* (Jackson and Armstrong, 1999, Stewart *et al.*, 2004, Ward *et al.*, 2007), may be important in explaining associated increases in methane emissions from blanket bog post burn in the long term, by increasing plant mediated transport to the atmosphere. Although this study did not show any relationship between CH_4 fluxes and cover or biomass of vegetation, fluxes were measured in the dark so the lack of correlation between the aerenchymatous *Eriophorum spp.* and CH_4 fluxes as has been demonstrated previously (McNamara *et al.*, 2008) could be a result of reduced active transport of CH_4 brought about by the closure of stomata (Frye *et al.*, 1994, Thomas *et al.*, 1996), although others have reported no differences in steady CH_4 flux in light and dark phases (Green and Baird, 2011). Overall the results here suggest that vegetation was not a good indicator of CH_4 emissions at the sites studied, a rejection of hypothesis [3], with the considerable variation in fluxes both between sites and sampling days more associated with abiotic conditions which did vary considerably both spatially and temporally.

Measured CH_4 fluxes have been shown to relate to the interplay between conditions such as the position of the water table and the vegetation within a chamber (Dinsmore *et al.*, 2009), so the large variability in conditions between sites, plots and sampling date may perhaps mask any more subtle associations between CH_4 and vegetation. The CH_4 fluxes recorded here varied considerably over time, between plots and sites with plot to plot variation within site explaining the greatest amount of variance in the mixed effects model. This high variability in CH_4 emissions has been commonly reported by studies which have measured CH_4 over longer periods (Lai, 2009)

Despite the position of the water table and soil temperature not being measured continuously, being more “snap-shot” measurements with some seasonal bias due to the dates of sampling, both were significant random effect terms in the model. This is consistent with the literature where water table and soil temperature have been found to correlate with CH_4 emissions (Moore and Knowles, 1990, Shannon and White, 1991, Funk *et al.*, 1994, Hargreaves and Fowler, 1998, Whalen and Reeburgh, 2000, Rydin and Jeglum, 2006). This, to a large extent, can help explain the significance of sampling date, plot and site in the models as conditions varied at all these scales. The model does however also suggest that using water table or soil temperature alone as indicators of CH_4 emissions, particularly when upscaling to estimate, for example annual or catchment carbon budgets, may underestimate the variability in emissions as there was a large amount of residual variation not explained by the model here.

2.6.2 Ecosystem Respiration

ER was found to be significantly lower on burnt plots compared to unburnt plots on two occasions from a total of 13 sampling days, but after considerably different periods of time from when the sites were burnt suggesting no trend in treatment effect. However, when taking the results of the model into account hypothesis [2] has to be rejected as ER of burnt plots was not significantly different to those of unburnt control plots in the vast majority of sampling times, with treatment not significant when considered a fixed effect and sampling date, site, plot and measured abiotic variables random effects in the model. This contradicts previous findings by Ward *et al.* (2007) who found that ER was higher at a site burned every 10 years compared to a no burn control site at the Hard Hill experiment at Moor House. Clay *et al.*, (2010) at the same site also found that burning had a significant effect on ER but only in conjunction with grazing. The results here show that fire did not have an effect on ER and contradicts the finding of Clay *et al.*, (2010) as both Glensaugh and Eastside were also grazed. The fires studied here were of course quick moving low severity fires which may make them different to those experienced at Hard Hill and again reiterates the importance of taking the characteristics of a fire into account when discussing the impact of a fire on carbon cycling.

As with the CH_4 fluxes recorded, ER varied between sites and sampling days and falls within the ranges previously reported for blanket bogs (eg. Bubier *et al.*, 1998, Bubier *et al.*, 2003, Lafleur *et al.*, 2005, Gazovic *et al.*, 2013, Strack *et al.*, 2014) including those recorded by Ward *et al.* (2007) at Hard Hill. The significance of sampling day found here is consistent with previous studies which have also found ER to vary significantly between sampling days as well as season and year (Ward *et al.*, 2007, McNamara *et al.*, 2008). Thermal regime and hydrology are considered important controls on soil respiration (eg. Bridgham and Richardson, 1992, Silvola *et al.*, 1996, Scanlon and Moore, 2000, Reichstein *et al.*, 2003) and will both vary over different temporal and geographic scales as was the case at the three sites studied here. Although the results here did not show any significant relationship between ER and soil temperature, water table or soil moisture this is not inconsistent with previous field studies on peatlands which have found no, or only weak, correlations between ER and thermal and hydrological regimes (Updegraff *et al.*, 2001, Lafleur *et al.*, 2005, Dimitrov *et al.*, 2010) with complex relations between the two (Bubier *et al.*, 2003, Lafleur *et al.*, 2003). There are also further interactions between ER and vegetation composition and micro-habitat (Bubier *et al.*, 2003). Previous research has shown for example that some species such as *Eriophorum* spp. (McNamara *et al.*, 2008) and *Juncus* spp. (Stockdale, 2012) are associated with higher ER than *Sphagnum* spp. and grasses. Here, however, no strong correlations between ER and *Eriophorum* spp. biomass, leaf area or any of the measures of vegetation were found so Hypothesis [3], ER would be related to vegetation, water table position soil temperature and soil moisture conditions, must also be rejected in this instance.

2.7 Conclusions

The hypotheses that CH_4 emissions and ER would be significantly higher in burnt plots, when compared to unburnt plots, immediately after a fire have to be rejected as there was no significant treatment effect detected when spatial and temporal variation were taken into account. Although a weak correlation was found between CH_4 emissions and position of the water table and soil temperature they did not vary significantly between treatments which means the results suggest that fires that do not change these conditions, for example by penetrating the peat increasing oxidation and drying, do not affect CH_4 emissions. There were no correlations found between CH_4 emissions and measures of vegetation, including the abundance of aerenchymatous species commonly associated with greater CH_4 emissions. This suggests that when considered alone fire induced changes in abundance of species such as *Eriophorum* spp. may not always result in an increase in CH_4 emissions.

Although this study only considers two components of a blanket bogs carbon cycle, CH_4 emissions and ER, important conclusions can be drawn which have a wider relevance. The results presented here show that there are complex controls on both CH_4 emissions to the atmosphere and ER, of which the fires here did not significantly modify to give a significant treatment effect. This means that the impact of fire on the carbon cycling of blanket bogs is difficult to predict, particularly if the characteristics of a fire, such as the extent it penetrates the peat and damages the moss layer, are not taken into consideration. The results here also contradict results from the Hard Hill experiment suggesting that the fires, the burning rotation times and site conditions may not be representative of fires on blanket bog burned for management purposes in differing circumstances. This shows the need for studies to be carried out over a wider geographic area, particularly pertinent when seeing the variability in CH_4 and ER between the three sites studied here.

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Appendix 2.1. Field Sites: Maps, Photographs and Sampling Times

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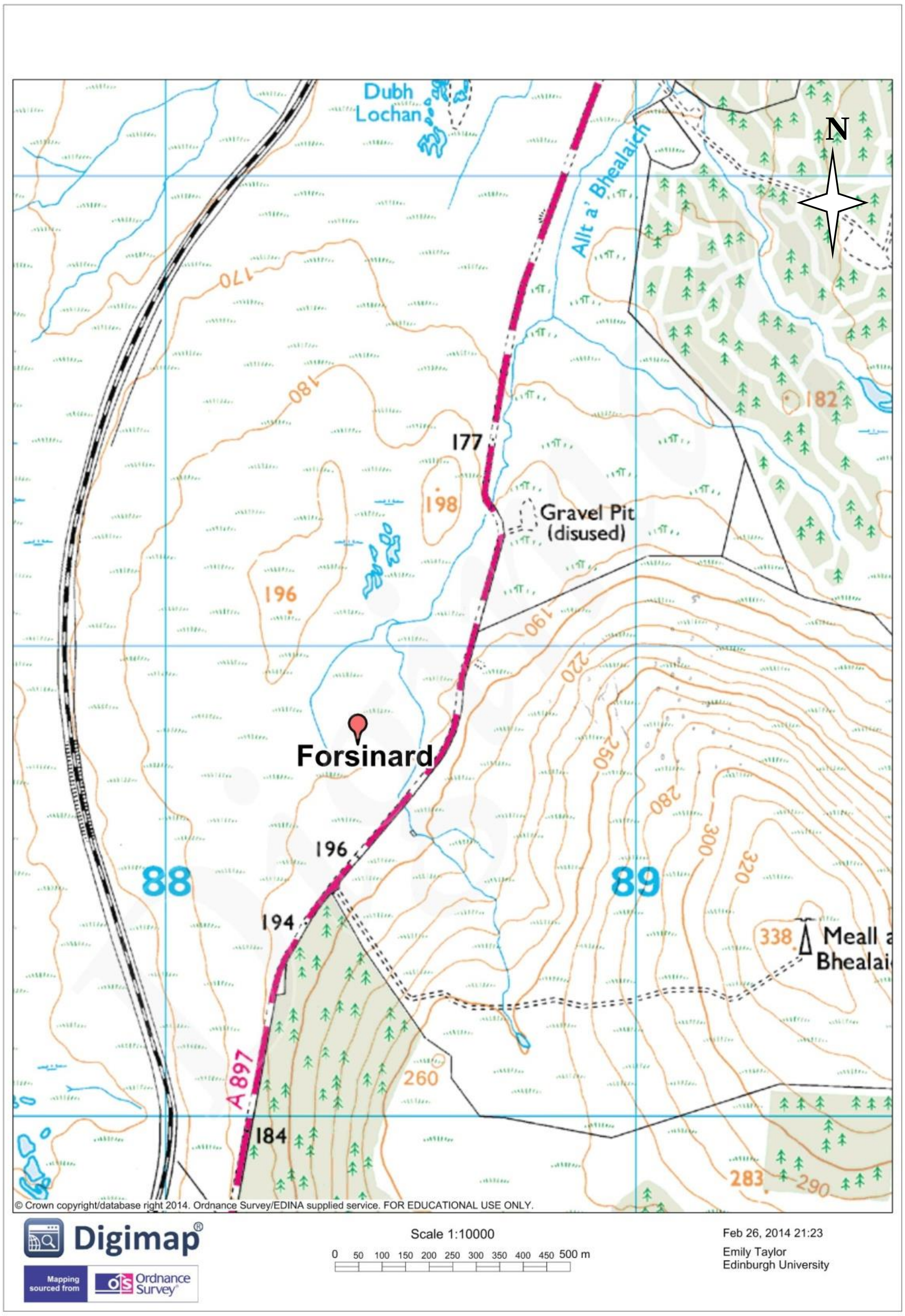
Emily Taylor
Edinburgh University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Gravel Pit (disused)
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Forsinard
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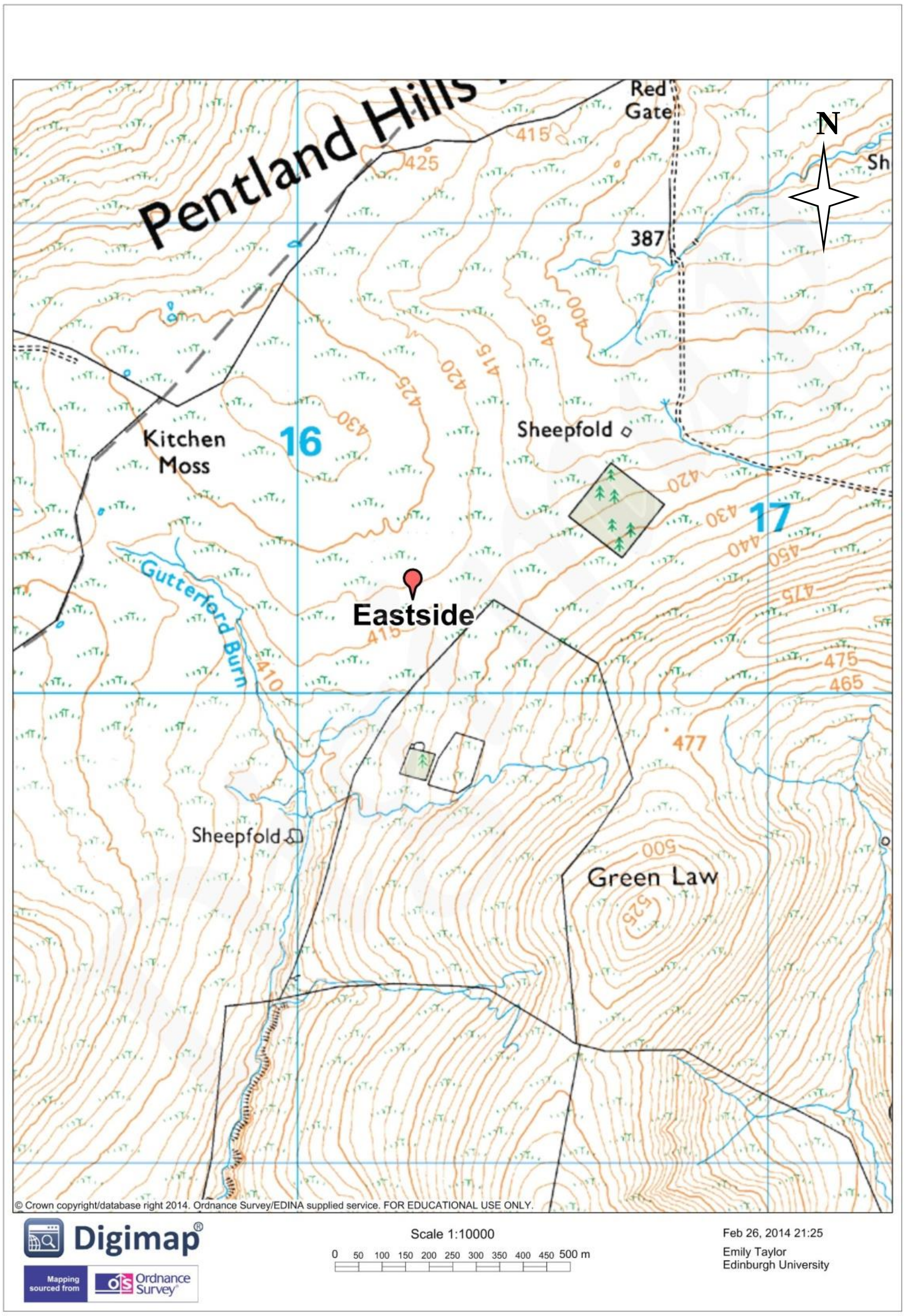
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Gutterford Burn
Eastside
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Sheepfold
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Green Law
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Edinburgh University

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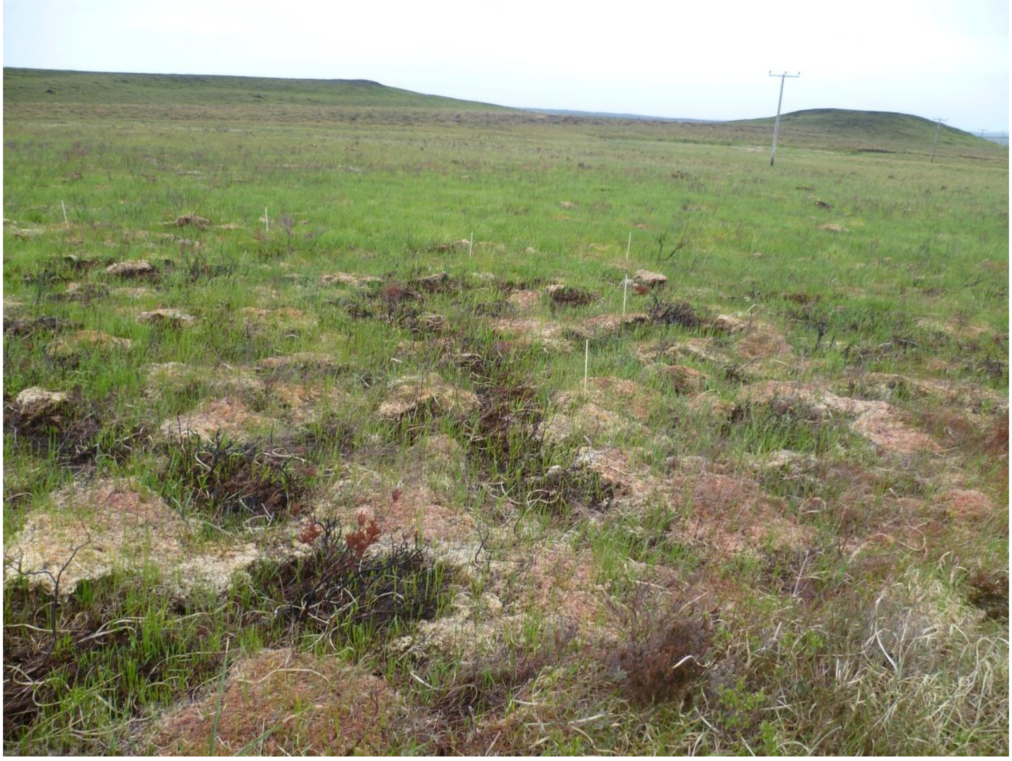


Area sampled at Forsinard following the fire in April 2011. This photograph was taken 38 days after the area was burned.

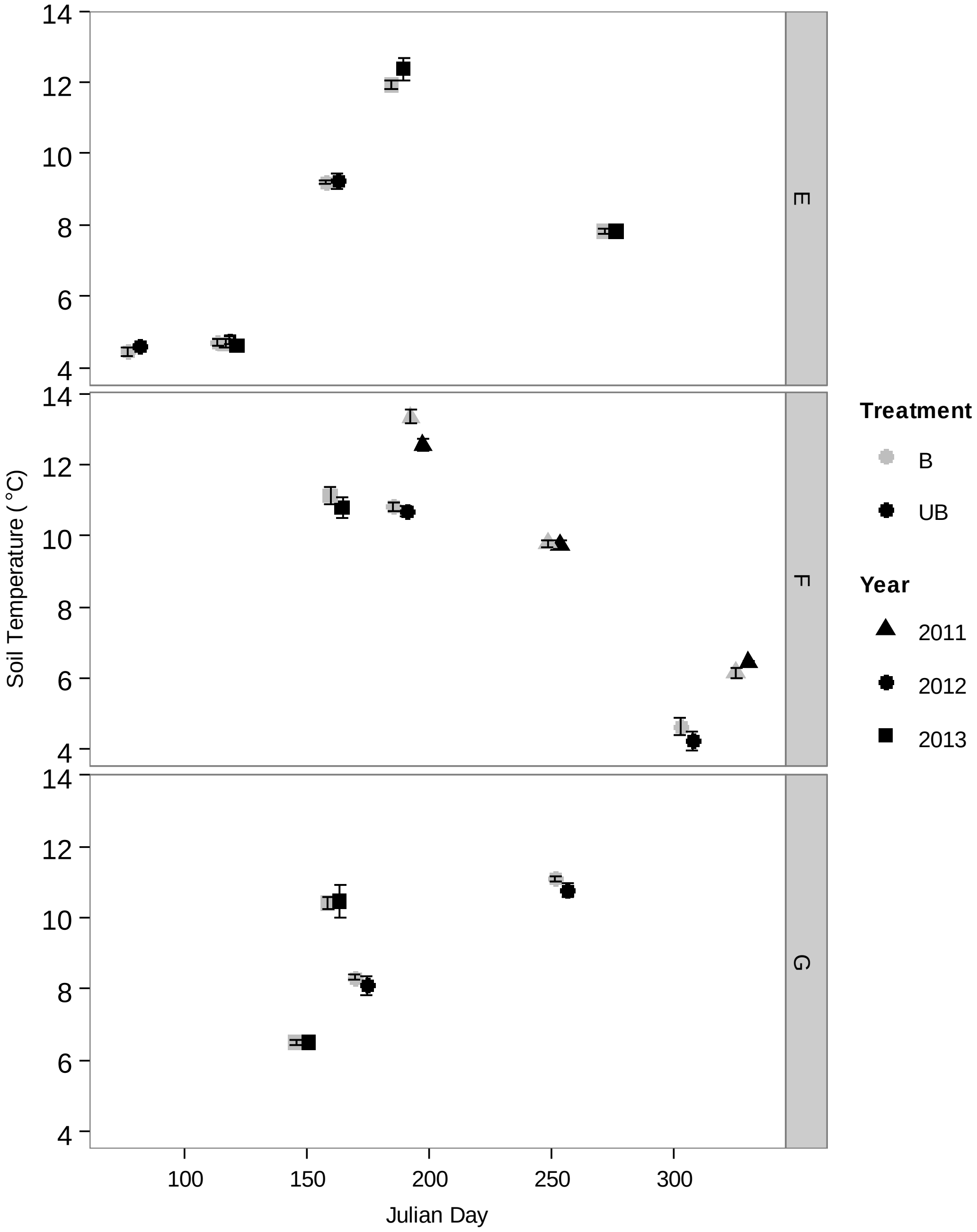
The area sampled at Eastside, immediately after the site was burned.

The area sampled at Glensaugh 81 days after the area was burned. Middle area shows the fire break, swiped prior to burning, with the area to left unburnt and the area to the right the burnt area.

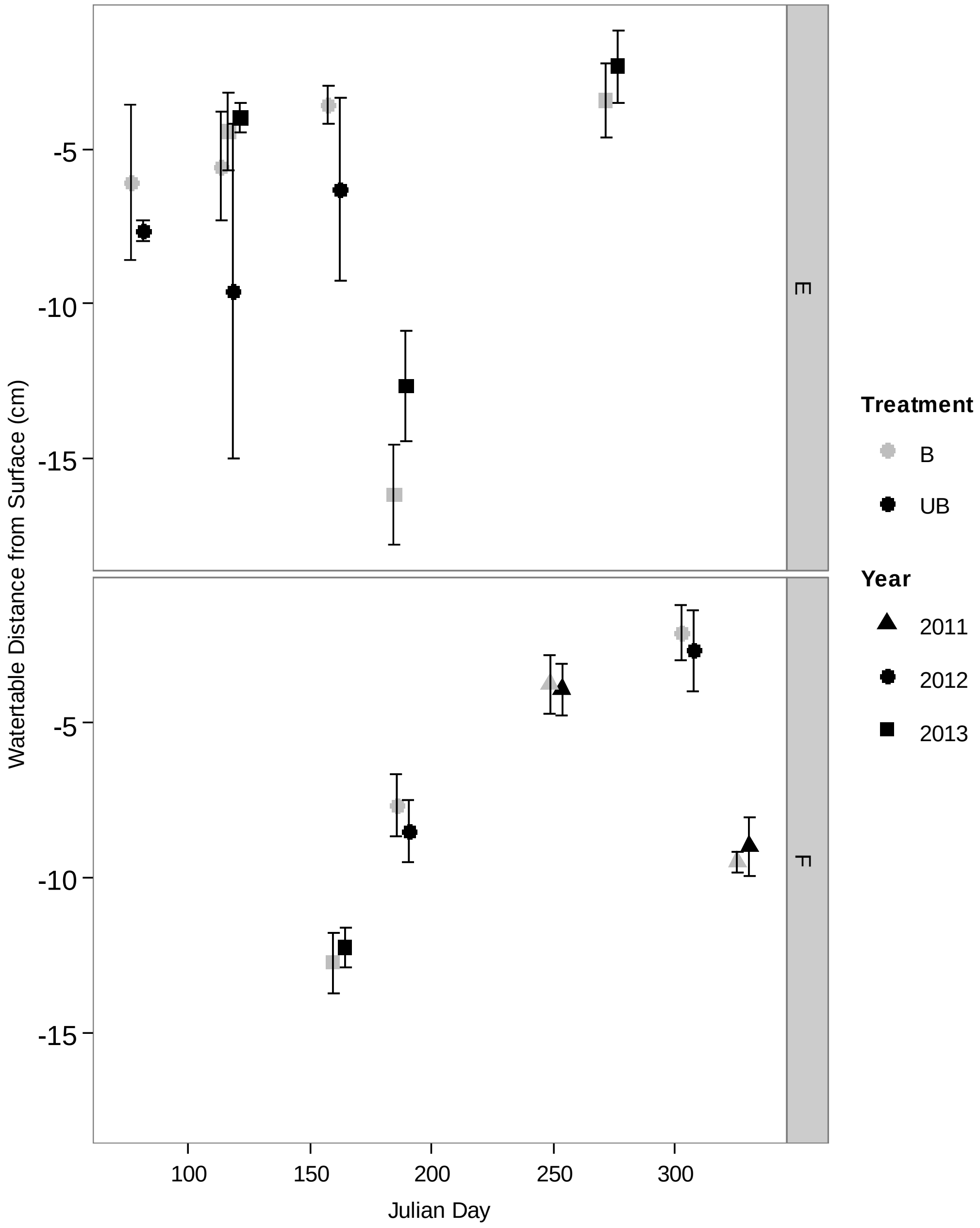
Sampling times at each site with Recovery Days (number of days since the site was burned) shown in brackets.

Eastside Burned 14th March 2012	**Forsinard** Burned 18th April 2012	**Glensaugh** Burned 27th March 2012
19th March 2012 (5)	4th July 2011(87)	20th June 2012 (85)
28th April 2012 (42)	29th August 2011 (143)	10th September 2012 (167)
6th June 2012 (86)	15th November 2011 (220)	28th May 2013(427)
28th September 2012 (198)	28th June 2012 (428)	10th June 2013 (440)
29th April 2013 (411)	23rd October 2012 (545)	
6th July 2013 (479)	11th June 2013 (766)	

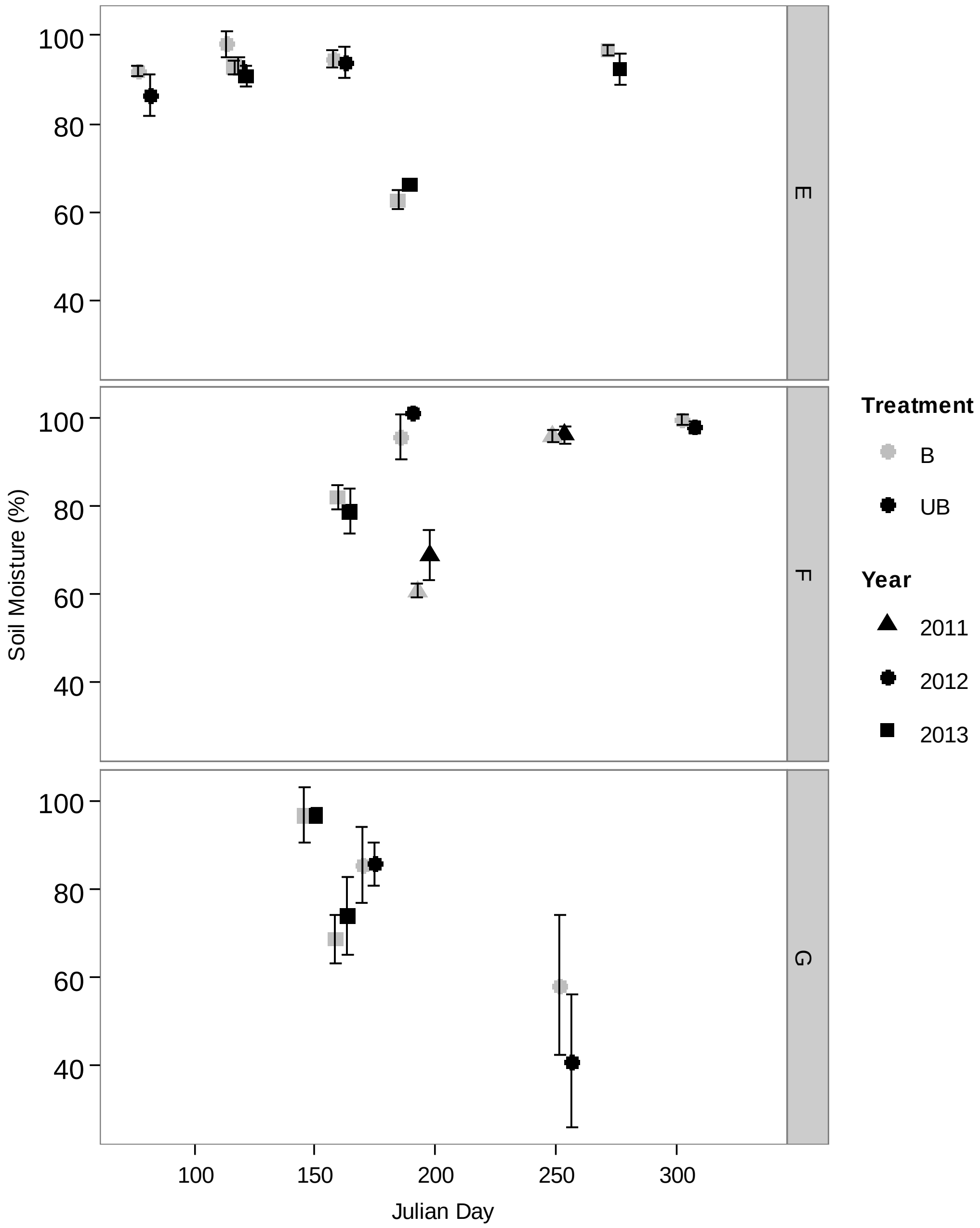
Appendix 2.2. Soil Temperature, Soil Moisture and Water table at the three field sites



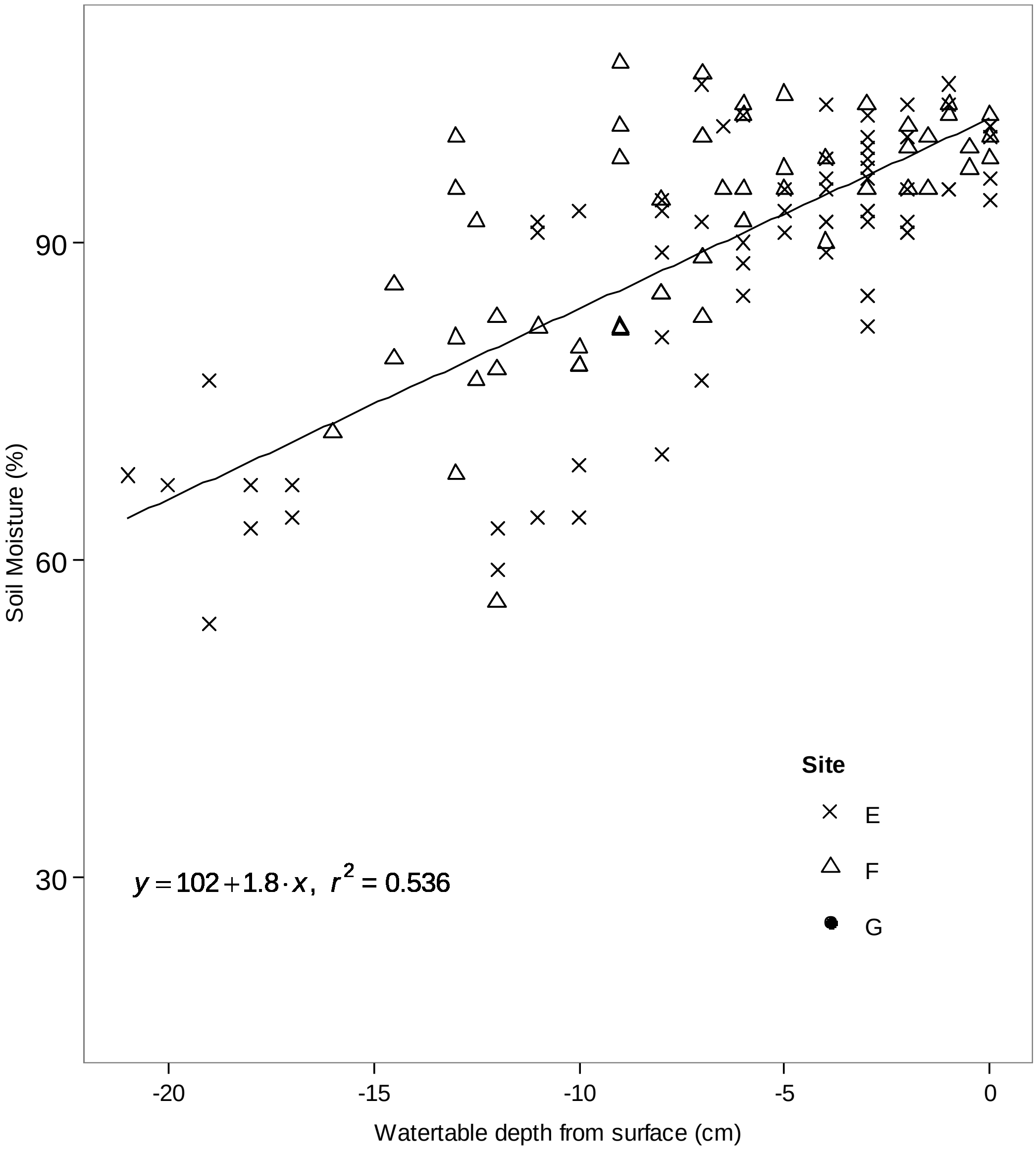
Soil temperature of plots at each of the three sites (E=Eastside, F=Forsinard, G=Glensaugh) in relation to day of the year and year sites were sampled. Points show mean with ±StEM error bars. No statistical differences were found between burnt and unburnt plots.



Distance from surface (defined as peat/*Sphagnum* interface) to water table at each plot at the two sites where dipwells were installed of the three sites (E=Eastside, F=Forsinard) in relation to day of the year and year sites were sampled. Points show mean with ±StEM error bars. No statistical differences were found between burnt and unburnt plots.

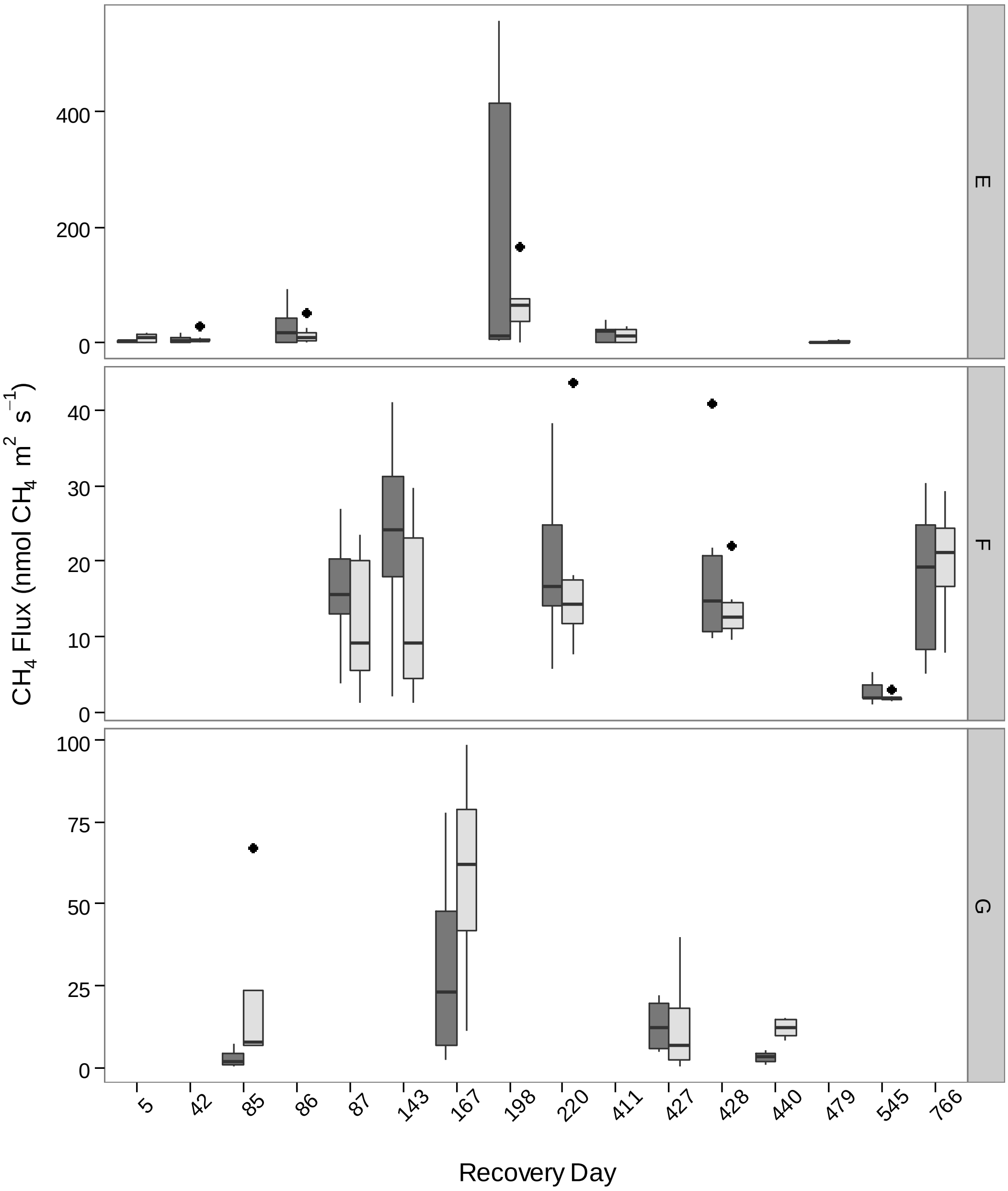


Soil moisture of plots at each of the three sites (E=Eastside, F=Forsinard, G=Glensaugh) in relation to day of the year and year sites were sampled. Points show mean with ±StEM error bars. No statistical differences were found between burnt and unburnt plots.

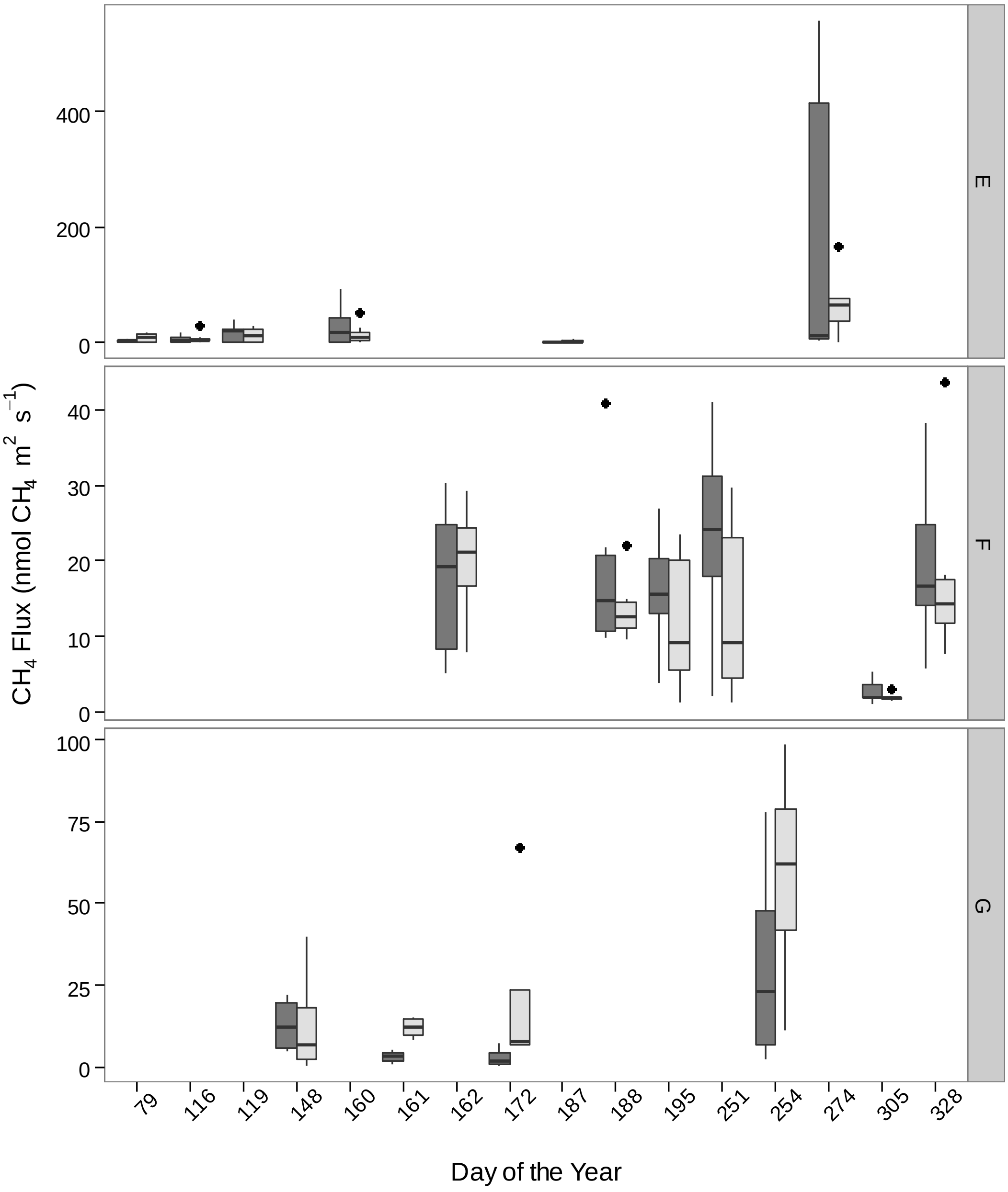


Soil moisture in relation to depth of the water table (distance the peat surface) in plots at Forsinard and Eastside plotted with linear regression line. Regression equation was subsequently used to estimate water table height at Glensaugh where no dipwells were installed.

Appendix 2.3. Methane fluxes at each site at each sampling time

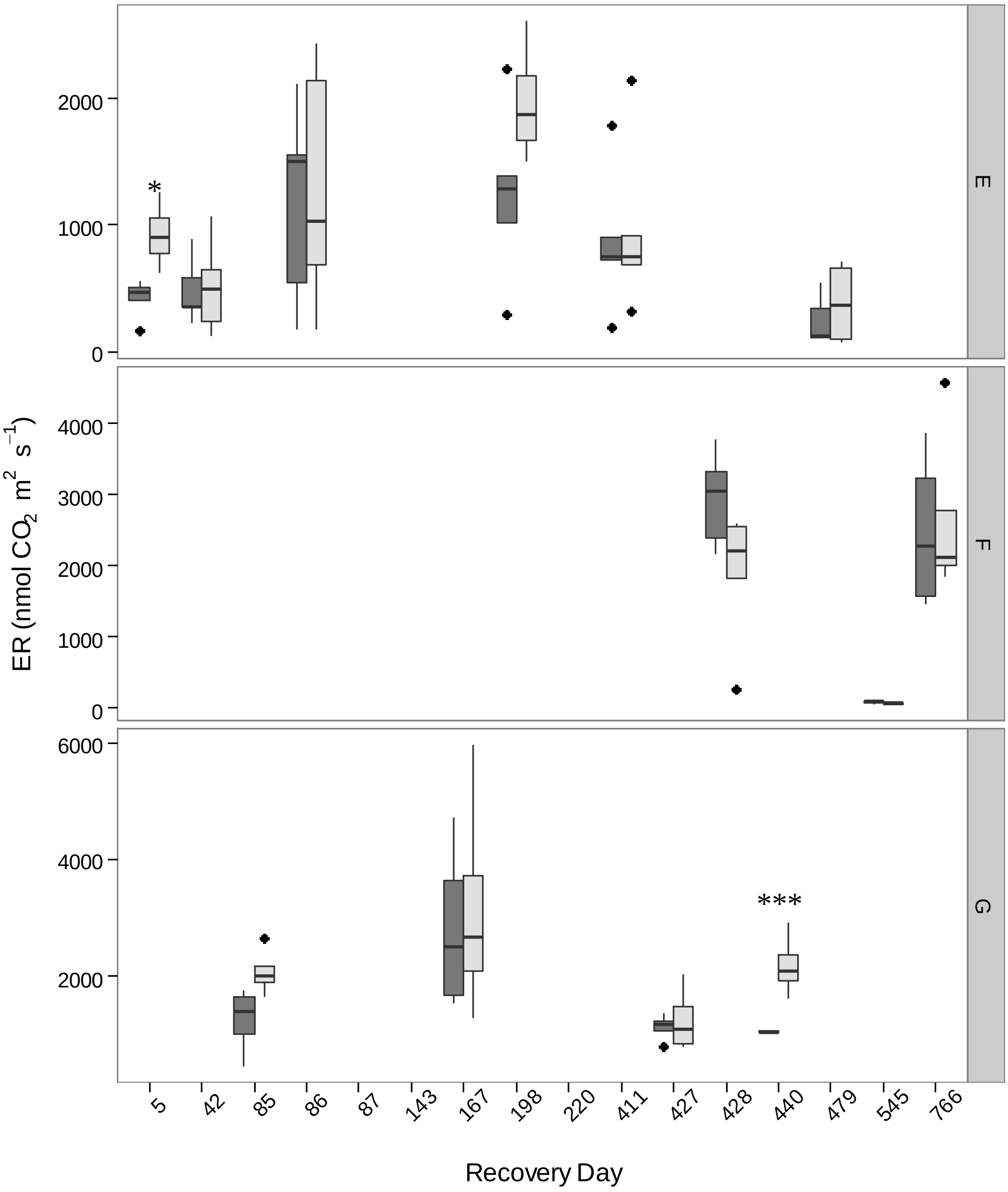


Methane fluxes at each field site on each sampling day plotted as **Recovery Day** (number of days since site was subjected to fire). Sites are E=Eastside, F=Forsinard, G=Glensaugh, dark grey boxes are burnt plots, light grey unburnt plots. Bold horizontal line shows median value, edge of boxes upper and lower quartiles, end points of whiskers smallest and largest values and circles outliers. Nb. Different scales on y axis. Treatment was not statistically significant on any Recovery Day at any site.

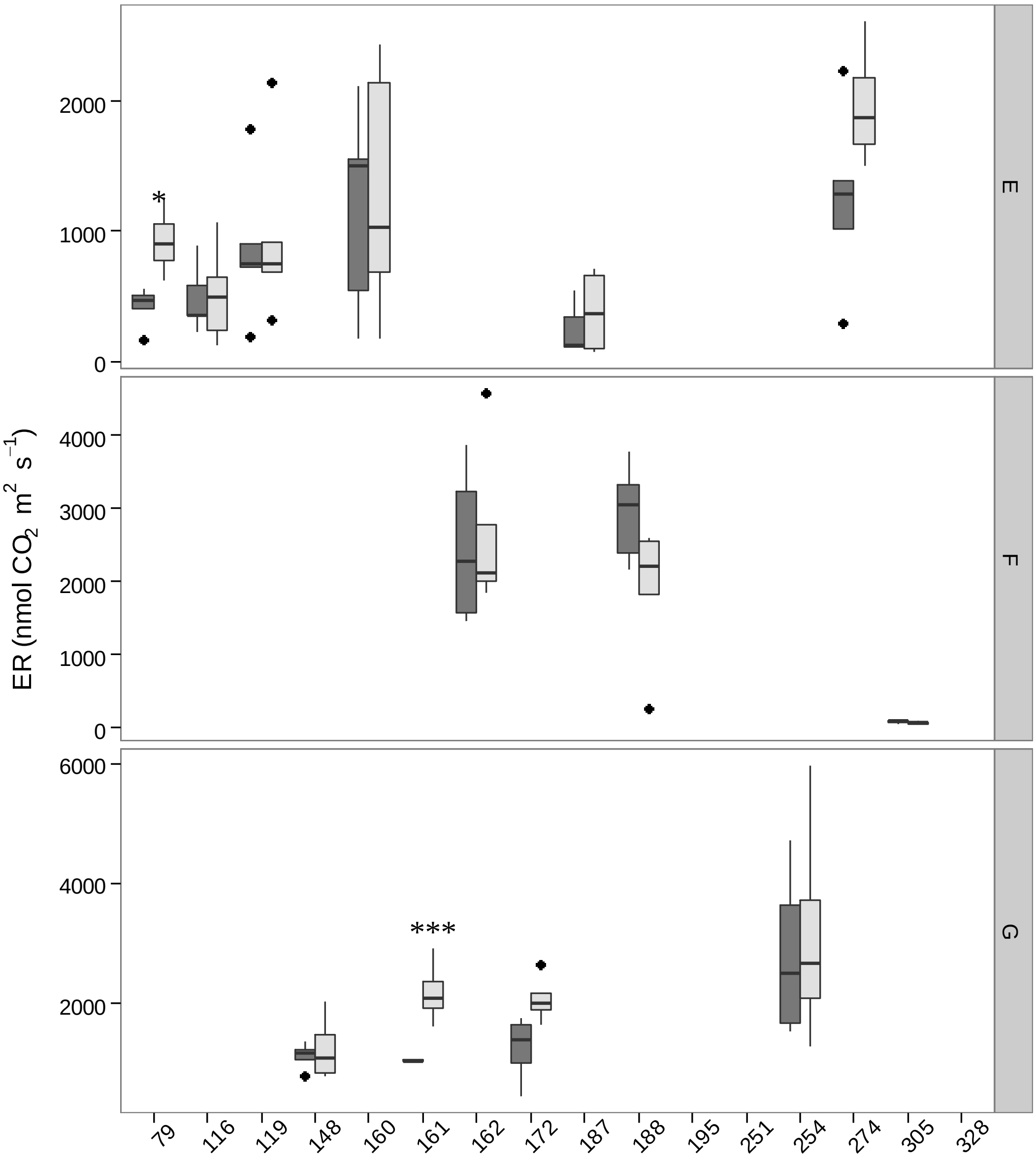


Methane fluxes at each field site on each sampling day plotted as **day of year** (from more than one year). Sites are E=Eastside, F=Forsinard, G=Glensaugh, dark grey boxes are burnt plots, light grey unburnt plots. Bold horizontal line shows median value, edge of boxes upper and lower quartiles, end points of whiskers smallest and largest values and circles outliers. Nb. Different scales on y axis. Treatment was not statistically significant on any Recovery Day at any site.

Appendix 2.4. Ecosystem Respiration at each site at each sampling time



Ecosystem Respiration at each field site on each sampling day plotted as **Recovery Day** (number of days since site was subjected to fire). Sites are E=Eastside, F=Forsinard, G=Glensaugh, dark grey boxes are burnt plots, light grey unburnt plots. Bold horizontal line shows median value, edge of boxes upper and lower quartiles, end points of whiskers smallest and largest values and circles outliers. Asterisk show where there was a significant difference between burnt and unburnt treatments (*indicates where $p<0.05$, ** $p<0.01$, ***$p<0.001$). Nb. Different scales on y axis.



Ecosystem Respiration at each field site on each sampling day plotted as **day of year** (from more than one year). Sites are E=Eastside, F=Forsinard, G=Glensaugh, dark grey boxes are burnt plots, light grey unburnt plots. Bold horizontal line shows median value, edge of boxes upper and lower quartiles, end points of whiskers smallest and largest values and circles outliers. Asterisk show where there was a significant difference between burnt and unburnt treatments (*indicates where $p<0.05$, ** $p<0.01$, ***$p<0.001$). Nb. Different scales on y axis.

3. The recovery of *Sphagnum capillifolium* following exposure to temperatures of simulated moorland fires: a glasshouse experiment

3.1 Abstract

In the UK blanket bog can be burnt by wildfires and deliberately for management purposes under government legislation and guidelines. *Sphagnum* mosses are considered a key component of a blanket bog system so their response to fire is important to understand for the formulation best practice burning guidance. Previous research on peatland fires has shown that the moss layer can be subjected to high, potentially physiologically damaging, temperatures and that frequent burning can lead to a decline in bryophyte cover. To date however there is no empirical evidence for the short term effects of fire on *Sphagnum.* Here we show that *Sphagnum capillifolium* has the ability to recover from exposure to high temperatures analogous to those previously recorded in managed peatland fires. We found that recovery of *S.capillifolium* as indicated by chlorophyll fluorescence, net primary productivity and new growth was related temperatures experienced at the *Sphagnum* layer surface, post-fire environmental conditions and pre-burn stem moisture content. The lowest rates of photosynthetic recovery were found when samples were heated to 400^{o}C for 30 seconds with the lowest rates of photosynthesis and new auxiliary growth during winter months. Our results demonstrate there are situations conducive to *S.capillifolium* recovery following a fire and that spring fires may allow for quicker recovery. We anticipate our results will help inform burning regimes that aim to do least damage to the *Sphagnum* layer. In addition the results provide important

evidence that seasonality and post-burn conditions should be considered when formulating assessments of the short term impacts of a fire on the *Sphagnum* layer.

3.2 Introduction

Sphagnum mosses are often considered the foundation or building block of ombrotrophic boreal peatlands (Rydin and Jeglum, 2006) and have unique capabilities which allow them to survive in the nutrient poor and acidic peatland environment. They can be considered 'ecosystem engineers' (Jones *et al.*, 1994) in the sense that the physical conditions they thrive in are in part determined and maintained by the plants themselves (Clymo and Hayward, 1982). Their water holding capacity, both internally within cells and externally due to their morphology, help maintain the wet and anoxic conditions of a peatland, while reducing the risk and amplitude of desiccation of their photosynthetically active capitulum (Hayward and Clymo, 1982). *Sphagnum* also produce the organic acids responsible for both creating and maintaining the acidic conditions of ombrotrophic and minerotropic boreal peatlands (Kuhry *et al.*, 1993) and have the ability to lock away nutrients making them unavailable to other species (Rydin and Jeglum, 2006), important factors in creating the unique environmental conditions and associated fauna and flora. The recalcitrant nature of *Sphagnum*, thought to be due to the intercellular concentrations of phenolic compounds and uronic acids (Børsheim *et al.*, 2001), also means it is very resistant to decay and is likely the most important component for peat formation worldwide (Malmer and Wallén, 2004). It is therefore important to understand the impact disturbance events may have on the *Sphagnum* layer, especially now when greater emphasis is given to maintaining peatlands as long term carbon stores. Furthermore *Sphagnum* species are significant components of habitats of conservation concern, with both active raised and blanket bog and transition mires and quaking bogs European Habitat Directive Annex I habitats. Active raised and blanket bogs are priority habitats, and the UK has special responsibility for their protection and so are often interest features of Special Areas of Conservation (SAC). At an individual species level some species are particularly vulnerable in the UK, with one species, *Sphagnum obtusum* Warnst., thought to have gone extinct during the 20th Century, with *Sphagnum balticum* (Russow) C.E.O.Jensen. and *Sphagnum skyense* Flatberg. classed as endangered and near threatened respectively. One such disturbance event which could have consequences for *Sphagnum* is fire, which could have both direct and indirect effects on the *Sphagnum* layer as a whole and at an individual species level.

In the UK peatlands, as well as being potentially burnt by wildfire, can be burned legally following guidance set out in the Muirburn Code in Scotland and the Heather and Grass Burning 2007 Code in England. In Scotland, management burning specifically on blanket bog can only occur during the muirburn season when heather (*Calluna vulgaris*) constitutes more than 75% of the vegetation cover while in England can only be burned as part of a pre-approved burning plan for conservation and restoration with the aim of not damaging the moss layer (Department for Environment Food and Rural Affairs, 2007, Scottish Executive, 2011). This makes understanding the response of *Sphagnum* species, such an important component of a blanket bog, important if damage to *Sphagnum* by burning is to be limited. To date, however, little direct research has looked at the direct effect fire has on the *Sphagnum* layer as a whole or at an individual species level in peatlands.

Studies looking at the characteristics of fires on peatlands have shown that although the bryophyte layer can be exposed to high temperatures, these temperatures are usually not as high as those found in the canopy vegetation (eg. Hobbs and Gimingham, 1984, Hamilton, 2000, Davies, 2005). In fires over *Calluna vulgaris* (L.) Hull (here after referred to as *Calluna*) dominated heaths it has been demonstrated that temperatures rarely exceed 50^{o}C 2cm below the surface of pleurocarpous mosses (Davies, 2005). However, temperatures lethal for bryophytes by which cell damage occurs are thought to be between 40 and 51 ^{o}C (Glime, 2007) so even temperatures significantly lower than those found in the canopy vegetation may still be physiologically damaging. At the ground/moss surface temperatures can be significantly higher, up to 600^{o}C, even if for relatively short (<30 seconds) periods of time (Davies, 2005, Hamilton, 2000). Such high surface temperatures could have an impact on *Sphagnum* growth particularly by damaging the capitulum, wherein the apical meristem and the site of the majority of photosynthesis resides (Rydin and Jeglum, 2006). However, as *Sphagnum* typically grows in vertical shoots it is possible that when fire only damages the capitulum and upper sections of stems *Sphagnum* could have the ability to re-grow from side shoots (Rydin and Jeglum, 2006) meaning recovery may be possible, which has indeed been observed in certain circumstances in the field (Hamilton, 2000). There are however instances when high temperatures may penetrate much deeper into the moss layer and peat, when the peat itself ignites and smoulders (Ashton *et al.*, 2007). This may be a result of the structure and distribution of fuel above the moss layer, with a high density of fuel increasing the temperature residence time within a fire in a confined area, causing greater evaporation and so lowering the moisture content of the vegetation and peat and allowing the fire to penetrate the peat. Such “hot spots” have been observed in *Calluna* fires (Davies, 2005) and in the moss layer in areas immediately around the woody stems of *Calluna* (Hamilton, 2000). Lab based burning experiments have demonstrated the importance of moisture status for allowing the smouldering of pleurocarpus mosses with a critical “fuel moisture threshold” existing at a moisture content of around 16%. Below this threshold the moss smouldered and often flamed, and above the threshold smouldering was slower, often self-extinguishing, and never igniting (Legg *et al.*, 2008). Peat below the moss layer has also been widely demonstrated to be more likely to ignite and smoulder in wildfires when drier (eg. Frandsen, 1997, Rein *et al.*, 2008, Davies *et al.*, 2013).

It is intuitive that the moisture content of the *Sphagnum* layer prior to burning will have an effect on the impact of high temperatures, as higher water contents can make vegetation less susceptible to being burned, as has been found in grasses (eg. Lloyd, 1968) and *Calluna* (eg. Kayll 1966, Hamilton 2000, Davies et al., 2009). The study by Legg *et al.*, (2008) also showed the importance of the bulk density of the moss layer for the probability of ignition, with low densities heated with igniters failing to smoulder, which the authors suggests is due to the rapid vaporisation of moss directly in contact with the igniter creating a small hollow where smouldering could not take hold. Although low densities may not be conducive to ignition and smouldering, low densities may increase the rate of evaporation (Titus and Wagner,

1984) reducing moisture content, subsequently increasing the risk of burning. In *Sphagnum* the looser arrangement of hollow and lawn forming species have been found to be more susceptible to burning than hummock forming species such as *Sphagnum fuscum* (Schimp.) H.Klinggr. which are more densely arranged (Benscoter *et al.*, 2011). These potential short term effects of fire on the *Sphagnum* layer may therefore have important repercussions for rates of recovery, primary production and if linked to density and morphology may be species specific and therefore important to long term species composition and succession.

Previously, a long term study at an experimental burning on blanket bog with a fire frequency rate of 10 years found that overall bryophytes declined with burning (Ward *et al.*, 2007) but that *Sphagnum spp*. increased in abundance (Lee *et al.*, 2013). Little work however has looked at the specific response of different *Sphagnum* species to burning, although Barkman (1992) reported differences in rates of recovery between species on a Dutch bog, with no studies relating *Sphagnum* recovery to fire characteristics and pre and post fire conditions. It is possible that fire may favour some *Sphagnum* species over others as has been found at some sites in the North York Moors where *Sphagnum capillifolium* (Ehrh.) Hedw. was found to be more abundant at sites burned more recently (Burch, 2009). However, studying the abundance and distribution of *Sphagnum* species in relation to fire distribution to infer the impact fire has on *Sphagnum* may be too simplistic as it is possible that the distribution of *Sphagnum* species may be associated more by the ecophysiology of species. *S.capillifolium* for example can thrive in much drier conditions than other *Sphagnum* species so is often found in areas of blanket bog that experience burning, as burning is usually confined to drier areas where fire can be ignited. A more direct and functional approach to determining the effect of fire on *Sphagnum* species is therefore also needed.

3.3 Aims

The aim of this study was to quantify the recovery of *S.capillifolium* following exposure to temperature treatments simulating different maximum temperature and residency times analogous to those during *Calluna* fires. *S.capillifolium* was chosen as it is a species often associated with *Calluna* dominated heaths (Rodwell, 1991) and is a common species found in areas managed by fire under the regulations set out in the Muirburn Code (Scottish Executive, 2011). Based on previous research on critical temperatures in bryophytes (Glime, 2007) it was hypothesised that: [1] the photosynthetic capacity of *S. capillifolium* would be reduced following exposure to high temperatures and be more adversely affected by higher temperatures and temperature residency times and [2] a critical temperature and temperature residency time exists above which the temperature treatments will be lethal to *S.capillifolium*.

3.4 Materials and Methods

3.4.1 Experimental Design

Sphagnum capillifolium was collected from Whim Moss, Penicuik, South East Scotland (NT203532), an ombrotrophic blanket bog classified under the National Vegetation Classification (NVC) as M19 *Calluna vulgaris-Eriophorum vaginatum* blanket mire which lies 280m above sea level with a mean air temperature

(2003–2009) of 8.6^{o}C (ranging from −9.2 to 27.7 ^{o}C) (Sheppard *et al.*, 2012). 6cm deep, 5cm diameter round clumps of *S.capillifolium* were collected a maximum of two days prior to start of each run of the experiment from 4 different, randomly selected, hummocks per run of the experiment, and placed into 5cm diameter round fibre pots (Grow It, Spalding, UK). While potting, the clumps were kept as intact as possible to ensure that the number of stems in each pot was representative of natural stem densities found within each hummock. For each run of the experiment 96 pots filled with *S.capillifolium* were placed within a tray containing a bed of *S.capillifolium* cuttings, to help maintain damp conditions and simulate a more natural habitat. For the duration of the experiment the tray kept within a glasshouse designed to track external air temperatures to within 2^{o}C. The surrounding *Sphagnum* bedding was watered regularly and each pot watered with distilled water individually using a syringe to maintain *S.capillifolium* moisture content to around 90%, the amount of water given to each pot varying in response to stem moisture content, which was calculated for individual stems on a dry weight basis each time throughout each run of the experiment. During dry and hot conditions in the glasshouse the entire tray was sprayed uniformly with distilled water up to three times a day to ensure samples did not dry out. A pilot study (Appendix 3.1) was conducted prior to the experiment to ensure *S.capillifolium* samples could remain healthy, with plant health monitored using chlorophyll florescence measurements which gave an indication of the photosynthetic capacity of individual stems as discussed in section 3.4.2.1.

The experiment was run three times with one of three different temperature treatments randomly assigned to each of the 96 pots per run (Table 3. 1). Each pot was also assigned randomly to one of 4 measurement procedures; chlorophyll fluorescence, CO_2 exchange, growth measurements and moisture content analysis. Multiple measurements could not be made on each pot as both the chlorophyll fluorescence and moisture content analysis were destructive (Appendix 3.2).

Table 3. 1 Temperature treatments used for each of the three runs of the experiment. Burn Season refers to the time of year the pots were exposed to each burn treatment. All pots were observed and recovery measurements made for a total of 100 days after being exposed to each temperature treatment which is termed Observation Period in the table. *400+D indicates where the treatment was carried out on pots of *S.capillifolium* subjected to three days of drying prior to the treatment.

Run	**Simulated Burn Season**	**Observation Period**	**Treatment Name**	**Maximum Surface Temp (^{o}C)**	**Maximum Temperature Residence Time at Surface (s)**	**Mean *Sphagnum* Moisture Content when burnt (% wet weight basis)**
1	Spring	Mar'12 – Jun'12	Control	Ambient (~9^{o}C)	-	
			100	100	3s at max surface temp	89.5
			400	400	3s at max surface temp	89.6
2	Autumn	Oct'12 – Jan'13	Control	Ambient (~16^{o}C)	-	
			400	400	3s at max surface temp	89.6
			400+	400	30s between 350 & 450^{o}C	92.5
3	Winter	Feb'13 – May'13	Control	Ambient (~3^{o}C)	-	
			400+	400	30s between 350 & 450^{o}C	92.5
			400+D*	400	30s between 350 & 450^{o}C	80.6

The temperature treatments were performed by placing each individual pot in a perforated steel heating chamber, which was heated by a butane-propane flame from a weed wand (Parasene Weed Wand 550, Parasene, UK). The flame was held in place until the surface of the pot of *Sphagnum* within the chamber reached the desired maximum temperature for the desired length of time. The perforated steel chamber was used to limit the consumption and charring of the whole pot as a consequence of being heated by a direct flame burning with a temperature of around 1000^{o}C. Temperature measurements logged every 2 seconds using k-type twisted thermocouple wire connected to a datalogger (CR21X, Campbell Scientific, Utah, USA). Thermocouples were places at the surface and at 2cm and 5cm depth within the pots. The surface temperature (displayed in real time on the data logger screen) was used to determine when to remove the flame to meet the desired temperature conditions of each treatment. The temperature treatments were designed to simulate temperatures and temperature residency conditions that have been recorded at the moss surface within *Calluna* fires on heaths in Scotland (Davies *per comn.* 2010). Due to the method of heating there was some variation around the maximum temperatures and maximum temperature residency times but each treatment did give distinctly different temperature conditions (Appendix 3.3). The 400+D treatment also involved drying the *Sphagnum* prior to burning by not watering the pots and keeping them in a separate tray without a bed of damp *Sphagnum* cuttings, surrounded by 6 small battery powered fans and kept at an air temperature of 18^{o}C for three days (all other treatments were potted into damp fibre pots and placed immediately into the tray of *Sphagnum* cuttings with no fans). Post-burn, the 400+D pots were placed with the others in the damp tray of *Sphagnum* cuttings and watered as per the others to maintain stem moisture content of around 90% (wet weight basis). *Sphagnum* stems were removed from pots assigned to each treatment through each run of the experiment for moisture content analysis (Appendix 3.4). The mean, minimum and maximum air temperature and light intensity (PAR) for each day of each run of the experiment were calculated from external ambient PAR and temperatures calibrated with actual measurements taken within the glasshouse over a period of weeks where internal measurements were available (Appendix 3.4).

3.4.2 Recovery Measurements

3.4.2.1 Chlorophyll Fluorescence

Chlorophyll fluorescence is a well established technique for measuring plant stress (Krause and Weis, 1991, Maxwell and Johnson, 2000) and has been demonstrated as a reliable method for evaluating stress and recovery in *Sphagnum* (eg. Manninen *et al.*, 2011, van Gaalen *et al.*, 2007, Hájek and Beckett, 2008). The technique works on the principle that, when damaged, Photosystem II (PS II) re-emits more energy when exposed to light as less is absorbed by chlorophyll for use in the photochemical process (Maxwell and Johnson, 2000). This energy, fluorescence, can then be measured as the variable florescence (F_v) which is the maximal florescence (F_m) when saturated with light, minus minimum florescence (F_o) when first exposed to light, with the ratio Fv/Fm, described as the maximum quantum yield of PSII, indicative of stress (Maxwell and Johnson, 2000). An Fv/Fm ratio of 0.75 to 0.84 is the widely accepted range expected in healthy vascular plants (Demmig and

Björkman, 1987) and mosses (eg. Bates *et al.*, 2009, Hájek and Beckett, 2008, Green *et al.*, 1998, Manninen *et al.*, 2011, Proctor, 2003, van Gaalen *et al.*, 2007).

Chlorophyll fluorescence measurements were made using a Continuous Excitation Chlorophyll Fluorimeter (HandyPEA, Hansatech Instruments Ltd, UK) on the capitulum of one stem from each individual pot assigned to the fluorescence measurement protocol for each treatment on 8 separate days starting from the first day after being exposed to the temperature treatments up to 100 days after exposure to the temperature treatments. Each capitulum was dark adapted for 20 minutes using a dark adaption clip (HPEA/LC, Hansatech Instruments Ltd, UK) prior to making the measurement at a light intensity of 1500 µmol m^{-2} s^{-1} (Carfrae, 2005). Concurrently a stem was removed from another 8 individual pots per treatment for moisture content analysis to ensure the *Sphagnum* samples were maintaining healthy moisture content of around 90% (wet weight basis). Chlorophyll fluorescence was also used to assess physiological damage from the capitulum downwards along a stem by making measurements at 5 mm intervals down a sub-sample of stems taken from pots from each treatment in Run2 at 100 days when pots were harvested.

3.4.2.2 CO_2 Exchange

Gas exchange measurements were made on 8 pots per treatment on 5 occasions from day 3 to day 99 of each run of the experiment. Measurements were made using a portable infra-red gas analyser (LI-6400XT, Li-Cor, Lincoln, NE, USA) with a purposely designed sample chamber to measure net primary productivity (NPP) of the whole pots of *Sphagnum*. Prior to embarking on the experiment, gas exchange measurements were made on the empty fibre plant pots used to hold the *Sphagnum* samples. Results of these tests showed that, particularly when wet, these pots did respire, increasing CO_2 concentrations in the sample chamber. Therefore, throughout each run of the experiment each pot of *Sphagnum* was carefully decanted into an inert plastic pot of the same size for the gas exchange measurements. After each measurement was made the samples were returned to their original peat pots. The sample chamber was connected to a flow meter (6400-18 RGB, Li-Cor, Lincoln, NE, USA) which contained silica gel beads to reduce humidity in the sample chamber. It was found that a method to reduce humidity in the chamber, caused by the high moisture content of the *Sphagnum* samples in comparison to plants the system was designed for, was vital for maintaining accuracy and to stop condensation on the infra-red gas analysers. The Licor LI-6400XT was set to maintain the sample chamber air temperature at 20^{o}C with an initial 400µmol of CO_2 with a flow rate to the sample chamber of 500 µmol s^{-1}. This temperature condition was chosen as it was the most maintainable in lab conditions throughout each run of the experiment. The light source used was a 6400-18 RGB (Licor, Lincoln, NE, USA) with NPP measured under a white light intensity of 2000µmol m^{2} s^{-1}, to give the highest rates of CO_2 assimilation (Appendix 3.5), and respiration under a light intensity of <1µmol m^{2} s^{-1}. NPP, measured in all three runs of the experiment, and respiration, measured during the second and third runs of the experiment, expressed as µmol CO_2 g^{-1} day^{-1}, were calculated on a dry air (equation 3.1) and dry weight basis (equation 3.2), where ***CO_2D*** is the concentration of CO_2 (µmol CO_2 mol $^{-1}$) on a dry air basis calculated for the air supplied to the sample chamber (**CO_2R_D**) and the air in the sample chamber (**CO_2S_D**), **H_2O** the concentration of water (mmol H_2O mol $^{-1}$) in the reference or sample air, ***Pr*** pressure (kg m^{-2}), ***FR*** flow rate (µmols s^{-1}) and ***M*** mass (kg).

$$CO_2D = \frac{CO_2}{[1 - H_2O\,]/Pr}$$

Eq.3. 1

$$RoP = [CO_2R_D - CO_2S_D]\; x\; \left[\frac{FR}{M}\right]$$

Eq.3. 2

The dry weight of *Sphagnum* was calculated by oven drying samples at the end of each run of the experiment (day 100) at 70°C for 5 days before weighing. In the more traditional two dimensional leaves of vascular plants surface area would be used to calculate photosynthetic rates. However, two dimensional area has little meaning for *Sphagnum* on the scale used here since *Sphagnum* have a three dimensional micro-canopy structure. In particular it was not possible to estimate the depth light penetrated into the *Sphagnum* sample and thus how much photosynthetically active surface was exposed to light. Therefore, as an alternative to area, dry weight was used to calculate NPP and respiration. CO_2 concentrations in the reference air and sample chamber air were logged at 10 second intervals and averaged across the times when CO_2 concentrations, humidity and temperature within the chamber were stable, typically over a period of 5 to 10 minutes. Average NPP and respiration could then be used in statistical analysis to compare between pots and treatments.

3.4.2.3 New Growth and Physical Damage

New growth in each pot assigned to the Gas Exchange and Growth Measurement protocols at the end of each run of the experiment was measured as the number and weight (dry mass) of new auxiliary stems that had grown from original stems. Pots assigned to the chlorophyll fluorescence and moisture content analysis measuring protocols were not harvested as these had stems removed throughout the experiment. New auxiliary stems were easy to identify as they were bright green in appearance and thinner in morphology than the pre-existing old stems so could be separated by eye. The length of the new stems was measured in a subset of samples. New stems were weighed after being oven dried at 70^{o}C for 5 days and new growth calculated as a ratio of total biomass dry weight (new growth plus original sample) to the original biomass (dry weight) of each pot. Calculating new growth as a ratio takes into account the difference in the number of stems between pots, and thus the number of stems that could potentially produce new auxiliary stems. Most observations and measurements used to indicate physical damage and new growth came from Runs 2 and 3 of the experiment.

The depth of physical damage and bleaching (loss of pigment), caused by the different treatments, was measured as the distance from the capitulum down the stem showing bleaching and/or reduced structural integrity. Reduced structural integrity equated to parts of a stem that were brittle and easy to pull apart with little force, with a capitulum that could be removed by gently running a finger across the surface of the pot. Only pots assigned to the whole pot gas exchange and new growth measurements were assessed in this way as these pots remained intact for the duration of the experiment. These measurements were only made at the end of Runs 2 and 3 of the experiment, as this was when the bleaching effect of the burn treatments was most notable. In total, 6 stems from 16 pots were measured for depth of physical damage per treatment per run.

3.4.3 Statistical Analysis

To compare differences in the extent of decay (the length of stem section from the capitulum) unpaired Welch's sample t-tests were used. New growth, calculated as the ratio of the dry weight of new biomass to original sample biomass, was compared between treatments using Welch's two-sample t-tests of the log (+1) or the square root of the ratio to meet test assumptions of normality.

Linear mixed effects models were used for analysing chlorophyll fluorescence, NPP and respiration as these measurements were made repeatedly on the same pots throughout each run of the experiment and so were not independent of each other, making the addition of random terms in the model to account for additional levels of variation necessary. Initial models composed all relevant fixed and random effect terms structured as appropriate to the data set to take into account the explicit nesting of terms (Table 3. 2). Initially random effects were selected using AIC criteria computed from Restricted Maximum Likelihood (REML) parameter estimates and models compared by assessing the amount of variance explained by each term, with the model with the smallest AIC value chosen. Secondly, using Maximum Likelihood (ML) parameter estimates, non-significant fixed effect terms were dropped one by one from the model to derive a model with the smallest AIC that consisted only significant fixed effect terms, as indicated by Wald tests. All statistics were carried out using the statistical program R (v R i386 3.0.1) (R Core Team, 2013) with mixed effects modelling computed using the package lme4 (Bates *et al.*, 2013).

Table 3. 2 Fixed and random effects terms used in mixed effects modelling of the repeated measures of chlorophyll fluorescence and CO_2 exchange.*Moisture content term only used in chlorophyll fluorescence model as stems were harvested for moisture content analysis only on days fluorescence measurements were made.

Model Term	**Abbreviation**	**Description**
Fixed Effects		
Treatment	Treat	Treatment applied to each pot
Day		The day measurement was made (between 1 and 100 per run). Treated as fixed effect as measurements made on same day each run of the experiment
Random Effects (accounting for variance within Treatment + Day fixed effect)		
Block		Block (1 to 4) within the tray pots were kept in
Run		Run of the experiment (1 to 3), synonymous with “Burn Season”
Hummock	Hum	Variance explained by the hummock from which potted *S.capillifolium* sample was taken (4 per run, 12 different hummocks in total)
Run:Hummock	Run:Hum	Hummock nested within run specifies variance between hummocks within the same run of the experiment (accounts for different hummocks used in each run)
Moisture Content*	MC	Moisture content of samples taken concurrently with fluorescence measurements
Pot		Random pot to pot variance
Run:Pot		Pot nested within run specifies variance between pots within the same run (accounts for different pots used in each run)

3.5 Results

3.5.1 Physical Damage

The majority of stems from pots assigned to the 4 burn treatments showed bleaching of the upper parts and capitulum to some extent (Appendix 3.6), with the 100^{o}C treatment showing the least amount of bleaching (Figure 3. 1). The control pots never showed permanent bleaching to the same degree as the burnt pots, with bleaching occurring for a short time only on one or two stems per pot after particularly warm and dry conditions in the glasshouse. It was also observed that bleaching in some pots could be more pronounced a few days after burning (Appendix 3.6), despite all pots being kept at similar moisture contents (Appendix 3.4), suggesting that bleaching was a product of physiological changes brought about by the treatments rather than desiccation which can also cause *Sphagnum* to bleach (Clymo and Hayward, 1982).

Depth of physiological damage was confined to the upper portion of stems. This was further demonstrated by chlorophyll fluorescence measurements made down stems from Run 2 where the Fv/Fm ratio of the top 20 mm of stems from the 400 and 400+ treatments was reduced when compared the control (Figure 3. 2). Following the scale of treatment severity used in this study, when looking at treatments where the surface temperatures reached 400^{o}C, the lowest maximum surface temperature residence time (treatment 400) showed the lowest depth of damage followed by treatment 400+ which had a higher 400^{o}C surface temperature residence time, with the greatest depth of damage was found in the 400+D treatment (Figure 3. 1). No damage was found down stems in control pots (Figure 3. 1, Figure

3. 2). Physical decay, defined as a total loss of structural integrity, was most severe in the capitula, with capitula loss occurring in the later stages of the experiment common in all 400+ treatments in runs 2 and 3 (Figure 3. 3).

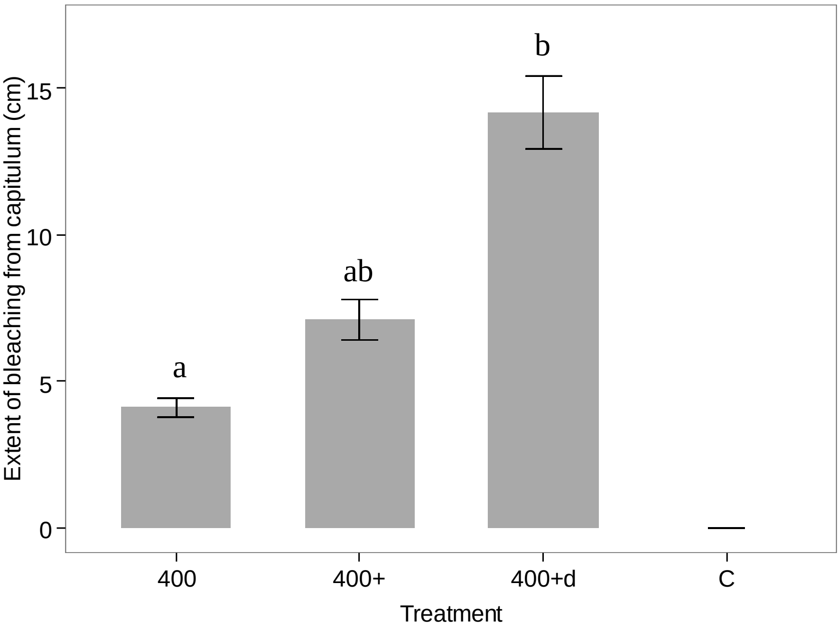


Figure 3. 1 Mean depth ± SEM of bleaching in a sub-sample of pots from runs 2 and 3 (n= 6 stems per pot, 16 pots per treatment, per run). No permanent bleaching was recorded in any control pots. All pots harvested on day 100. Means with different letters are significantly different (Welch Two Sample t test: t=-4.6, df=39.6, p=<0.05 and t=-5.1, df=25.1, p=<0.05 respectively).

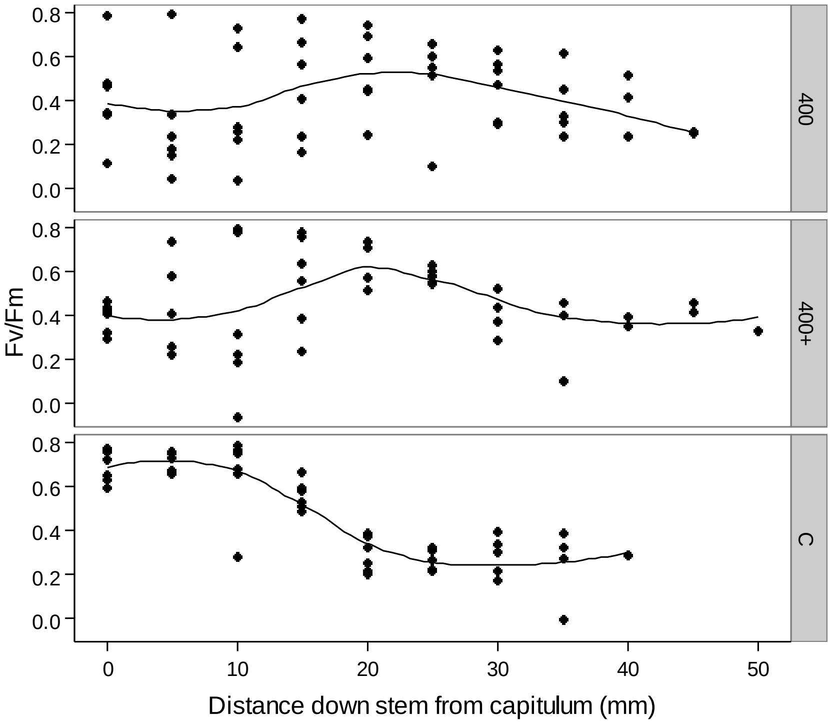


Figure 3. 2 Fv/Fm ratio of 5mm sections of stem starting from the capitulum (position 0mm) from a sub-sample of pots exposed to the three treatment in Run2 of the experiment (n=6 per treatment). Plots fitted with locally estimated scatterplot smoothing (LOESS) regression lines (fitted over all points by weighted least squares with a smoother span of 0.75).

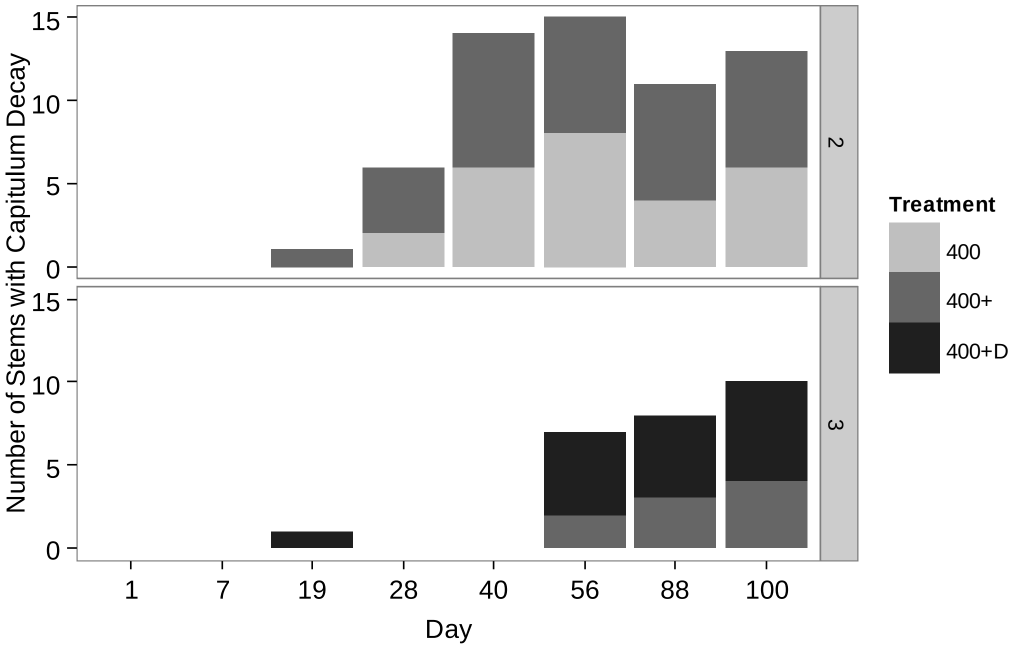


Figure 3. 3 The number of stems showing capitulum decay, defined as the distance from the capitulum down the stem showing bleaching and/or reduced structural integrity, at each sampling time for each treatment during runs 2 and 3 of the experiment (n=8 stems per treatment per sampling time per run). No capitulum decay occurred in control pots.

3.5.2 Chlorophyll florescence

Throughout each run of the experiment the control pots had an Fv/Fm ratio closest to 0.7 but with distinct low periods during Run 1 and Run 3 (Figure 3. 4). In Runs 1 and 2 of the experiment the control stems had higher Fv/Fm ratios than stems from pots exposed to the temperature treatments. The most appropriate linear mixed effects model showed that both the fixed terms of Day and Treatment were significant as well as the interaction between Day and Treatment while pot was found to be the best random effects term to account for additional variation in the data beyond the fixed effects (Table 3.3, Figure 3. 5).

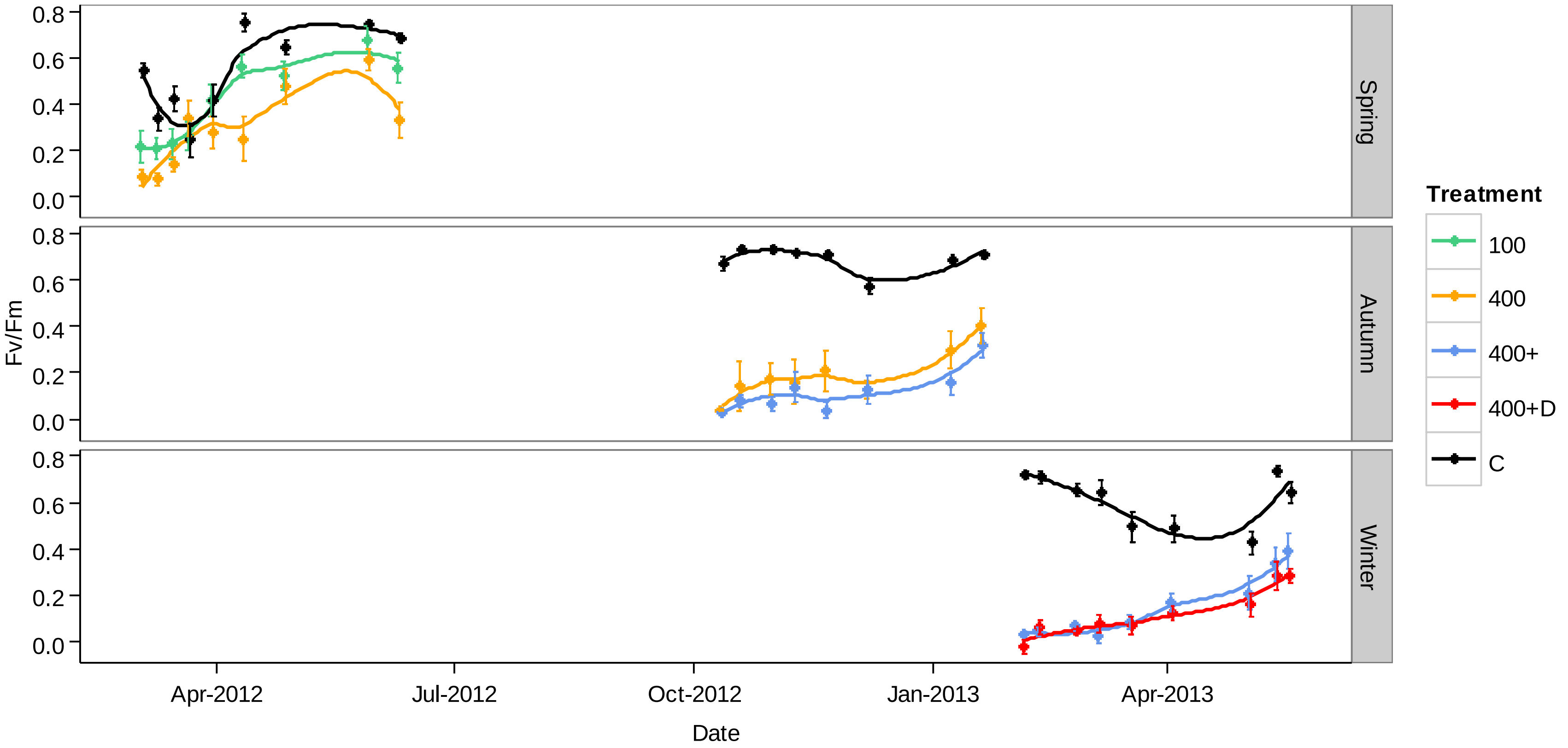


Figure 3. 4 Fv/Fm ratio of stems taken from pots subjected to each treatment over the three runs, Spring, Autumn and Winter of the experiment (n=8 per treatment per sampling time). Points show mean Fv/Fm ±SEM bars fitted with LOESS regression lines (parameters as in Figure 3. 2).

Table 3.3 Results of linear mixed effects model of the Fv/Fm ratio (transformed using Arc Sine transformation) with appropriate model selected using AIC criteria to determine random and fixed effects and a Wald test for fixed term significance. Models with the lowest AIC criteria and thus largest negative delta AIC (ΔAIC) were selected. MC = moisture content of *Sphagnum* stems at time of measurement.

Model	**AIC**	**ΔAIC**
Random Effects		
MC+Pot+Run:Pot+Block+Run+Hum+Run:Hum	-220.7	–
MC+Pot+Run:Pot+Block+Run+Hum	-222.7	-2.0
MC+Pot+Run:Pot+Block+Run	-224.7	-4.0
MC+Pot+Run:Pot+Block	-226.7	-6.0
MC+Pot+Run:Pot	-225.2	-4.5
MC+ Pot	**-227.2**	**-6.5**
MC	-211.5	+9.2
Fixed Effects		
Treatment+Day	-280.8	–
Treatment	-275.4	+5.4
Day	-151.8	+129

Wald Test of Final Model

Fixed Effect Treatment+Day *Random Effect* MC+ Pot

	Chi Sq	**Df**	**P value**
Treatment	226.4	4	<0.001
Day	26.1	8	0.001026

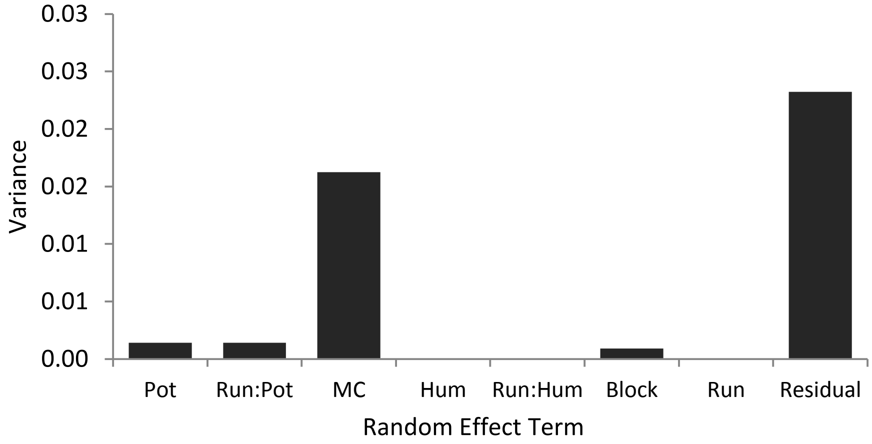


Figure 3. 5 Amount of within treatment variance explained by the different random effects terms in the largest mixed effect model described in Table 3.3. The final model only included the random effect terms Pot and MC (moisture content).

3.5.3 CO_2 Exchange

NPP, CO_2 exchange measured at a light intensity of 2000 µmol m^2 s^{-1}, varied considerably between runs, across sampling times and treatments ranging from -84±13 to 252±26 µmol g^{-1} (dry weight) day^{-1} with greatest NPP in control pots during Run 2, the Autumn run (Figure 3. 6). NPP of temperature treated pots was only noticeably lower during the first half of runs 1 and 2, with generally less obvious treatment differences when NPP was lower. In general respiration rate, measured when light intensity was <1 µmol m^2 s^{-1}, was less variable between treatments than NPP (Figure 3. 7) during both runs 2 and 3 (no respiration measurements were made during run 1 and measurements made on only three occasions during the first half of run 2, as pots in all treatment groups became infected with mould making gas exchange measurements on whole pots inappropriate). Respiration rate also varied less between runs, ranging from -105±33 to -13±22 µmol g-^{1} (dry weight) day^{-1} in Run 2 and -103±11 to 17±12 µmol g-^{1} (dry weight) day^{-1} in Run 3.

The most appropriate linear mixed effects model of NPP, respiration and fluorescence showed that both the fixed terms of Day and Treatment were significant (Table 3. 4). In contrast, Day was not found to be significant in models of respiration rate (Table 3. 5) with Hummock and Block the best random effects terms to explain the variance beyond the Treatment effect (Figure 3. 8). Common to both the models of NPP and respiration was that the random effects described in the models explained little of the within treatment variance.

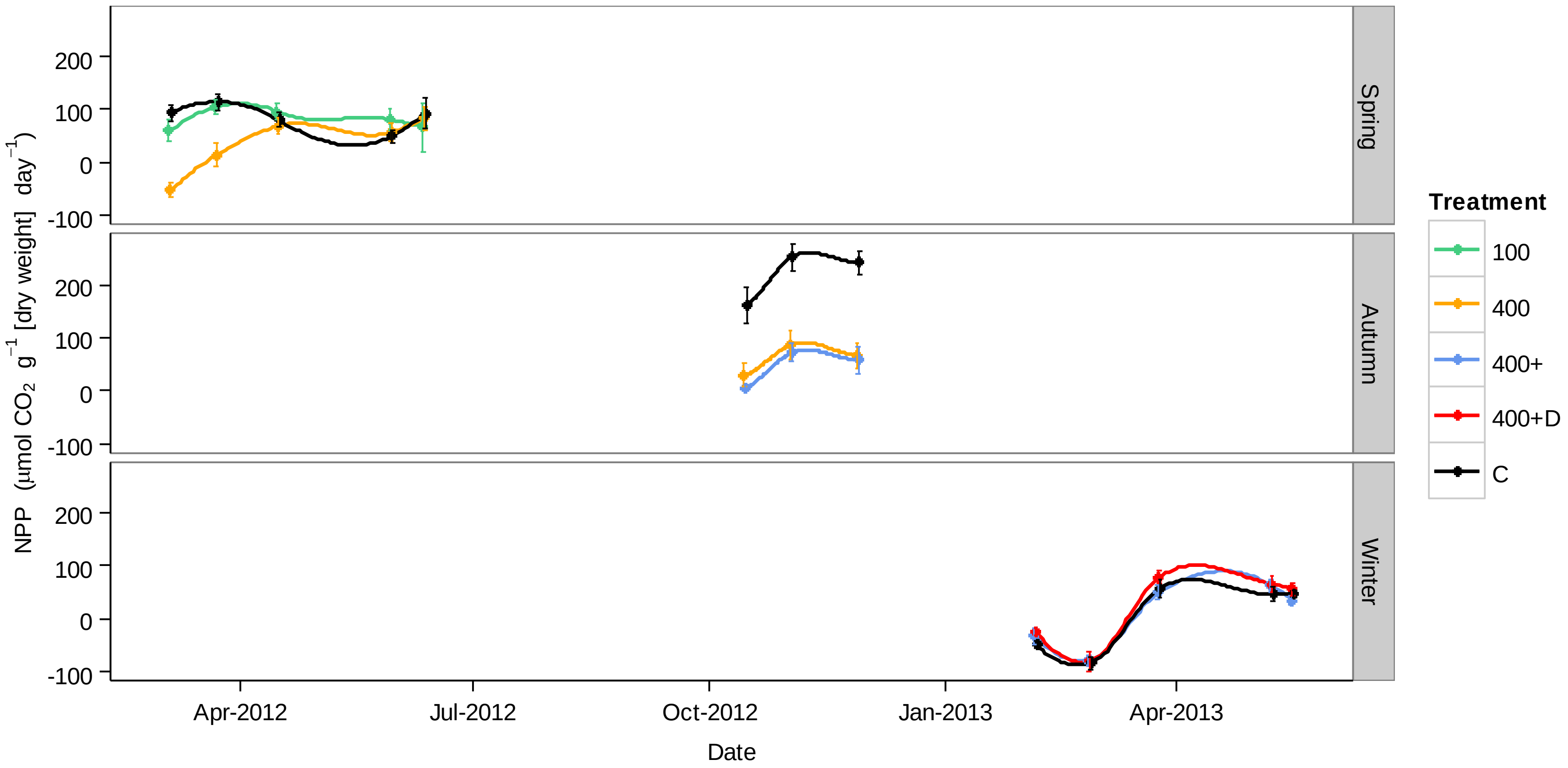


Figure 3. 6 NPP of pots in each treatment group during each run when PAR=2000 µmol m^2 s^{-1}. Points show mean ±SEM bars fitted with LOESS regression line (parameters as in Figure 3. 2). Positive values show CO$_2$ uptake (indicating photosynthesis).

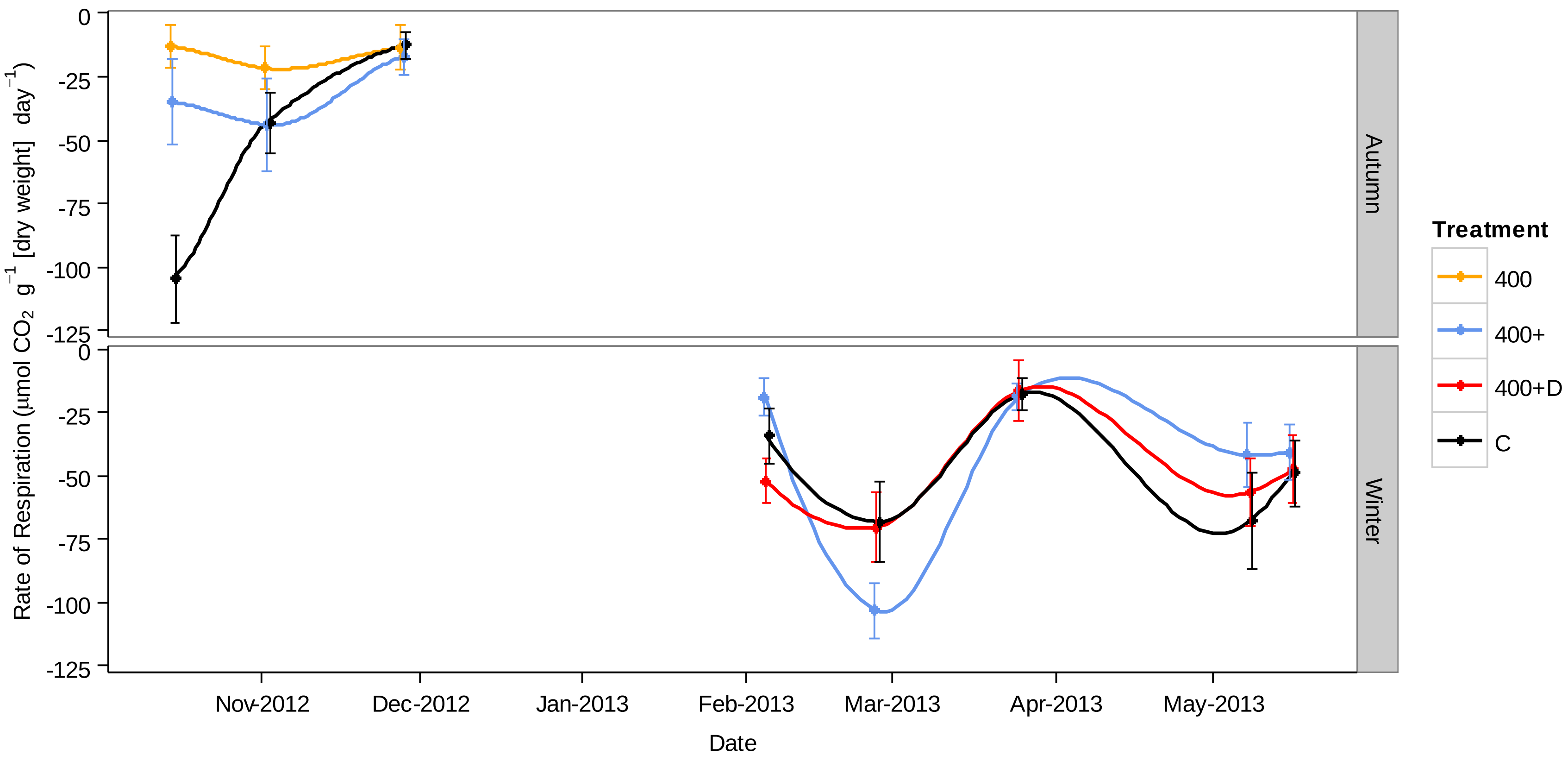


Figure 3. 7 Respiration of pots in each treatment group in runs 2 and 3 of the experiment measured when PAR = <1 µmol m^2 s^{-1}. Points show mean ±SEM bars fitted with LOESS regression line (parameters as in Figure 3. 2). The lower the negative values, the higher the rate of respiration.

Table 3. 4 Results of linear mixed effects model of **NPP** (µmol CO_2 g[dry weight]$^{-1}$ day^{-1}) with smallest model with the lowest AIC shown in bold.

Model	**AIC**	**ΔAIC**
Random Effects		
Run+Pot+Hum+Run:Hum+Run:Pot+Block	3409	–
Run+Pot+Hum+Run:Hum+Run:Pot	3407	-2
Run+Pot+Hum+Run:Hum	3405	-4
Run+Pot+Hum	**3403**	**-6**
Run+Pot	3404	-5
Run	3423	+14
Fixed Effects		
Treatmment+Day	**3467**	**0**
Treatment	3520	+53
Day	3486	+96

Wald Test of Final Model

Fixed Effect Treatment+Day *Random Effect* Pot

	Chi Sq	**Df**	**P value**
Treatment	33.13	4	<0.001
Day	70.73	4	<0.001

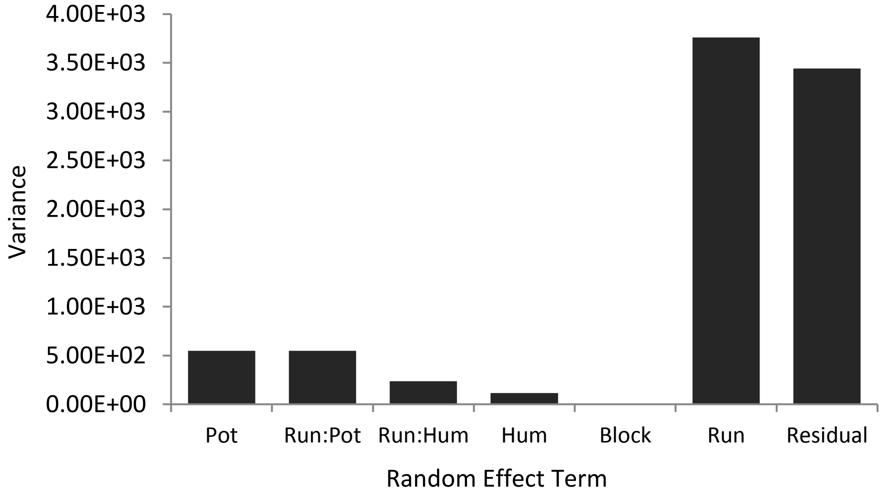


Figure 3. 8 Amount of within treatment variance explained by the different random effects terms in the largest mixed effect model described in Table 3. 4. The final model, with the lowest AIC, only included the random effects terms Pot.

Table 3. 5 Results of linear mixed effects model of **respiration** (μmol CO_2 g[dry weight]$^{-1}$ day^{-1}). The most appropriate model with lowest AIC shown in bold. Random effects calculated using REML estimates and fixed effects using ML estimates.

Model	AIC	ΔAIC
Random Effects		
Pot+Block+Hum+Run:Hum+Run:Pot+Run	1825	–
Pot+Block+Hum+Run:Hum+Run:Pot	1823	-2
Pot+Block+Hum+Run:Hum	1821	-4
Pot+Block+Hum	1819	-6
Pot+Block	1818	-7
Block	**1818**	**-7**
Fixed Effects		
Treatmment+Day	**1863**	–
Treatment	1872	+9
Day	1891	+28

Wald Test of Fixed Effects

Fixed Effect Treatment+Day *Random Effect* Block

	Chi Sq	Df	P value
Treatment	15.58	3	0.001382
Day	39.93	1	<0.001

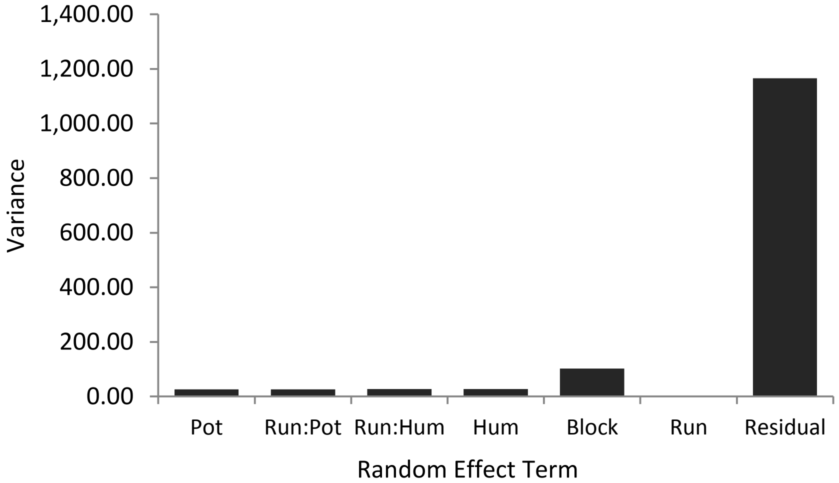


Figure 3. 9 Amount of within treatment variance explained by the random effects terms in the largest mixed effect model described in Table 3. 5. The final model, with the lowest AIC, included only the random effects term Block.

3.5.4 New Growth

New growth during the duration of the experiment arose in the form of new, smaller and more elongated auxiliary stems and was found in all treatments after 100 days in Run 1 and Run 3 of the experiment. No new growth was found in any of the pots harvested in Run 2 (Figure 3. 10). Two distinct zones of growth were apparent in both Run 1 and Run 3 with new stems growing from the upper portions of stems (here after referred so as side innovations) and stems which grew from the lowest portion of an original stem (base innovations) (Figure 3. 11a, Appendix 3.7). In both Run 1 and 3 most new growth occurred in pots which had been subjected to the higher temperature treatments as opposed to control pots (Figure 3. 10). Significantly more new growth was seen in Run 1 in both control and temperature treatment pots than in Run 3 (Figure 3. 10).

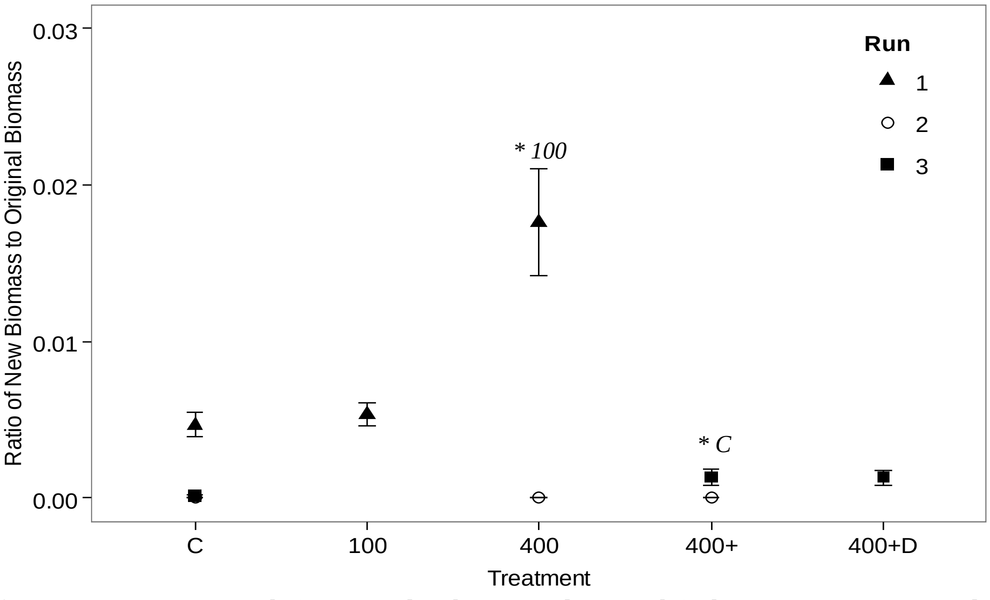


Figure 3. 10 New growth (measured as biomass dry weight) shown as a ratio to total original sample biomass dry weight for each treatment and run of the experiment. Points show the mean percentage ±SEM (n=16 per treatment per run). **C* shows significantly higher growth than control treatment group in run3 (*t=-2.4, df=15.9, p=0.03*), **100* shows significantly higher growth than 100 treatment group in run 1(*t=-3.8332, df=22.9, p=<0.001*). No new growth was observed in any treatment group in run 2.

The location (distance from capitulum) at which new side innovations grew correlated to the depth of bleaching (Figure 3. 11) with new side innovations growing from unbleached original stem immediately below the area of bleaching (Appendix 3.10). A greening of the area immediately below this was often observed in stems which did not show any auxiliary growth (Appendix 3.7).

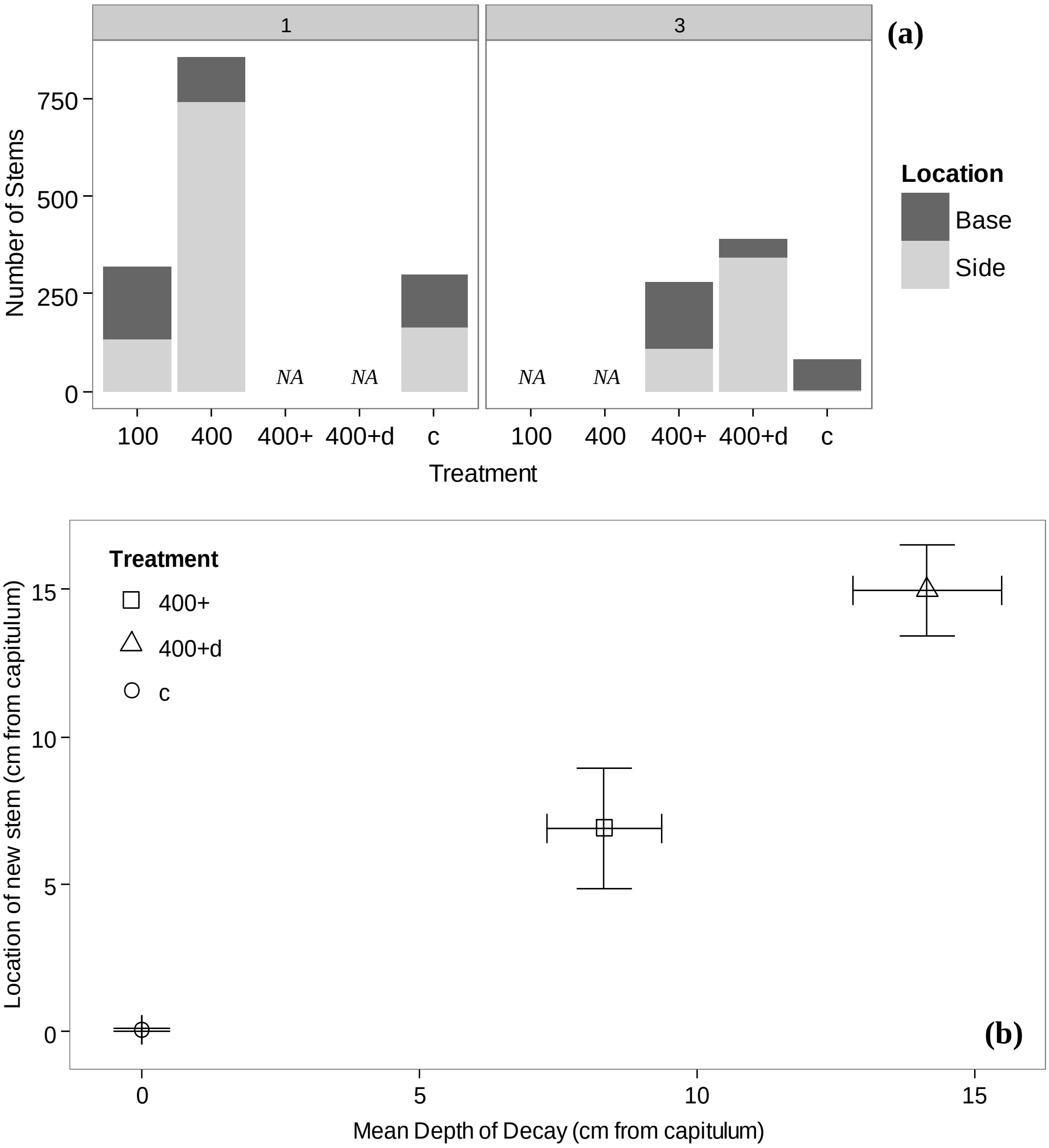


Figure 3. 11 The location of new growth found in a subsample of 16 pots per treatment per run showing (a) the total number of new side and base innovations seen in runs 2 and 3 and (b) the mean location of new auxiliary side innovations in relation to the mean depth of bleaching in the same pot shown with StE bars.

3.6 Discussion

3.6.1 Photosynthetic Capacity and CO_2 Exchange

The photosynthetic capacity, as indicated by chlorophyll fluorescence and CO_2 assimilation, of the upper most sections and capitula of *S. capillifolium* stems was found to vary considerably between temperature treatments, throughout and between each run of the experiment. The highest maximum quantum yield of photosystem II (MQY), shown by the Fv/Fm ratio (Maxwell and Johnson, 2000), in every run, and the closest to the accepted healthy plant ratio of around 0.75 (Demmig and Björkman, 1987), was found in control pots which had not been subjected to a temperature treatment. Pots which were subjected to the temperature treatments showed a general increase in MQY throughout the duration of each run, with perceivably quicker recovery to healthy Fv/Fm ratios in the less severe treatments with lower maximum surface temperatures and residency times.

The least amount of damage, in terms of reduction in photosynthetic capacity, was seen in pots exposed to the temperature treatment of 100^{o}C where capitula had an Fv/Fm ratio closest to those of the control pots throughout the duration of the spring run of the experiment. This being the least damaging treatment is consistent with the observation that it induced the least amount of bleaching, which suggests that surface temperatures and residence time of this magnitude do not cause severe damage in *S.capillifolium* with a pre-burn moisture content of around 90%. Pots treated with a maximum surface temperature of 400^{o}C showed the greatest reduction in MQY when compared to control pots, however little difference was detected in MQY between 400^{o}C treatments when the maximum surface temperature residence time and pre-burn moisture content was varied. This shows measure of the maximum temperature reached at the surface of the *Sphagnum* layer may be a sufficient indicator of the potential short term impact on photosynthetic capacity and that mechanisms for damage in plant cells brought about by fire, such as protein denaturation or lipid mobility shown in other plants (Levitt, 1972) can be brought about by exposure to surface temperatures of around 400^{o}C for just 3 seconds in *S.capillifolium* at a pre-burn moisture content of around 90%.

Another important observation beyond the effect of high temperatures on photosynthetic capacity was that the MQY varied both within a run over time and between runs suggesting that short term changes in environment and seasonality are also important. This was demonstrated by the control pots, which did not show the steady increase in MQY over time as seen in temperature treated pots, rather considerable variation between sample days.

An optimum stem moisture content for photosynthesis has widely been shown in *Sphagnum* with declining rates of CO_2 assimilation coupled with a reduction in stem moisture content with the water needed for optimum photosynthesis varying between species (eg. Clymo, 1973, Williams and Flanagan, 1996, Schipperges and Rydin, 1998, Adkinson and Humphreys, 2011, Silvola and Aaltonen, 1984, Robroek *et al.*, 2009, Titus *et al.*, 1983, Grace, 1973, Titus and Wagner, 1984, Strack *et al.*, 2009) and seasonally (eg. Johansson and Linder, 1980, Titus *et al.*, 1983). Specifically, the MQY measured using chlorophyll fluorescence has been shown to decline with reduced stem moisture content in *Sphagnum* (van

Gaalen *et al.*, 2007). Although the aim of this study was to limit environmental variation by maintaining steady moisture conditions to help show the effect of the temperature treatments, inevitably stem moisture content did vary to some degree within and between runs of the experiment. The effect of stem moisture content was demonstrated here in the mixed effects model of Fv/Fm measurements in which stem moisture content accounted for the most within treatment and sample day variation with lowest MQY in control pots corresponding to lower stem moisture content and a particularity warm period during Run 1. During Run 3, the winter run of the experiment, it was also found that the lowest MQY found in control pots occurred after a period of a few days when the *Sphagnum* had frozen. This suggests that the variation in the MQY in control pots reflected environmental conditions and furthermore that photosynthetic capacity was able to recover from the stem moisture content and the temperature ranges experienced during the experiments.

Sphagnum has been shown to tolerate desiccation up to a critical moisture threshold (Schouwenaars and Gosen, 2007), the point at which net photosynthesis ceases (Schipperges and Rydin, 1998), suggesting that the drying experienced in control pots during this study was survivable and did not drop below this threshold. An important avenue for future experimentation would be to determine the interaction between exposure to fire and periods of post burn desiccation as there was some evidence for this here in the 400+D treatment. *Sphagnum* samples from this treatment were dried to a moisture content of 80% prior to burning, but even when placed in the same conditions as all other treatments and watered frequently were consistently drier up to 88 days post burning. This could be caused by the water transport and holding capacity of the *Sphagnum* being compromised by drying and subsequent exposure to high temperatures suggesting that fire may make *Sphagnum* more vulnerable to long term damage brought about by drought by increasing the likelihood of drying below the critical threshold.

Post burn conditions are also important when considering the use of chlorophyll fluorescence for quantifying recovery in the field, as these experiments show that measurements on burnt *Sphagnum* have to be made concurrently with un-burnt samples from the same site to take account of variation in MQY brought about by environmental conditions. Confounding this is that short term changes in environment may have long term influences on primary productivity in *Sphagnum* (Backéus, 1988, McNeil and Waddington, 2003) making it necessary for fluorescence measurements, and indeed other measures of photosynthetic capacity, to be a long term form of monitoring rather than a “snap-shot” measurement which may not be representative of differences in MQY brought about by burning alone.

It is important to note here that the chlorophyll fluorescence measurements in this study were not made on the same capitula over time but on different capitula or part of stem which made up the surface of pot, often the uppermost part of a stem if there was capitulum loss or new auxiliary capitula, at each sampling time. These measures of photosynthetic capacity must not therefore be interpreted as recovery in the photosynthetic capacity of one capitulum following exposure to high temperatures, but rather a reflection of whole pot recovery. However, it has been shown that isolated capitula are more susceptible to damage than those within a tighter cluster of other stems (Schipperges and Rydin, 1998) so single capitula measurements may not always be representative of the whole pot. Understanding how larger samples, better representative of a hummock, respond to burning was the basis for whole pot measurements of CO_2 exchange.

Whole pot measurements of CO_2 assimilation, NPP, largely reflected the treatment effects on MQY indicated by chlorophyll fluorescence but with the notable exception of the lack of treatment effect on NPP in the winter (Run 3). During Run 1 and Run 2, the spring and autumn runs respectively, the control pots showed higher NPP than the 400°C temperature treatments with some degree of recovery in the temperature treated pots in Run 1, indicated by a return to similar NPP as the control pots. Recovery of the temperature treated pots was not seen in either Run 3 or Run 2, but this may be a reflection of measurements not being continued throughout the duration if the Run 2 due to the presence of mould in the latter weeks of the run. Unlike the 400°C treatments NPP in the 100°C treatment did not differ significantly to the rate measured in the control pots and so again suggests that the higher temperature treatment had a more detrimental effect on photosynthesis. This supports the observations made of MQY that the temperatures experienced at the *Sphagnum* surface during a fire may be a good indication of the degree of physiological damage to *Sphagnum*. When comparing respiration between treatments there is not such a clear treatment effect, despite it still being a significant term in the mixed effects model. This however is likely due to the pronounced differences in respiration rates observed on day 1 between the control pots and temperature treated pots in Run 2. Again there was considerable variation between sampling days particularly in Run 3, the winter run, when, as with NPP, there was considerable temporal variation but no detectable difference between treatments. During both Runs 2 and 3 the NPP of temperature treated pots followed the same temporal pattern of NPP of control pots. This suggests that NPP in all pots was determined by other factors beyond the temperature treatments as was also indicated from the chlorophyll fluorescence results.

Sphagnum has been found to exhibit strong seasonal variation in production with short day photoperiods (Gerdol, 1995) and low temperatures associated with up to a five-fold reduction in growth (Gerdol *et al.*, 1998). The findings here support this seasonality shown here by the lack of CO_2 assimilation during the winter run of the experiment. However this is confounded by the lower stem moisture content experienced throughout the winter run which as discussed previously could account for low NPP in the control pots. However, the implications for this in the context of prescribed burning is that if photosynthesis and growth rates are lower during the colder and shorter photoperiod days of winter months, then rates of recovery could be much slower following fires which have taken place early in the legal burning season (October through to February) when compared to burns which happen at the tail-end of the legal burning season (March/April). Seasonality is also an important consideration when formulating monitoring systems to determine the impact of fire on *Sphagnum*, as making CO_2 assimilation measurements during winter alone may not allow for the full detection of the impact burning has had on *Sphagnum* as comparative unburnt *Sphagnum* may naturally show lower rates of photosynthetic capacity and thus any differences between burnt and unburnt may be less pronounced.

3.6.2 New Growth

New growth in the form of side and base innovations growing from original stems were only found in Run 1 and 2 of the experiment. These runs were classed as summer and spring runs respectively with Run 2 occurring throughout the winter months (October to January). *Sphagnum* productivity has been found to be lower in winter months (Clymo, 1970, Clymo and Hayward, 1982) with higher growth rates correlating well with longer photoperiods in *Sphagnum magellanicum* and *Sphagnum papillosum* (Li and Glime, 1991). Low light levels, as recorded for Run 2, the winter run of the experiment, could therefore account for the lack of new growth observed. An additional control on growth is night-time temperature and *S.capillifolium* has been demonstrated to have a five-fold increase in growth at a night-time temperature of 15^{o}C compared to 5^{o}C (Gerdol *et al.*, 1998). The temperatures recorded during Run 2 declined from around day 50, making them lower than those in Run 1, so these low temperatures could also contribute to the lack of growth observed. Run 3, which ran over a particularly cold spring, had lower growth rates in the control pots than Run 1 which again could be due to the shorter day lengths and lower temperatures experienced throughout the run.

Although intuitive, it is important to highlight the differences in growth rates, in relation to biomass production, found across the experiment at different times of year, as it shows the need to take into account post burn conditions when assessing

Sphagnum recovery. Management burns for instance occurring in the spring time may show faster rates of *Sphagnum* recovery due to the more favourable growing conditions after burning, while autumn burns may show much slower apparent rates of recovery. This has implications for using *Sphagnum* damage, as indicated by lack of recovery, as a post-burn indication of fire severity as time of year may be more important for recovery than actual characteristics of the fire. In addition, other post fire conditions, most notably the moisture status of the *Sphagnum* layer and height of the water table may retard or promote growth with responses varying between species (Robroek *et al.*, 2007, Rochefort *et al.*, 2002). This would make it necessary to include post burn environmental variables and a method to assess *Sphagnum* over time when formulating a system to assess damage to the *Sphagnum* layer post burn.

A common observation regarding new growth throughout the experiment was the very distinct zones in which the new innovations originated. The side innovations appeared to be very similar to those described by Clymo and Duckett (1986), appearing bright green and originating at the base of existing branches from an area of outer stem cortex distinctly greener than the surrounding stem. Clymo and Duckett suspected that the ability of *Sphagnum* to produce new shoots in this manor was a widespread and important mechanism to overcome random or systematic disturbance events and has since been demonstrated in a number of species including *S.capillifolium* (Clymo and Duckett, 1986, Hamilton, 2000, Rochefort *et al.*, 2002). The production of new innovations in response to fire has been observed in the field (Hamilton, 2000) suggesting the side innovations observed here were not just a product of experimental conditions. Building on these observations, here it was found that the more severe temperature treatments, in terms of maximum surface temperatures and temperature residency time, induced more production of side innovations with the least severe temperature treatment (100 ºC for 3 seconds at the surface) promoting a similar quantity of new innovations as the control pots in Run1. The results suggest that this difference in recovery was likely due to the temperatures experienced at the *Sphagnum* surface and associated subsequent loss of capitula. Stems have the ability to recover from lower surface temperatures, which may not permanently damage the capitulum, and thus plants do not need to replace capitula, the site of greatest photosynthesis. However, when capitula are severely damaged side innovations are induced to replace the capitula and thus restore the photosynthetic ability at the surface. During Run1 it was evident that during the 100 day period of the experiment new capitula had reached the surface of the pots, replacing those lost. This substantiates the observations of Hamilton (2000) who noted some patches of *Sphagnum* in the field produced new green capitula on the surface as well as other areas in which capitula regained colouration after bleaching. The treatment which was intended to be fatal to *S.capillifolium* (treatment 400+D) was still found to result in new growth suggesting it would take even higher surface temperatures and temperature residency times to stop *S.capillifolium* regenerating in this way. However, as Clymo and Duckett (1986) demonstrated discs of *Sphagnum* cores taken up to 30cm below the *Sphagnum* surface still produced new innovations from apparent dead material suggesting that the detrimental effects of high temperatures would potentially have to penetrate very deep within the *Sphagnum* layer to stop this type of regeneration. However, Clymo and Duckett also found that light was the key stimulus for inducing the production of new innovations meaning this could ultimately limit regeneration after fire deep within the *Sphagnum* layer.

The results of this experiment also showed innovations growing from the base of stems suggest the cutting of the *Sphagnum* stems to achieve potted samples of a consistent depth may have induced new growth too. It was found most new growth in the control pots came from the area of stem closest to the cut surface with more side stems in the most severe treatments of the two runs than bottom stems. This suggests a potential physiological control on the site of new growth in response to the severity and location of damage. The correlation between the maximum depth of bleaching found within a pot and the mean depth at which new innovations grew also suggests that damage to the capitulum triggers growth from the area immediately below the area of stem damaged, overriding any growth from lower sections and the production of what were observed here as base innovations.

3.7 Conclusions

The aim of this research was to determine some of the short term responses of *Sphagnum* to fire by carrying out multiple measurements of recovery on *S.capillifolium*, a hummock forming species common to areas of blanket in the UK, after exposure to simulated temperatures of *Calluna* fires. Firstly in regards to hypothesis [1], that the photosynthetic capacity of *S. capillifolium* would be reduced following exposure to high temperatures, there was evidence that rates of, and capacity, for photosynthesis was affected by being exposed to high surface temperatures akin to those found in the *Calluna* fires. Importantly the higher 400^{o}C treatments caused the most pronounced reduction in photosynthesis. The 400^{o}C treatments having the most detrimental effect on *Sphagnum* was also mirrored in the extent of bleaching and capitulum loss, which was minimal in the lowest 100^{o}C treatment. Secondly it was hypothesised that [2] a critical temperature and temperature residence time exists above which the temperature treatments will be lethal to *S.capillifolium*. Within the range of surface temperatures and temperature residence times used here a critical threshold was not ascertained, evident by new auxiliary stem growth found in the temperature treatment designed to be lethal, where *S.capillifolium* was exposed to surface temperatures of 400^{o}C for 30 seconds after being dried. It must be stressed that these experiments only concerned one species studied over three month periods within comparatively narrow maximum burn temperature and stem moisture content ranges so cannot be used to entirely reject the potential lethality of fire on other *Sphagnum* species beyond these conditions. Instead these results give evidence that *S.capillifolium* has the ability to recover from fire in certain circumstances. Beyond this there is strong evidence here that the rate of recovery of *S.capillifolium* is in response to maximum temperatures experienced at the surface as well as environmental conditions with the least amount of re-growth during the winter months. This is an important observation to consider when formulating assessments using *Sphagnum* re-growth as an indicator of the ecological severity of a fire.

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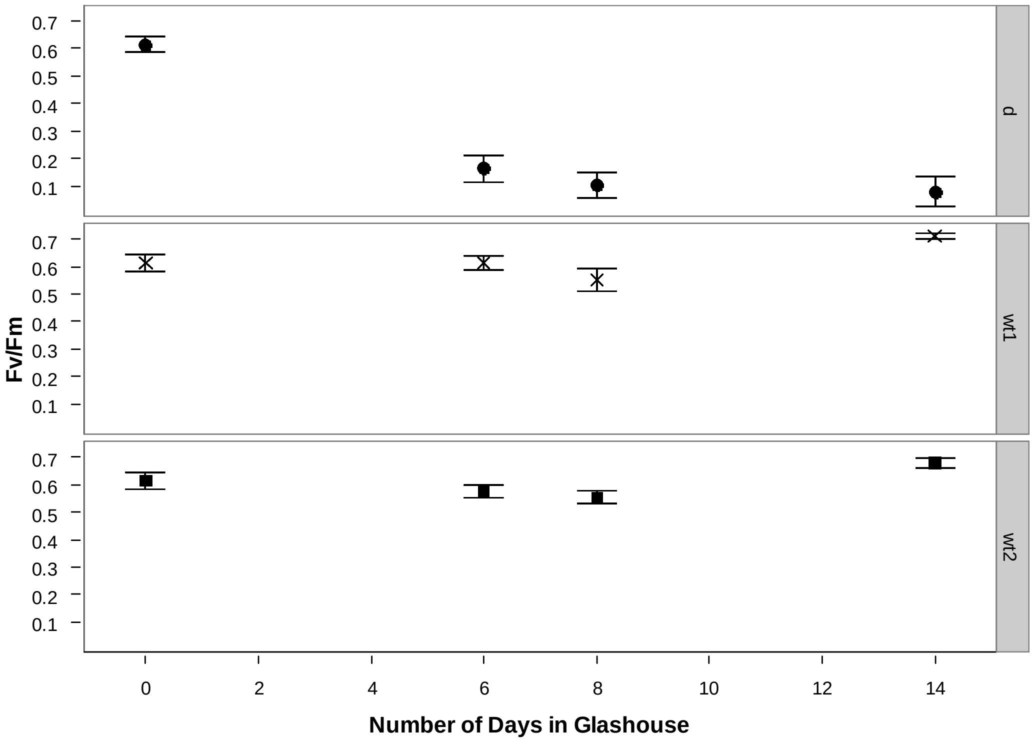
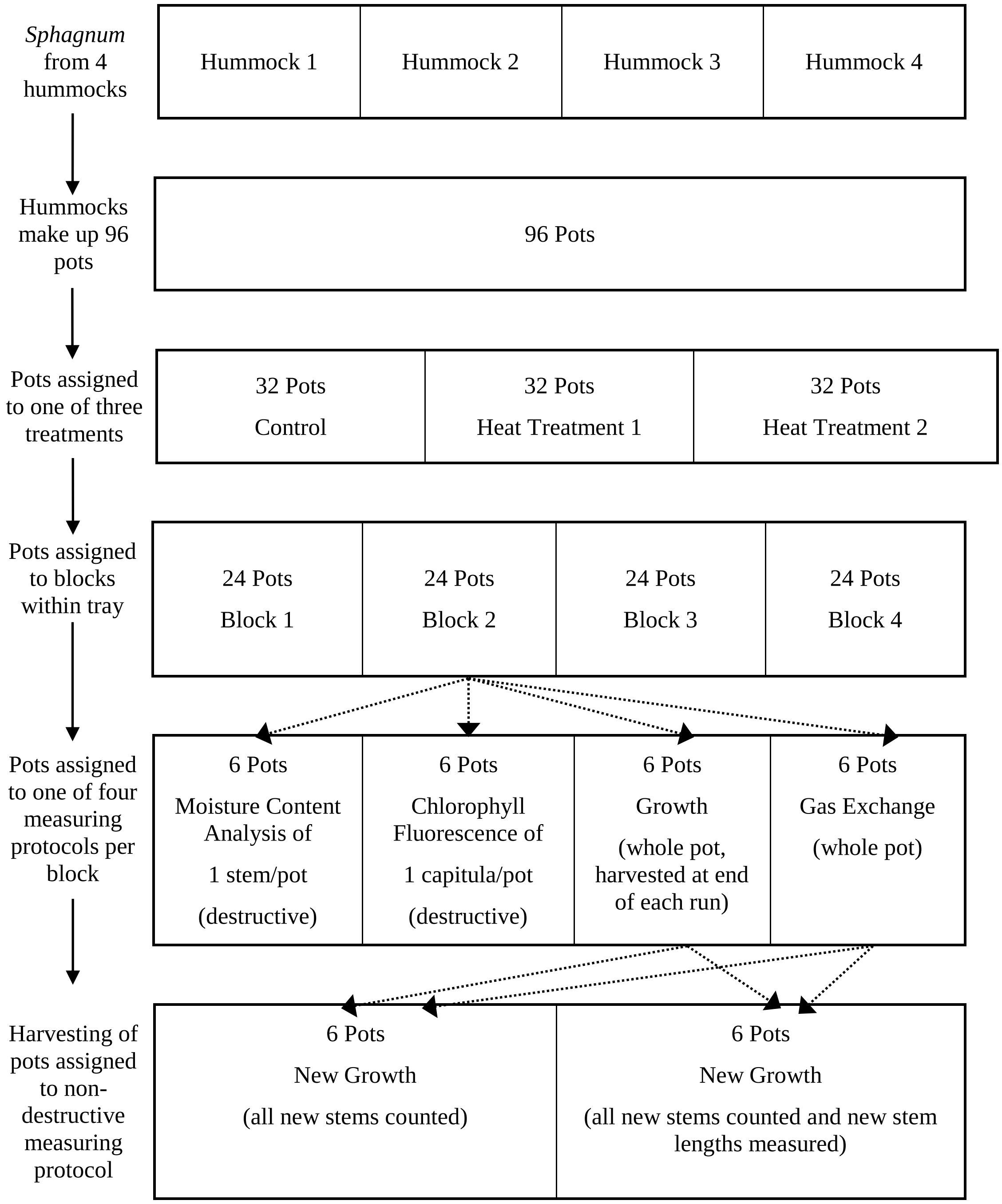
Appendix 3.1 Glasshouse Watering Trial

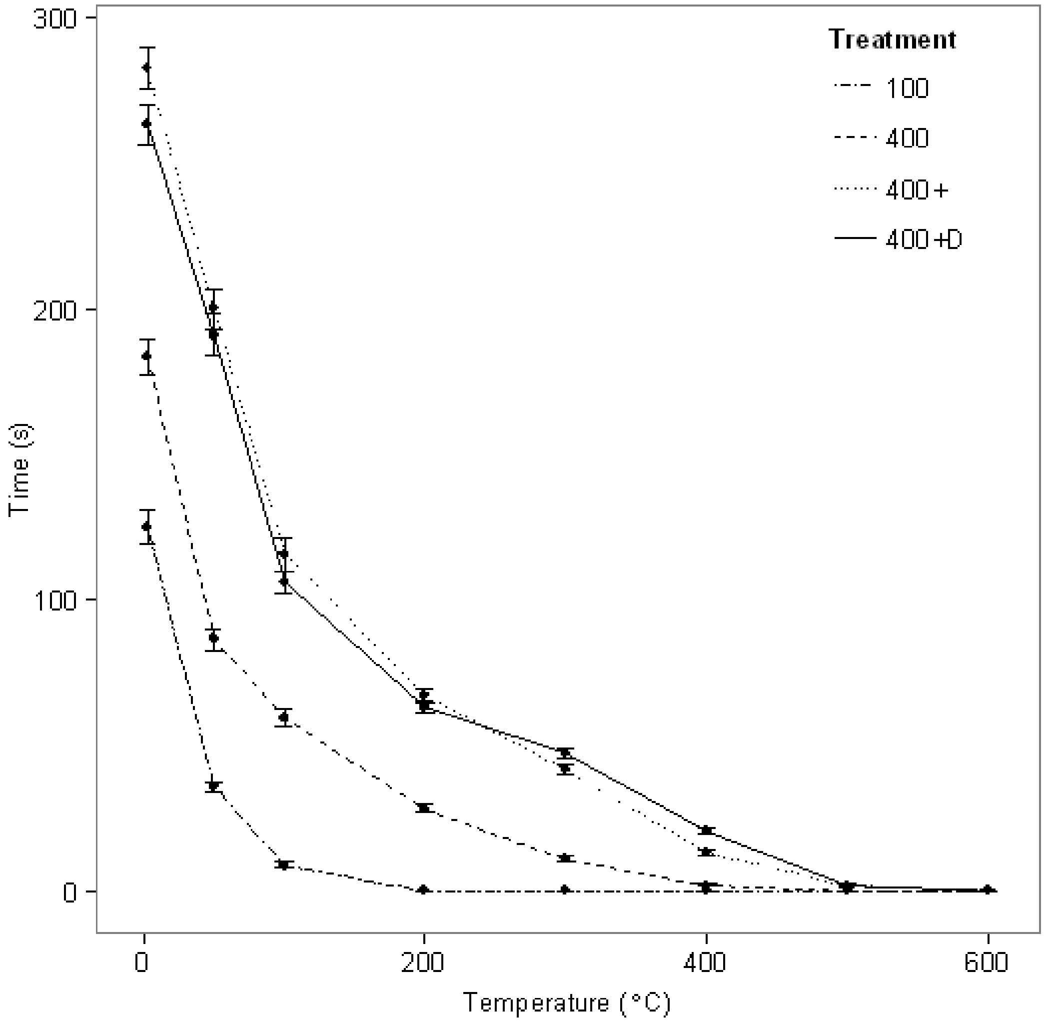


Fv/Fm ratio of the capitula of one stem per pot (n=12/treatment) under 3 watering treatments over a 2 week period in a glasshouse designed to track external air temperatures. d = no water applied to pots, wt1=5ml distilled water applied to each pot using a syringe, and wt2= 10ml distilled water applied to each pot via syringe. The bed of *Sphagnum* cuttings surrounding pots was kept moist by watering with tap water throughout the trial.

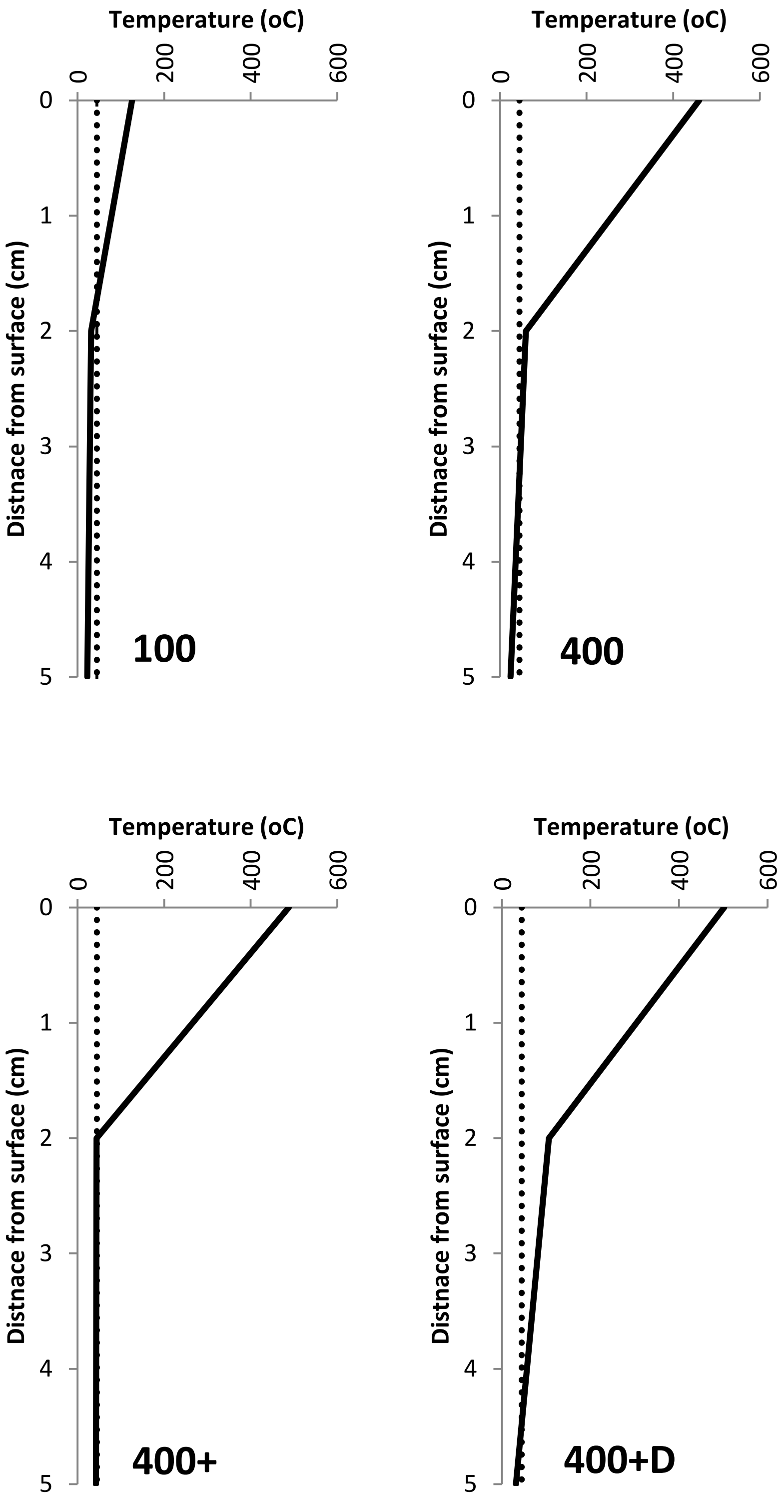
Appendix 3.2 Schematic of experimental design and sampling procedure



Appendix 3.3 Maximum temperatures and temperature residency time of each treatment

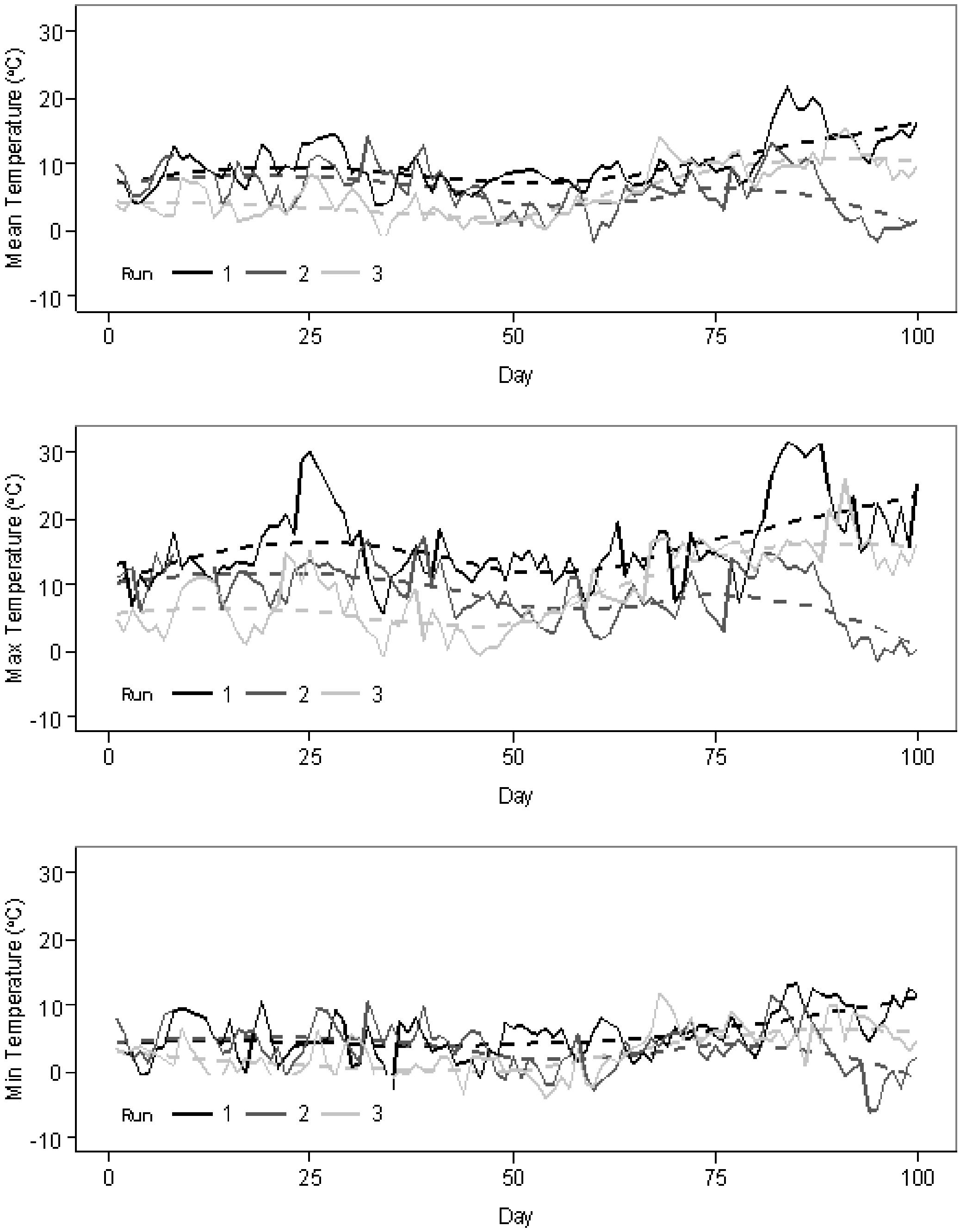


Time (s) surface temperatures achieved for each treatment used in the experiment. Points represent the mean time the surface was above each temperature ± StE bars (Treatment 100 n=32, Treatment 400 n=64, Treatment 400+ n=62, Treatment 400+D n=32).

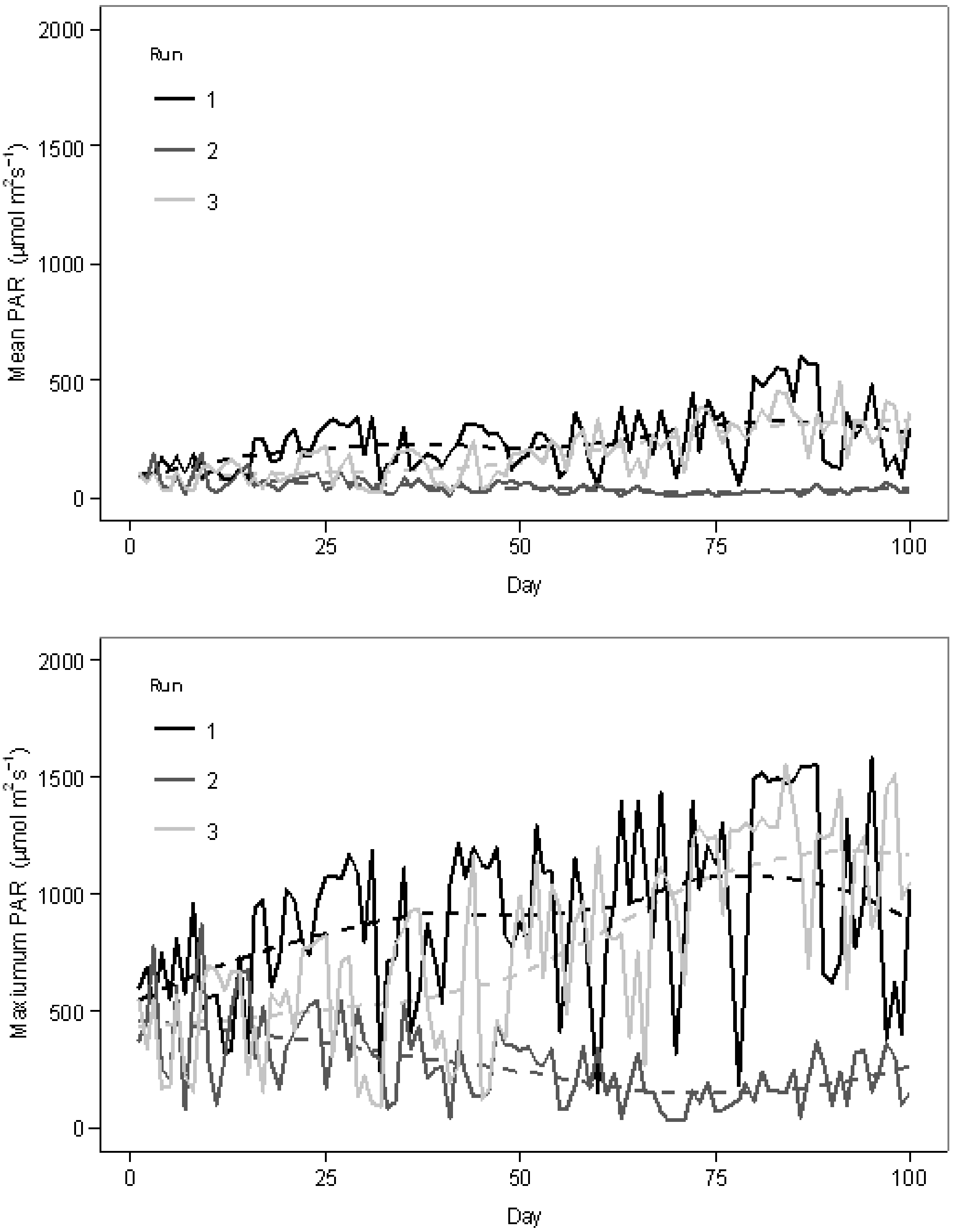


Surface temperatures and temperatures reached at 2cm and 5cm below the surface in samples of *Sphagnum capillifolium* exposed to the four different treatments. Solid line shows maximum temperature reached at the three locations, dotted line represents the potentially physiologically damaging temperature (45^{o}C).

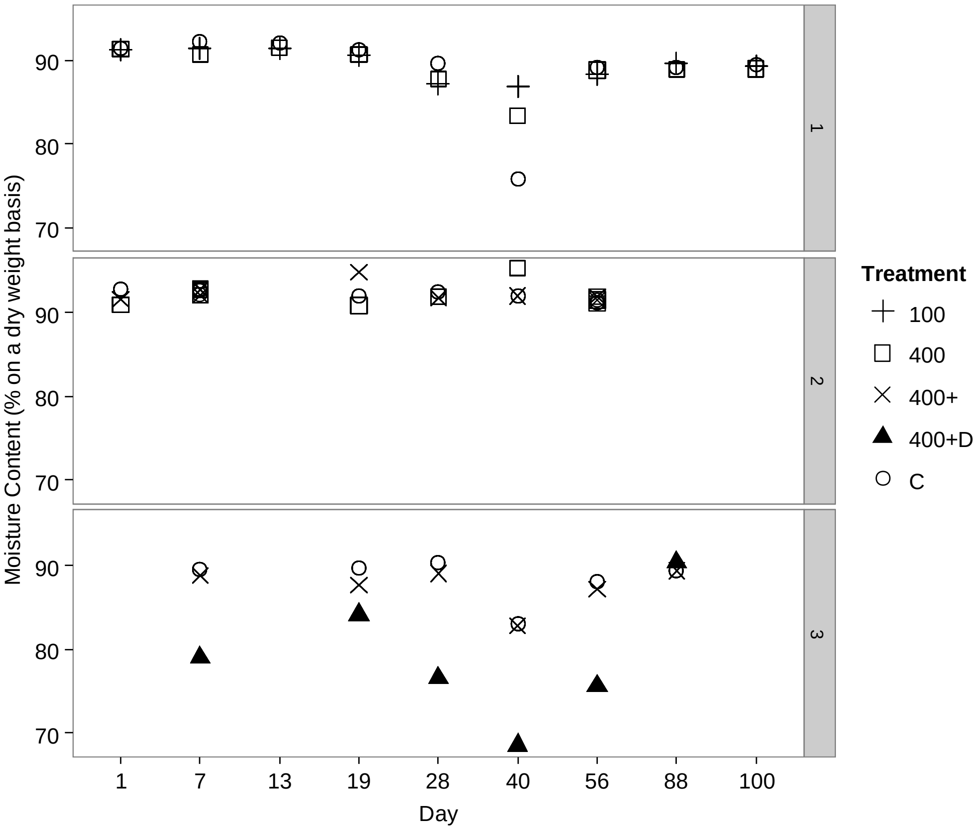
Appendix 3.4 Glasshouse conditions



Calculated mean (a), minimum (b) and maximum (c) temperatures in the glasshouse where the *Sphagnum* samples were kept for the duration of three runs of the experiment. Solid lines show calculated temperatures with dashed showing temperature trend (calculated using LOESS smoother).



Observed mean (a) and maximum (b) external PAR (umol m^{-2} s^{-1}) recorded in the vicinity of the glasshouse in which the *Sphagnum* samples were kept for the duration of each run of the experiment. Solid lines show actual recorded PAR with dashed lines showing trend (calculated using loess smoother).

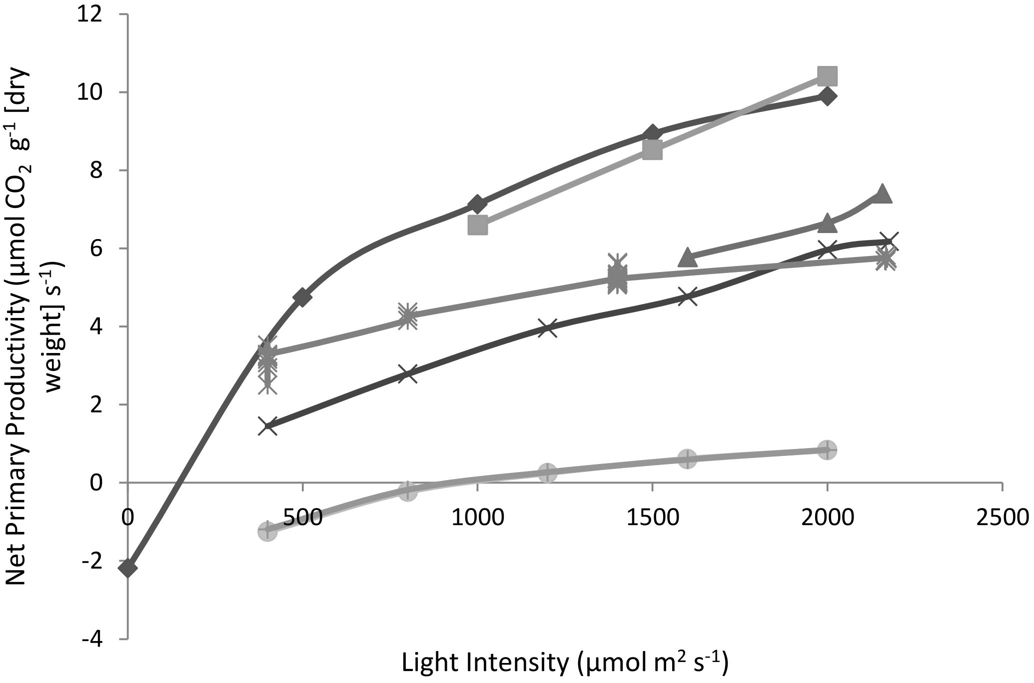


Moisture content (on a wet weight basis) of *Sphagnum* sampled from pots of each treatment during each run where n=8 per treatment per sampling time.

Mean moisture contents for each treatment are shown below:

Run	Treatment	Mean Moisture Content (% wet weight basis)	Mean Moisture Content (fresh /dry weight)
1	Control	88.6	9.9
	100	89.3	9.6
	400	88.9	9.3
2	Control	92.1	10.9
	400	91.2	12.6
	400+	91.5	12.5
3	Control	88.9	6.9
	400+	88.5	8.2
	400+D*	79.1	6.1

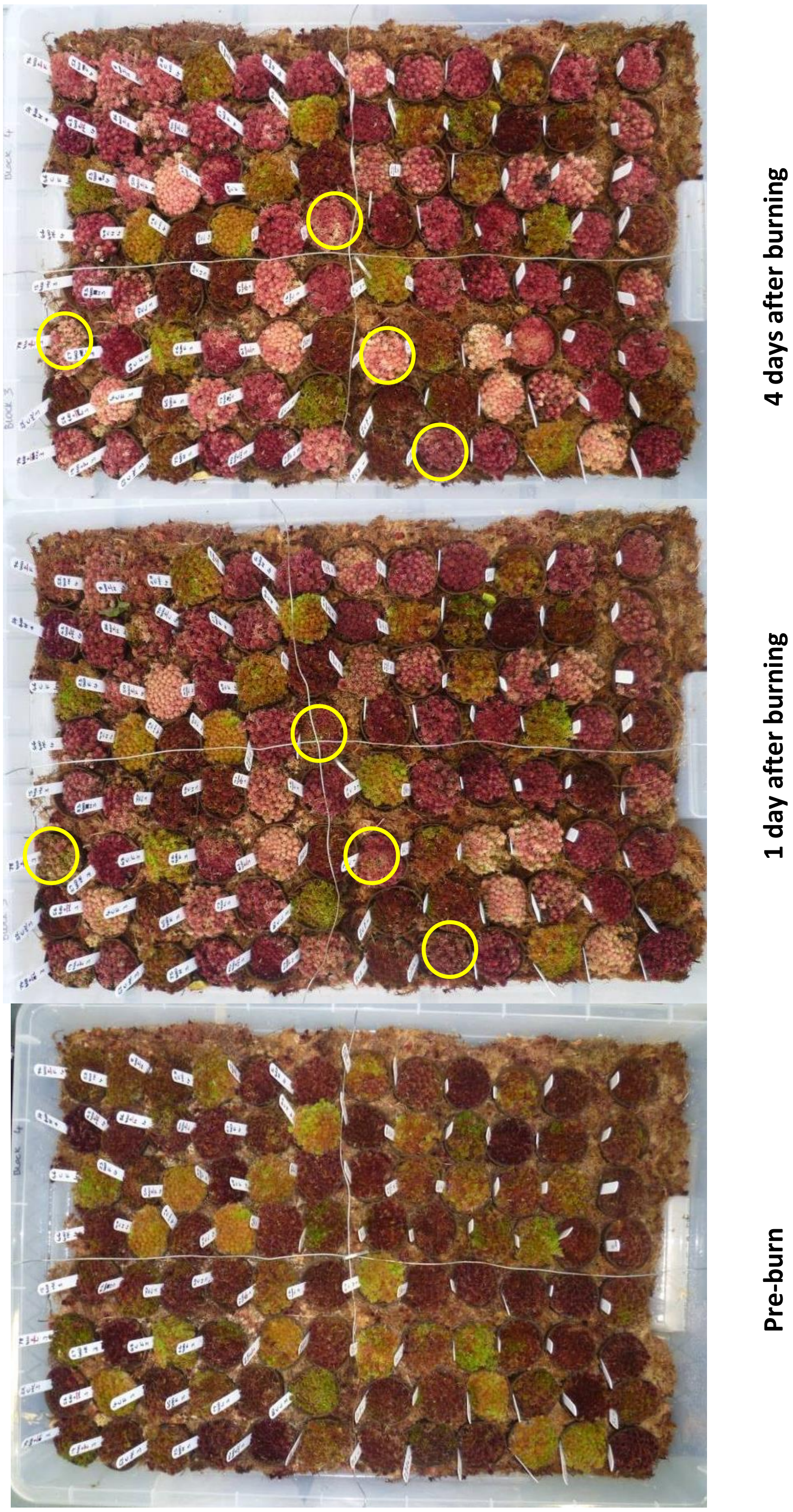
Appendix 3.5 Rates of Photosynthesis in *Sphagnum capillifolium* at different light intensities using Licor Li-6400 and specifically designed sample chamber



Rates of photosynthesis measured in seven samples of *Sphagnum capillifolium* at different light intensities. Measurements were made using the light curve logging function on the Licor Li-6400 and set to maintain sample chamber temperature at 20ºC with an initial CO_2 concentration of 400µmol.

Rates of photosynthesis never stabilised or declined with an increase in PAR. It was hypothesised that this was due to the large samples of *Sphagnum* used within the sample chamber, as the samples would become light saturated at different depths in relation to light intensity. Thus damage or saturation at the surface of the sample could be masked by the photosynthetic activity of lower sections of the sample.

Appendix 3.6 Bleaching evident prior to burning, 1 day after burning and 4 days after burning in Run 2 of the experiment. Yellow circles highlight pots which showed a delay in bleaching



Appendix 3.7. Photographs of new auxiliary stem growth observed 100 days after burning in runs 1 and 2 of the experiment

New side innovation growing from original stem with capitulum decay and eventual loss.

New side innovation growing from original stem showing bleaching.

Difference in morphology of new side innovations (top of image) and base innovations which grew from the bottom cut surface of the stem (bottom of image).

A pot from the 400ºC treatment (Run1) 100 days after burning showing new capitula (green). The capitula of most of the original stems were heavily bleached with widespread capitulum loss observed throughout the pot.

An example of stems (subjected to the 400+ treatment in Run 3) showing the characteristic bleaching of the capitulum and the apparent greening of the area of stem immediately below.

Examples of base innovations found growing from the bottom of original stems.

4. Methanotrophy in *Sphagnum* and the potential impact of fire

4.1 Abstract

Methanotrophic bacteria can be found living in symbiosis with *Sphagnum* mosses in peatlands across the world (Kip *et al.*, 2010). Their role in intercepting and oxidising CH_4 naturally produced by peatlands is increasingly being emphasised within the context of the global atmospheric greenhouse gas budget (Chen and Murrell, 2010). Fire, which occurs both naturally and anthropogenically on peatlands, could potentially reduce or change the methanotrophic community and have consequences for net CH_4 emissions from peatlands. CH_4 oxidation has been reported in a large number of *Sphagnum* species from different microhabitats, with rates of CH_4 oxidation of up to 80 µmol CH_4 g^{-1}dw (dry weight) day^{-1} (Kip *et al.*, 2010). However, there are potential problems with the methodology used, and as yet there is no research looking at the specific effect of fire on methanotrophy. Here we show that experimental errors can account for oxidation rates seen in samples using the standard methodology; we found that empty flasks produced statistically similar CH_4 fluxes to those of *Sphagnum-filled* flasks. *Sphagnum papillosum* was the only species studied that showed detectable methanotrophy but no differences were found between burnt and unburnt samples. These results emphasize the need for well considered controls when estimating potential CH_4 oxidation in *Sphagnum* using this methodology. The results also reiterate that rates of CH_4 oxidation may vary considerably within *Sphagnum* and that a better understanding of the controls on CH_4 oxidation in the *Sphagnum* layer is needed if the role of methanotrophic bacteria can be incorporated into carbon budget models of *Sphagnum*-dominated peatlands.

4.2 Introduction

Peatlands store up to one third of terrestrial carbon (Gorham, 1991) making them a significant component of the terrestrial carbon cycle. Carbon can however be lost directly to the atmosphere from peatlands in the form of carbon dioxide (CO_2) and methane (CH_4), both important greenhouse gases. CH_4 has a global warming potential (GWP) 34 times that of CO_2 over a 100 year time horizon (IPCC, 2013) and is estimated to account for 18% of global warming (Butler, 2012). Understanding the controls on CH_4 efflux to the atmosphere is therefore important if peatlands are to be maintained and managed in ways to best maximise their carbon storage potential and their role in mitigating climate change. Methanotrophic bacteria, predominantly found in the aerobic zone of peat and in the *Sphagnum* layer, are responsible for oxidising significant amounts of CH_4 as it is transported through peat soils to the atmosphere (Whalen, 2005), converting CH_4 to CO_2 and thereby reducing the GWP of the gas emissions. This makes the balance between the production of CH_4 and the oxidation of CH_4 by methanotrophic bacteria a significant component of the peatland carbon cycle and is increasingly recognised as integral to the global atmospheric greenhouse gas budget (Chen and Murrell, 2010, Singh *et al.*, 2010, Chowdhury and Dick, 2013).

Methanotrophic bacteria use CH_4, produced from the breakdown of organic material under anoxic conditions, as their sole source of carbon and energy through a process which is oxygen-dependent, confining them mainly to the upper aerobic layers in wetlands (Hanson and Hanson, 1996), although anaerobic CH_4 oxidation may also be widespread (Gupta *et al.*, 2013). Methanotrophic bacteria, which are classified as Type I or Type II, based on their physiology and phylogeny (Hanson and Hanson, 1996), can live in mutualistic symbiosis with *Sphagnum* (eg. Larmola *et al.*, 2010, Kip *et al.*, 2010, Parmentier *et al.*, 2011, Stępniewska *et al.*, 2013), living in hyaline cells and on leaf surfaces (Raghoebarsing *et al.*, 2005, Kip *et al.*, 2010). The CO_2 they release provides an important source of carbon for *Sphagnum* photosynthesis (Raghoebarsing *et al.*, 2005, Parmentier *et al.*, 2011) and is estimated to make up to 10 to 30 % of total carbon assimilated by *Sphagnum* (Raghoebarsing *et al.*, 2005, Larmola *et al.*, 2010). The critical role of methanotrophic bacteria associated with the aerobic peat and *Sphagnum* layer in balancing CH_4 production with oxidation means that *Sphagnum*-dominated peatlands often have lower CH_4 emissions than other wetland types (Nykänen *et al.*, 1998) with methanotrophs having been found to oxidise up to 100% of CH_4 (Whalen, 2005). Reducing the number, or changing the community structure, of methanotrophs in the *Sphagnum* layer could therefore have a significant impact on the carbon balance of a peatland.

A potential mechanism to reduce the number of methanotrophs and thus rates of CH_4 oxidation could be fire. Fires occur both naturally on peatlands and due to anthropogenic causes, including the routine intentional burning to clear and manage land and for agricultural. The understanding of the interaction between fire and the *Sphagnum* layer is limited but studies have shown that *Sphagnum* may experience potentially biologically lethal temperatures (Davies, 2005, Glime, 2007) as well as be consumed by a fire (Hamilton 2000). The direct consumption and heating of the *Sphagnum* layer could be lethal to methanotrophic bacteria residing there and so potentially reduce the amount of CH_4 intercepted and oxidised. There is limited research into the effect of fire on the bacterial community of peatlands and peat soils, particularly in relation to the impact on methanogenic and methanotrophic bacteria (Andersen *et al.*, 2013) but a general reduction in methanotroph population size together with an increase in the dominance of type II methanotrophs has been demonstrated on a burned *Calluna vulgaris*-(L.) Hull dominated peatland (Chen *et al.*, 2008) this suggests that fire has the ability to alter the methanotrophic community so the potential to change rates of CH_4 oxidization.

4.3 Aims

The aim of this research was to investigate the magnitude of CH_4 oxidation by methanotrophic bacteria associated with three *Sphagnum* species common in UK blanket bog, and to examine the potential influence of fire, via its effect on the methanotrophic populations. A lab-based experiment was used to enable CH_4 oxidation rates in samples of *Sphagnum* to be determined in non-CH_4-limiting conditions following the methodology set out in Larmola *et al.* (2010). The potential impact of fire on methaotrophic activity in the *Sphagnum* layer was investigated by subjecting samples to a temperature treatment designed to simulate a temperatures of a heath fire. It was hypothesized that: [1] CH_4 oxidation would differ between species collected from different microhabitats using the experimental technique and that [2] *Sphagnum* samples subjected to a temperature treatment would show lower CH_4 oxidation rates, because temperatures experienced during the fire treatment would be lethal to methanotrophs.

4.4 Methodology

4.4.1 Sampling Site

Sphagnum capillifolium (Ehrh.) Hedw., *Sphagnum papillosum* Lindb. and *Sphagnum fallax* H. Klinggr. were collected from Whim Moss, an ombrotrophic CH_4 producing blanket bog at an altitude of 282m situated near Penicuik, South East Scotland (NT203532) (Sheppard *et al.*, 2014). A National Vegetation Classification (NVC) M19, *Calluna vulgaris/Eriophorum vaginatum* blanket mire (Rodwell 1991), Whim Moss has a mean air temperature (2003–2009) of 8.6°C (ranging from −9.2 to 27.7 °C) (Sheppard *et al.*, 2012).

4.4.2 Experimental Methodology

Based on the methodology set out in Larmola *et al.* (2010) samples of *Sphagnum* were allocated randomly to a 1000ml glass jar (Kilner®) and sealed with a metal vacuum lid and metal screw band (Kilner®) in which a 3-way valve (Discofix® 3-way Stopcock) with 4cm section of Bev-a-Line® tubing on the underside had been sealed into a gas tight hole (Figure 4. 1). Prior to each run of the experiment jars were washed and sterilised using 1% Nuetracon® (Decon Laboratories Ltd) solution and dried at 70°C for 24 hours. Once filled with *Sphagnum* and sealed, 10 ml of headspace air was removed from each jar using a syringe attached to the valve before being injected with 10 ml of pure CH_4 to give a starting CH_4 concentration just above 10,000 ppm, exact concentration being dependent on volume of *Sphagnum* and thus headspace volume in the jar. Once spiked with CH_4 each jar was shaken by hand for 10 seconds to help the mixing of CH_4 and headspace air. Once shaken, a 4 ml sample was removed with a syringe via the valve. Each sample was withdrawn from the jar after two flushes of the syringe to aid mixing (a flush entailing 4 ml being drawn into the syringe and pushed back into the jar). Immediately after being withdrawn from the jar, the entire 4 ml sample was manually injected into a Gas Chromatographer (5890 Series II, Hewlett Packard) with flame ionization detector (FID). Samples were taken from each jar and analysed at 0 hours (immediately after sealing, spiking with CH_4, shaking and syringe flushing), 5 hours, 24 hours, 29 hours and 48 hours during Runs 1 and 2 of the experiment and at 0 hours, 24 hours and 48 hours during Runs 3 to 5. Prior to each sample being removed the jars were shaken by hand for 10 seconds to help ensure gases in the jars were well mixed.

Figure 4. 1 Experimental set up showing jars filled with *Sphagnum* samples and the valve mechanism and syringes used to remove headspace gas samples.

The experiment was run once with no *Sphagnum* to ensure the methodology was sound and four times with the freshly collected *Sphagnum* samples, the sampling procedure being varied for each run in order to maximize the chance of sampling areas of *Sphagnum* demonstrating methanotrophy (Table 4.1). In all *Sphagnum* runs 10 jars contained samples subjected to a temperature treatment (where the surface of a sample was exposed to ~350^{o}C for 30 seconds) prior to sealing within the jars (here after termed the “burnt” treatment), and 10 jars contained samples not subjected to the temperature treatment (termed “unburnt”). Throughout each run each jar was kept in the dark in a temperature controlled room at 9 ^{o}C, only being exposed to light during the time it took to collect a headspace sample. Within each run, the wet weight of all samples was kept as uniform as possible, but did vary between runs and species. At the end of each run, samples were dried for 7 days in an oven at 70^{o}C and the dry weight recorded.

Table 4. 1 Sampling methodology for each run of experiment (species are S.cap=*S.capillifolium*, S.fal=*S.fallax*, S.pap=*S.papillosum*), the date of each run and mean moisture content (MC) of samples calculated on a percentage wet weight basis.

Run	Species	Collecting Procedure	MC	Date
1	No *Sphagnum*	-	-	May 2012
2	*S.cap*	All samples collected from 1 hummock, half (10 samples) subjected to temperature treatment	93%	May 2012
3	*S.fal*	All samples collected from 1 lawn, half (10 samples) subjected to temperature treatment	95%	April 2013
4	*S.cap*	Samples collected from 10 areas, divided into two samples and randomly assigned to temperature treatment or no temperature treatment	93%	April 2013
5	*S.pap*	Samples collected from 4 areas and half (10 samples) subjected to temperature treatment	94%	April 2013

4.4.3 Verification of methodology

A number of steps were taken to ensure sound methodology, primarily to ensure the jars used were well sealed and CH_4 could not leak from the jars, lowering CH_4 concentrations and thus giving the appearance of an oxidative flux. During the first run of the experiment all sterilised jars were empty but spiked with 10,000ppm of CH_4 and sampled as per the other runs. In addition the CO_2 concentration of each sample was analysed concurrently by the Gas Chromatograph allowing rates of respiration to be calculated. It could then be assumed that if CO_2 concentrations showed a linear increase from the starting concentration within the *Sphagnum-filled* jars over time then it was unlikely the jar was leaking and that oxygen was not limiting for either plant or bacteria since respiration (as indicated by a build up of CO_2 within the *Sphagnum*-filled jars) had been observed. Runs 2 to 5 were run with

20 jars containing *Sphagnum* samples and an additional 4 *Sphagnum*-free jars. Runs 3 to 5 differed slightly as the 4 *Sphagnum*-free jars contained aluminium pieces to aid mixing of the headspace air and CH_4.

4.4.4 Calculating concentrations and oxidation rates

At each sampling time four standard samples of known CO_2 and CH_4 concentrations of 100.9, 5,000, 10,000 and 15,000 ppm of CH_4 and 200, 344, 678 and 4941 ppm of CO_2 (BOC Ltd, U.K.) were analysed before and after every 6 jar samples. The area under each output peak (in mV) of each standard sample could then be calculated using Clarity Chromatography Software (v.3.0.6.589). The standard samples allowed for linear regression and calibration of the peak area (mV.s) with the known concentrations of the four standard samples and the subsequent calculation of the concentrations of CO_2 and CH_4 in the unknown jar samples. Fluxes of both CO_2 and CH_4 were calculated on a jar basis as opposed to a dry weight basis so *Sphagnum-free* jars could be used as a comparison using equations 4.1 to calculate *p* (molar density of air in mol/m^3) and 4.2 to calculate the flux (f) where *P* is pressure (Pa), *R* is the Universal Gas Constant and *T* is temperature (K), *dC* change in concentration, *dt* is change in time, and *V* volume.

$$\rho = \frac{P}{R \times T}$$

Eq4. 1

$$f = \frac{dC}{dt} \times p \times V$$

Eq4. 2

4.4.5 Statistical Analysis

One-way ANOVA’s were used to look at treatment and sampling location effects on CH_4 and CO_2 fluxes with unpaired two-sample t-tests used to identify differences between species and temperature treatment.

4.5 Results

4.5.1 CH_4 Oxidation

Analysing CH_4 oxidation rates over all runs of the experiment the CH_4 fluxes of *Sphagnum*-filled jars were not significantly different to those of *Sphagnum*-free jars (Figure 4. 2). There was however considerable variation in calculated CH_4 fluxes where *Sphagnum*-free jars showed fluxes between -74 and +16μmol CH_4 jar^{-1} day^{-1}, while *Sphagnum*-filled jars showed a range of between -25 to +20 μmol CH_4 jar^{-1} day^{-1}. These fluxes show comparatively small changes in methane concentration over time when considering the mean initial concentration per jar measured at Time 0 across the whole experiment was 10364±50 ppm jar^{-1} (438±52 μmol jar^{-1}). At a species level CH_4 fluxes were only found to be significantly lower in jars containing *S.papillosum* when compared to *Sphagnum*-free jars from all 5 runs of the experiment (Table 4. 2). However, when compared to the *Sphagnum*-free jars from only that individual run no significant differences between treatments were found ($F(2,52)=0.01, p=0.99$). No significant differences were found between burnt and unburnt samples in any run (Figure 4. 2) and no clear relationship between CH_4 fluxes and *Sphagnum* dry weight detected. For the runs of the experiment which involved a variation in sampling location, be it hummock or lawn, no statistical difference was found in CH_4 fluxes in Run4 where *S.capillifolium* was sampled from 10 hummocks

(F(9,8)=0.772, p=0.648), however statically different CH_4 fluxes were found between the 4 lawns where *S.papillosum* was sampled for Run 5 (*F(3,14)=5.899, p=0.008)*. However, this significant result is likely skewed by two points which show a positive CH_4 flux (Figure 4. 3).

In terms of methodological error, higher fluxes were often observed in *Sphagnum*-free jars without added mixers (Figure 4. 4, Figure 4. 5). Despite this difference not being statistically significant (*t(21.8)=1.89, p=0.07*) it was still important to take this into consideration when assessing for methanotrophy in the *Sphagnum* samples as when compared to empty jars without mixers there was seemingly lower CH_4 concentrations in the *Sphagnum*-filled jars (Figure 4. 5a). This difference however was not seen when empty jars that did not contain mixers were removed from the analysis (Figure 4. 5b). A number of calculated CH_4 fluxes in *Sphagnum*-filled jars were also removed from statistical analysis when comparing fluxes between treatments as it was believed to be likely that there was insufficient mixing of headspace gases leading to artificially high CH_4 concentrations when sampled at time zero and thus an over-estimated CH_4 oxidation rate (Appendix 4.1).

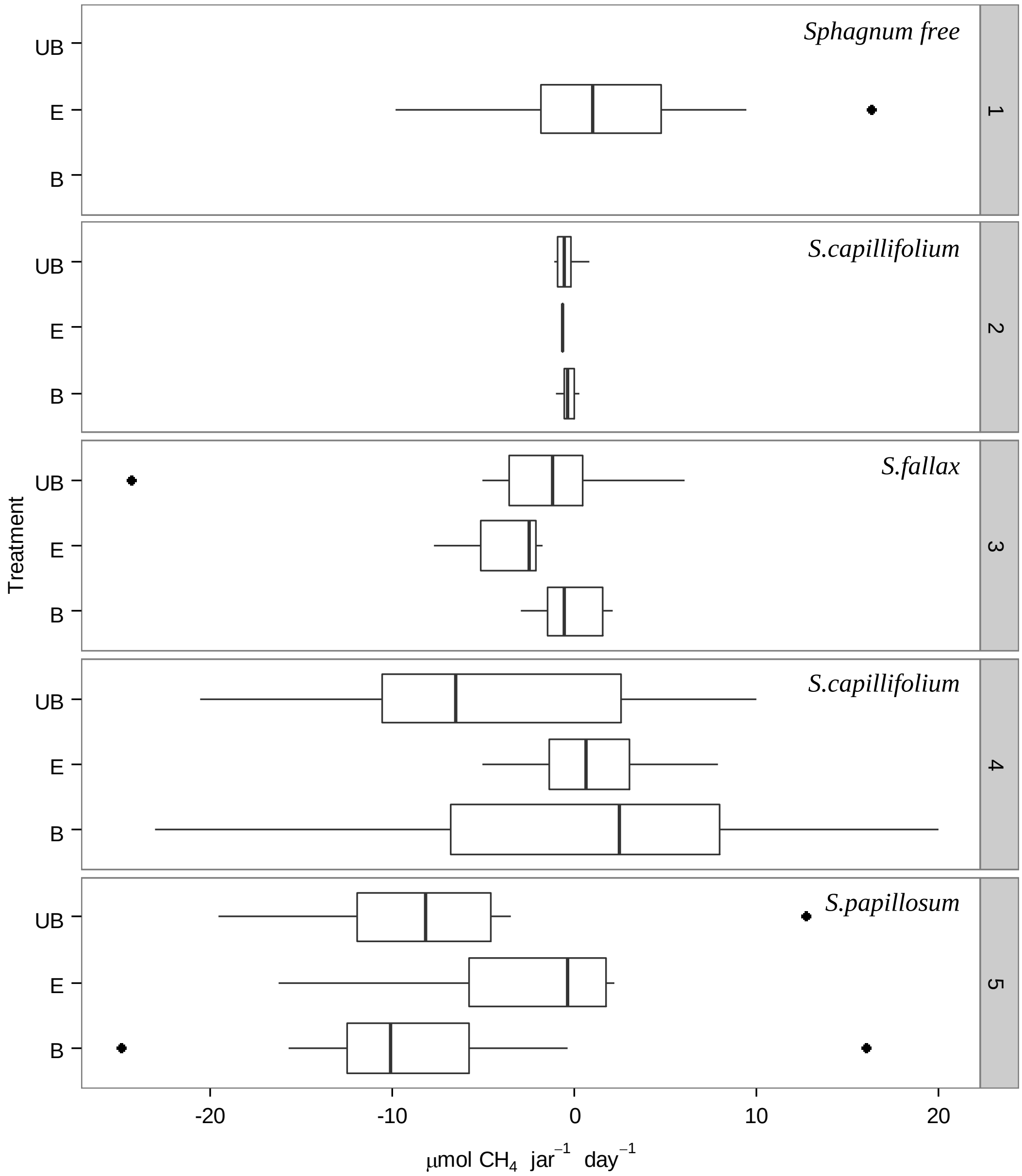


Figure 4. 2 CH_4 fluxes for each treatment (UB=unburnt, B=burnt, E=empty) per run of the experiment. Solid vertical lines show the median, boxes the lower and upper quartiles, whiskers the extent of upper and lower values within 1.5*inter quartile range and points outliers. Outliers associated with assumed mixing problems not plotted (Appendix 4.1).

Table 4. 2 Results of One-Way ANOVA tests between all three treatments for each run of the experiment where burnt (B) and unburnt (UB) *Sphagnum-filled* jars were compared to **all** empty (E) jars analysed across the 5 runs of the experiment. Significant differences between groups shown in bold.

Run/Species	**Test Statistics**	**Mean flux ± StError** **(**µmol CH_4 jar $^{-1}$ day^{-1}**)**
1 .No Sphagnum	–	E 0.08 ±1.04 (n=34)
2. S.capillifolium	F(2,50)=0.05, *p=0.951*	B -0.30±0.14 (n=10) UB –0.40 ±0.19 (n=9)
3. S.fallax	F(2,50)=0.894, *p=0.415*	B –0.22 ±0.58 (n=10) UB –2.94 ±2.91 (n=9)
4. S.capillifolium	F(2,49)=1.049, *p=0.358*	B –0.89 ± 4.63 (n=9) UB –4.67 ± 3.73 (n=9)
5. S.papillosum	F(2,49)=5.963, ***p=0.005***	B –8.06 ± 3.39 (n=10) UB –7.03 ± 3.36 (n=8)
All species	F(1,72)=0.389, *p=0.535*	B –2.40 ± 1.43 (n=39) UB –3.67 ± 1.43 (n=35)

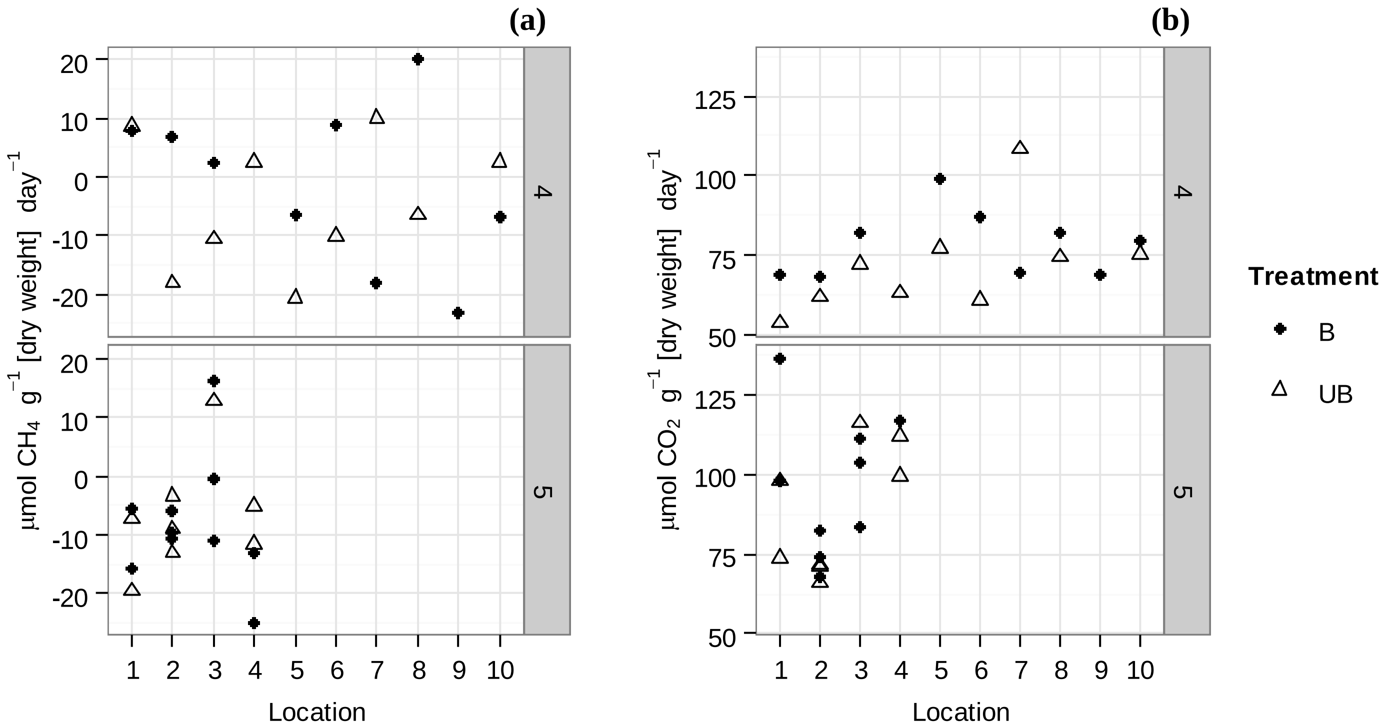


Figure 4. 3 CH_4 (a) and CO_2 (b) fluxes in relation to sampling location used in Runs 4 and 5 where *S.capillifolium* was sampled from 10 hummocks in Run 4 and *S.papillosum* taken from 4 lawns in Run 5. A significant difference in both CH_4 and CO_2 fluxes was found between sampling locations in Run 5 where *F(3,14)=5.9, p=0.008* and *F(3,14)=7.3, p=0.004* respectively.

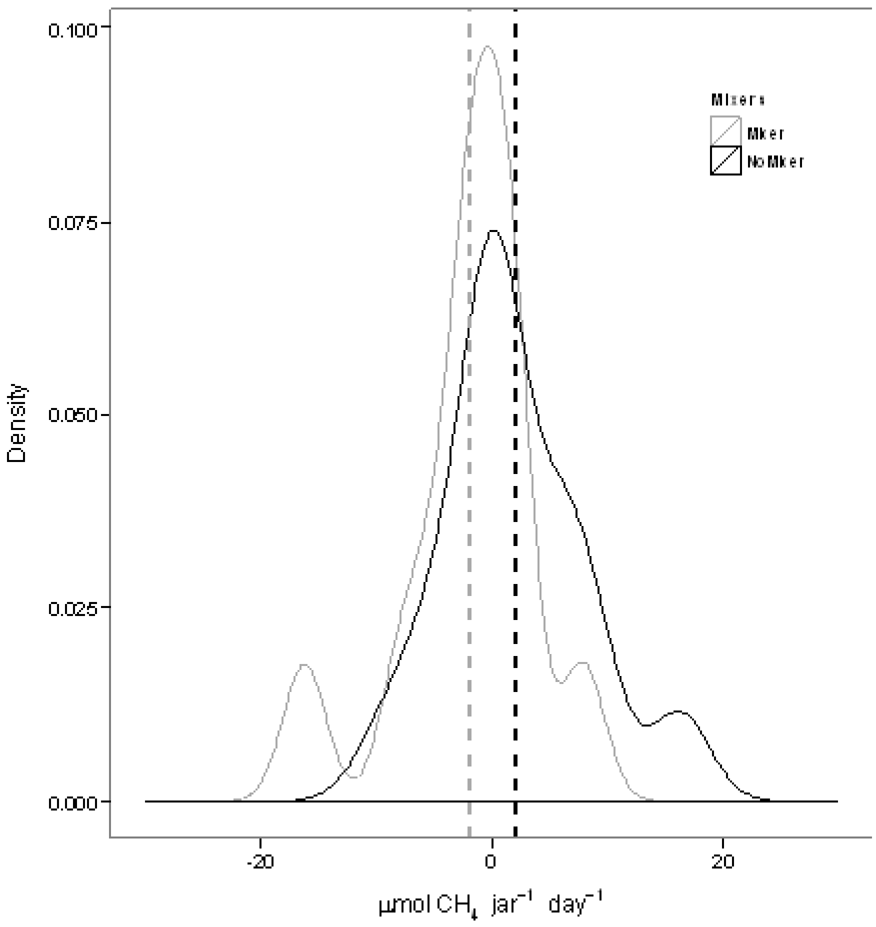


Figure 4. 4 Conditional kernel density plot of CH_4 fluxes observed in *Sphagnum* free jars with (n=11) and without (n=23) the addition of mixers where dashed lines represent means.

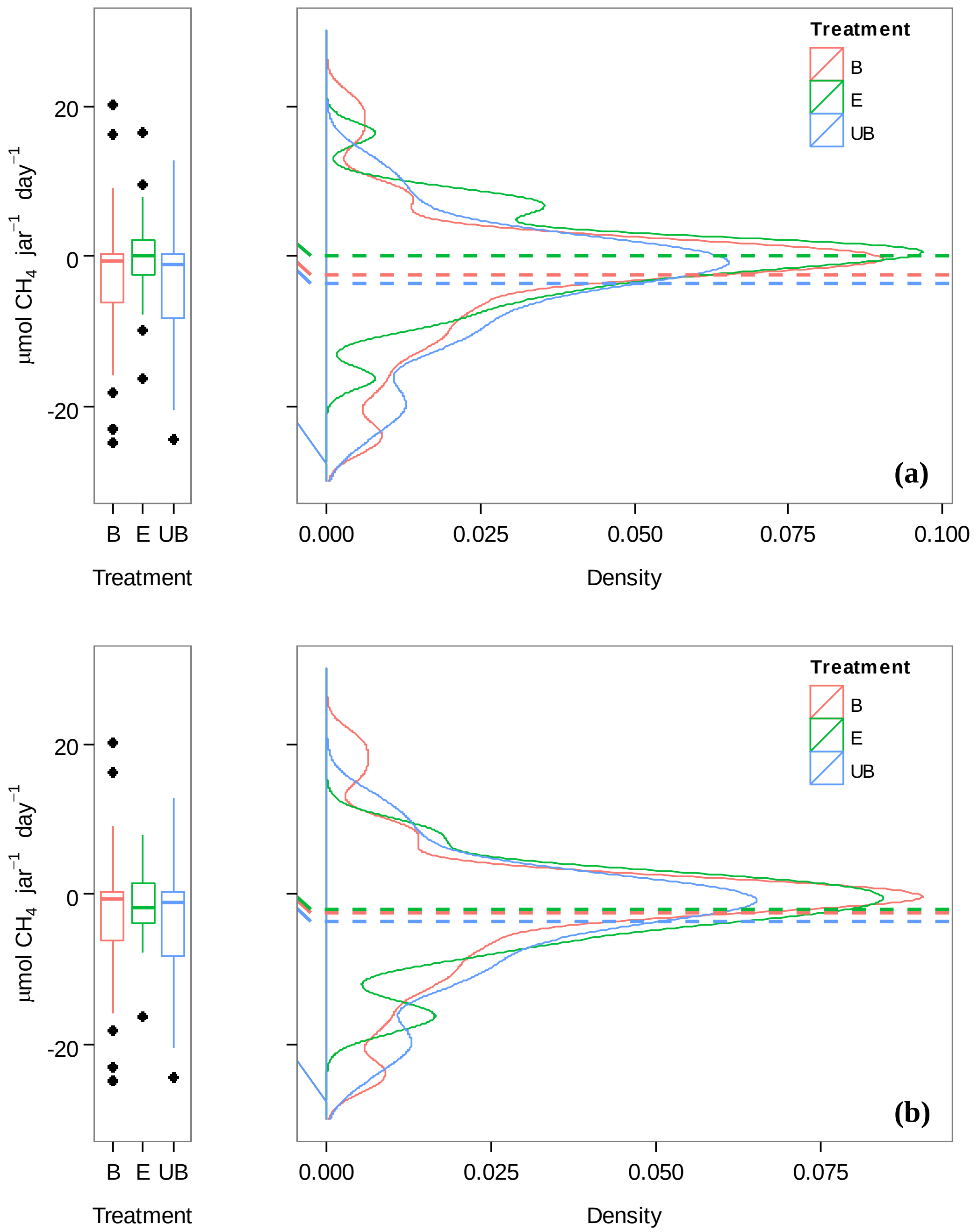


Figure 4. 5 Boxplots (left) and conditional kernel density plots (right) of CH$_4$ fluxes calculated per jar per day for each temperature treatment compared to (a) all *Sphagnum*-free jars and (b) only those *Sphagnum*-free jars containing mixers (B are burnt, UB unburnt and E *Sphagnum* free jars). Dashed lines in density plot represent Treatment means and boxplot solid lines the median, boxes the lower and upper quartiles, whiskers the extent of upper and lower values within 1.5*inter quartile range with points outliers.

4.5.2 CO_2 fluxes

CO_2 fluxes in *Sphagnum*-free jars were not statistically different from zero, as expected (mean = –0.2±SE0.2 µmol CO_2 jar^{-1}day^{-1}, *t=-0.9, df=39, p=0.38*), while *Sphagnum* filled jars had a mean CO_2 flux of 204.2±SE10.5µmol CO_2 jar^{-1}day^{-1} (Figure 4. 6). No significant differences however were found between the mean fluxes of burnt and unburnt *Sphagnum (t=0.13, df=76, p=0.89)* (Figure 4. 7) but significantly higher CO_2 fluxes were observed in *S.papillosum* when compared to *S.capillifolium* (Figure 4. 7). This, together with the good positive relationship between *Sphagnum* dry weight and CO_2 concentrations (Figure 4. 8), indicates respiration taking place in the *Sphagnum-filled* jars. It also suggests that the lack of methanotrophy observed was unlikely due to methanotrophic bacteria being O_2 limited.

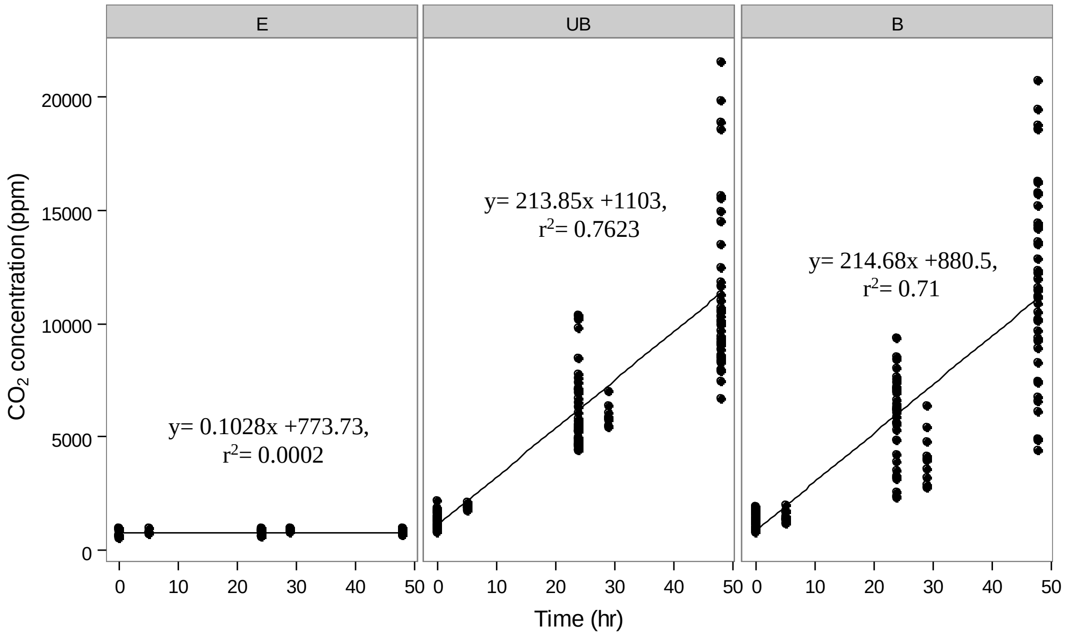


Figure 4. 6 CO_2 concentrations over time for each treatment (B=Burnt, UB=Unburnt, E=*Sphagnum-free* jars) with regression lines for each. Burnt *Sphagnum* jars had a mean flux of 207.6±SE15.1 µmol CO_2 jar^{-1} day^{-1}, unburnt *Sphagnum* jars had a mean flux of 202.1±SE14.5 µmol CO_2 jar^{-1} day^{-1}, and *Sphagnum* free jars had a mean flux of -0.2±SE0.2 µmol CO_2 jar^{-1} day^{-1}.

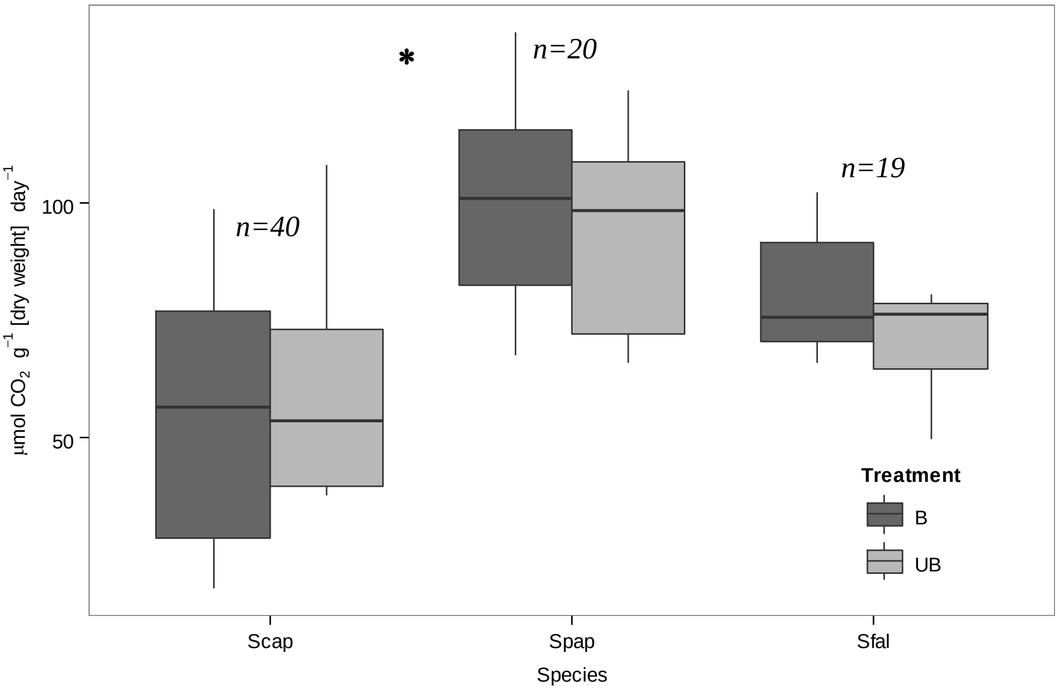


Figure 4. 7 CO_2 fluxes for each species where Scap=*S.capillifolium*, Sfal=*S.fallax*, Spap=*S.papillosum*, n=40, 19, 20 respectively. ∗ indicates significant difference between adjacent species, where (sqrt transformed) t=-6.9, df=53, p=<0.001. Middle line shows median, boxes show lower and upper quartiles, whiskers show extent of upper and lower values within 1.5 inter quartile range, and points outliers.

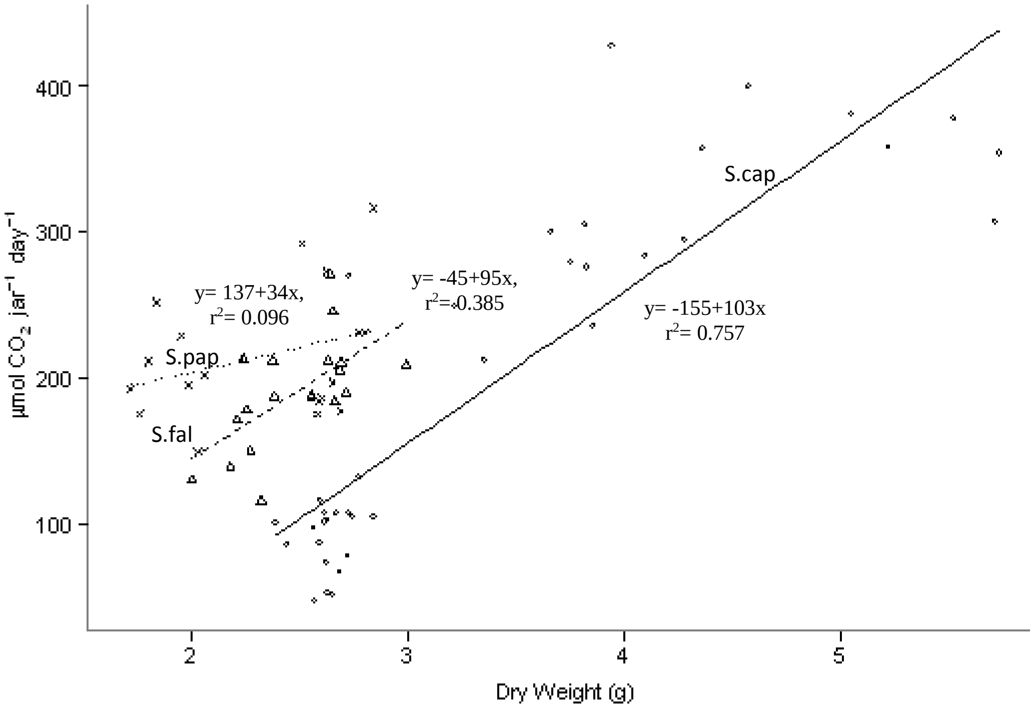


Figure 4. 8 CO_2 fluxes in relation to *Sphagnum* dry weight with linear regression lines for each sample by species where Scap=*S.capillifolium*, Sfal=*S.fallax*, Spap=*S.papillosum*.

4.6 Discussion

Results from the empty jars can be used to calculate a detection limit associated with the methodology, defined here as the standard deviation in the flux in empty jars. This gives a value of 0.08±SD6.05 µmol CH_4 jar^{-1} day^{-1}. Fluxes in the *Sphagnum-filled* jars were mostly of a similar magnitude to this with the exception of jars filled with *S.papillosum*, meaning we cannot confidently conclude that CH_4 oxidation has occurred in *S.capillifolium*, or *S.fallax*. Consequently we can only accept or reject our null hypothesis that samples subjected to the temperature treatment would show lower CH_4 oxidation rates based on our observations of *S.papillosum* where we assume genuine oxidation was taking place. Within this species no significant differences were found between burnt and unburnt samples. Beyond these observations the results also raise important issues associated with the methodology, a variation of which has been used in a number of studies looking at CH_4 oxidation rates in *Sphagnum*, and any assumptions that *Sphagnum* will always host an active methanotrophic community.

4.6.1 Experimental Error

Despite being a widely used lab-based method for measuring CH_4 oxidation rates in samples of *Sphagnum,* the substantial number of control jars used in this experiment suggests that there are errors associated with the experimental procedures. The *Sphagnum-free* jars, representative of a *Sphagnum* dry weight of 0g, gave a mean calculated CH_4 flux of 0.08±SD 6.05 µmol CH_4 jar^{-1} day^{-1}, suggesting that the variation of the methodology used here was not refined enough to confidently determine genuine fluxes in *Sphagnum-filled* jars within the range of ±6 µmol CH_4 jar^{-1} day^{-1}. No significant differences in CH_4 oxidation rates on a jar basis were found between empty jars and jars filled with *S.fallax* or *S.capillifolium*, which when corrected for dry weight showed CH_4 oxidation rates of –0.6±SD2.6 and -0.5±SD2.2µmol CH_4 g [DW]^1 day^{-1} respectively, which are within the range of oxidation rates calculated for a number of *Sphagnum* species in previous studies (eg. Basiliko *et al.*, 2004, Raghoebarsing *et al.*, 2005, Kip *et al.*, 2010, Larmola *et al.*, 2010, Stępniewska *et al.*, 2013) but not within the detection limit of our methodology. The only species that could confidently be reported as exhibiting CH_4 oxidation was *S.papillosum* which had a mean CH_4 oxidation rate of -3.7 ±SD4.5µmol CH_4 g [DW]^1 day^{-1} which is consistent with what has previously been reported (Raghoebarsing *et al.*, 2005). However, even CH_4 fluxes in this species showed considerable variation between jars and between sampling locations with some relatively high positive fluxes recorded.

One of the sources of variation in CH_4 fluxes, which could account for both positive fluxes and the perceived CH_4 oxidation in *Sphagnum-free* jars, could be insufficient mixing of headspace gases, which was particularly apparent in *Sphagnum-free* jars which did not contain the additional aluminium mixers. Jars with poorly mixed headspace samples at time zero, where ambient air inside the jar did not uniformly mix with the injected CH_4, could have caused high initial CH_4 concentrations and give an overall negative flux as CH_4 concentrations lowered throughout the run after the additional mixing at each sampling time. Conversely, poorly mixed headspace samples could give rise to high CH_4 concentrations being measured at sampling times throughout each run of the experimental which could give the false impression of CH_4 being produced over time and hence positive CH_4 fluxes. Positive CH_4 fluxes have been recorded before using a similar methodology and it was suggested that this could be due to small amounts of CH_4 being produced at anaerobic microsites in the *Sphagnum* (Basiliko *et al.*, 2004). In this study however positive fluxes were found in both *Sphagnum-free* and *Sphagnum-filled* jars so it can be assumed that positive fluxes were likely due to errors associated with the methodology. This study did use larger jars than those used by Kip *et al.*, (2010), Larmola *et al.*, (2010) and Raghoebarsing *et al.*, (2005) so insufficient mixing of the headspace gases may be more apparent here. To compensate however for the larger jars the *Sphagnum* samples were bigger to give larger, and it was hoped more measurable, CH_4 fluxes. The methodology is also inherently susceptible to apparent CH_4 oxidation actually being a product of leaking containers. However, this is not thought to be the case here as CO_2 fluxes were found to increase linearly over time in *Sphagnum*-filled jars with CO_2 fluxes in *Sphagnum*-free jars not statistically different to zero.

4.6.2 CH_4 Oxidation

The results of this experiment imply that it can only be stated with confidence that CH_4 oxidation was taking place in *S.papillosum* due to the large errors associated with the methodology meaning the calculated fluxes found in *S.fallax* and *S.capillifolium* have to be rejected. However, even if all calculated fluxes for *Sphagnum-filled* jars were accepted they still show lower oxidation rates than previously reported in the same species. *S.capillifolium*, a hummock forming species, has been found to oxidise around 5 µmolCH_4 g^{-1}[DW] day^{-1} (Larmola *et al.*, 2010, Basiliko *et al.*, 2004), while *S.fallax* and *S.papillosum*, both lawn forming species, have been found to oxidise more than 10µmolCH_4 g^{-1}[DW] day^{-1} (Raghoebarsing *et al.*, 2005, Larmola *et al.*, 2010). Although rates of methanotrophy are controlled by a number of biotic and abiotic factors (Chowdhury and Dick, 2013) fundamentally at lower atmospheric CH_4 concentrations there will be lower rates of oxidation, with artificial concentrations of CH_4 greater than 10,000 ppm shown to result in the most methanotrophy (Bender and Conrad, 1995). The concentrations used in this experiment should therefore have promoted towards the maximum potential CH_4 oxidation rates since CH_4 was not limited, and so should not be responsible for the very low oxidation observed. This leads to the assumption that the low oxidation rates observed must be a genuine reflection of the presence/absence of methanotrophs or environmental controls on CH_4 oxidation potential in the *Sphagnum* sampled.

Most research looking at the controls on methanotrophy in peatlands have focussed on CH_4 oxidation in the soil where it has been found that pH (Dunfield *et al.*, 1993), soil temperature (Chowdhury and Dick, 2013), soil water content (Le Mer and Roger, 2001) and nutrient availability (Crill *et al.*, 1994) can all affect oxidation rates with different optimum conditions for different methanotrophs (Dunfield *et al.*, 2003, Dedysh *et al.*, 2000). However, it is the position of the water table which ultimately determines the extent of the aerobic zone and a CH_4 oxidation gradient which exists downwards in the peat layer (Sundh *et al.*, 1995). In *Sphagnum* dominated areas of a tundra bog it has been shown that most oxidation occurs at the interface between the peat and *Sphagnum* layers (Vecherskaya *et al.*, 1993) where the optimum O_2:CH_4 ratio exists (Chowdhury and Dick, 2013). Less is understood about the controls on methanotrophy in *Sphagnum* above this interface but the position of the water table has been found to be particularly important for CH_4 oxidation (Larmola *et al.*, 2010) linking rates of oxidation to microhabitat and species.

Sphagnum species associated with pools tend to show much larger potential rates of CH_4 oxidation than lawn or hummock species (Larmola *et al.*, 2010, Kip *et al.*, 2010, Raghoebarsing *et al.*, 2005), with an increase in the distance between the moss layer and water table being negatively correlated with CH_4 oxidation (Basiliko *et al.*, 2004). However, the lowering of the water table and the associated reduction in CH_4 oxidation (Basiliko *et al.*, 2004, Larmola *et al.*, 2010) may not necessarily reduce CH_4 oxidation in the long term as methanotrophic bacteria can re-colonise *Sphagnum* from surrounding water when re-wetted (Putkinen *et al.*, 2012). There were no periods of drought prior to sampling the *Sphagnum* used in this experiment with *Sphagnum* sampled at a field moisture content of between 93 and 95% which suggests that low rates of CH_4 oxidation were not related to low precipitation and change in moisture status as has been found before (Basiliko *et al.*, 2004, Larmola *et al.*, 2010). Seasonal effects, be it position of the water table or temperature, on oxidation rates cannot, however, be verified by this study since all samples came from spring months with similar temperature and water table conditions. In addition to the abiotic controls on CH_4 oxidation, which may vary temporally and spatially across a bog, rates of oxidation may also change at a much smaller scale within *Sphagnum* plants themselves.

Sphagnum grows from the top of its stem (capitulum) and naturally breaks down from the bottom (Clymo and Hayward, 1982) leading to stems which change in physical and biological characteristics along their length. Lower oxidation rates have been associated with the top and middle parts of stems of the non-submerged lawn species *S. papillosum* and *Sphagnum magellanicum* Brid. (Raghoebarsing *et al.*, 2005) with significantly higher CH_4 oxidation found in the lower segments of the stems with a loss in physical structure in *S.capillifolium* and *S.magellanicum* (Basiliko *et al.*, 2004). The rate of CH_4 oxidation however may also be influenced by habitat, namely if a plant is submerged or not submerged, as demonstrated in *Sphagnum fallax* (H.Klinggr.) H.Klinggr. by Stepniewska *et al.*, (2013) where in contrast the highest oxidation rates were in the top parts of the stem. This change in oxidation rate along stems could perhaps account for low the CH_4 oxidation found in this study, as only the top, more physically intact, 5cm of *Sphagnum* was sampled. Oxidation rates measured here are indeed more comparable to those of the upper parts of stems of lawn forming *S.magellanicum* and *S.papillosum* found by Raghoebarsing *et al.*, (2005).

4.7 Conclusions and Future Research

The results of this experiment suggest that inherent methodological errors can be responsible for an over estimation of CH_4 oxidation rates using closed flasks with artificial CH_4 concentrations, shown here by the negative CH_4 fluxes recorded in *Sphagnum*-free jars. This highlights the need for the methodology to be rigorously tested and the need to include more controls, specifically empty flasks, as part of the experiment. However, the problems found here with insufficient mixing may be associated with the large size of the flasks used as its not been reported as a problem in previous studies using smaller flasks.

Due to the errors in the methodology the very low oxidation rates found in *S.fallax* and *S.capillifolium* cannot be accepted and leads to an assumption that it is just as likely that no oxidation was occurring in these species. *S.papillosum* was the only species to exhibit CH_4 oxidation, meaning hypothesis [1] can be accepted as oxidation rates were found to differ between species. As *S.papillosum* was the only species to show CH_4 oxidation it was the only species in which hypothesis [2] could be tested and showed no significant difference in rates of CH_4 oxidation in burnt and unburnt *Sphagnum* leading to a rejection of hypothesis [2] in this instance. This finding would have to be further tested, particularly between species, as differences in pre-treatment moisture content and differences in morphology between species could be important in determining the full effect of fire on the methanotrophic community in *Sphagnum*. The role of methanotrophs is increasingly being recognised for their significance to the carbon balance of peatlands and if fire were found to have a negative impact on CH_4 oxidation rates it could better inform best practice management guidelines and carbon budget models. However it is also important to extend the research to look at the long term impact of fire on the methanotrophic community and rates of CH_4 oxidation in the *Sphagnum* layer *in situ* as the re-colonisation of *Sphagnum* by methanotrophs in the surrounding water (Putkinen *et al.*, 2012) could negate any initial impact of fire.

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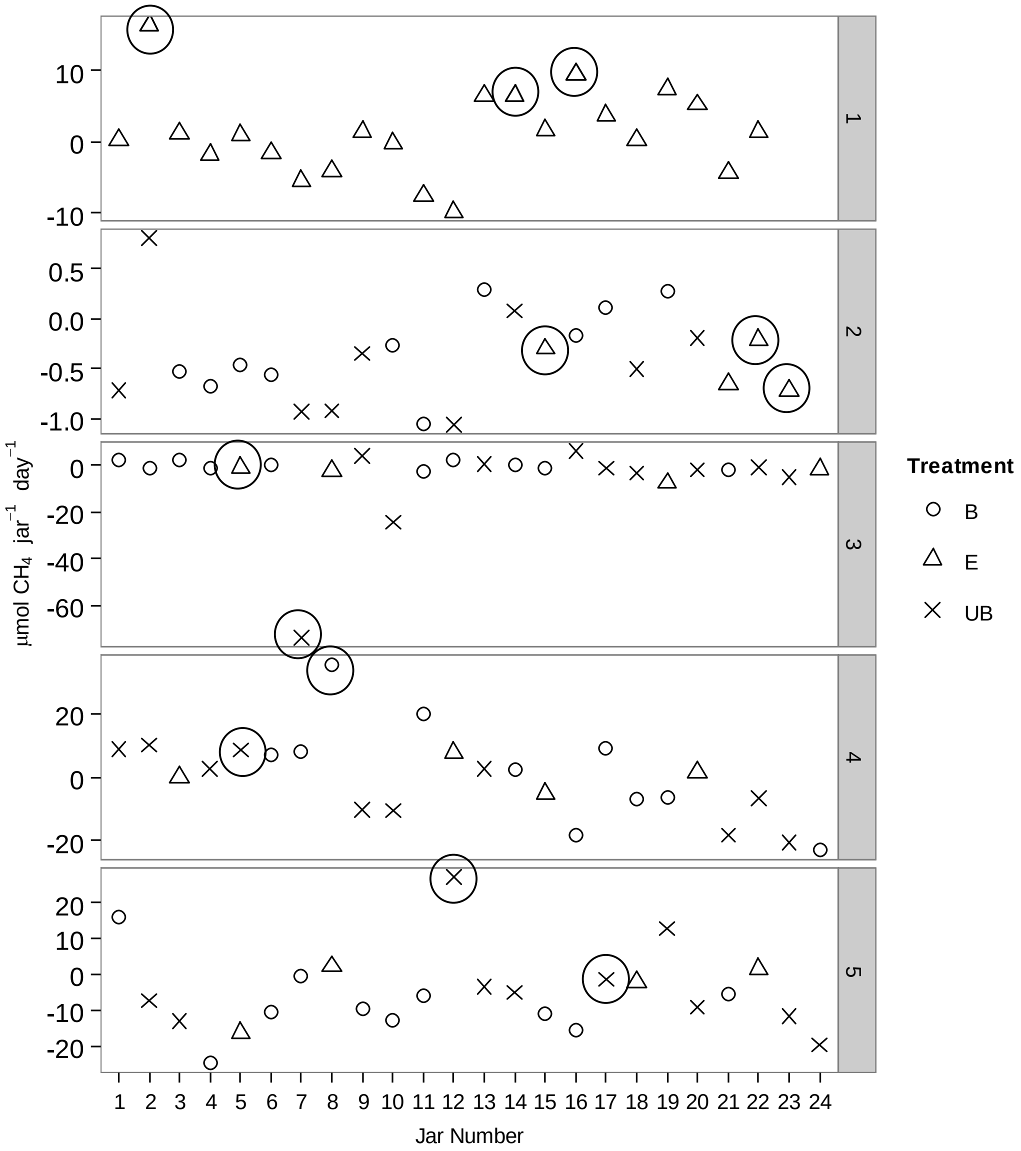
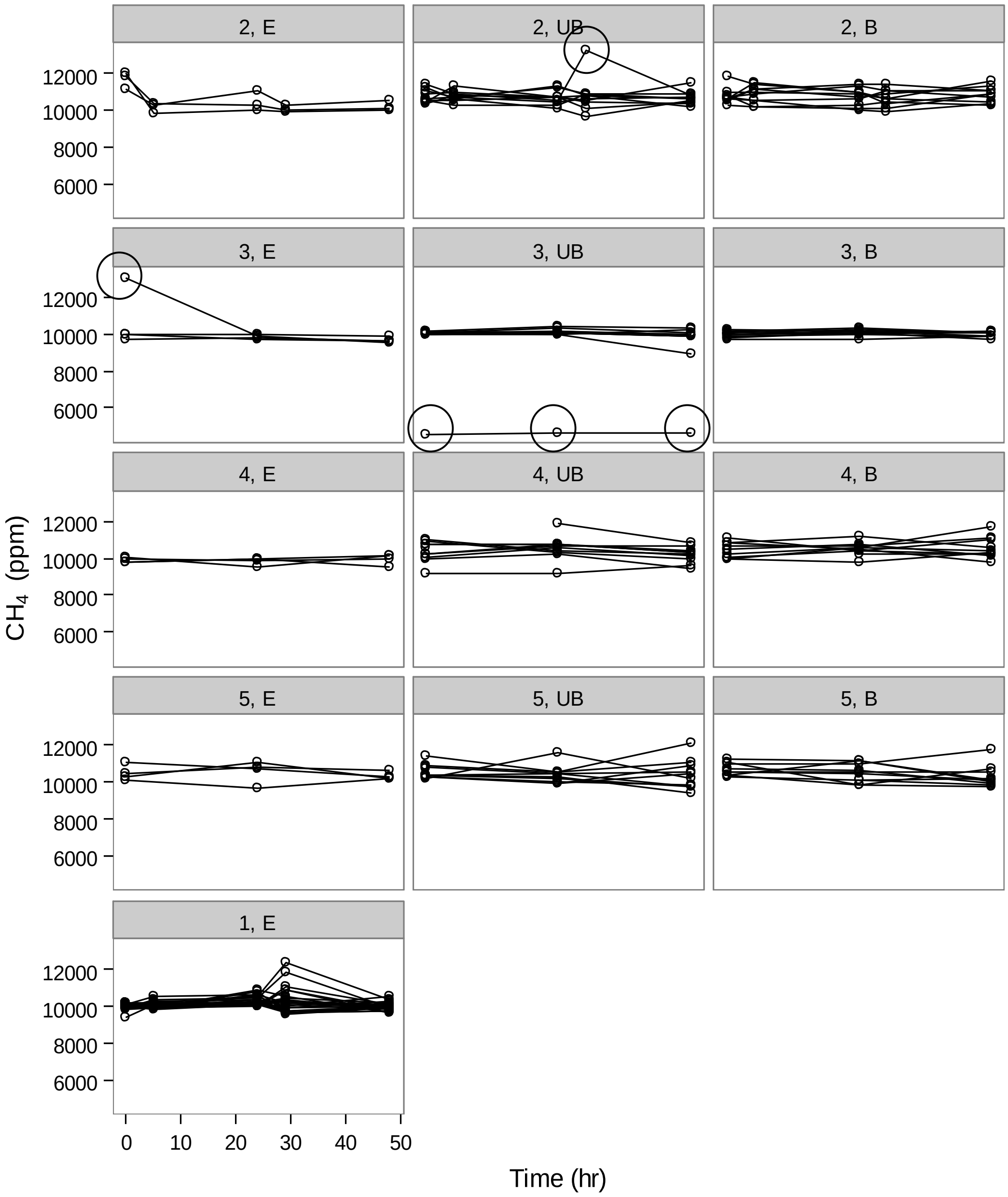
Appendix 4.1. Concentrations of CH_4 and CO_2

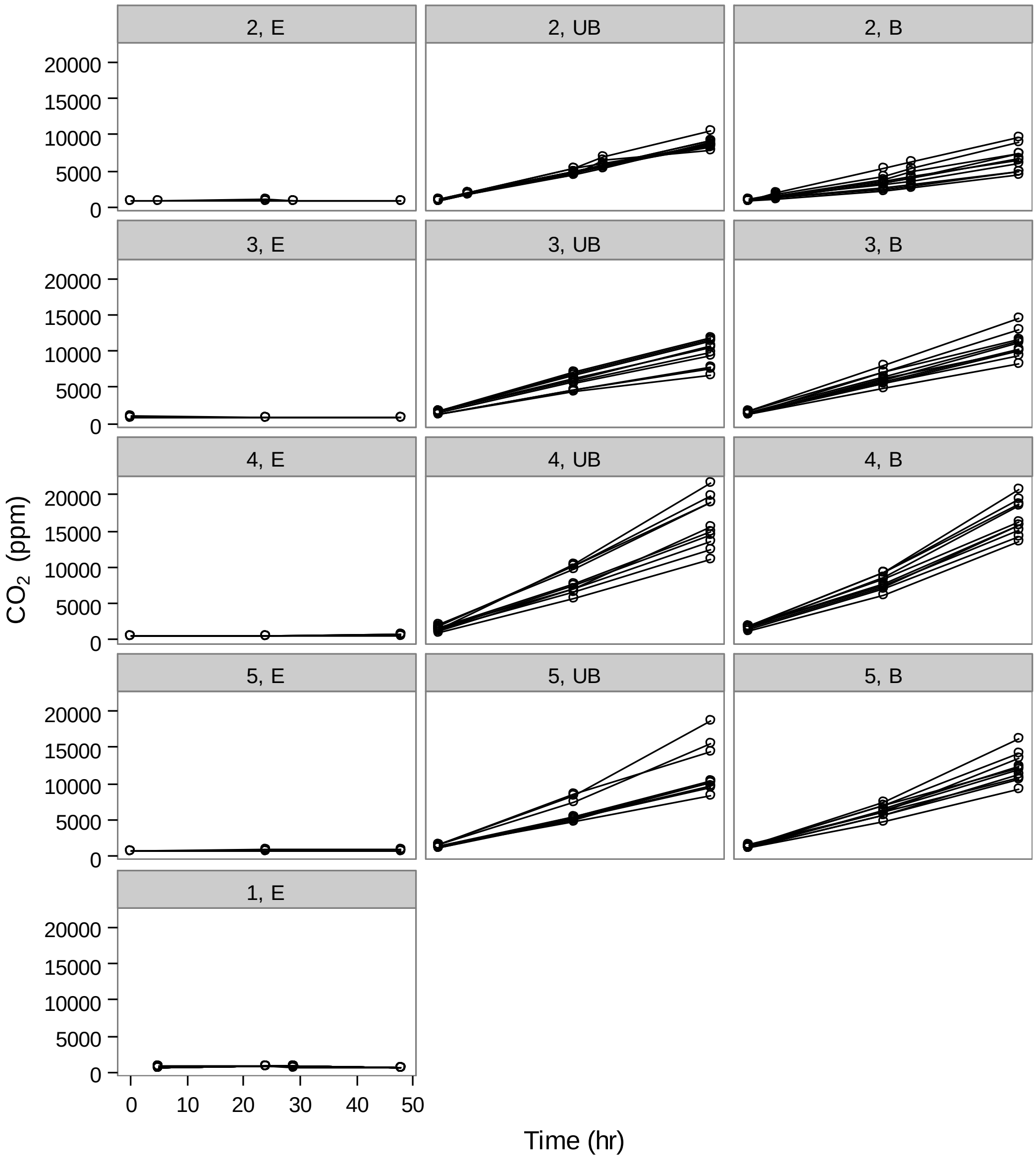


Calculated CH_4 fluxes for each jar per run of the experiment. Circles highlight jars removed from analysis. Jars removed from analysis were:

- Run 1 – Jars 2 and 14 (very high CH_4 concentrations at 29hours) and Jar 16 (very CH_4 at 0 hours attributed to poor mixing)
- Run 2 – Jars 22 and 23 (mixing problem at 0 hours) and Jar 15 (very high CH_4 value at 29 hours)
- Run 3 – Jars 7 (underspiked so CH_4 concentrations too low) and Jar 5 (mixing problem at 0 hours)
- Run 4 – Jar 5 (very high CH_4 concentration at 24 hours) and Jar 8 (mixing problem at 48 hours)
- Run 5 – Jar 12 (very high CH_4 concentration at 48 hours) and Jar 17 (mixing problem at 24 hours)



Concentration of CH_4 over time for each jar (1 to 24) in each run (1 to 5) of the experiment for each treatment (E is Sphagnum free, UB is unburnt Sphagnum and B burnt Sphagnum). Circles highlight the reason some jars were removed from statistical analysis.



Concentration of CO$_2$ over time for each jar (1 to 24) in each run (1 to 5) of the experiment for each treatment (E is Sphagnum free, UB is unburnt Sphagnum and B burnt Sphagnum). All jars were kept in the statistical analysis of CO$_2$ fluxes.

5. The impact of burning on vegetation of three blanket bogs in Scotland

5.1 Abstract

In the UK fire is used as a tool to manage vegetation for livestock and grouse, and blanket bog can be burned in special circumstances under existing legislation and best practice guidance. Burning, however, has the potential to cause the loss of fire sensitive species and modify processes such as carbon cycling and peat formation. The aim of this study was to look at the changes in vegetation brought about by low severity fire events, which burned only the canopy vegetation and did not penetrate the peat, at three blanket bogs in Scotland. To further assess the impact these fires had on the critical *Sphagnum* layer, *Sphagnum capillifolium* was monitored to quantify any reduction and recovery in photosynthetic capacity. The results show that the fires caused the dominance of graminoids over shrubs, which is consistent with the literature, and that this was to some degree reflected in National Vegetation Classification classifications. Changes in vegetation composition could be linked to both fire severity and time since burning. The photosynthetic capacity of the capitula of *S.capillifolium* was reduced by burning for over two years after the fire events, but this was shown to be less critical in some instances in the long term as some damaged stems had the capacity to grow new healthy stem and capitula. These results show that even low severity fires have the potential to change vegetation composition for a number of years after burning and that the impact on the *Sphagnum* layer can vary at the micro-scale. The results also reiterate that fire is

highly variable in its impacts and will have different implications for vegetation depending on pre-burn vegetation composition, age and structure, and fire behaviour.

5.2 Introduction

The impact of fire on the vegetation of peatlands in the UK is best understood in the context of *Calluna vulgaris* (L.) Hull (from here expressed as *Calluna*) dominated heaths, primarily due to the need to inform management on grouse moors. Traditionally heather is burned to encourage new more palatable growth and structural diversity as in the right circumstances *Calluna*, a low growing perennial shrub, responds to fire by putting up new shoots or growing from new seed. The age at which *Calluna* heaths are burned is important as older plants have been found to have less capacity for vegetative growth (Miller and Miles 1970). The length of the burning rotation is therefore important in ensuring optimal heather regeneration and since the early 20th century rotation periods and optimum burn sizes have been prescribed for heather dominated heaths on this basis (eg. Lovat, 1911, Gimingham, 1972). The Muirburn Code for Scotland, for instance, has based best practice rotation times directly on the amount of annual growth of *Calluna* (Scottish Executive, 2011). Fire has, however, also long been used to deliberately manipulate vegetation composition in the long term, promoting more palatable graminoids over older shrubs. Understanding the response of vegetation to fire on blanket bog is therefore an important consideration when aiming to maintain blanket bogs as an important habitat and carbon store with best practice burning guidelines.

Previous reviews have shown that the impact of burning blanket bog, in the context of the Joint Nature Conservations Committees defined “favourable condition" (Joint Nature Conservation Committee, 2006), is contradictory, with species composition change being both either a positive or negative deviation from favourable condition (Stewart *et al.*, 2004) with little empirical evidence for fire having a damaging effect on blanket bogs (Stewart *et al.*, 2005). However, common observations are that fire can promote the dominance of a small number of species, lead to an increase in bare ground and result in a change in abundance of species, the majority of datasets showing a decrease in abundance of key species (Stewart *et al.*, 2004). Graminoids such as *Eriophorum* spp. (Rawes and Hobbs, 1979, Stewart *et al.*, 2004, Gray, 2006, Ward *et al.*, 2007) and *Molinia caerulea* (Hamilton, 2000, Ross *et al.*, 2003) can increase in abundance over *Calluna* following burning. However, the frequency of burning has been demonstrated to be an important factor in facilitating long term changes in species composition (Gray 2006), with 10 year rotations having a greater effect than 20 year rotations (Rawes and Hobbs, 1979) with shorter rotations favouring graminoids (Lee *et al.*, 2013).

A plant's ability to recover from a fire will be related to its physiology and pre and post burn environmental conditions, which in turn can be related to fire behaviour and severity. Regeneration may relate to the life histories of the pre-burn plant community, and can be dependant on the timing of critical stages in a plants growth cycle in relation to the timing of a fire event (Mallik and Gimingham, 1983, Hobbs *et al.*, 1984). Fire behaviour and the temperature gradient found in a fire also have implications for vegetation recovery, with lower ground surface temperatures important for *Calluna* regeneration form lateral meristems at the stem base after fire (Kayll, 1966), and the temperature below ground important when considering seed banks and seed viability within the soil. Schimmel and Granstrom (1996) for example demonstrated that plant survival following experimental burning of understory vegetation in a Boreal pine forest in Sweden, at sites dominated by *Vaccinium vitis-idaea* L., *Vaccinium myrtillus* L. and *Deschampsia cespitosa* (L.) P.Beauv. was dependant on the depth to which temperatures increased below ground in a fire, and the depth within the soil that plants held regenerative structure. This supports observations of wildfires in the UK where regeneration of blanket bog vegetation in areas which were severely scorched and turned to ash, indicative of burns where high temperatures penetrated deeper into the peat layer (Ashton *et al.*, 2007), showed little or no recovery (Maltby *et al.*, 1990). Post fire input of nutrients from ash deposition (Allen, 1964) and the reduction in competition may also favour some more competitive species over others. In addition, confounding the effect of fire is the relationship between burning and grazing as post fire grazing pressure may increase (Hamilton, 2000), resulting in a cumulative management effect which may have wider implications such as soil compaction (Gray, 2006).

5.3 Aims

The aim of this study was to increase our understanding of the effects of fire on vegetation composition of blanket bogs by assessing how fire changed the vegetation composition in the short to medium term (months to 3 years). It was also intended that any changes in species composition over this timescale be considered in relation to CH_4 emissions and ecosystem respiration measured at the same plots (see Chapter 2). Species composition was assessed over time to determine how the change in vegetation composition related to the time since burning and to see if there were trends in plant succession at different sites. Species composition was also matched to National Vegetation Classification (NVC) communities (Elkington *et al.*, 2001) to examine if this method of classification, used widely by ecologists, could sufficiently show the short term change in vegetation community brought about by burning. Previously there has been some doubt whether this system is appropriate for showing the effects of fire on vegetation composition (Gray, 2006). In addition, and in response to the limited information available on how *Sphagnum* is affected by burning (as discussed in Chapter 3), the surface of lawns and hummocks of *Sphagnum capillifolium* (Ehrh.) Hedw. at each site were assessed with a specific measure of photosynthetic capacity, chlorophyll fluorescence, to quantify impacts and show any recovery.

It was hypothesised that [1], although there would be differences in species composition between the three sites, there would be a common trend of fire increasing the abundance of graminoid species, while reducing shrub cover in the short term but in the medium term promoting the growth of new shrub plants. That [2] the differences between the vegetation communities of the burnt plots and unburnt reference plots would be reflected in NVC classifications. In regards to the effect of fire on *S.capillifolium* it was hypothesised that [3] the capitula, when not entirely consumed, would show a long term reduction in photosynthetic capacity due to physiologically lethal temperatures being reached at the moss surface during the fires, with recovery slow and dependent on new regenerative growth.

5.4 Methodology

5.4.1 Site description and survey methodology

The plots used in this study were the same as those used for sampling CO_2 and CH_4 (described in Chapter 2) as samples were taken using a closed chamber system. This meant a permanent circular collar, 43cm in diameter, remained in-situ for the duration of the study period, providing a constant area to monitor species composition. However, the vegetation assessment needed to cause minimal disturbance within each collar for the natural CO_2 and CH_4 fluxes to be measured. Therefore, percentage top cover of each species was assessed throughout the duration of the study while harvesting of the vegetation within each collar and total percent cover and dry weight only calculated when flux measurements had ceased. By concurrently monitoring unburnt plots at each site, the change in vegetation in the burnt plots over time could be compared to control plots to give an indication of recovery to pre-burn composition.

As described in Chapter 2 each site had been subjected to a fire; two for management purposes and one by an accidental wildfire, and an equal number of plots were located either side of the fire line at each site to allow for comparisons to be made between burnt plots and unburnt reference plots (Table 5. 1). The fires at all sites were similar in character, mostly only removing the canopy vegetation of graminoids and *Calluna vulgaris* (L.) Hull (from here expressed as *Calluna*) while not penetrating the peat. The moss layer was only consumed in small discrete areas, with the drier pleurocarpous and acrocarpous mosses suffering more damage than *Sphagnum* species. The fire at Glensaugh removed the least amount of biomass, with the finer branches of *Calluna* left intact in places, compared to mostly just the woody stems of *Calluna* remaining after the fires at Eastside and Forsinard (Appendix 2.1). Fuel loads, as indicated from the harvesting of 6 unburnt plots adjacent to the areas burned at Forsinard and Eastside, showed that Eastside was characterised by a much greater dry weight of shrubs, predominantly *Calluna*, when compared to Forsinard although total graminoid and sedge biomass were similar (Chapter 2, Table 2.2). Glensaugh was similar to Eastside in terms of vegetation composition and structure, with similar *Calluna* biomass at the time of burning.

5.4.2 Percentage top cover assessment

Digital photographs were taken of each plot throughout the study period to show changes in vegetation composition. However, images from only three time points at each site were used in the analysis, as often the images were of poor quality due to low light levels and weather conditions making identification to an individual species level difficult. Since each area within the collars being monitored was circular, images of each plot were assessed digitally with an 8 sector grid superimposed onto each image (Figure 5. 1). The total area of each plot was 1452cm^2, with each 8 sector segment covering 363cm^2. This meant percentage top cover could be assessed in each of the 8 sectors more easily by eye, and combined to give a more accurate estimation of the whole plot. Each species was identified non-destructively in the field or from a representative specimen taken from areas adjacent from the plots if more comprehensive identification was needed.

Table 5. 1 Vegetation survey site descriptions (See Appendix 2.1 for maps and images of the sites). [M] measured, [1]Levy *et al.* (2012), [2]Centre for Ecology and Hydrology (2012), [3]Ball *et al.* (2012) , [4]UK Environmental Change Network (2012).

Site Name	**Grid Ref**	**Date of Burn**	**Plots Surveyed**	**Mean ST** (°C)	**Mean Precipitation** (mm/yr)	**Altitude** (m above sea level)	**Slope** (°)	**Aspect**	**Easting**	**Northing**
Forsinard	NC 884 408	18/04/2011	6 Burned, 6 Unburned	9.2 [M]	825 [2]	190	0.6	S	288450	940850
Eastside	NT 162 602	14/03/2012	7 Burned, 7 Unburned	7.3 [M]	789 [3]	420	2	SE	316250	660250
Glensaugh	NO 664 810	27/03/2012	4 Burned, 4 Unburned	7.3 [1]	1130 [4]	410	9	N	366450	781050

Figure 5. 1 Example image of a plot where percentage top cover of each plant species was surveyed, showing the superimposed digital 8-sector layer to aid assessment.

5.4.3 Total percentage cover and dry weight

On the last day of flux measurements each plot was surveyed, by eye, in the field for total percentage cover of each species. This gave a summed total percent cover of all species >100% as opposed the top cover survey which gave a maximum 100%. Once surveyed each plot was harvested by removing all vegetation above the peat layer and sorted into each species component. Each harvested species was dried at 70°C for up to 7 days (or when weight was no longer decreasing) to achieve a dry weight for each species. Species lists for each of the three sites can be found in Appendix 5.1. Small fragments of vegetation and longer lengths of dead graminoids were considered “litter”. *Calluna* was further sorted into woody stems and finer branch material.

The vegetation community at each site in the burnt and unburnt plots were attributed to NVC sub communities (Elkington *et al.*, 2001) using the NVC classification software ComKey (Legg, 2008). Plots were split into burnt and unburnt communities for each sampling time per site and matched to an NVC community by: matching species, counting the number of species which occurred in the matched community, by a weighted species match which, in addition to counting the number of species occurring in the matched community species were given weight according to their fidelity, and finally by frequency weighted match which accumulated scores for species common with matched community weighted by the fidelity of the species. The community which ranked #1 for each match method was chosen, however, results were sense checked with the literature (Rodwell, 1991, Elkington *et al.*, 2001) to ensure matched communities were appropriate. NVC classifications were also compared between the top cover survey method, employed throughout the study period, and the full survey method used on the final day of sampling to show if the top cover survey underestimated cover of any species.

5.4.4 Assessment of Sphagnum recovery

To assess the effect the fires had on *Sphagnum* recovery photosynthetic capacity was estimated using chlorophyll fluorescence as an indicator of *Sphagnum* health. Chlorophyll fluorescence is a technique that has been widely used to assess recovery in *Sphagnum* following stress (eg. van Gaalen *et al.*, 2007, Hájek and

Beckett, 2008, Manninen *et al.*, 2011). A more detailed account of the technique is given in Chapter 3 (section 3.4.2.1).

Measurements were made on *Sphagnum capillifolium* (Ehrh.) Hedw. a widespread species in the UK, and common to all three field sites. At each site measurements were made on the capitula of plants from the burnt area and concurrently from the adjacent unburnt area. Sampling design did vary between sites as *S.capillifolium* abundance and the number and size of fires varied making a consistent sampling design difficult (Table 5. 2). Due to the small size of the fires and lower abundance of *Sphagnum spp.* at Eastside, *S.capillifolium* was sampled from three hummocks from a total of three different fires (each however were burned only minutes apart on the same day in the same weather conditions), with unburnt *S.capillifolium* sampled from an adjacent unburnt area. At Forsinard, where vegetation was more uniform with *Sphagnum spp.* found throughout, 10 discrete patches of *S.capillifolium* were identified both sides of the fire line in the same area. At Glensaugh five sampling areas were identified along a transect through the burnt area and unburnt *S.capillifolium* sampled from the adjacent unburnt area. Measurements were always made on the capitula of stems taken from the same sampling locations. However, due to the destructive nature of the technique measurements were not made on the same stems at each sampling time. Prior to making each fluorescence measurement, made at a light intensity of 1,500 µmol m^{-2} s^{-1}, each capitula (3 per sampling location) were dark adapted for 20 minutes using a dark adaption clip (HPEA/LC, Hansatech Instruments Ltd, UK). Samples from each hummock/lawn area were also removed for moisture content analysis, each sample being weighed prior to being oven dried at 70°C for 1 week, after which the sample was weighed again and moisture content (MC), on a percentage wet weight basis, calculated using equation 5.1 where w is wet weight, and d is dry weight.

$$MC = \frac{w - d}{w} \times 100$$

Eq 5. 1

Table 5. 2 Sampling procedure for chlorophyll fluorescence measurements at each field site where *S.capillifolium* was sampled from hummocks or areas of lawn at various time points after the site was burnt.

Site Name	Fire	Sampling Location	Total number of capitula sampled/site	Time period sampled (number days since fire)
Forsinard	1	10 burnt 10 unburnt	60	38 -766
Eastside	1 2 3	3 burnt 3 burnt 3 burnt 3 unburnt	36	5 - 439
Glensaugh	1	5 burnt 5 unburnt	30	81 - 440

5.4.5 Statistical Analysis

5.4.5.1 Analysis I

To investigate if there were significant site level differences in species composition an unconstrained detrended correspondence analysis (DCA) using CANOCO 5 (ter Braak and Šmilauer, 2012) was used on the total percentage cover data from the final day of sampling. The environmental terms soil temperature (ST), mean soil moisture (SM) and mean height of the water table (WT), which had all been measured at a plot level over the duration of the study period, with the exception of WT at Glensaugh which had been calculated from SM (Appendix 2.2), were plotted as supplementary variables. A detailed account of how these measurements were made is given in Chapter 2 (section 2.4.2). Plotting the environmental variables as supplementary variables allowed for a projection of the environmental variables onto the species data, without influencing the species and sample ordination which would be problematic due to the unbalanced experimental design (some sites sampled more than others) and repeated measures (samples from same plots over time). To further assess the differences between the three sites, mean precipitation, altitude, steepness of slope, aspect and location (easting/northing) were also included in the DCA. The plotted ordination diagram of the DCA results allow the dissimilarity of distribution of species to be evaluated, the closer the species are plotted on the ordination diagram the more often they occur together. The DCA ordination diagram can also show the dissimilarity between environmental variables in the same way. The continuous environmental variables are plotted as arrows in the direction of the steepest increase in value and show the marginal effects of the environmental variable upon species sample scores.

5.4.5.2 Analysis II

To assess the differences between burnt and unburnt vegetation communities at each site and how species composition changed in the burnt plots over time Principle Response Curves (PRC), a multivariate constrained ordination approach

(Van den Brink and ter Braak, 1999), were computed using CANOCO 5 (ter Braak and Šmilauer, 2012). These used logged percentage top cover survey data from the three sampling times at each site. The effect of treatment, including its interaction with time point, was calculated using a Monte Carlo Permutation Test for time series data.

5.4.5.3 Recovery of Sphagnum capillifolium

Statistical differences in Fv/Fm of burnt and unburnt *S.capillifolium* capitula at the three sites on each sampling day were identified using the non-parametric Mann-Whitney-Wilcoxon test, as data were not normally distributed, on Fv/Fm ratios for each sampling day. A Kruskall-Wallis test was used to test if there were significant differences in the distribution of Fv/Fm between burnt, unburnt, and new growth samples, as again data were not normally distributed. All tests were carried out using R (R Core Team, 2013).

5.5 Results

5.5.1 Change in vegetation following fire

5.5.1.1 Analysis I

In total 28 species recorded across all three field sites from 34 samples were used in the correspondence analysis. The unconstrained DCA indicated that although there was high variation in the data, shown by the low eigenvalues, there were associations between site and the environmental variables with axis 1 and 2 accounting for 15% and 12% percent of the variation respectively (Table 5. 3). However, the close proximity of the centroids showing Treatment in the ordination diagram (Figure 5. 2) indicates that Treatment did not have a strong association with vegetation. The ordination diagram shows that the strongest (negative) correlation with the first axis was with Northing, with the second axis correlating positively with Easting, Slope and Precipitation, which were most attributable to the Glensaugh site. The DCA ordination diagram also showed that the vegetation communities at each site were different making it appropriate to analyse the differences between bunt and unburnt communities by site in Analysis II, so differences in vegetation composition would not mask any treatment effect. The strongest differences between sites were, predictably, geographic position (Northing and Easting) and altitude, with Forsinard having the highest soil temperatures. In general the DCA showed that there was greater similarity in conditions and vegetation between Eastside and Glensaugh.

Table 5. 3 Summary of DCA ordination analysis for Analysis I (total % cover of each species on final day of sampling) showing eigenvalues, which indicate high variation within the data, and the proportion of cumulative variation explained by axis 1 and 2. Supplementary variables accounted for 25.6% (adjusted explained variation 14.9%)

	Axis 1	**Axis 2**
DCA		
Eigenvalues	0.5438	0.4344
Proportion variation explained (%)	14.68	11.73

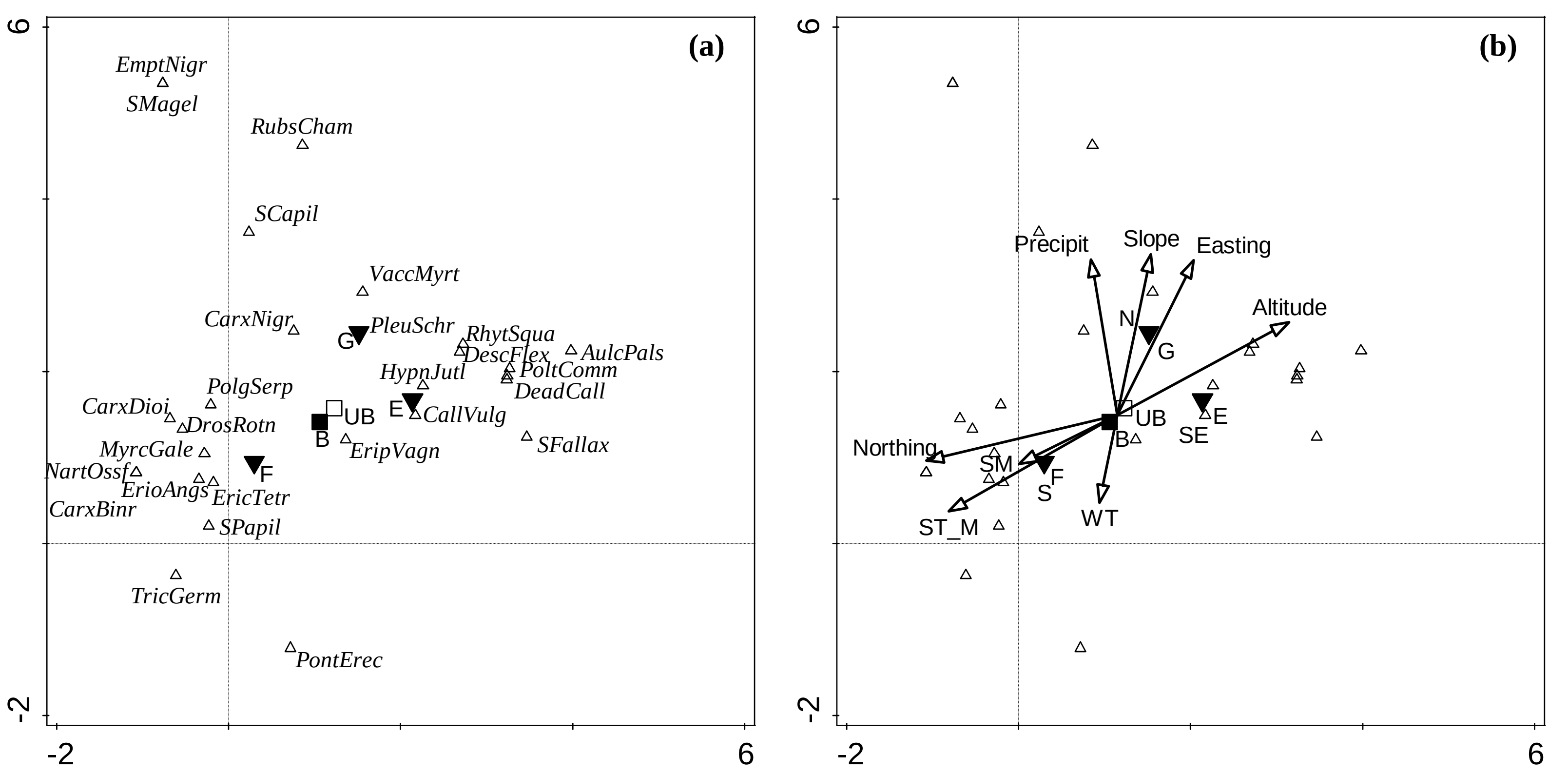


Figure 5. 2 DCA ordination diagram showing treatment (squares) with **(a)** species composition assessed by total percent cover on final day of sampling plotted with site (G=Glensuagh, E=Eastside, F=Forsinard), where empty triangles denote species and large filled triangles denote site and **(b)** a projection of the environmental variables; site, altitude, aspect, slope, cardinal and intercardinal direction (Easting/Northing), precipitation (Precipit), water table (WT), mean soil temperature (ST_M) and soil moisture (SM), onto the species data. Full species names and authors given in Appendix 5.2. Plot (b) shows that the correlation between the measured environmental variables was strongest between SM and ST, and lowest between altitude and SM and ST.

5.5.1.2 Analysis II

To assess the differences between burnt and unburnt communities, and the change in vegetation composition over time in the burnt plots, each site was assessed separately using Principle Response Curves. All plots showed a one dimensional direction of departure from the unburnt plots (vertical scores) with the greatest difference in vegetation composition between burnt and unburnt plots found at T1 (Figure 5. 3 to 5.5). Common to all sites was a greater abundance of *Eriophorum vaginatum* in the unburnt plots with the higher cover of litter (fragments of unidentifiable plant material) in the burnt plots the most significant difference between treatments at Eastside and Glensaugh.

At Forsinard (Figure 5. 3) there was greater cover of the *Sphagnum* mosses *S.capillifolium* and *S.papillosum* as well as *Eriophorum angustifolium* and *Narthecium ossifragum* in the burnt plots when compared to the unburnt plots. At both Eastside and Glensaugh there was more dead *Calluna* in the burnt plots and in general there were more dwarf shrubs in the unburnt plots at all sites: *Erica tetralix* and *Myrica gale* at Forsinard and Glensaugh and *Calluna vulgaris* and *Vaccinium myrtillus* at Eastside and Glensaugh. There was also greater cover of *Rubus chamaemorus* in the burnt plots at Glensuagh, the only site at which it was found (Figure 5. 5). Treatment was, however, only found to be significant at Eastside (Table 5. 4) and that was the only site where there was a clear trend for the vegetation composition of burnt plots becoming more like that of the unburnt reference plots over the three sampling times (Figure 5. 4).

In general, the percentage top cover of shrubs and graminoids was consistently lower across the burnt plots than the unburnt plots with a strong trend for graminoids increasing in the burnt plots over time (Figure 5. 6). Over the study period however, graminoid cover in the burnt plots did not significantly exceed the cover in the unburnt plots. There was not such a clear trend in shrubs, although shrub cover in the burnt plots was consistently much lower than in unburnt plots at the first sampling time. This remained the case at Eastside and Glensaugh at all sampling times, however shrub cover was recorded as higher at time 2 in the burnt plots at Forsinard. This is likely an artefact of the sampling method used as the shrubs at Forsinard were smaller and lower growing, in contrast to the dominant shrub *Calluna* at Glensaugh and Eastside, making them easily obscured by taller vegetation.

Table 5. 4 The amount of total and partial variance explained by Treatment and Time for each site and the significance of Axis 1 (significant result shown in italics)

Site	**Amount of Total variation explained by**		**Amount of Partial Variance explained by**	**Test on 1st Axis**
	Time	**Treatment**	**Treatment**	
Forsinard	6%	20%	21.7%	F=4.7 (p=0.15)
Eastside	23%	12%	15.9%	F=5.5 *(p=0.01)*
Glensaugh	3%	5%	5.4%	F=0.8 (p=0.54)

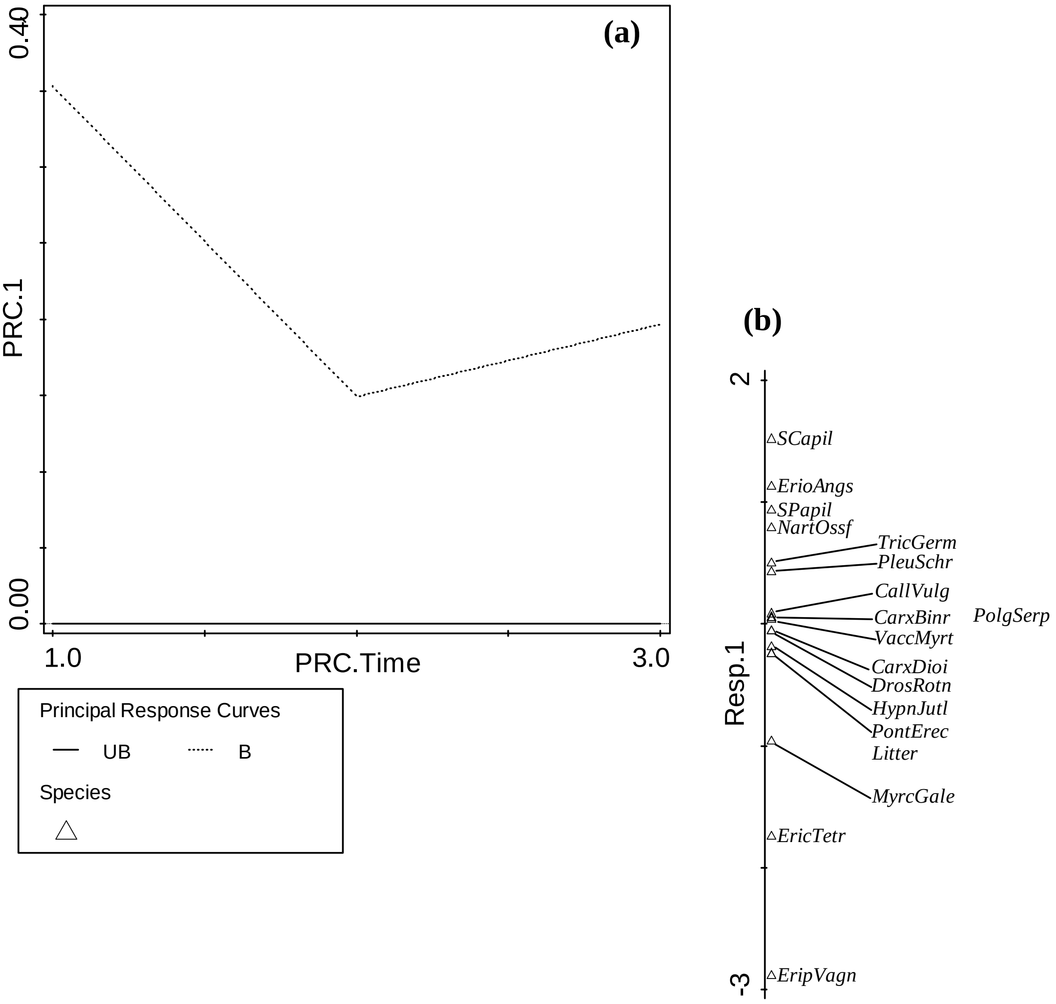


Figure 5. 3 Principal Response Curve of **Forsinard** vegetation at the three sampling times where burnt plots were compared to unburnt control plots and individual species scores (full species names given in Appendix 5.2) for Axis 1 (a), (b). The effect of treatment and it's interaction with timepoint according to Monte Carlo permutation test was not significant (p=0.148).

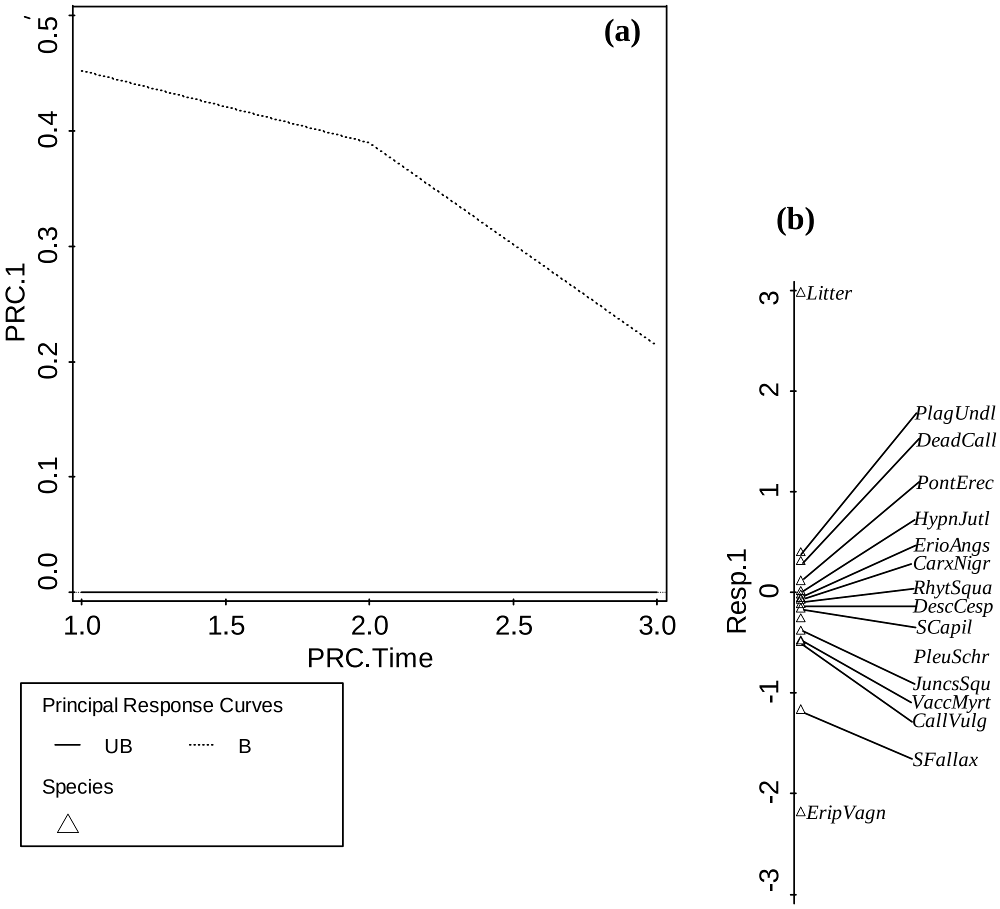


Figure 5. 4 (a) Principal Response Curve of **Eastside** vegetation at the three sampling times where burnt plots were compared to unburnt control plots and (b) individual species scores (full species names given in Appendix 5.2).The effect of treatment and it's interaction with timepoint according to Monte Carlo permutation test was significant (p=0.01).

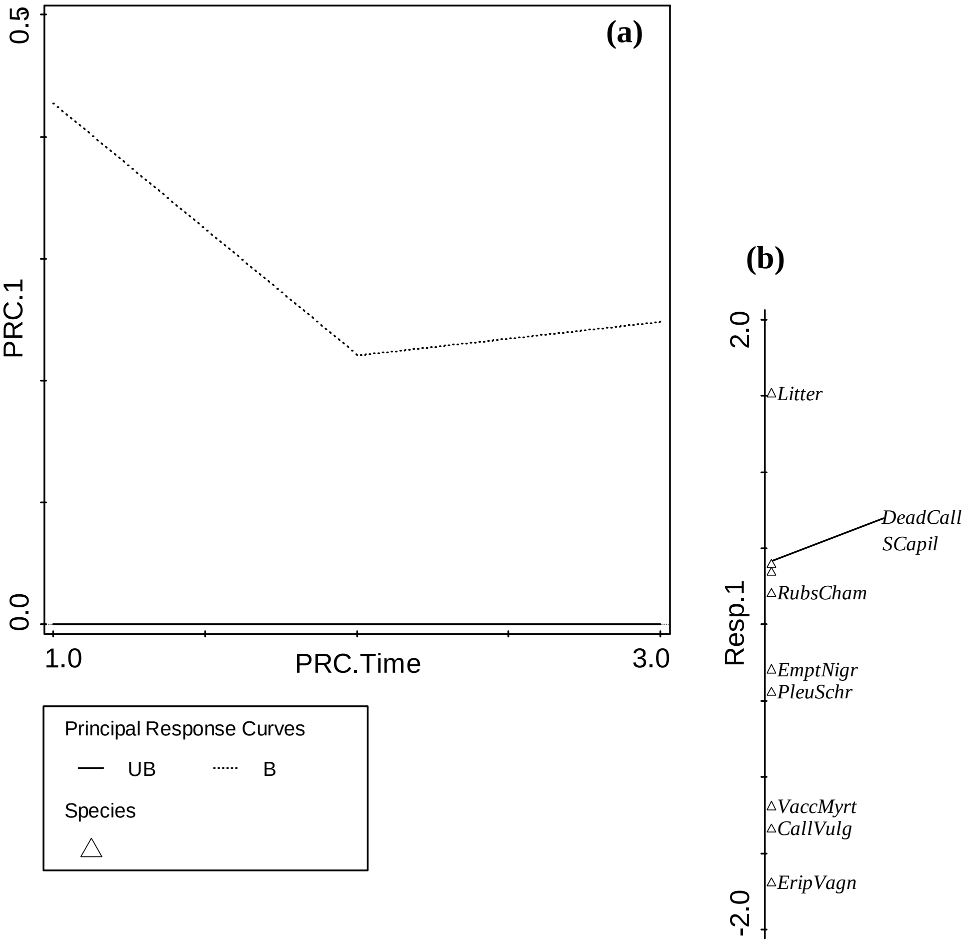


Figure 5. 5 (a) Principal Response Curve of **Glensaugh** vegetation at the three sampling times where burnt plots were compared to unburnt control plots. The effect of treatment and it’s interaction with timepoint according to Monte Carlo permutation test was not significant (p=0.258) and (b) individual species scores. Full species names given in Appendix 5.2.

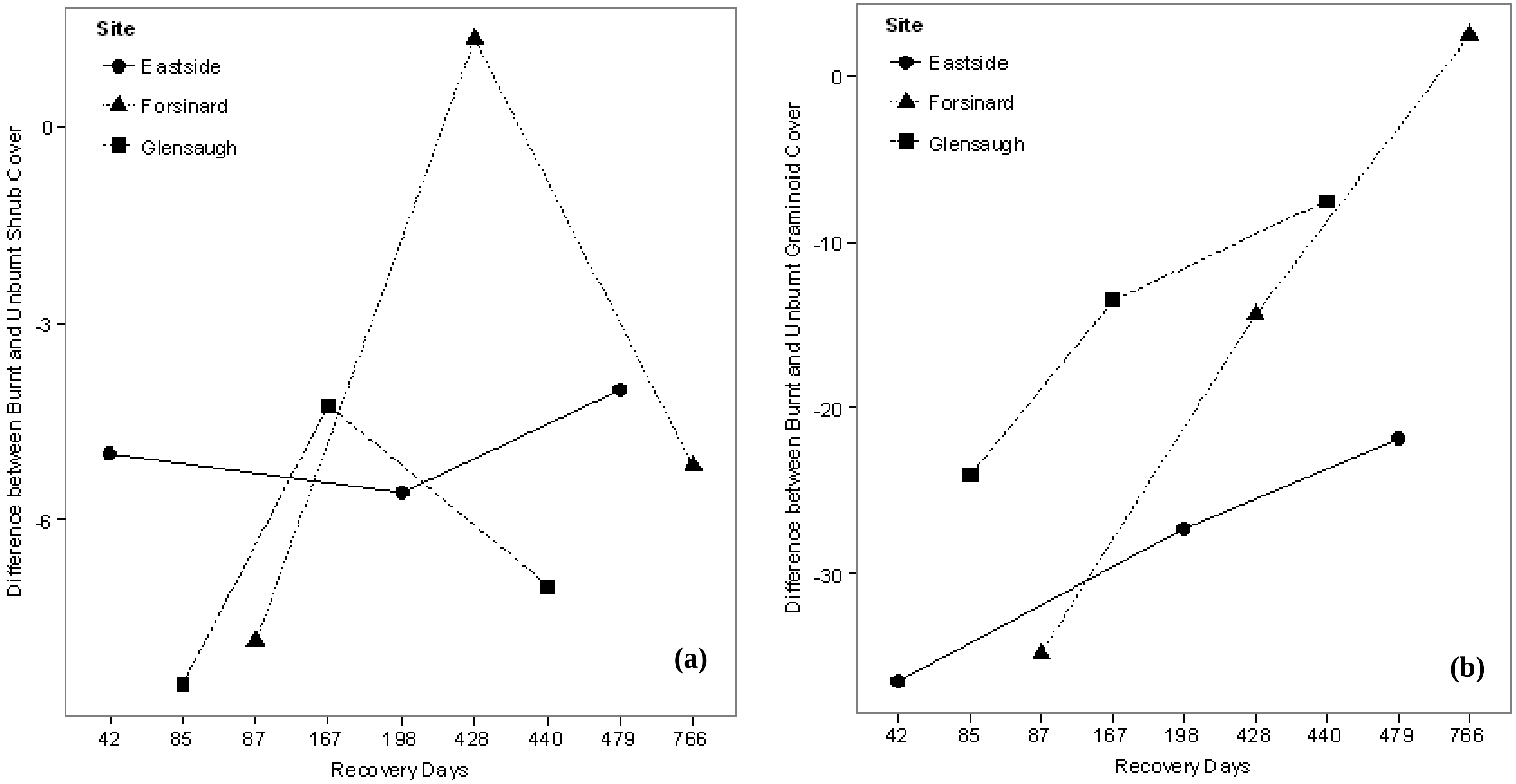


Figure 5. 6 Difference in percentage cover of shrubs (a) and graminoids (b) at each site at each sampling time in the burnt and unburnt plots (calculated as Burnt minus Unburnt percentage cover) where minus values represent a lower cover in the burnt plots when compared to unburnt plots. The shrub group consisted *Calluna vulgaris* (dominant), *Vaccinium myrtillus*, *Myrica gale* and *Erica tetralix*. The graminoid group was made up of *Eriophorum vaginatum* (dominant), *Eriophorum angustifolium* and *Deschampsia flexuosa*.

5.5.1.3 NVC Classifications

All three sites were matched to different NVC sub communities with classifications changing over time and occasionally, rather than consistently, showing differences in NVC community between treatments (Table 5. 5,

Figure 5.7). Notably, NVC classifications were found to change over time in both the unburnt plots and the burnt plots at all three sites. At some sampling times there were relatively few species recorded, particularly in the burnt plots at Eastside and at Glensaugh at the first sampling time, which meant matched sub-communities were verified with the literature to ensure sensible matches.

Eastside was most often matched to M15b *Scirpus cespitosus- Erica tetralix* wet heath however at sampling time 1 (T1) the unburnt plots were most closely matched to M20b *Eriophorum vaginatum* mire: *Calluna vulgaris- Cladonia* sub community. On the final day of sampling (T3) the burnt plots deviated from the M15b classification, being more closely associated with M19b *Calluna vulgaris – Eriophorum vaginatum* mire: *Empetrum nigrum* sub-community. This change in community from M15 to M19 is likely due to the increase in graminoids cover in the burnt plots, in particular an increase in *E.vaginatum* and *Calluna* with the lack of *Sphagnum spp.* recorded in the burnt plots at T1 responsible for the M15/M20 split between the burnt and unburnt communities.

The NVC classifications matched to the vegetation communities at Forsinard varied from M17a *Scirpus cespitosus – Eriophorum vaginatum* blanket mire Drosera – Sphagnum sub community to M15b *Scirpus cespitosus – Erica tetralix* wet heath typical sub community in both the burnt and unburnt plots. The burnt plots at Forsinard were matched to the same communities as the unburnt plots at T2 and T3 while at T1 the best NVC match was M15c *Scirpus cespitosus – Erica tetralix: Cladonia* sub community which could be a reflection of less *Sphagnum* being detected in the burnt plots.

Table 5. 5 NVC sub communities matched to burnt and unburnt control community at each site and sampling time (T1, T2, T3) showing the number of species in each community and match statistics.

	T1		**T2**		**T3**	
	B	**UB**	**B**	**UB**	**B**	**UB**
Eastside						
Number of spp.	3	5	8	11	8	12
Matched Community	M15b	M20b	M15b	M15b	M19b	M15b
Matching spp.	3/3	4/5	8/8	9/11	7/8	10/12
Weighted spp. match	100	100	100	91	90	92
Freq. Weighted match	86	94	75	74	68	73
Forsinard						
Number of spp.	10	6	9	7	15	14
Matched Community	M15c	M17a	M17a	M17a	M15b	M15b
Matching spp.	10/10	6/6	9/9	7/7	15/15	13/14
Weighted spp. match	100	100	100	100	100	94
Freq. Weighted match	82	76	68	73	70	68
Glensaugh						
Number of spp.	4	4	6	4	8	5
Matched Community	M20b	M20b	M20b	M20b	M19a	M20b
Matching spp.	4/4	4/4	6/6	4/4	8/8	5/5
Weighted spp. match	100	100	100	100	100	100
Freq. Weighted match	86	78	87	79	70	84

Glensaugh only showed a difference in NVC community between burnt and unburnt plots at T3 where the burnt plots were most appropriately matched to M19a *Calluna vulgaris – Eriophorum vaginatum* blanket mire: *Erica tetralix* sub-community with the unburnt plots and both treatments at T1 and T2 matching M20b *Eriophorum vaginatum* blanket & raised mire: *Calluna vulgaris – Cladonia spp.* sub-community. The difference in species cover likely to be responsible for the unburnt plots being matched to an M19a community at T1 is the presence of *E.tetralix* which was absent at all other sampling times.

A comparison made between the two survey methods, comparing the full survey carried out in the field on the last day of sampling (T3), to the top cover survey assessed using the photographs taken on the same day (Appendix 5.1), showed that at all three sites the top cover assessment using the digital photographs gave a lower species number when comparing the total number of species found at each site. In general the species which were under recorded were moss species such as *Pleurozium schreberi* (Brid.)Mitt., *Polytrichum commune* Hedw and *Hypnum jutlandicum* Holmen & Warncke. Percentage cover was also found to be underestimated in some species using the top cover methodology, particularity so for mosses, low growing shrubs such as *Vaccinium myrtillus* L. and some graminoids which did affect NVC community classification (Appendix 5.1).

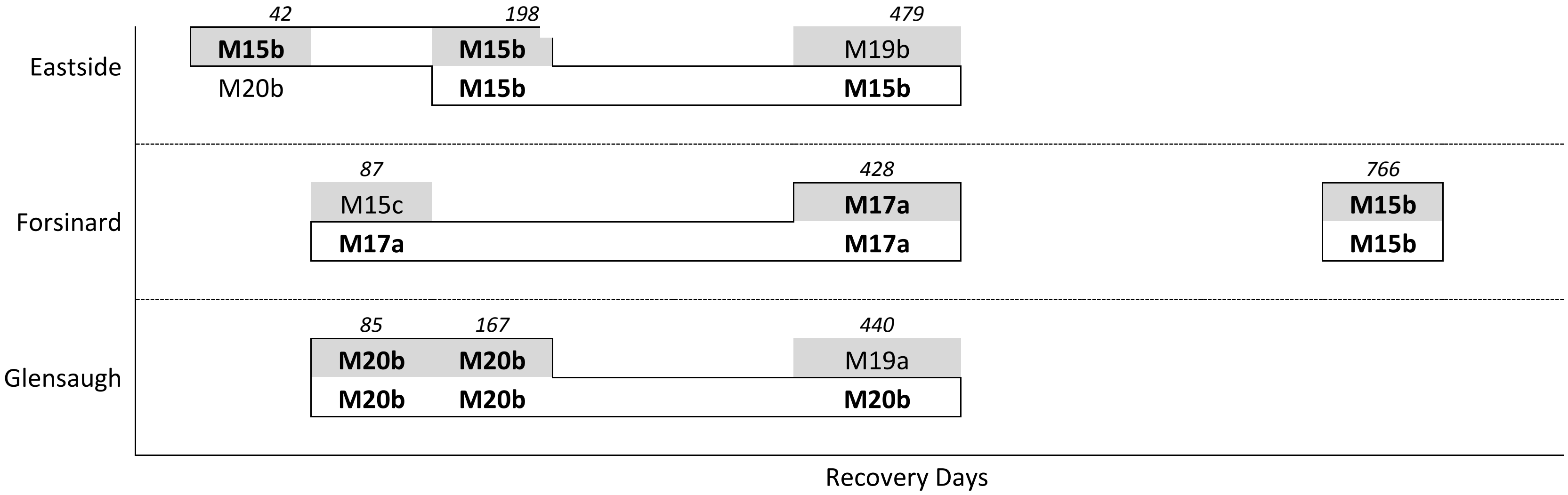


Figure 5.7 NVC sub-communities matched to the vegetation at each site over time and treatments using top cover survey method. Grey boxes show the NVC community matched to the burnt treatment plots, white boxes the unburnt control plots. Consistent classifications are outlined. Numbers in italics are recovery day (number of days since fire) on which the sites were surveyed. All sub-communities were ranked #1 matches by the software apart from Glensaugh T3 where the burnt plots rank #1 match M18a was rejected as it is a community of lower altitude and raised bogs and dominated by *Sphagnum*, and rank #2 M19c rejected due to the complete absence of *Vaccinium vitis-idaea* a constant of this community. Rank #1 sub-community for the unburnt plots was M17c however this was rejected due to it being more associated with lower altitudes in the west, which favoured rank #2 M20b which had the same match statistics.

5.5.2 Recovery of S.capillifolium

A reduction in photosynthetic capacity as indicated by chlorophyll fluorescence Fv/Fm ratios was found in *S.capillifolium* sampled from burnt areas when compared to samples taken from unburnt areas (Figure 5. 8). This reduction in Fv/Fm was seen as much as 545 days from the time of the fire with lower Fv/Fm in burnt samples found at all three sites. At a site level Glensaugh saw least differences between burnt and unburnt samples, with a statistical difference between treatments found on only one occasion. The most statistically different Fv/Fm ratios between treatments were found at Forsinard with differences highly significant, particularly at sampling times closest in time since the site was burnt (Figure 5. 8). This was also seen at Eastside where among the lowest Fv/Fm ratios were seen. There was some evidence that Fv/Fm increased in burnt samples to values closer to those of unburnt samples in time, particularly at Eastside and Forsinard, however, statically significant differences were still seen between treatments well over a year from the time of burning.

At Forsinard unburnt samples were also found to vary in their photosynthetic capacity between sampling times, suggestive of conditions beyond that of treatment having an effect on photosynthetic capacity. Stem moisture content, measured at each sampling location (lawn/hummock) at each sampling time, did not show any significant relationship with Fv/Fm, however, greater variation in stem moisture content was observed in burnt samples (Figure 5. 9).

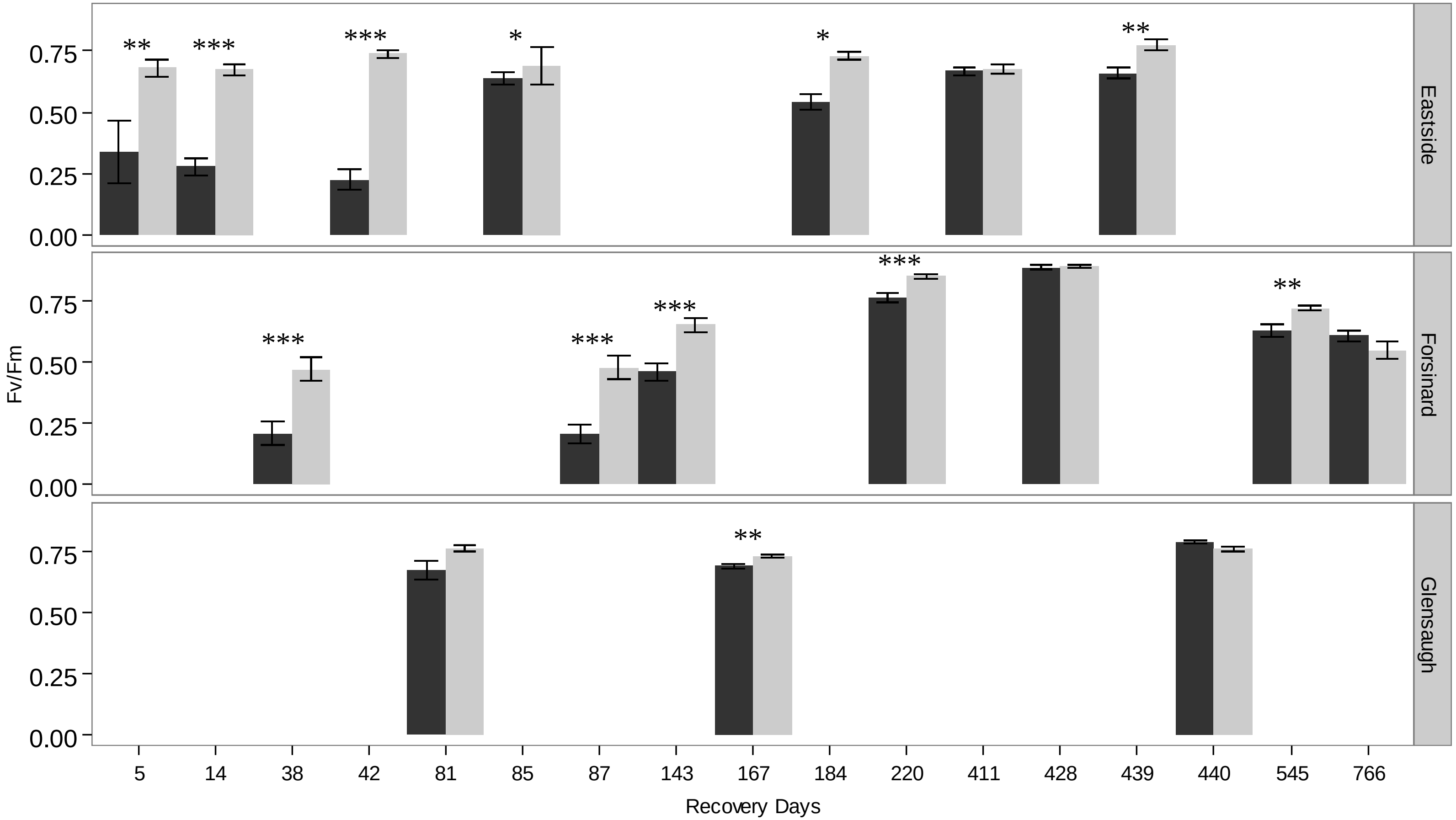


Figure 5. 8 Fv/Fm of the capitula of *S.capillifolium* at each site in the days after the site was subjected to burning where dark grey bars are burnt samples and light grey unburnt. Bars show mean Fv/Fm ratio ± SE of the mean with statistical differences between burnt and unburnt capitula shown by significance level (*** p=<0.05, ** p=<0.01, *** p=<0.001).

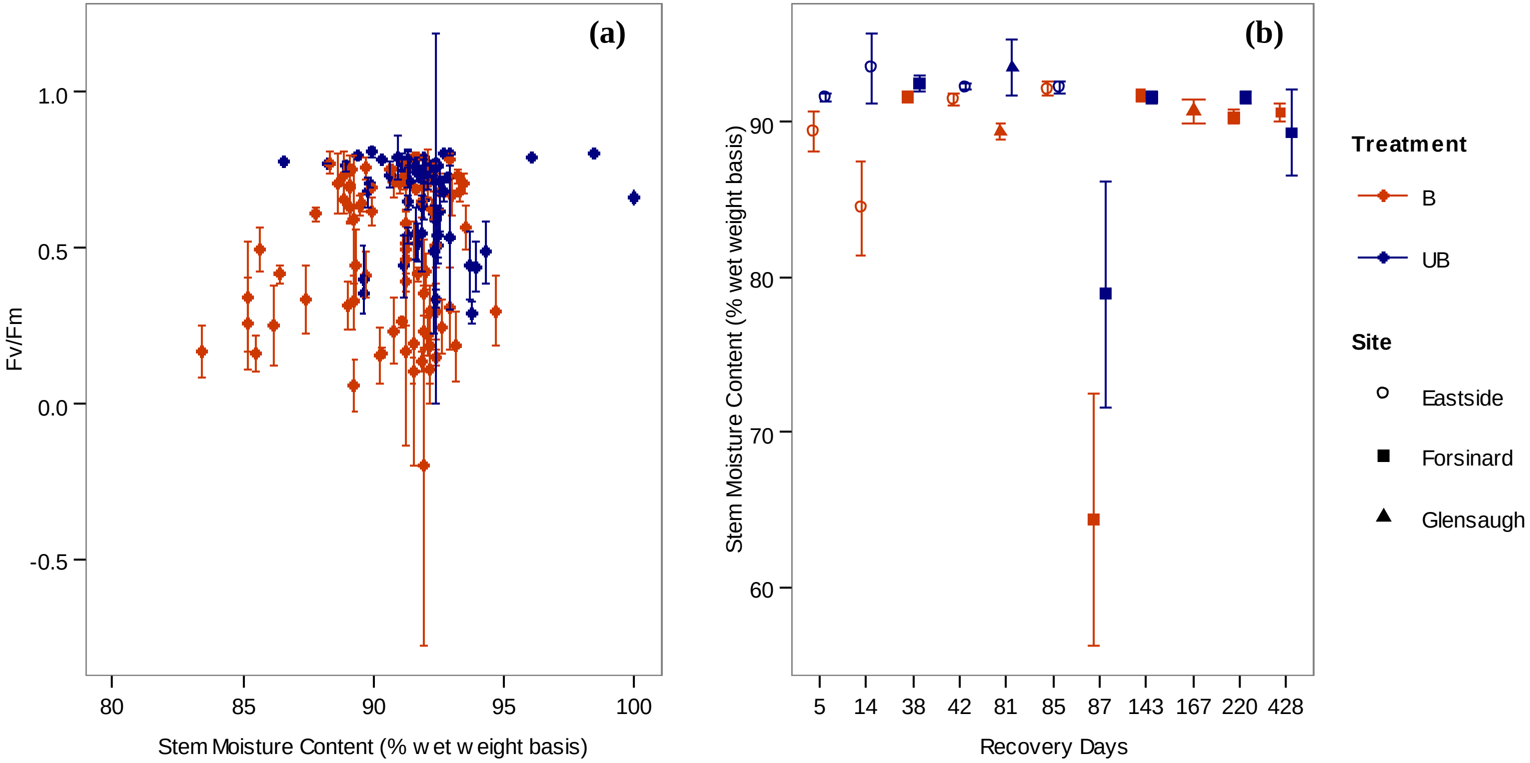


Figure 5. 9 Stem moisture content of a sample of *S.capillifolium* removed from each hummock plotted with mean Fv/Fm (±StE bars) of the capitula of and (b) mean (±StE bars) stem moisture content of burnt and unburnt samples at each site and sampling day where recovery day was the number of says since sites were burned.

As hypothesied, the photosynthetic capacity of *S. capillifolium* capitula was related to new growth, with higher Fv/Fm measured on new capitula growing in the burnt areas (Figure 5. 10). The new auxillay stems and capitula, which grew from the old fire damaged stems, was observed at all three field sites (Figure 5. 11). At each field site the hummocks and lawns of *S. capillifolium* where this new growth was found appeared “speckled”, with new red (or green in some instaces) capitula a stark contrast with the bleached old stem material, with no capitula, surrounding them (Figure 5. 12). In some instance these areas of new growth were observed in hummocks which were significantly damaged by the fire in parts, with extensive bleaching and no apparent regrowth (Appendix 5.3).

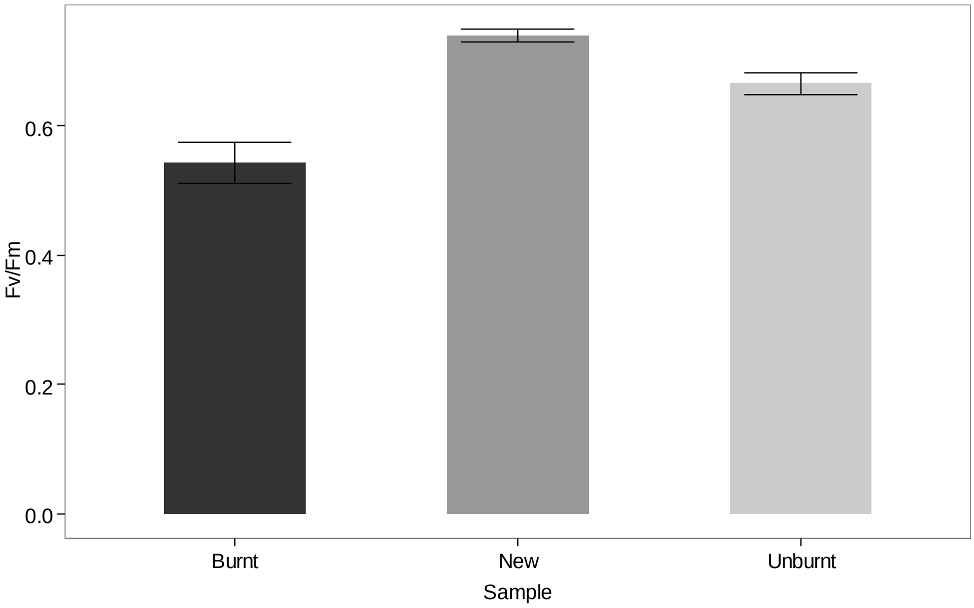


Figure 5. 10 Mean (±StE bars) Fv/Fm of the capitula of *S.capillifolium* at Eastside which had been burned 184 days previously (Burnt), compared to unburnt hummocks (Unburnt) and new auxiliary capitula (New) found growing on stems in hummocks which had been damaged by the fire (see Figure 5. 12). The results of a Kruskal–Wallis test were significant (*df=2, p=<0.001*).

Figure 5. 11 New auxiliary growth observed on *S.capillifolium* stems that had been subjected to burning at Eastside (photograph taken 184 days after the fire had occurred). The same auxiliary growth was seen at all three sites.

Figure 5. 12 A hummock of *S.capillifolium* at Forsinard which had been burnt 428 days previously showing the new auxiliary growth which appear as red capitula surrounded by bleached material (the remainder of the original stem) (enlarged in inset)

5.6 Discussion

5.6.1 Changes in vegetation composition

There were distinct differences in vegetation composition between the three sites studied, reflected by the different NVC sub-communities each site could be most confidently assigned to. The sites most similar, both in terms of vegetation composition and environmental conditions, were Eastside and Glensaugh. The most species rich, in terms of species number, was Forsinard. Already this shows that there were fundamental differences in pre-burn conditions even though the field sites were established because they were similar, could be described as blanket bog with peat deposits greater than 50cm, and were all burned by low severity fires. These site level differences in vegetation composition and structure highlight the potential variability in pre-burn conditions which may exist and shows how, even fires similar in behaviour, could have different implications for vegetation. The results therefore confirm the initial hypothesis [1], that there would be differences in species composition between the three sites. Despite these differences however, as hypothesised, there were common trends in composition change over time and between treatments.

As would be expected by the visual observations of the fires, which removed mostly just the canopy vegetation, both graminoids and shrubs were lower in the burnt plots. Graminoid cover did, however, increase over time to levels seen in the unburnt plots. Frequent burning is associated with the promotion of graminoids over shrubs (eg. Stewart *et al.*, 2004, Lee *et al.*, 2013) but it is important to make the distinction here, that graminoid cover could not be said to be increased by fire, rather that it recovered to levels seen in unburnt plots. This shows the importance of having good control sites, as without the monitored unburnt control plots, the effect of the fires could have been interpreted as promoting graminoids. Instead it is more accurate to describe this response as a reflection of the quicker recovery of graminoids. However, the sites were only monitored for a maximum of two and a half years, so the results can only be related to the relatively short term impacts of the fires, and there is perhaps some evidence to show that graminoid cover may exceed pre-burn levels at Eastside.

The correspondence analysis showed that *E.vaginatum* was found to be more abundant in unburnt plots at all three field sites, while *E.angustifolium* was more associated with burnt plots. It is also likely that the strong trend for burnt plots becoming more like the unburnt control plots over time at Eastside, the only site where treatment was significant, was due to *E.vaginatum* cover increasing. A change in the cover of *Eriophorum spp.* could have wider implications, as it has been shown that both species can increase CH_4 emissions, as their aerenchyma act as a conduit for CH_4 to reach the atmosphere, and can increase rates of mathonogenesis by providing substrates for methanogenic bacteria through root exudation (Öquist and Svensson, 2002, Green and Baird, 2011, Greenup *et al.*, 2000). As described in Chapter 2, however, no relationship was demonstrated between *Eriophorum spp.* cover and CH_4 emissions at the plots studied here.

When considering graminoids alone, the recovery in percentage cover to unburned levels shows that one-off burning events, with the characteristics of those studied here, have limited impact in the short term. There was however, a greater impact on shrub communities, with no clear trend for recovery to pre-burn levels. This could be an artefact of the monitoring technique as only top cover was estimated, so some taller graminoids and sedges may have obscured low growing shrub plants, particularly *Erica tetralix*. Despite this, it was generally observed that it took longer for new shrub plants to start growing, which was particularly evident at Eastside where new *Calluna* seedlings were still emerging two years after burning. This may be a reflection of the older stand age of the *Calluna* at Eastside, with growth having to come from seed rather than vegetatively (Miller and Miles, 1970). This highlights the importance of considering the vegetation state, the vegetation composition and structure, at the time of burning, as this will have implications for rates and modes of recovery (Davies *et al.*, 2010). Stand age and structure can also influence temperature gradients within a fire and fire intensity (Hobbs and Gimingham, 1984a), which could be important to plant survival and recovery. This suggests that future fires at the three sites studied could well have different implications for the vegetation due to the potentially different pre-burn vegetation and environmental conditions as well as due to differences in fire behaviour.

The dominance of graminoids over shrubs may also have wider implications for carbon cycling as graminoid dominant systems have different carbon assimilation rates and retention potential in the long term than woody shrub dominated systems (eg. Knapp *et al.*, 2008, Barger *et al.*, 2011, Quin *et al.*, 2014). This would imply that even fires, like those here, which do not penetrate the peat change carbon dynamics indirectly, at least in the short term, by changing vegetation composition. However, the correspondence analysis found that burning only had a significant effect on vegetation composition at Eastside, despite similar pre-burn vegetation composition, structure and fuel loads to Glensaugh. This suggests that the fires behaved differently, evident in the greater amount of *Calluna* biomass left by the fire at Glensaugh indicating a fire lower in severity, and confirms that fire behaviour is also important to consider. In addition, Eastside was surveyed closer to the time of fire, when vegetation composition in burnt and unburnt plots was most different. Together this highlights the dynamic impact of fires on vegetation, related to fire behaviour and time since a fire. This would be important to build into any model of the impact of fire on vegetation and carbon cycling in blanket bogs, and makes it necessary that methods to assess the impact of a fire have the ability to relate to fire behaviour and time since burning.

5.6.2 NVC Classifications

In respect to the hypothesis that the NVC system would offer a way of reflecting differences in vegetation composition brought about by a fire, NVC community matches were found to vary with site and treatment. However, they also varied in both burnt and unburnt communities over time. The NVC communities ascribed to each site and treatment did reflect the changes in dominant vegetation, particularly the graminoids such as *E.vaginatum*, brought about by the fires. However, the inconsistency in the NVC classifications given to the unburnt control communities at two of the sites suggests that, to a degree it reflected seasonal changes in dominant vegetation cover as well as the surveying procedures. There is evidence of a seasonal effect on the NVC classifications as more vigorous growth may have obscured mosses, often key to prescribing an NVC community. However, this will be an artefact of the surveying method as only top cover estimates were used to assess change over time. This does highlight the importance of carrying out a full assessment of cover, including the moss layer, to robustly assign an NVC community. Despite only using top cover estimates, however, the results do indicate both the capability and the limitations of using the NVC system to evaluate the impact of fire on blanket bog vegetation.

The results show that the NVC communities assigned to Glensaugh were most consistently the same between treatments and time points. This agrees with the observation that this was the least severe fire. This suggests that the NVC system can show, to some degree, the severity of the fire in terms of the degree of difference between burnt and unburnt vegetation communities. Where it is limited however, is in describing some of the changes in vegetation potentially important to the wider functional condition and ecology of a blanket bog system. For example, structural changes in vegetation cover are not described by NVC, so a shift in mature or degenerate heather stands to pioneer seedling cover is not distinguished. This would have particularly important implications for managed burning and rotation times as for example, *Calluna* has different modes for re-growth depending on age and structure, with post fire recovery shown to be slower in old *Calluna* stands (Hobbs and Gimingham, 1984b, Davies *et al.*, 2010). Plant biomass and structure have also been related to fire behaviour (eg. Kayll, 1966, Hobbs and Gimingham, 1984a, Molina and Llinares, 2001, Davies *et al.*, 2010) which will be important to plant survival and recovery. Post fire, the change in structure, particularly of canopy species, may be important to low growing plants, such as the bryophytes which will have to be able to tolerate greater light exposure and potentially different moisture conditions. This was shown here in an apparent increase in cover *S. capillifolium* in burnt plots, but as the survey estimated top cover this only reflected the loss of the canopy. In addition, the stem moisture content of *S. capillifolium* was shown to be much more variable in the burnt plots, which may have implications for photosynthesis (Schipperges and Rydin, 1998, van Gaalen *et al.*, 2007, Strack *et al.*, 2009).

Over the timescale studied here some of the more subtle changes in species cover were shown in the NVC matches, such as the presence of *Rubus chamaemorus* only in the burnt plots, a species capable of dominating after fire due to spreading rhizomes (Hobbs, 1984). However, using NVC to assess longer term changes in vegetation composition, particularly if there are no control plots for comparison, does not solely show the impacts of fire, rather it is a representation of the vegetation community at a particular location and time point, where vegetation may be strongly associated with environmental conditions and long term management. The cumulative effect of management, climate and environmental conditions is difficult to unravel and thus attributing change to one element of disturbance, such as fire, is difficult using a vegetation classification system alone. This suggests that it is preferable that other indicators of the ecological impact of a fire event are assessed along with vegetation composition, such as extent of bare peat and percentage consumption of the moss layer, which can be associated directly to burning.

5.6.3 Sphagnum Survival and Recovery

It was hypothesised that the capitula, when not consumed, would show a long term reduction in photosynthetic capacity. This was confirmed at all three sites as, even after over a year from the time of the fire, the photosynthetic capacity of the capitula was significantly lower in *S.capillifolium* in the bunt area. The site which showed the least difference between treatments was Glensaugh, which again indicates the lower severity of the fire. However, despite the observed reduction in photosynthetic capacity, long term this may not be important due to the observed propensity for rapid re-growth of new healthy auxiliary stem and capitula. The results show that *S.capillifolium* has the ability to recover from low severity fires, and that this can be common as it was observed at all three sites studied. It would now be important to see if this response extends to other species and under what conditions, both in terms of fire severity and behaviour, do plants lose this ability. However, even in these light fires there was significant variation in the extent of damage and bleaching, found even within the same hummock or lawn area. This suggests that variation in fire behaviour at the micro-scale is significant for the impact of a fire on the *Sphagnum* layer. This again highlights the potential for significant variability in the impacts of fire on vegetation and wider ecology of blanket bog, and suggests that fire behaviour at different spatial scales is critical.

5.7 Conclusions

Hypothesis [1] can be accepted as, despite differences in vegetation communities between sites, there was a common trend of fire increasing the abundance of the more competitive graminoid species, while reducing shrub cover in the short term. There was, however, no clear trend for shrubs to increase to cover levels of unburnt areas over the time monitored. This supports previous observations and also suggests that even fires which remove mostly only the canopy vegetation and do not penetrate the peat, could indirectly affect rates of carbon assimilation and retention in the short term. The change in vegetation composition brought about by the fires was reflected to some degree by the NVC system, confirming hypothesis [2]. However, NVC did not show more subtle changes in species cover over time, and would not be sufficient for showing the effect on rare, low frequency, species. In addition, it does not describe other impacts of fire which could have important implications for the ecology of a blanket bog system, such as vegetation age and structure or extent of damage to the *Sphagnum* layer or peat. Hypothesis [3] was also confirmed, as the capitula of *S.capillifolium* which had been burned did have lower photosynthetic capacity throughout the monitoring period. Despite this however, *S.capillifolium* was shown to be fairly robust and able to recover from the fires studied here by growing new healthy stem and capitula. More widely the results show how the impact of a fire on the vegetation of a blanket bog is dependent on fire behaviour as well as pre burn vegetation structure and composition.

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Appendix 5.1 Species lists and comparison of top and full cover vegetation surveys

Forsinard		
Survey Type	**Full**	**Top**
Number of plots	12	12
Species		
Calluna vulgaris	II	II
Carex binervis	I	I
Carex dioica	I	
Drosera rotundifolia	III	
Erica tetralix	**V**	**III**
Eriophorum angustifolium	IV	IV
Eripophorum vaginatum	V	V
Hypnum jutlandicum	I	I
Myrica gale	IV	IV
Narthecium ossifragum	I	I
Pleurozium schreberi	II	
Polygala serpyllifolia	**III**	**I**
Pontella erecta	I	I
Sphagnum capillifolium	**II**	**I**
Sphagnum papillosum	V	IV
Trichophorum germanicum	**IV**	**III**
Vaccinium myrtillus	I	I
Total Number Species	**17**	**14**
Burnt NVC Community	M15b	M15b
Unburnt NVC Community	M15b	M15b

Species found in all 12 plots at **Forsinard** in the full cover survey (full) carried out on the last day of sampling and the top cover survey (top) carried out using photographs of each plot taken on the last day of sampling. Species which were only identified in one of the surveys shown by shading and species with different estimated cover in each survey shown in bold.

Eastside		
Survey Type	**Full**	**Top**
Number of plots	14	14
Species		
Eripophorum vaginatum	V	V
Deschampsia flexuosa	III	III
Pleurozium schreberi	**III**	**I**
Sphagnum fallax	**III**	**I**
Rhytidiadelphus squarrosus	**II**	**I**
Vaccinium myrtillus	**II**	**I**
Carex nigra	I	I
Eriophorum angustifolium	I	I
Hypnum jutlandicum	I	I
Plagiothecium undulatum	I	I
Polytrichum commune	I	
Pontella erecta	I	I
Sphagnum capillifolium	I	I
Sphagnum papillosum	I	
Calluna vulgaris	III	III
Deschempsia cespitosa		
Juncus squarrosus		I
Total Number Species	**15**	**14**
Burnt NVC Community	M19b	M15b
Unburnt NVC Community	M15d	M19b

Species found in all 14 plots at **Eastside** in the full cover survey (full) carried out on the last day of sampling and the top cover survey (top) carried out using photographs of each plot taken on the last day of sampling. Species only identified in one of the surveys shaded, species which had different estimated cover in each survey shown in bold.

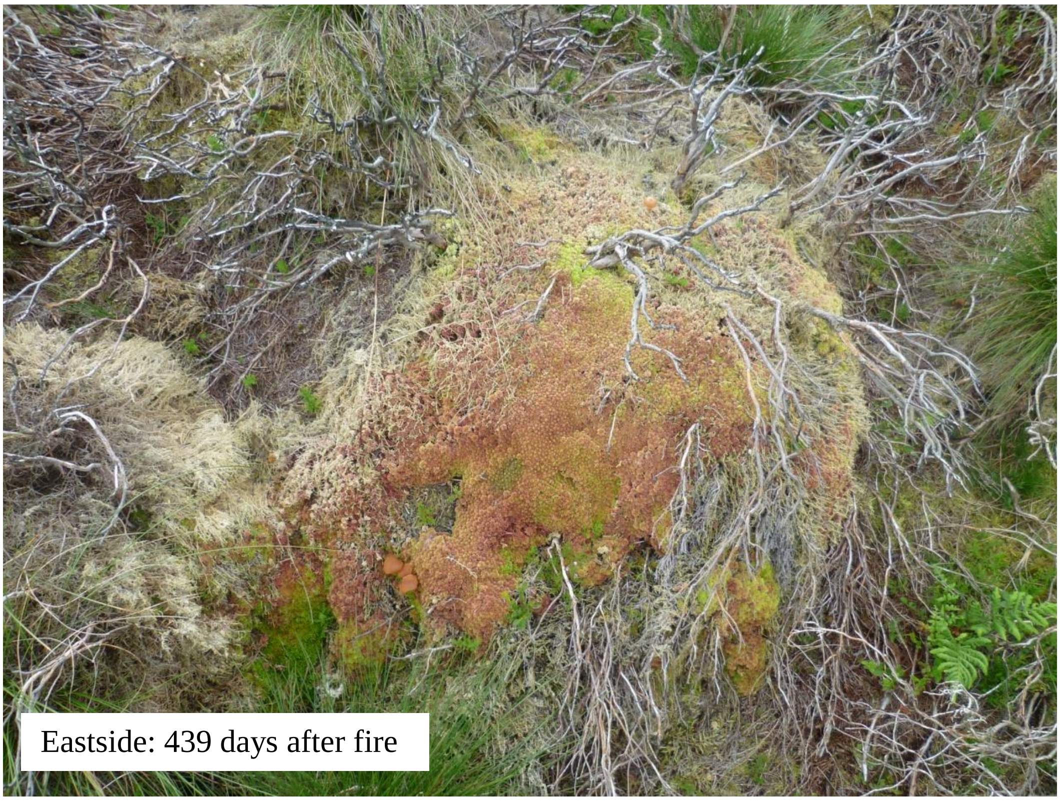
Glensaugh		
Survey Type	**Full**	**Top**
Number of plots	8	8
Species		
Aulacomnium palustre	I	
Calluna vulgaris	II	II
Empetrum nigrum	**I**	**II**
Erica tetralix	**II**	**I**
Eripophorum vaginatum	**IV**	**V**
Hypnum jutlandicum	I	
Pleurozium schreberi	**IV**	**II**
Rubus chamaemarus	**II**	**I**
Sphagnum capillifolium	III	III
Sphagnum magellanicum	I	
Vaccinium myrtillus	IV	IV
Total Number Species	**11**	**8**
Burnt NVC Community	M18a	M18a
Unburnt NVC Community	M19c	M17c

Species found in all 8 plots at **Glensaugh** in the full cover survey (full) carried out on the last day of sampling and the top cover survey (top) carried out using photographs of each plot taken on the last day of sampling. Species only identified in one of the surveys shaded, species which had different estimated cover in each survey shown in bold.

Appendix 5.2 Full species names and species author

Species name	**Abbreviation**
Aulacomnium palustre (Hedw.) Schwägr.	AulcPals
Calluna vulgaris (L.) Hull	CallVulg
Dead Calluna	DeadCall
Carex binervis Sm.	CarxBinr
Carex dioica L.	CarxDioi
Carex nigra (L.) Reichard	CarxNigr
Drosera rotundifolia L.	DrosRotn
Empetrum nigrum L.	EmptNigr
Erica tetralix L.	EricTetr
Eriophorum angustifolium Honk.	ErioAngs
Eriophorum vaginatum L.	EripVagn
Hypnum jutlandicum Holmen & Warncke	HypnJutl
Myrica gale L.	MyrcGale
Narthecium ossifragum Ker Gawl.	NartOssf
Pleurozium schreberi (Brid.) Mitt.	PleuSchr
Polygala serpyllifolia Hose.	PolgSerp
Potentilla erecta (L.) Raeusch.	PontErec
Rubus chamaemorus L.	RubsCham
Sphagnum capillifolium (Ehrh.) Hedw.	SCapil
Sphagnum magellanicum Brid.	SMagel
Sphagnum papillosum Lindb.	SPapil
Sphagnum fallax (Klinggr.) Klinggr.	SFallax
Trichophorum germanicum Palla.	TricGerm
Vaccinium myrtillus L.	VaccMyrt
Deschampsia flexuosa (L.) Trin.	DescFlex
Rhytidiadelphus squarrosus (Hedw.) Warnst.	RhytSqua
Plagiothecium undulatum (Hedw.) Schimp.	PlagUndl
Polytrichum commune Hedw.	PoltComm

Appendix 5.3 Images of *Sphagnum* damaged by fire


Eastside: 439 days after fire


Eastside: 439 days after fire

Forsinard: 428 days after fire

Forsinard: 428 days after fire

6. Synthesis

The aim of this research was to better understand some of the impacts of burning on carbon cycling and the vegetation of blanket bogs. Through controlled laboratory experiments and sampling at three fire sites over two and a half years, the impacts of fire could be quantified and specific potential mechanisms for fire modifying greenhouse gas emissions and damaging the *Sphagnum* layer could be investigated. To address some of the gaps in our understanding of the impacts of burning, important when prescribing best practice management, there were four broad questions this research set out to answer:

1) Does fire increase methane emissions from blanket bogs? Is a reduction in methanotrophy in the *Sphagnum* layer a potential mechanism for this?

2) Does ecosystem respiration change due to the changes in vegetation and abiotic conditions after a fire that does not penetrate the peat?

3) How does *Sphagnum* respond to burning? Is there a critical temperature at which *Sphagnum* cannot recover?

4) What short-term changes in blanket bog vegetation composition does fire bring about? Do changes have wider implications for carbon cycling?

Despite these being distinct questions, and presented and discussed as such in each chapter, the results need to be examined as a whole and considered in the context of management guidance and policy. From this perspective the most important results relate to the effect low-severity fires have on greenhouse gas emissions, and the critical factors for *Sphagnum* survival and recovery.

6.1 The impact of burning on greenhouse gas emissions from blanket bogs

Evaluating the impact of fire on blanket bogs, and whether it has a positive or negative effect on their carbon budget, is increasingly relevant as more emphasis is being placed on peatlands as carbon stores within the context of greenhouse gas emissions from land use and land use change. This makes it necessary to revisit management legislation and guidance to ensure it remains appropriate for this new emphasis for good practice management. To do this, there has to be a sound evidence base on which to amend the best practice guidelines. Historically in the UK guidelines have been centred on the optimum management of heather, limiting the risk of severe and dangerous fires, and potential damage to the wider environment and wildlife. Therefore, this research set out to answer the specific questions of whether fire increased CH_4 emissions and ecosystem respiration from blanket bogs, and if these increases were associated with changes in abiotic conditions, vegetation composition and bacterial communities.

It was found that CH_4 emissions were not significantly higher on burned blanket bog when compared to adjacent areas that had not been burned. Likewise, there was no trend for increased ecosystem respiration on the burned plots. This suggests that the low severity fires studied (which did not penetrate the peat and left the majority of the moss layer intact) did not increase carbon loss via these flux pathways in the short (months) or medium term (less than 3 years). Both ecosystem respiration and CH_4 emissions were found to be highly variable both within and between sites and could not be related well to the vegetation composition of the plots where fluxes were measured. There was a weak correlation between CH_4 fluxes and position of the water table and soil temperature, which is consistent with the literature, but no differences were found in soil temperature, soil moisture and position of the water table between the burned and unburned plots.

As the field study did not find any significant differences between burned and unburned plots at any time, no short-term increase in methane emissions from the burned plots was detected, as had been hypothesised. A mechanism that was proposed for a potential short term increase in methane emissions from blanket bogs after burning was a reduction in methanotrophy in the *Sphagnum* layer, caused by high temperatures at the moss surface being lethal to methanotrophic bacteria. In the laboratory experiment the only species of *Sphagnum* in which methanotrophy was detected was *Sphagnum papillosum* Lindb., but no significant differences in CH_4 oxidation rates of burned and unburned samples was detected. However, despite testing various species from different micro-habitats the lack of methanotrophy detected suggests that methanotrophic bacteria may not be as wide spread in *Sphagnum* as previously reported. This would have broader implications for our understanding of carbon cycling in blanket bogs, and it would be important to do more widespread sampling of sites and species to better determine if the impact of fire on methanotrophs has the potential to have any serious consequences for CH_4 release from blanket bogs.

In general the results indicate that low-severity fires, with the characteristics of those studied here, do not significantly increase carbon loss via CH_4 emissions and CO_2 emissions as a result of increased rates of ecosystem respiration. However, the results should not be viewed in isolation, instead considered alongside the known potential impacts of fire on the other carbon flux pathways not measured here.

Burning will directly increase carbon loss to the atmosphere through the combustion of biomass, although the carbon lost in this way will only be that which was sequestered by plants over relatively short timescales. More important therefore, in terms of long term carbon storage, is carbon loss through the combustion of the organic matter within the peat, formed over much longer timescales. There can be significant carbon losses when fire penetrates the peat (eg. Turetsky and Wieder, 2001, Mack *et al.*, 2011, Davies *et al.*, 2013), and fire can change the structure and functionality of a peatland in the long term (Maltby *et al.*, 1990). Significantly, this has been shown to be a mechanism for fire to turn peatlands from a net carbon sink to a net source (Turetsky *et al.*, 2011). As discussed fire may also have more subtle interactions with components of the carbon cycle, such as changing the methanotrophic community (Chen *et al.*, 2008) or increasing decomposition through the addition of nutrients in ash (Hogg *et al.*, 1992). Carbon loss in run-off waters, in the form of dissolved organic carbon (DOC), has also been shown to be higher after a fire (Clay *et al.*, 2009) and on blanket bog burned frequently as part of a management regime (Yallop and Clutterbuck, 2009, Clutterbuck and Yallop, 2010). As discussed in Chapter 5 frequent burning can also change vegetation composition, which could lead to lower carbon sequestration rates (Garnett *et al.*, 2000, Quin *et* *al.*, 2014). At the sites studied here there was lower shrub and graminoid cover on burned areas, although graminoid cover increased over the two and a half years studied, so it is likely that carbon assimilation was affected at least in the short term as a result of the fires. When considering all the potential impacts fire has been shown to have on carbon cycling, it is important to appreciate the limitations of the research and the results presented here. A major question, not directly answered by this research, but pertinent to prescribing best practice guidance for managed burning, is that of what are the most appropriate rotation times, the time period between burns.

The consequences of repeated burning for the carbon cycle and vegetation of a blanket bog will be the cumulative effect burning has on all carbon flux pathways, most of which are inherently linked in some way to vegetation. Evident here was that a single fire event brought about at least a short term change in vegetation composition. Plants all have different traits in relation to lifecycle, growth, rates of photosynthesis and decay with subsequent implications for carbon sequestration and retention (eg. Belyea and Malmer, 2004, Quin *et al.*, 2013, Quin *et al.*, 2014). A burning regime which favours one dominant vegetation type over another could therefore have important implications for the long term carbon assimilation of a blanket bog. In addition, different vegetation types have been associated with different rates of DOC export (Limpens *et al.*, 2008). Despite this however, there may be reason to mitigate against severe fires with frequent, managed, low severity fires to reduce fuel-load build up and the long-term risk of more severe fires. The frequency and extent of the direct loss of carbon to the atmosphere via biomass combustion, and in severe fires the combustion of the peat, must be taken into consideration when assessing the impact of different regimes on carbon budgets. In addition, all the potential impacts of burning will be related in some way to the pre-burn vegetation composition, plant survival, recovery and the viability of the existing seed banks, and the behaviour of the fires. Therefore, not only will the optimum burning rotation time, to reduce the likelihood of long term negative impacts on the carbon cycle and carbon storage potential of a blanket bog, inevitably be site specific, but it will have to strike a balance between these different potential impacts of burning. This complexity makes it a challenge to model and predict the total impact of different burning regimes, particularly when the vast majority of research has occurred on frequently burned *Calluna* dominated systems. To better understand the impact of different rotation times in different systems it is therefore essential to monitor the consequences of different burning regimes in different blanket bog vegetation communities as more refined, site specific, best practice guidelines are likely needed. However, a key recommendation that can be made from the results presented here, is that as low severity fires did not increase ecosystem respiration or CH_4 emissions from a blanket bog, it is important that burning does not take place in circumstances which may allow for more severe fires which consume more than just the canopy vegetation and penetrate the peat. This therefore makes it important that any best practice burning guidance and legislation strives to mitigate the risk of more severe fires, which could lead to significantly more short and long-term losses of carbon.

6.2 The Impacts of burning on *Sphagnum*

To better understand the impact of burning on the *Sphagnum* layer, how *Sphagnum* responded to fire and whether there is a critical temperature at which *Sphagnum* cannot recover was investigated. Lab based experiments and field monitoring were carried out on *Sphagnum capillifolium* (Ehrh.) Hedw., chosen as it is a species common to *Calluna* dominated blanket bog which can, in certain circumstances, be burned as part of a moorland management regime (Scottish Executive, 2011, Department for Environment Food and Rural Affairs, 2007).

The results of the laboratory experiment showed that the rate of recovery was related to the temperature and temperature residency times experienced at the *Sphagnum* surface. Samples exposed to 100^{o}C for 3 seconds had the quickest recovery, as indicated by photosynthetic capacity, while those which reached a surface temperature of 400^{o}C had slower rates of recovery and suffered more physiological damage the longer the surface was at 400^{o}C. The results also showed that significant factors determining the rate of recovery and total damage sustained were seasonality and pre burn stem moisture content. When samples were exposed to the temperature treatments prior to cold winter months, recovery was slower which, together with the very low rates of CO_2 exchange found in unburned samples, reflect a winter ‘dormancy’ period in *S.capillifolium*. Pre-burn conditions were also shown to be important, with samples dried prior to burning, suffering a greater extent of damage and decay. However, despite samples being artificially dried prior to being exposed to the most severe heat treatment, 400^{o}C for 30 seconds, designed to be lethal, plants still showed signs of recovery. Thus, no critical lethal temperature treatment was demonstrated. However, taken with observations of some areas of *S.capillifolium* at the field sites which showed no signs of recovery after comparatively low-severity fires, it suggests that even these types of fires can be lethal to *Sphagnum*. This may be because a combination of factors, beyond fire behaviour and temperatures not simulated in the laboratory experiments, are important. For instance, there was evidence here that stem moisture content was more variable in burned *S.capillifolium*, which may make it less able to tolerate desiccation. Trampling by grazing animals has also been shown to reverse recovery of *Sphagnum* after burning (Hamilton, 2000). Nutrient input via ash deposition (Niemeyer *et al.*, 2005, Mohamed *et al.*, 2007, Marcos *et al.*, 2009) may also have important consequences for *Sphagnum* survival. Nonetheless, the temperatures experienced at the *Sphagnum* surface were shown to be directly related to how *S.capillifolium* responded to the fires.

S.capillifolium, both at the three field sites and in the laboratory, was shown to produce new auxiliary growth if the capitulum was damaged and lost. This response was not identified in any lab samples which were exposed to the least severe 100°C treatment in the laboratory experiment, where the capitulum remained intact and recovered its photosynthetic capacity. This also suggests that the plants monitored in the field had experienced temperature conditions exceeding those of the least severe 100°C treatment simulated in the lab. This shows that even in low-severity fires temperature conditions experienced at the *Sphagnum* surface in excess of this are common. When new auxiliary stems were produced the location at which they grew from the original stem related to the depth of decay from the capitulum down the stem. The depth of decay was related to the severity of the temperature treatment with the most severe treatment, when stems were artificially dried, showing the greatest depth of decay.

The depth of decay may be particularly critical for the ability of stems to produce new auxiliary growth when the capitulum is lost. As *Sphagnum* grows from the top of the stem while simultaneously decaying from the bottom, should physiologically damaging temperatures penetrate down to the naturally decaying lower sections, there may be not be the capacity for new growth from the original stem if they are too physiologically degraded. There are also wider implications for the deeper penetration of higher temperatures as it has been shown that, when present, more methanotrophic bacteria can reside in these lower, decaying sections (Basiliko *et al.*, 2004, Raghoebarsing *et al.*, 2005). Should temperatures exceed those that are survivable by methanotrophic bacteria then this could be expected to have implications on CH_4 emissions from a bog. However, as discussed previously, further investigation is needed as this was not confirmed by the experiments carried out here.

Temperatures between 100°C and 400°C at the ground/bryophyte surface have been shown to be common in *Calluna* dominated heath fires, but temperatures remaining at 400°C and above for up to 30 seconds are less common (Davies, 2005). Similar temperature ranges have been demonstrated in *Calluna* fires on blanket bog but with a greater proportion of temperatures at the lower end of those recorded (Hamilton, 2000). What is demonstrated here is that the temperatures and the temperature residency times at the ground/moss layer will be significant for *Sphagnum* and are among the critical factors in determining the ability for the plants to recover. Fuel load can be linked to the spatial variability in temperatures reached at the ground surface in fires although high fuel loads may not necessarily increase temperatures at the surface. This has been demonstrated in *Calluna* dominated heath fires, where fires with low to medium fuel loads could experience the same ground temperatures as high fuel load fires, associated with older stands of *Calluna* (Davies, 2005), suggesting that fuel structure is also important. The spatial variability in fuel load and structure within and between fires (eg. Hobbs and Gimingham, 1984, Davies, 2005, Davies *et al.*, 2009) makes it difficult to quickly and effectively predict the temperatures likely to be reached at the *Sphagnum* surface and thus their potential impact on the *Sphagnum* layer. Therefore, low *Sphagnum* moisture content, another critical factor in determining the impact on the *Sphagnum* demonstrated here, may be a more useful field indicator of when not to carry out managed burning on blanket bog if *Sphagnum* damage is to be limited.

Discussed thus far are the potential short term responses of one common species of *Sphagnum*, but the affect of frequent burning on the *Sphagnum* layer and the responses at a species level are also clearly important, particularly when considering management regimes. Different *Sphagnum* species have been shown to recover from fire at different rates (Barkman, 1992), which suggests that identifying the key determinants for rates of recovery is complex beyond just the fire characteristics, such as the temperatures experienced at the *Sphagnum* surface studied here. As demonstrated, stem moisture content is likely to be critical in determining the extent of physiological damage and, as stem moisture content can be related to morphology and growth habits, could make some species more tolerant to burning than others. Dense, hummock forming species such as *S.capillifolium*, grow in such a way to survive being further away from the water table, making them more desiccation tolerant and better capable of retaining water (eg. Clymo, 1973, Luken, 1985). Interestingly, the field and lab evidence for new auxiliary growth to replace lost capitula could mean that hummocks and lawns of *S.capillifolium* could become denser, in terms of capitula number, as often the original stem would grow a number of new auxiliary stems. However, these new auxiliary stems often appeared finer, and not as robust as the original, which may have impactions for desiccation tolerance and water retention in the long term. This would be an interesting avenue for further research as not only could the differences in morphology mean some species are more capable of surviving a fire, frequent burning may induce a change in morphology in the long term which could either improve or reduce fire tolerance. Another important factor which may be species specific is how tolerant a species is to the post burn conditions, primarily the loss of the canopy vegetation. How well a species recovers after burning is therefore related to a host of factors: pre burn conditions such as stem moisture content, fire behaviour such as ground surface temperatures, species morphology, and the post burn environmental conditions. This makes the potential implication of a fire on the *Sphagnum* difficult to predict. However, the results here would suggest that measures could be adopted to help limit damage, the most obvious being not burning when the *Sphagnum* layer is particularly dry.

Although not studied here, but especially important when considering management regimes and burning guidance, are burning frequency and rotation times. Burning every 10 years compared to 20 years has been shown to have different outcomes for the vegetation at the long term experimental burning site of Hard Hill in the North Pennines (Gray, 2006, Rawes and Hobbs, 1979, Lee *et al.*, 2013), and a greater abundance of *S.capillifolium* has been found in the more frequently burned plots (Lee *et al.*, 2013). There is however, beyond the Hard Hill experiment, little robust evidence of the effect of rotation times on *Sphagnum* and it is clearly still vital for best practice management to research this further.

Another relevant aspect of the results, which may have implications for how the severity of a fire can be assessed in the field, was the strong seasonal difference in the rate of recovery. Delayed recovery due to winter dormancy means that in the months after a fire the *Sphagnum* layer may seem more severely damaged because there is no new growth and production of replacement capitula. This suggests that October fires could seem to be more damaging than spring fires, purely due to the rate of recovery and evidence of new growth being delayed until the spring months. This makes using the damage caused to *Sphagnum* as an indicator of fire severity potentially difficult, as in addition the response of losing capitula was delayed after the time of burning. There is some evidence here however, that the loss of capitula may indicate the temperatures experienced, with extensive capitula loss and a greater depth of decay associated with higher surface temperatures and temperature residency times.

6.3 Conclusions and Implications for Management in the UK

What is demonstrated here is that to limit the detrimental effects of fire on greenhouse gas emissions and the *Sphagnum* layer of blanket bogs, burning should only take place in conditions which mitigate the risk of severe fires which burn more than just the canopy vegetation. Critical to this will be moisture content of the bryophyte layer, both to increase the chances of recovery in *Sphagnum* and to reduce the risk of fire penetrating the deep into the Sphagnum layer and into peat. Currently blanket bog in Scotland can be burned if heather constitutes more than 75% of the vegetation (Scottish Executive, 2011) and in certain circumstances with agreed management plans in England and Wales (Department for Environment Food and Rural Affairs, 2007, Environment Agency Wales, 2008). To further mitigate the risk of burning, when agreed and approved, on blanket bog where *Sphagnum* is an important component of the vegetation, further provision should be made to ensure conditions are conducive to low severity fires. This could include prescribing a basic pre-burn assessment of the wetness/dryness of the moss layer and imposing restrictions on burning in spells of prolonged dry weather. There will however be a fine balance in achieving a burn on a blanket bog in the wet conditions necessary for limiting damage, which may act to inherently reduce the occurrence of prescribed burning on blanket bogs.

However, there is need for further research, particularly when considering the effect of long term rotational burning on greenhouse gas emissions and vegetation, as well as further investigation of the species level response of *Sphagnum* to fire. In addition, this research supports the need to develop a system of categorising the ecological severity of a fire and their distribution and frequency at a national scale. This is particularly important if burning is to be incorporated into national statistics and frameworks for reporting green house gas emissions from land use and land use change. Fire is ultimately a highly variable treatment, with both short term and long term implications for vegetation and the carbon cycle of a blanket bog. Considering the impact of fire on blanket bogs as one defined outcome, for example by assigning it a standard emission factor, is therefore not appropriate and efforts have to be made to understand the mechanisms behind the variability in effects. Only by understanding the mechanisms which determine the severity of these effects, such as the temperatures sustained at the moss surface or extent of peat consumption, can we predict the outcome of fire on carbon cycling and vegetation and mitigate the risk of detrimental fires through management guidance and legislation.

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