A Burning Issue: Assessing the impact of alternative grouse moor managements on vegetation dynamics and carbon cycling on UK blanket bogs

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Environment

September 2016

Abstract

Blanket bogs are a globally rare habitat and store vast quantities of carbon in the form of peat. In the UK, blanket bogs are subject to a variety of anthropogenic activities which threaten their ability to maintain this carbon store long term. Release of this carbon is likely to exacerbate climate change. Burning peatlands to encourage *Calluna vulgaris* on grouse moors is thought to be detrimental to peat-forming vegetation, water quality and the peatland carbon balance but lacks robust evidence. This study aimed to assess the effects of different methods of *Calluna* management on the carbon balance, vegetation dynamics and water quality of blanket bogs.

A paired catchment manipulation was combined with plot-scale manipulations and replicated across three English blanket bogs managed as grouse moors to examine the effects of burning, mowing, no management and variations thereof on the carbon balance and vegetation changes.

Carbon balances indicated that unmanaged areas were a carbon sink whereas both burning and mowing caused carbon release. Taking the quantities of burnt plant biomass and tractor fuel into account, burnt areas were a stronger carbon source than mown areas. Mowing increased both height and cover of *Calluna* compared to burning, promoted growth of *Eriophorum vaginatum*, a peat-forming species, and had less bare ground. The nutritional content of *Calluna* increased under management, being slightly higher following burning than mowing.

A pot experiment was combined with radiocarbon analysis to explore whether *Calluna*-associated ericoid fungi break down recalcitrant matter in the peat. The radiocarbon dates strongly indicated that ericoid fungi decomposed recalcitrant ancient compounds within the peat, releasing these as gaseous and aquatic carbon.

Altering *Calluna* management practices by replacing burning with mowing, where feasible, could potentially bring benefits for the peatland carbon balance and water quality by increasing abundance of peat-forming species without negatively impacting upon grouse.

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To Sarah (Shayesy),
who should have
shared this journey
with me, and to Nan
and Grandad, whom
I know had hoped
they would get to
hold this thesis.

Acknowledgements

Funding for my research, studentship and fees was generously provided by Defra, Natural England and The Moorland Association. I am thankful to these organisations for giving me the opportunity to complete my studies. The radiocarbon analysis work was supported by the NERC Radiocarbon Facility NRCF010001 (allocation number 1841.1014).

I would like to thank my supervisor, Dr. Andreas Heinemeyer, for his advice, support and encouragement over the past four years. I would also like to thank all the members of my thesis advisory committee, Prof. Phil Ineson, Dr. Colin McClean, Dr. Astrid Hanlon and Dr. Tim Thom.

I am very grateful to all the enthusiastic people who have helped with fieldwork and labwork throughout this project. I am eternally indebted to Tom Sloan, who was always willing to drop everything at a moment's notice to, amongst other things, fix machines, assist with sample preparation or aid me in relocating 48 incredibly heavy plant pots from office to lab to greenhouse to courtyard and back to greenhouse! Mel Meredith-Williams, Harry Vallack, Scott Lambert, Anda Baumerte, Jose Vega Barbera, Lewis Paxton, Becky Berry, George Rowley, Stephen Harrison, Natalie Weldon and Rachel Pateman have all been on great assistance on the numerous field trips. The Environment Department technicians have always been incredibly helpful and I would particularly like to thank Rebecca Sutton and Debs Sharpe for allowing me to spread soil, water and heather across the lab many times over without ever appearing annoyed. A special thank you to Dr. Clare Rickerby for her moss identification skills.

I would like to thank all the gamekeepers and land owners of the three estates where the majority of this study was conducted, along with United Utilities and the Yorkshire Peat Partnership for allowing and securing land access. Without your support and goodwill, none of this would have been possible.

I am grateful to Jonathan Leake for supplying the ericoid fungus culture for use in the pot experiment, and to Irene Johnson, Thorunn Helgason and David Sherlock for their helpful advice on culturing fungi.

A big thank you to Dr. Mark Garnett of the NERC Radiocarbon Facility, without whom it is unlikely the radiocarbon analysis would have happened. I thank you for your advice in preparing the funding applications, for the loan of the molecular sieve sampling system, for prioritising the samples processing and for all your help with mass balance equations.

Within the university, there are many staff I am grateful to, even if they will insist they were just doing their job. To Colin Abbott, Alison Fenwick, Chris Lancaster, Paul Scott and the rest of the horticultural team, thank you for patiently explaining how best to culture plants, as well as the holiday watering. Mark Benton from Biology Mechanical Workshops has always been a huge help, carrying out all the requests I asked, however bizarre. He has also generously (and possibly, unadvisedly) lent me tools whenever he was unable to lend a hand at that moment.

I would also like to thank Olivier Missa for his stats lectures and James Hodgson for his statistical advice.

I am incredibly grateful to the whole of SEI-York for their support throughout the whole process and for adopting me as one of them from the beginning.

Thank you to YUSAC for helping to keep me sane and active by dragging me on trips and throwing me into the sea every so often. In particular, a massive thank you to Sarah Leith, Alex Harvey and Izzy Neligan for feeding me at regular intervals and making sure I was still functioning.

I would like to thank both of my parents for both the financial and mental support they have provided throughout my PhD, even if they didn’t necessarily understand what I was doing to start with. And thanks Mum for the proofreading and constant reminders that most sentences really do require verbs. Thanks also to my brother, Edmund, for those long Monday morning chats from China about everything and anything non-PhD related.

Finally, I would like to thank Luke for his unending support, advice, proofreading and hugs, both real and virtual. I am sure it has been as tiring for you some days as it has been for me. I hope I have used enough full stops to satisfy even you.

Author's declaration

I declare that the work presented in this thesis is my own, and is written by me, except where outlined below:

Access to the sites used in Chapters 2 and 3, and the site set up was secured and arranged by Dr. Andreas Heinemeyer, amongst others, as part of the Defra project BD5104. I was present for and undertook field measurements of all the gaseous fluxes detailed in Chapter 2 with the help of Dr. Andreas Heinemeyer, Dr. Harry Vallack, Tom Sloan, Dr. Mel Meredith-Williams, Scott Lambert, Anda Baumerte and numerous student volunteers. I collected and analysed only a few of the water samples detailed in Chapter 2, with the majority collected and analysed by Tom Sloan, Mel Meredith-Williams, Scott Lambert and Anda Baumerte. Dr. Andreas Heinemeyer upscaled some of the NEE flux measurements detailed in Chapter 2 and I upscaled the rest under his guidance. He also provided the stream flow rate data for all catchments. I carried out all the statistical analysis and upscaling of other carbon measures.

I designed and conducted the vegetation surveys detailed in Chapter 3 with the help of Dr. Andreas Heinemeyer and Dr. Clare Rickerby. I took the photographs of the vegetation with the help of Dr. Andreas Heinemeyer and reassessed for percentage cover myself. I cut the majority of the *Calluna* samples, with the remainder cut by Tom Sloan. I analysed the *Calluna* samples, both physically and statistically, and all the vegetation data.

I prepared all the components of the pot experiment detailed in Chapter 4 and assembled the experiment. I measured all the CO_2 fluxes from the pots and collected and analysed all the DOC samples. I collected the samples for radiocarbon dating and these samples were analysed by the NERC Radiocarbon Facility. This work was supported by the NERC Radiocarbon Facility NRCF010001 (allocation number 1841.1014). I performed the mass balance with the radiocarbon data. Mass balance interpretation was aided by Dr. Mark Garnett.

The maps in Chapters 2 and 3 were created by Steve Cinderby under my guidance. Erik Willis made the species labels on the redundancy analysis graph in Chapter 3 readable.

I declare that this work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as References.

1 General Introduction

1.1 *Sphagnum* moss: The foundation 'stone' of peat

Peatlands occur on all continents across the world (Joosten & Clarke, 2002), globally covering about 4 million km^2 in total, which equates to approximately 3% of global land area (Rydin & Jeglum, 2006). Peatlands are commonly considered to be areas consisting of peat deposits more than 30 cm deep, where peat is defined as a soil containing over 30% organic matter (Joosten & Clarke, 2002). The vast majority of peatlands (80%) are found in the northern hemisphere, with substantial peat deposits also found in the tropics (Joosten & Clarke, 2002; Limpens *et al.*, 2008). Boreal and sub-arctic peatlands are estimated to store 270-547 Pg (1 Pg = 10^{15} g) of carbon (C), which represents over one third of the world's total soil C store (Gorham, 1991; Turunen *et al.*, 2002; Yu *et al.*, 2010). By comparison, tropical peatlands contain 82-92 Pg C (Page *et al.*, 2011), the global vegetation C stock is 550 Pg C and the atmosphere contains about 780 Pg C (Houghton, 2007), thus making northern peatlands one of the most important global stores of terrestrial C.

Peat is formed from dead vegetation which has not fully decomposed due to a constantly high (i.e. near surface) water table depth (WTD) creating anoxic conditions (Joosten & Clarke, 2002). Not all vegetation is 'peat forming' and not all peat is formed of the same vegetation. In the tropics, peat largely consists of tree remains (Page *et al.*, 2011) whereas New Zealand peat is predominantly formed from plants in the *Restionaceae* family (Rydin & Jeglum, 2006). Northern hemisphere peats are usually composed of *Sphagnum* mosses (Gorham, 1991), although *Saxifraga* species , reeds and sedges tend to be the main peat formers around springs (Gorham, 1991; Lindsay, 2010).

Peatlands are a specific type of wetland, with mires being peatlands which actively form peat (Joosten & Clarke, 2002). Mires are classified into two broad groups based on hydrology: ombrotrophic mires, or bogs, which are solely fed by precipitation and thus hydrologically detached from any groundwater sources; and minerotrophic mires, or fens, which are also fed by water which has been in contact with the mineral bedrock and can thus bring in nutrients from external sources (Lindsay, 2010). Bogs are further split into raised bogs, constituting domed mounds of peat which are raised above the general land surface and tend to be found in lowland areas (Brooks & Stoneman, 1997), and blanket bogs, comprising extensive areas of peat which cover the underlying bedrock, often following the contours of the mineral ground (Lindsay, 2010).

Blanket bogs are found across the world (Gallego-Sala & Prentice, 2013), predominantly in upland areas as cool temperatures and high precipitation are required for their formation (Lindsay, 2010). This cool damp climate creates low evaporation rates (Lindsay *et al.*, 1988), typically giving rise to the formation of an ironpan by podzolisation of the original soils, leading to waterlogging (Brooks & Stoneman, 1997). Most *Sphagnum* species prefer wet conditions therefore, when present in the area, they are likely to colonise. All bryophytes, including *Sphagnum* mosses, grow from the tip as the base dies (Glime, 2007), which allows layers of dead vegetation to build up (Clymo, 1992). Due to the low hydraulic conductivity of semi-decomposed *Sphagnum* (Ingram, 1982), the water level remains at or close to the surface, reducing the rate of oxygen infiltration to the point where it is used more rapidly than it is replaced, thereby creating anaerobic conditions and greatly slowing the rate of decomposition (Clymo & Hayward, 1982).

Additionally, the large empty hyaline cells in *Sphagnum* leaves store water even after they have died (Lindsay, 2010), further aiding maintenance of a high WTD. In living plants, the hyaline cells enable the *Sphagnum* to cope with the wet conditions by providing a large surface area for cation exchange, the process through which *Sphagnum* exchanges hydrogen ions for nutrients (e.g. Ca, K) dissolved in the water (Clymo, 1963; Daniels & Eddy, 1990). This release of hydrogen ions acidifies the water surrounding the plants (Clymo, 1963) which, combined with the antibacterial properties of sphagnan (Børsheim *et al.*, 2001), a chemical which *Sphagnum* produces, further retards decomposition.

Despite the anoxic conditions, decomposition still occurs, albeit at a much reduced rate to that above the water table. This effectively creates two distinct layers within the peat, the acrotelm and the catotelm (Ivanov, 1981), with the boundary between the two usually defined as the lowest depth to which the water table falls except during drought conditions (e.g. Clymo, 1992; Evans *et al.*, 1999). The acrotelm, the layer above the WTD boundary, tends to be at least 10-20 cm deep and consists mainly of dead moss, intermingled with the roots of vascular plants, topped by the living *Sphagnum* layer (Ivanov, 1981). Beneath, the catotelm constitutes the bulk of the peat, made mainly of partially decomposed plant fragments (Ivanov, 1981), with a less ordered structure which is compressed slightly by the weight of the upper layers (Clymo, 1992). In the acrotelm, aerobic microbes are present and thus decomposition in this layer is much more rapid than that beneath (Ingram, 1982). However, a small amount of the acrotelm matter is passed to the catotelm, as the collapse and settling of the vegetation structure slows water movement, causing the water table boundary between the layers to rise at approximately the same rate as the surface extends upwards (Clymo, 1992). Once within the catotelm, decomposition slows and the process is predominantly driven by *Archaea* which can cope with the anoxic conditions (Lindsay, 2010). The growth rate of a bog is therefore equal to the quantity of material reaching the catotelm (minus the small amount of decomposition products produced below the water table) which tends to be between 0.1 and 1 mm y^{-1} (Tallis, 1995; Yu *et al.*, 2001; Heinemeyer *et al.*, 2010). Estimates of the apparent long-term peat accumulation derived from peat depth and age measurements, indicate that this equates to 14-26 g C m^{-2} y^{-1} (Gorham, 1991; Turunen *et al.*, 1999, 2002; Roulet *et al.*, 2007).

The anaerobic conditions in the catotelm result in methane (CH_4) being the main product of decomposition. Much of the CH_4 produced within the peat does not reach the surface but is stored in micro-bubbles in the catotelm and consumed by methanotrophs for energy (Brown, 1995). Additionally, much of the CH_4 travelling to the surface is consumed and oxidised to CO_2 as it passes through the oxygenated layers of the acrotelm (Calhoun & King, 1997). Some CH_4 does reach the surface, mainly by ebullition (bubbles of gas expelled to the atmosphere) or by transport through aerenchyma, which are hollow tubes found within the sedge stems, thus meaning the CH_4 bypasses the aerobic zone (Ström *et al.*, 2003).

Globally, wetlands are estimated to release between 38 and 157 Tg CH_4 y^{-1}, making them the largest natural source of CH_4 (Petrescu *et al.*, 2010). As CH_4 is a greenhouse gas 28 times as potent as CO_2 over a 100-year timespan (Myhre *et al.*, 2013), peatlands appear a substantial contributor to global climate change. However, because peatlands accumulate C over time due to the waterlogged conditions preventing decomposition, they are a net sink of C (Bain *et al.*, 2011) and have exerted a net cooling effect on global temperatures (Frolking *et al.*, 2011).

1.2 Digging deeper into British bogs

In the UK, peatland formation is thought to have begun approximately 8,000-10,000 years ago at the end of the last ice age, due to changing climatic conditions (Charman, 2002) and forest loss (Moore, 1973) leading to wetter soil conditions. About 7% of the UK's land surface is covered by peatlands (Rydin & Jeglum, 2006). The majority of these peatlands are blanket bogs (Bain *et al.*, 2011), meaning that approximately 13% of the world's blanket bog area is found within the UK (Ratcliffe & Thompson, 1988).

Peat depth of British bogs can range from 0.3 m (the minimum depth required for the area to be classed as a peatland) to over 10 m in some raised bogs, although depths rarely exceed 6 m in blanket mires (Lindsay, 1995) and depth measurements are sometimes truncated at 1 m (e.g. Garnett *et al.*, 2001). The bulk density (the weight per unit volume of dry material) of UK peat is often accepted to be 0.03 g cm^{-3} for the acrotelm peat and 0.12 g cm^{-3} for the catotelm peat (Clymo, 1992), although there are relatively few bulk density measurements (Lindsay, 2010). Nonetheless, current best estimates indicate that UK peatlands store at least 3.2 Pg C, which is equivalent to 20 times the C stored in UK forests (Bain *et al.*, 2011).

As well as playing a role in regulating global climate by storing C, British peatlands also provide a range of ecosystem services, including flood regulation, water filtration, biodiversity and cultural benefits (Millennium Ecosystem Assessment, 2005). There is a temporal mismatch between the precipitation input and the water release because the *Sphagnum* creates a rough surface, slowing overland water flow and allowing infiltration (Holden *et al.*, 2008). Due to the low hydraulic conductivity within the peat (Ingram, 1982), movement of water is slow meaning that water release occurs gradually, helping to prevent flooding after heavy rain events (Holden *et al.*, 2007a). Released water has a low pH because of the *Sphagnum* exchanging hydrogen ions for nutrients (Clymo, 1963; Daniels & Eddy, 1990), thus reducing bacteria (Børsheim *et al.*, 2001). This slow water movement also filters out particles making water cheap to purify (Bain *et al.*, 2011).

Blanket bogs support unique assemblages of plants (Thompson *et al.*, 1995) and, in turn, these provide nesting habitats for many rare bird species, such as golden plovers, dunlin and peregrine falcons (Holden *et al.*, 2007a; Carroll *et al.*, 2011). As the surface of most bogs is undulating and many of the plant species require different sets of hydrological conditions, each area of a bog will have a different assemblage of species, although *Sphagnum* species occur throughout all but the very driest parts (Lindsay *et al.*, 1988). In very wet areas and shallow pools, *S. cuspidatum* usually dominates (Hill *et al.*, 2007), often dotted with common cotton-grass (*Eriophorum angustifolium*), other sedges, bogbean (*Menyanthes trifoliata*) and sundews (Lindsay, 2010). Where the water table dips just beneath the surface, other *Sphagnum* species appear, such as *S. fallax*, *S. palustre* and *S. papillosum* (Hill *et al.*, 2007; O'Reilly, 2008), along with a few vascular plants, such as *Erica tetralix* (Lindsay, 2010). Areas with deeper WTDs support hummock-forming *Sphagnum* species, such as *S. fuscum* and *S. capillifolium* (Hill *et al.*, 2007), along with other mosses, such as *Racomitrium languinosum*, and more vascular plants including heather (*Calluna vulgaris*), hares-tail cotton-grass (*E. vaginatum*) and berry species, such as cranberry (*Vaccinium oxycoccus*), bilberry (*V. myrtillus*) and crowberry (*Empetrum nigrum*) (Lindsay, 2010).

Hummock-forming *Sphagnum* species tend to grow more slowly than those in pools but they are also the main peat forming species as they tend to decompose more slowly (Belyea & Malmer, 2004). This is because the hummock species have a more stable cell water content, are less prone to drying out and therefore the hummock can maintain a moist sub-surface in all but the driest conditions, enabling continuation of growth and limiting amounts of aerobic decomposition (Lindsay, 2010). It is this feature which enabled bogs to continue growing at a relatively constant rate through the various changes in climate which have occurred over the last 10,000 years, whereby the assemblage of *Sphagnum* species changed with the climate (Belyea & Malmer, 2004).

However, despite the resilience of *Sphagnum* to previous changes in climate, there are concerns that anthropogenic climate change may negatively affect peatlands (e.g. Gorham, 1991). Clymo *et al.* (1998) demonstrated that a mean annual temperature of 5-10°C, combined with wet conditions is most conducive to peat accumulation. This is because, although colder and wetter conditions retard photosynthesis, they also suppress decomposition of organic material. Warmer and drier conditions result in greater plant production but also cause a drop in water table depth, hence increasing aerobic decay of organic matter (Clymo, 1987; Clymo & Pearce, 1995). The UK is on the southern edge of the climatic envelope for northern hemisphere peat formation (Wieder & Vitt, 2006), having a milder and wetter climate than much of continental Europe. Therefore, there is concern that UK peatlands will be more vulnerable to climate change than other northern hemisphere peatlands, which could result in a reduction or possibly even reversal of peat accumulation (Gorham, 1991). This is particularly pertinent given that the climate change predications for the UK indicate a decrease in summer precipitation and an increase in summer temperatures (Murphy *et al.*, 2009), which is likely to increase evaporation rates, leading to a drop in WTDs.

In theory, given the mechanisms *Sphagnum* mosses employ to maintain constantly damp conditions, climate change could merely result in a shift in the dominant *Sphagnum* species, thus enabling mires to continue accumulating peat. However, the assumption would be that all British blanket bogs are hydrologically stable, peat-forming mires: this is not the case. The IUCN Peatland Programme estimate that over 80% of all UK bogs are in a damaged state (Bain *et al.*, 2011). This figure is even lower for England, with Natural England (2010) estimating that only 1% of English deep peats are undamaged.

1.3 A potted and rather dry recent history of bogs

There are a variety of reasons for this degradation, many with a long history, and include drainage, fertilisation, afforestation, peat excavation for fuel and horticulture, atmospheric pollution, overgrazing and rotational burning (Holden *et al.*, 2007a; Natural England, 2010; Evans *et al.*, 2014). Although this list covers a broad range of activities, all items hold at least two things in common. Firstly, all are, at least in part, carried out by humans (Evans *et al.*, 2014). Secondly, all result in a lower WTD, leading to an increase in decomposition of organic matter from higher rates of oxygenation, detrimentally affecting and sometimes even reversing peat accumulation (e.g. Frolking *et al.*, 2011). Additionally, a combination of the activity itself and a lower WTD has resulted in the loss of much of the surface layer of *Sphagnum* mosses and other peat forming species (Natural England, 2010). In some cases, this has resulted in the loss of the entire acrotelm, exposing catotelm peat to aerobic decomposition and creating a 'haplotelmic' peatland (Ingram & Bragg, 1984).

Although many peatlands may have their origins in woodland clearance and deliberate burning to create pastures and enable crop cultivation (Simmons, 2003), peatlands tend to have a low nutrient content due to the high WTD preventing decomposition and nutrient cycling (Clymo, 1992). Therefore, to counter this, many bogs have had shallow drainage ditches or 'grips' dug across them to speed up water movement, preventing waterlogging (Holden *et al.*, 2004). Gripping occurred on the largest scale in the mid-20th century due to agricultural intensification, and was often combined with liming and fertiliser application to improve grassland for livestock (Natural England, 2010). Digging of drainage ditches for commercial forestry planting also increased at a similar time (Condliffe, 2009). Many lowland peatlands, especially fens, also had water pumped out to improve drainage. One such fen, Holme Fen, has a fixed iron post inserted through the bedrock - since its insertion in 1848 when the peat was 6.7 m deep, it had lost over 3.5 m by 1978 (Hutchinson, 1980), thus illustrating the impact of drainage upon peat. Approximately 21% of blanket bogs in England are gripped, with 24% of deep peat under cultivation, although these areas overlap (Natural England, 2010). There is extensive evidence that drainage by humans can substantially lower the water table depth (see Holden *et al.* (2004) for a review), increasing oxygen ingress and hence decomposition.

Peat cutting for use as a fuel has been prevalent across much of the UK for centuries (Smart *et al.*, 1986), with Somerset peat being cut since Roman times (Somerset County Council, 2009). Before commercialisation, the peat was cut by hand into blocks and stacked to dry before being burnt in homes, as fuel for both cooking and heating (Smart *et al.*, 1986). It is estimated that 11% of all UK blanket bogs have been affected by past peat cutting (Bain *et al.*, 2011) and commercial peat extraction still continues in some areas (Smart *et al.*, 1986), especially in Ireland, with large quantities milled, dried and removed each year – just one of the Irish-based companies, Bord na Móna, produces 4 Tg milled peat per year for fuel use alone (Bord na Móna). Peat is also extracted for horticultural purposes (Evans *et al.*, 2014) due to its high water holding capacity. Removal of both the surface layer, which is necessary to extract the peat, and the peat itself can have profound effects on the peatland hydrology (Smart *et al.*, 1986). Additionally, combustion of the peat releases much of the stored C to the atmosphere as CO_2 and peat used in horticulture dries out and eventually decomposes to CO_2 as well (Lindsay, 2010).

Many atmospheric pollutants have been generated since the Industrial Revolution, largely through combustion of fossil fuels, including sulphur dioxide (SO_2), nitrous oxides, ammonia and ozone (Holden *et al.*, 2007a). Despite *Sphagnum* species not only tolerating acid environs but also acidifying the water surrounding them (Clymo, 1963), surface acidification through the deposition of SO_2 can damage *Sphagnum*, to the point where it has been virtually eliminated in the southern Pennines (Ferguson & Lee, 1983). This leads to areas of bare peat which are then subject to drying and erosion (Evans *et al.*, 2006), with haggs and gullies forming, further drying peat. Natural England (2010) estimates that at least 14% of blanket bogs are hagged and gullied. Overgrazing can compound the problems caused by SO_2 pollution by animals trampling vegetation, which can kill *Sphagnum* and cause compaction of the peat surface, altering water flow and leading water runoff and further erosion (Holden *et al.*, 2007a).

Erosion not only presents the immediate problem of C loss from the catchment but also provides an unstable surface for revegetation, especially on slopes (Holden *et al.*, 2007b). Additionally, erosion can greatly increase levels of particulate organic C (POC) in stream water (Evans *et al.*, 2006), which can decompose to dissolved organic C (DOC) downstream (Worrall & Moody, 2014). Higher concentrations of DOC make the water harder to treat and can react with compounds used in the chlorination process used to disinfect drinking water, resulting in the formation of carcinogenic disinfection by-products, such as trihalomethanes and haloacetic acids (Singer, 1999; Clay *et al.*, 2012).

Whilst many of the aforementioned issues have greatly affected peatlands and peat formation in the UK, there is growing recognition that peatlands are of great value, both economically and culturally (Millennium Ecosystem Assessment, 2005; Evans *et al.*, 2014). Grips have been blocked across many peatlands, with over €250 million spent on peatland drain blocking since the late 1980s (Armstrong *et al.*, 2009). There has been a great reduction in SO_2 deposition, with deposition more than halving in the last 15 years of the previous century, largely caused by a reduction in emissions (Fowler *et al.*, 2005). Whilst peat cutting is still prevalent for fuel purposes in some areas (Smart *et al.*, 1986), there have been calls from the government to phase out the use of peat for horticultural purposes (HM Government, 2011). Combined with these measures, there is also a concerted effort being made by organisations such as The Moorland Association and Moors for the Future to revegetate large areas of peatland which are actively eroding. There is however one other major activity affecting blanket bogs which has received less remedial attention than many of the others: rotational burning.

1.4 Peatlands under fire!

It is estimated that 30% of English blanket bogs are subject to rotational burning (Natural England, 2010). Burning has been used periodically by humans on upland vegetation to clear areas or stimulate new growth to improve sheep grazing since Neolithic times (Fyfe *et al.*, 2003; Simmons, 2003) and has been common practice in some areas since at least Mediaeval times (Rackham, 1986; Worrall *et al.*, 2011). There has been an intensification in burning over the past 100-200 years, but more recently, analysis of aerial imagery has revealed that the area of new burns in the uplands almost doubled between the 1970s and 2000 (Yallop *et al.*, 2006). Although wildfires are a natural phenomenon on peatlands, the prescribed burning currently used on many blanket bogs occurs much more frequently (Allen *et al.*, 2013), usually on an 8-25 year rotation (Clay *et al.*, 2015). Thus, although *Sphagnum* mosses are capable of recovery following infrequent burning (i.e. wildfires), regular exposure to fire causes damage and drying (Holden *et al.*, 2007a), which can increase fire intensity (Turetsky *et al.*, 2011).

Burning is predominantly used to manage grouse moors, although this usually coincides with improved sheep grazing and there are areas burnt solely for sheep (Holden *et al.*, 2007a). Depending on the intention, the length of the burn rotation can be used to encourage different species. In areas which already have high cover of *Molinia caerulea*, a moorland grass, burning can increase this cover, providing grazing for sheep (Grant *et al.*, 1963). On *Calluna-Eriophorum* bog, both Hobbs (1984) and Lee *et al.* (2013) found that a short (10 year) burning rotation favoured *Eriophorum vaginatum* whilst longer rotations of 20 years or more led to *Calluna* dominance.

Burning is usually carried out over many small areas at a time, which helps to keep fires under control. The aim is produce a quick-moving cool burn (Defra, 2007), which should usually be aided by a steady breeze (of about 8-12 mph or Force 3) blowing downhill and be burnt uphill into the wind on slopes (Defra, 2007; The Scottish Government, 2011), to remove old woody growth and litter, leaving the root stock and ground cover of bryophytes largely untouched. However, these ideal conditions rarely occur, necessitating burning on stiller days, which can produce slower-moving hotter burns killing most or all of the plants (including bryophytes) present, or windier days, which can cause fires to burn out of control. In exceptional circumstances, fires can burn for weeks, consuming large quantities of peat, with vegetation taking years to recover (Radley, 1965; Davies *et al.*, 2013).

As well as the weather conditions, the standing biomass of the vegetation and the soil conditions can influence the speed and temperature with which a fire burns (Allen *et al.*, 2013). In areas with a high proportion of old *Calluna*, fires tend to burn more intensely as there is a high wood content meaning damage to the underlying peat is therefore more likely (Albertson *et al.*, 2010). The opposite can happen if the peat is very wet or frozen – the fire will be unable to burn for very long and the water or ice are likely to protect the bryophyte layer, and hence the peat, from the heat (Rowell, 1988).

The idea of regularly burning small areas rotationally for the management of red grouse (*Lagopus lagopus scoticus* (Latham)) appears to have primarily been endorsed and encouraged by Lovat (1911). Before, old *Calluna* seems to have been burnt on a less structured basis, with burning for grouse occurring since the 1840s in Scotland and the early 1800s in England (Holden *et al.*, 2007a). The main aim of burning is to provide new shoots of *Calluna* because this constitutes much of the diet of the adult red grouse (Grant *et al.*, 2012). After the age of about 20-30 years, *Calluna* stems lignify, turn woody and their growth slows (Gimingham, 1975). Burning removes much of this old growth and leaf litter as well as encouraging heather seed germination and regeneration from mature heather root stock (Liepert *et al.*, 1993).

However, whilst burning to encourage regeneration may be necessary on dry ground, *Calluna* growing on deep wet peat can regenerate naturally by layering (i.e. adventitious rooting) of stems (MacDonald *et al.*, 1995), which brings the necessity of burning for regeneration on blanket bogs into question. In fact, government guidelines (the Heather and Grass Burning Code in England and Wales and The Muirburn Code in Scotland) recommend against burning on areas where peat is deeper than 50 cm (Defra, 2007; The Scottish Government, 2011). However, there are also exceptions - Defra (2007) allow burning on deep peat in England and Wales under special pre-agreed circumstances, whilst The Scottish Government (2011) allow burning on blanket bogs in Scotland where *Calluna* makes up more than 75% of the vegetation. Given that many of these blanket bogs have been burnt for well over 100 years, *Calluna* often dominates, therefore giving the appearance on the surface of not being blanket bog. Additionally, these guidelines are not legally binding. The only parts of either code which have legal implications are the dates of burning which encompass the period between 1st October to 15th April in upland areas (Defra, 2007; The Scottish Government, 2011).

These burn dates are usually adhered to as they coincide with the breeding and shooting seasons. Birds begin nesting from mid-April and so burning after this would risk scorching eggs or killing chicks who cannot fly for at least the first few weeks after hatching (Savory, 1977). The shooting season begins on 12th August and so burning during this period could disperse the grouse and jeopardise shoots (Lovat, 1911). As the grouse shooting is worth approximately £10 million per year to the British economy and employs about 2500 people (Thirgood *et al.*, 2000), yet many moors in England run at the margins of their financial limits (Dougill *et al.*, 2006), great efforts are made to protect grouse through breeding and shooting.

Whilst *Calluna* is found in many parts of oceanic Europe, about 75% of the world's *Calluna*-dominated moorland occurs in Britain (Tallis *et al.*, 1998) and this habitat is thus considered of international importance (Thompson *et al.*, 1995; Thirgood *et al.*, 2000). As well as the financial returns of shooting to the economy, many people value *Calluna* moorland for its aesthetics, particularly when it is in bloom in August, and thus tourism further benefits the rural economy (Fischer & Marshall, 2010).

However, there is evidence that burning can also disrupt the C accumulation of blanket bogs. The loss of the 'active' peat-forming *Sphagnum* layer, which can occur if bogs are burnt under non-ideal conditions (Holden *et al.*, 2007a), causes a drop in WTD and aeration of the peat. Additionally, *Calluna* itself further dries the peat due to its high transpiration rate, thus lowering the WTD and aiding the decline in peat-forming *Sphagnum* (Worrall *et al.*, 2007). This decline towards a haplotelmic state (Ingram & Bragg, 1984) enables aerobic microbes to break down the peat faster. Combined with a decline in sphagnan and hydrogen ions in the peat from the loss of *Sphagnum*, this can cause blanket bogs to change from a net C sink to a net C source, having implications for climate change (Davidson & Janssens, 2006).

The net ecosystem C balance (NECB) is the net rate of C accumulation or loss from an ecosystem, with negative values indicating C gain and positive values C loss (Chapin *et al.*, 2006). Measurements of the NECB are relatively rare but appear similar on unburnt peatlands in Canada (-22 g C m^{-2} y^{-1}; Roulet *et al.*, 2007) and Sweden (-24 g C m^{-2} y^{-1}; Nilsson *et al.*, 2008). In the UK, the NECB can be more variable, with measurements showing both higher (-56 g C m^{-2} y^{-1} and -72.4 g C m^{-2} y^{-1}; Worrall *et al.*, 2009 and Dinsmore *et al.*, 2010, respectively) and lower (+8.3 g C m^{-2} y^{-1}; Billett *et al.*, 2004) NECBs than the long-term estimates, although a longer term study (>10 years) gave similar values to the Canadian and Swedish NECBs (-28 g C m^{-2} y^{-1}; Helfter *et al.*, 2015).

In comparison, studies which have specifically investigated the NECB on rotationally burnt blanket bogs in the UK have all demonstrated a net loss of C. Ward *et al.* (2007) showed burnt areas lost an average of 25.5 g C m^{-2} y^{-1} at Moor House National Nature Reserve, whilst Clay *et al.* (2010) showed losses of 117.8 g C m^{-2} y^{-1} at the same site. Clay *et al.* (2015) demonstrated a range of losses of between 4 g C m^{-2} y^{-1} and 269 g C m^{-2} y^{-1} for areas of different burn ages in northern England. Even when the longer term NECB was considered using depth of a layer of spheroidal carbonaceous particles as a marker in the peat and quantifying the C store above this, areas on a 10 year burn cycle had an average reduced sequestration rate of 73 g C m^{-2} y^{-1} after three burn cycles compared to the unburnt areas on the same site (Garnett *et al.*, 2000).

1.5 Muddying the waters

This represents a substantial loss of C when considered across the whole of the UK. As *Sphagnum* is still being lost in many areas, whether through burn damage, drainage or from some other causes, the rate of C loss may increase. One component of the C budget for which there is evidence of a long term increase is DOC. Since at least 1962, the colour of water from peat covered catchments has been increasing due to higher DOC concentrations in the stream water (Worrall *et al.*, 2003a). This has not been a trend restricted to the UK however: water colour and DOC concentrations have increased across the northern hemisphere since at least 1990 (Stoddard *et al.*, 2003; Skjelkvåle *et al.*, 2005; Monteith *et al.*, 2007).

About 70% of the UK's drinking water comes from surface waters, much of which originate from peat-covered upland areas (Bain *et al.*, 2011). The higher levels of DOC and browner water therefore pose a problem for the water companies, who must abide by regulations to provide water without colour that is safe for human consumption (Defra, 2016). The problem is further complicated by the fact that DOC is a complex mixture of both coloured and non-coloured substances. The coloured substances are humic, hydrophilic, amorphous and acidic compounds of high molecular weight (Thurman, 1985; Wallage *et al.*, 2006a) and are divided into humic acids and fulvic acids. The humic acids are darker coloured (dark brown to black) than the fulvic acids (pale brown to yellow) and have a higher molecular weight (Thurman, 1985). The non-coloured substances consist mainly of simple compounds such as carbohydrates, fats, proteins and waxes, which are easily broken down by microorganisms so have a shorter residency time than the humic substances (Schnitzer & Khan, 1972; Thurman, 1985).

DOC is removed from water in treatment plants by adding an amount of coagulant which varies with the quantity and colour of the DOC in the water (Clay *et al.*, 2012). However, whilst this removes the darker and heavier humic acids fairly easily, it is harder to remove the fulvic acids and non-coloured substances (Worrall & Burt, 2009). If these substances remain in the water when chlorine is added to disinfect it, they can form trihalomethanes and haloacetic acids (Singer, 1999; Clay *et al.*, 2012), many of which are considered to be carcinogenic. Therefore, there is great need to reduce DOC production at its source in order to improve water quality, thus reducing treatment costs and the risk of creating unsafe drinking water.

However, reduction of DOC concentrations in peatland stream waters presents a great challenge, not least because the reasons for its increase are still unclear. Explanations for this long term DOC increase include more severe and prolonged droughts (Worrall & Burt, 2004), increasing temperatures due to climate change (Freeman *et al.*, 2001a; Worrall *et al.*, 2004), land management such as drainage (Worrall *et al.*, 2003a) and recovery from acidification (Evans *et al.*, 2005) as a result of a reduction in nitrate and sulphate deposition (Stoddard *et al.*, 2003; Monteith *et al.*, 2007; Dawson *et al.*, 2009). Whilst many of these factors are widespread and have been shown to correlate significantly with the DOC trend in the catchments or streams studied, there is still much uncertainty associated with the causes of DOC increase, because not all catchments show increased DOC, with some even exhibiting a decrease in DOC concentrations (Skjelkvåle *et al.*, 2001; Worrall *et al.*, 2003a). Monteith *et al.* (2007) demonstrated that DOC concentrations in rivers and lakes across Europe and North America increased proportionally to the rates at which sulphate deposition declined, indicating that DOC concentrations are returning to pre-industrial, pre-acidification levels. Experimental evidence from field manipulations in the UK supported this relationship (Evans *et al.*, 2012), suggesting that this is the main reason for DOC concentration increases.

As burning peatlands is not widespread across the whole northern hemisphere, with the majority of intense rotational burning occurring in Britain, it is therefore unlikely to be a major cause of increasing DOC concentrations. There are suggestions, however, that burning can lead to browner water, although there is debate as to whether it directly increases DOC and POC production (Holden *et al.*, 2012). Yallop & Clutterbuck (2009) observed a correlation between bare peat caused by burning and higher DOC concentrations, whilst Clutterbuck & Yallop (2010) linked changes measured in humic coloured DOC over four decades to the increase in moorland burning within the catchments of the water bodies studied, after accounting for changes in sulphate deposition. Conversely, Clay *et al.* (2012) found that, although burning caused elevated water colour in the first few years after burning, this did not affect DOC concentrations, whilst Clay *et al.* (2009) found no difference in water colour or DOC concentrations between burnt and unburnt areas.

A possible mechanism as to why burning does not produce consistent effects in DOC production could be due to different burn rotation lengths producing different species compositions (Hobbs, 1984; Lee *et al.*, 2013). It has also been shown that different plant functional types can influence DOC production in both soil and drain waters, with areas dominated by *Calluna* having higher DOC concentrations than areas of predominantly sedge or *Sphagnum* cover (Armstrong *et al.*, 2012). There are also suggestions that this is linked to the release of labile C compounds from vascular plants into the soil (Bragazza *et al.*, 2013), 'priming' microbial decomposition of soil C (Fontaine *et al.*, 2007; Hartley *et al.*, 2012; Lindén *et al.*, 2013; Wild *et al.*, 2016). Specifically, burning results in an increase in C uptake in the plants by photosynthesis which leads to greater transfer of this recently fixed C below ground (Ward *et al.*, 2012). Warming increases respiration of old soil C from areas dominated by *Calluna*, indicating that the *Calluna* does prime microbial decomposition (Walker *et al.*, 2016). It has been suggested that ericoid fungi, which form mycorrhizal associations with *Calluna* roots, could be responsible for much of this decomposition (Walker *et al.*, 2016), due to them possessing saprotrophic abilities (Haselwandter *et al.*, 1990; Varma & Bonfante, 1994; Burke & Cairney, 1998). Therefore, these ericoid fungi may also be partially responsible for the observed increase in DOC concentrations and thus indirectly encouraged by burning.

1.6 Thesis overview

Blanket bogs are a globally rare habitat, with the UK supporting 13% of the world's blanket bogs by area (Ratcliffe & Thompson, 1988). However, only 1% of England's deep peats are in a favourable state and over half of the blanket bogs have lost much or all of their peat forming vegetation (Natural England, 2010). Inappropriate land management appears to be one of the major threats to blanket bogs and has the potential to interact with and exacerbate climate change through release of the vast quantities of C stored within the peat (Holden *et al.*, 2007a).

The release of C as greenhouse gases is not the only issue associated with peatland degradation and loss. Peatlands provide an array of ecosystem services including water storage and filtration, and are the source of much of the UK's drinking water (Holden *et al.*, 2007a; Bain *et al.*, 2011). Recent increases in stream water colour and DOC release into peatland waters (Worrall *et al.*, 2003a) are creating a greater and more expensive challenge for water companies to provide clear and safe water to the population (Worrall & Burt, 2009; Clay *et al.*, 2012).

Burning to encourage *Calluna* regeneration for red grouse is thought to be detrimental to peat forming vegetation, to water quality and to the peatland C balance (Holden *et al.*, 2007a; Ward *et al.*, 2007; Clutterbuck & Yallop, 2010), although conclusive evidence is lacking. Furthermore, the increase in *Calluna* cover caused by burning and the effect of this on soil microorganisms (Ward *et al.*, 2012) has yet to be fully assessed. Given the importance of grouse shooting to the UK upland rural economy (Thirgood *et al.*, 2000) and the vital need to conserve blanket bogs for their ability to store and sequester C as well as provide multiple additional ecosystem services (Evans *et al.*, 2014), there is an urgent need to assess different forms of upland management in order to satisfy all of these requirements.

This aim of this thesis is to investigate the effects of different methods of grouse moor management on the C balance, water quality and vegetation dynamics of blanket bogs in order to determine which management is the most sympathetic towards active peat formation whilst still allowing sufficient *Calluna* regrowth of a high enough quality to enable continuation of a grouse moor. This thesis first presents field research using a paired catchment approach on the C balance of three English blanket bogs and the C balance of various grouse moor management methods. This field experiment is then considered in terms of management effects on vegetation composition, as well as specific effects on *Calluna* metrics. Finally, the specific effects of *Calluna* and its belowground constituents on C release are examined in an experimental pot scale manipulation. Figure 1.1 gives an overview of how the ideas and concepts around peatlands and management are related to one another and form the basis for the different chapters.

Specifically, the remaining chapters in this thesis cover the following:

Chapter 2 describes a multiple site catchment scale field experiment which examines the effects of different types of grouse moor management on the C balance of blanket bogs. Each component of the C balance is considered individually for each of six management options. The components are then drawn together to determine the C balance for each of the three field sites studied and for the three main management options.

Chapter 3 investigates the vegetation responses to the different managements described in Chapter 2 on the same three field sites. Species richness and diversity are assessed, along with the species composition to determine which managements could promote the recovery and longevity of peat forming species. The effects of the different managements on *Calluna* growth and biomass production are explored, and the nutrient content of the *Calluna* is quantified and compared to the nutritional requirements of red grouse.

Chapter 4 utilises a fully crossed replicated pot experiment containing ericoid fungi, *Calluna* plants and charcoal to assess the potential of ericoid fungi, both when in mycorrhizal association with *Calluna* and when free living, to decompose recalcitrant organic matter. Flux measurements are used to determine plant and fungal contributions to C release and combined with radiocarbon dating to investigate the origins of the liberated C.

Chapter 5 discusses the findings of the preceding chapters and places them in the wider context of upland management. The impacts of different *Calluna* management techniques on both peatlands and grouse moors are considered, along with directions for future work and longer term implications.

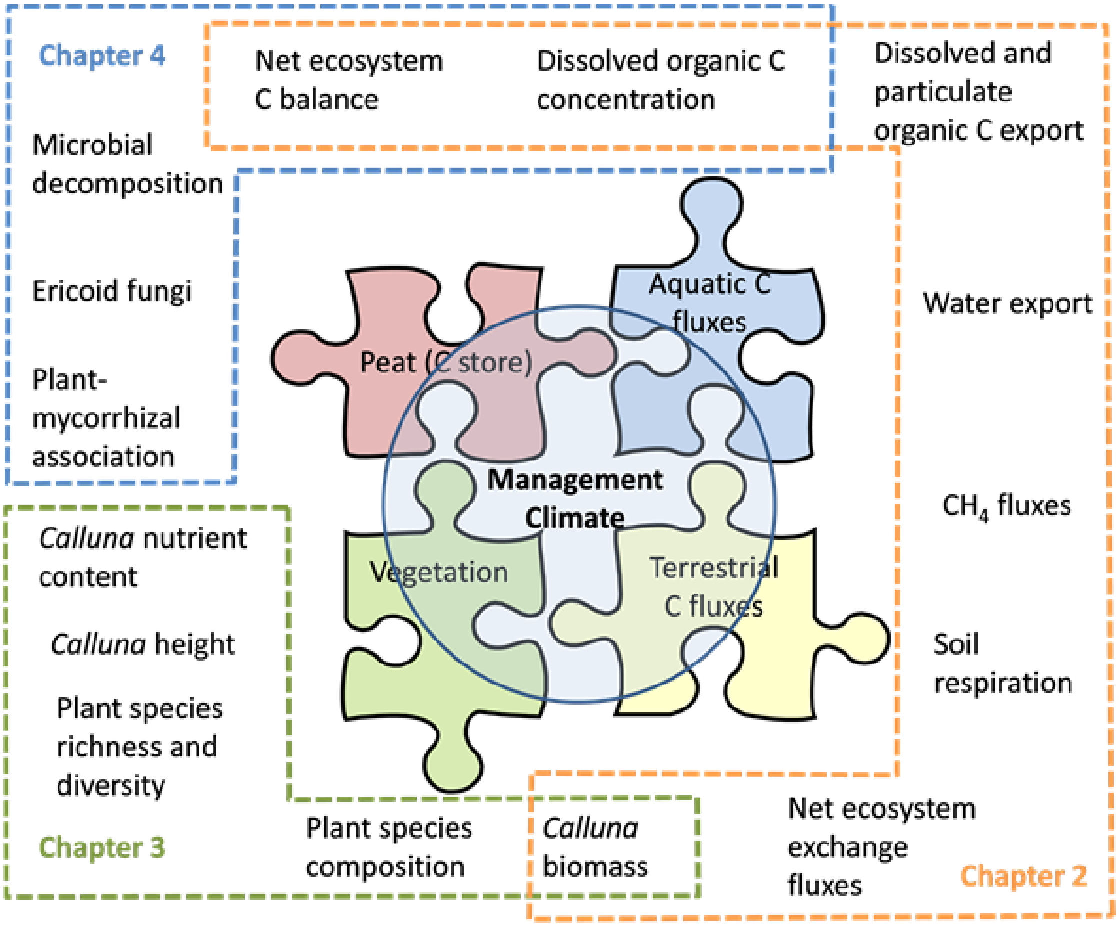


Figure 1.1 Schematic diagram showing the relationships of concepts and processes within peatlands.

The central concepts are shown within puzzle pieces. Factors with an overarching impact on the peatland system are shown in the circle. Individual concepts and processes surround the central concepts and dashed boxes indicate which chapter these are covered in.

2 To burn or not to burn? Comparing the carbon balance of three UK peatlands managed as grouse moors and three grouse moor management techniques

2.1 Introduction

Globally peatlands cover less than 3% of the world's land surface (Rydin & Jeglum, 2006), yet represent a vast carbon (C) store. Northern hemisphere peatlands alone are estimated to store 270-547 Pg C (1 Pg = 10^{15} g), which equates to over one third of the world's total soil C pool (Gorham, 1991; Turunen *et al.*, 2002; Yu *et al.*, 2010). In the UK, peatland formation is thought to have begun approximately 8,000-10,000 years ago at the end of the last ice age, due to changing climatic conditions (Charman, 2002) leading to wetter soil conditions. This led to large swathes of upland areas becoming blanketed in a layer of peat, resulting in the UK today supporting up to 13% of the world's blanket bog by area (Ratcliffe & Thompson, 1988).

The net ecosystem C balance (NECB) is the net rate of C accumulation or loss from an ecosystem, with negative values indicating C gain and positive values C loss (Chapin *et al.*, 2006). Net ecosystem exchange (NEE), which is the balance between CO_2 uptake by photosynthesis and CO_2 loss by respiration from plants and soil, is often the largest component of the NECB in peatlands (Billett *et al.*, 2010) and is thus often considered the most important component. Measurements of NEE encompass values of -40 g C m^{-2} y^{-1} (range: -2 to -112 g C m^{-2} y^{-1}) for a bog in Canada (Roulet *et al.*, 2007), -52 g C m^{-2} y^{-1} (range: -48 to -55 g C m^{-2} y^{-1}) for a Swedish mire (Nilsson *et al.*, 2008), -56 g C m^{-2} y^{-1} (range: -32 to -80 g C m^{-2} y^{-1}) for a bog in Ireland (McVeigh *et al.*, 2014) and -64 g C m^{-2} y^{-1} (range: -5 to -136 g C m^{-2} y^{-1}) for a Scottish peatland (Helfter *et al.*, 2015). Although the variability of NEE fluxes between - and especially within - these peatlands is large, all values represent a substantial drawdown of C from the atmosphere and demonstrates the importance of peatlands in helping regulate global CO_2 concentration, and hence climate (Billett *et al.*, 2010). The only other C input is the deposition of organic C via precipitation, although this is generally considered to be small, in the region of 1-3 g C m^{-2} y^{-1} (Billett *et al.*, 2004; Neal *et al.*, 2005; Nilsson *et al.*, 2008), and is rarely measured (e.g. Worrall *et al.*, 2009; Dinsmore *et al.*, 2010).

Respiration, which is included in the NEE flux, is the main form of terrestrial C loss (Nilsson *et al.*, 2008; Dinsmore *et al.*, 2010), with CH_4 release representing a much smaller but still considerable form of C loss. Globally peatlands represent a substantial source of CH_4 (Bartlett & Harriss, 1993; Huttunen *et al.*, 2003), due to microbes decomposing organic matter under the anaerobic conditions produced by the waterlogged soils (Lai, 2009). The rest of the C loss from peatlands occurs via the aquatic pathway, in the form of dissolved organic C (DOC), particulate organic C (POC), dissolved inorganic C (DIC), dissolved CO_2 and dissolved CH_4 (Billett *et al.*, 2010). The aquatic C flux is usually dominated by DOC, with POC, DIC and dissolved CH_4 making relatively minor contributions (Billett *et al.*, 2004; Nilsson *et al.*, 2008; Dinsmore *et al.*, 2010), although POC exports can be higher than DOC (Worrall *et al.*, 2003b), particularly in areas subject to erosion (Evans *et al.*, 2006). Inclusion of dissolved CO_2 in NECB calculations has been both advocated (Dinsmore *et al.*, 2010), due to its contribution to the aquatic C flux often being of the same order of magnitude as that of DOC (Nilsson *et al.*, 2008; Worrall *et al.*, 2009), and questioned, due to its age suggesting that its origins may sometimes be geogenic (Billett *et al.*, 2015). DOC and POC are included in the NECB as they are a C form which is transported from peatlands. Whilst much of this C will decompose and be released to the atmosphere as CO_2 or CH_4 (Billett *et al.*, 2004; Worrall & Moody, 2014), a small fraction may be incorporated into marine dissolved organic matter instead (Meyers-Schulte & Hedges, 1986), thereby not necessarily representing a complete C loss.

Rates of peat accumulation vary over time, largely due to variations in climate (Clymo *et al.*, 1998). Colder and wetter conditions not only suppress decomposition of organic material but also retard photosynthesis, whereas warmer and drier conditions result in greater plant production but also cause a drop in water table depths (WTDs) and hence an increase in aerobic decay of organic matter (Clymo, 1987; Clymo & Pearce, 1995). The UK is on the southern edge of the climatic envelope for northern hemisphere peat formation (Wieder & Vitt, 2006), having a milder and wetter climate than much of continental Europe. Therefore, there is concern that UK peatlands will be more vulnerable to climate change than other northern hemisphere peatlands, possibly reducing or even reversing peat accumulation (Gorham, 1991), particularly given mounting evidence of long-term increases in DOC concentrations (Worrall *et al.*, 2003a; Worrall & Burt, 2007) and the relationship of DOC release to rising temperatures (Freeman *et al.*, 2001a). This is of particular important since much of the UK's drinking water supply comes from peatlands (Holden *et al.*, 2007a).

As well as being under threat from a changing climate, many UK peatlands are also subject to human pressures, including periodic burning. Although wildfires are a natural phenomenon on peatlands, prescribed burning is much more frequent (Allen *et al.*, 2013), usually on a rotation of 8-25 years (Clay *et al.*, 2015). Despite areas of the English uplands having been managed by burning for centuries to improve sheep grazing (Simmons, 2003), there has been a substantial increase in burning, with the area of new burns almost doubling between the 1970s and 2000 (Yallop *et al.*, 2006). The vast majority of recent burning is undertaken to encourage the development of new shoots of *Calluna vulgaris* for red grouse (*Lagopus lagopus scoticus*

(Latham)) to eat, in order to increase grouse densities and provide a shootable surplus for the game industry. Although government guidelines recommend against burning on areas of peat deeper than 50 cm (Defra, 2007), it is estimated that 16% of all deep peat in England is rotationally burnt, including 30% of blanket bog (Natural England, 2010).

Ideally when burning, gamekeepers aim to produce ‘cool’ burns which rapidly move through small patches of mature *Calluna*, burning the majority of the living leaves and stems and scorching the dead litter on the ground, whilst leaving the root stock, and hence peat, largely intact (Albertson *et al.*, 2010). However, it is not always possible to burn under ideal conditions and fires can be unpredictable, leading to both hotter burns and burns covering greater areas than intended. In exceptional circumstances, fires can burn for weeks, consuming large quantities of peat (Radley, 1965). Even when controlled, burning can damage or remove other vegetation, including the moss layer, leading to bare ground, which causes drying and erosion (Holden *et al.*, 2007a). Over 70% of peatlands in England are classed as degraded, with over 30% of deep peats currently lacking typical peatland vegetation (Natural England, 2010), including peat forming *Sphagnum* species.

Eroding peat has been shown to release high quantities of POC, sometimes leading to a neutral or positive NECB (Evans *et al.*, 2006), but there have been very few studies of the effects of rotation moorland burning on the NECB of deep peat in the UK. Unmanaged peatlands appear to take up C relatively consistently across the northern hemisphere, based on NECB measurements from Canada (-22 g C m^{-2} y^{-1}; Roulet *et al.*, 2007), Sweden (-24 g C m^{-2} y^{-1}; Nilsson *et al.*, 2008) and Scotland (-28 g C m^{-2} y^{-1}; Helfter *et al.*, 2015). However, the few studies which have specifically investigated the NECB on rotationally burnt blanket bogs in the UK have all demonstrated a net loss of C. Burnt areas at Moor House National Nature Reserve lost 25.5 g C m^{-2} y^{-1} nine years into a 10 year burn cycle (Ward *et al.*, 2007) , whilst Clay *et al.* (2010) estimated losses of 117.8 g C m^{-2} y^{-1} at the same site shortly after burning occurred. A study of two other peatlands in northern England demonstrated a range of losses of between 4 g C m^{-2} y^{-1} and 269 g C m^{-2} y^{-1} for areas of different burn ages (Clay *et al.*, 2015). The amount of C lost from vegetation during the burning process was not included in the latter estimates.

Despite these studies all pointing to burning negatively impacting the peatland C balance, burning is still a widespread management practice across the UK (Natural England, 2010). There are other methods which can be used to manage *Calluna* moorland, namely mowing, but this can necessitate buying expensive machinery or employing a subcontractor. There are also concerns that the weight of a tractor on such a wet surface could damage or compact the peat. However, mowing could be less damaging to vegetation, especially *Sphagnum* mosses, than burning because the brash left by mowing may hold moisture and prevent the peat surface drying out. Additionally, mowing would return the cut biomass to the system, potentially increasing C sequestration. Although large quantities of brash may increase the risk of wildfire, brash is used in peatland restoration and therefore could be removed and used for restoration work elsewhere.

This study aimed to examine the effects of different types of *Calluna* management on the NECB on three English blanket bogs. The impact of traditional rotational burning was compared to that of mowing on a catchment scale, with the effects of leaving or removing the brash generated from mowing, and the effect of adding *Sphagnum* fragments after mowing, also assessed at a plot scale. Specifically, the magnitude of C losses and gains for each component of the NECB were compared for the six different plot level managements and measurements were upscaled to provide an estimate for the NECB of each peatland site. The NECB was also calculated for burnt, mown and unmanaged areas of the peatlands to test the hypothesis that mowing would be less detrimental than burning to the peatland C balance.

2.2 Methods

2.2.1 Site descriptions

The three study sites were all located in north-west England (Figure 2.1). The names used to identify the sites throughout this thesis are Nidderdale, Mossdale and Whitendale. The sites were chosen because all were classed as blanket bogs with peat over 1 m deep and were managed as grouse moors. Typically, the sites were managed with a 10-15 year burn rotation and all had a long history of burning (more than 100 years based on local knowledge). All sites had more than 50% *Calluna* cover, with at least some existing bog vegetation in the form of *Eriophorum* and *Sphagnum* species, and had a stocking density of <0.5 ewes ha^{-1}. The sites had similar altitudes and weather conditions and allowed for a pair of similar sized sub-catchments, each with a main stream.

Nidderdale is located on the Middlesmoor estate in the Nidderdale valley, which lies within the Yorkshire Dales National Park, UK, at 54°10’07”N; 1°55’02”W (UK Grid Reference SE055747) about 450 m above sea level. The site had an average annual air temperature of 7.1°C and annual precipitation of 1651 mm during the four year study period. It is situated on mudstone from the Millstone Grit group with intermingled sandstone (Kidd *et al.*, 2007). The soil is a poorly draining organic peat in the Winter Hill series with an average depth of 1.5 m at the experimental plots; peat depth ranges from 0.2 m to 2.9 m (according to measurements made on the study area in 2012 using manual peat depth rods). Most of the grips within the study

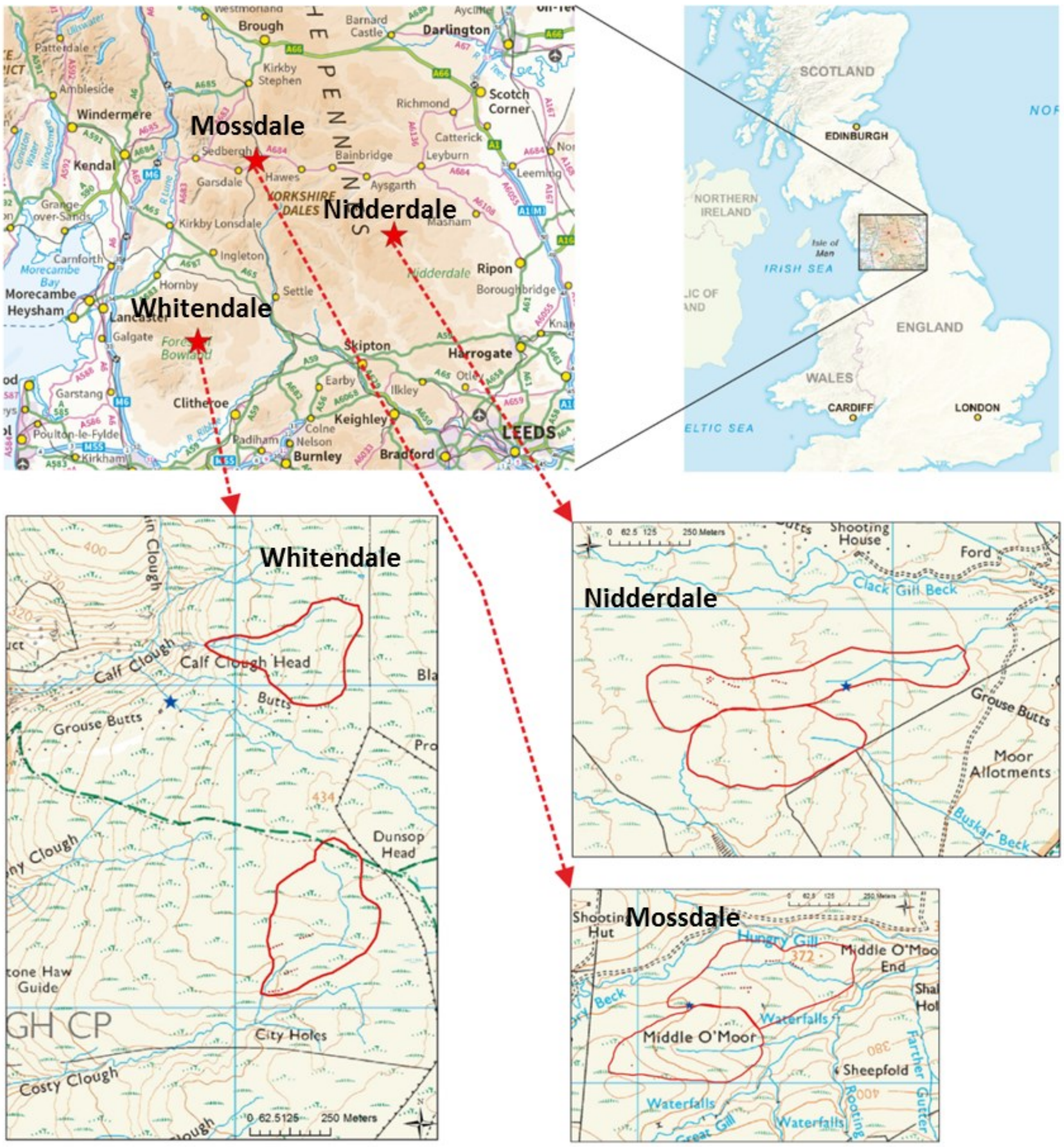


Figure 2.1 Location of the three study sites in north-west England (top maps, red stars). The catchment boundaries (thick red lines) and weather station (blue star) are detailed in the lower maps (from left star to right star) at Whitendale, Mossdale and Nidderdale.

Rights statement: MiniScale® [TIFF geospatial data], Scale 1:1000000, Tiles: GB, Updated: 3 December 2015, Ordnance Survey (GB), Using: EDINA Digimap Ordnance Survey Service, http://digimap.edina.ac.uk, Downloaded: 2016-09-09 14:35:01.73

area were blocked within the last 10 years but none were blocked during the study period. The two sub-catchments were ~11 ha and ~14 ha.

Mossdale is located in Upper Wensleydale within the Yorkshire Dales National Park at 54°19’01”N; 2°17’18”W (UK Grid Reference SD813913) about 390 m above sea level. During the four year study period, the average annual air temperature was 7.2°C and annual precipitation was 2115 mm. The site lies on limestone which is overlain by thin sandstone and covered with mudstone (Hall, 1979). The soil is a poorly draining organic peat in the Winter Hill series with an average depth of 1.0 m at the experimental plots; peat depth ranges from 0.3 m to 2.1 m (according to measurements made on the study area in 2012 using manual peat depth rods). Most of the grips that were within the study area have been blocked within the last 10 years. Three were unintentionally blocked during the study period on the control catchment on 20th November 2013. The two sub-catchments were ~8 ha and ~10 ha.

Whitendale is located within the Forest of Bowland AONB, Lancashire, at 53°59’04”N; 2°30’03”W (UK Grid Reference SD672543) about 410 m above sea level. The average annual air temperature was 7.6°C and the site had 1863 mm of precipitation per year during the four year study period. The site is situated on interbedded sandstone and mudstone with areas solely of mudstone (Ewen *et al.*, 2015). The soil is a poorly draining organic peat in the Winter Hill series (Ewen *et al.*, 2015) with an average depth of 1.5 m at the experimental plots; peat depth ranges from 0.2 m to 4.5 m (according to measurements made on the study area in 2012 using manual peat depth rods). This study area had no grips, although gullies similar to grips were present in some areas. The two sub-catchments were ~8 ha and ~11 ha.

2.2.2 Site set up

In March 2012, automated weather stations (AWS; MiniMet AWS, Skye Instruments Ltd, Llandrindod Wells, UK) were erected between the sub-catchments at each site. The AWS recorded hourly values for wind speed and direction, soil temperature, air temperature, air pressure, relative humidity, precipitation, total radiation and photosynthetically active radiation (PAR). Sub-catchment boundaries were defined based on the watershed. The rough outline of a catchment was identified using contour lines on a map. The top of the ridge around the edge of each sub-catchment was walked around with a GPS to accurately record the outline. A V-notch flow weir (with a notch angle of 90°) was constructed at the outflow of each sub-catchment. A water table depth (WTD) meter (WT-HR 1000, TruTrack, New Zealand) was positioned inside plastic tubing within the upstream weir pool to monitor the stream flow.

One sub-catchment of each site was assigned to a business-as-usual burning management with the other being assigned to management by mowing. Within each sub-catchment four blocks were defined (Figure 2.2). In the burning sub-catchment, each block contained one plot; FI plots were solely burnt. In the mown catchment, each block contained five plots; LB plots were mown with the brash left, BR plots were mown with the brash removed, LB+Sph plots (see "*Sphagnum* addition" below) were mown with the brash left and *Sphagnum* propagules added, BR+Sph plots were mown with brash removed and *Sphagnum* propagules added and DN plots were left uncut as the no management control (Figure 2.2).

All plots were 5 m x 5 m and were marked out with wooden corner posts protruding approximately 50 cm from the peat surface. In one corner of each plot (see Figure 2.2 for diagram of a typical plot), a temperature logger (Tinytag Plus 2 – TGP -4017 data logger, Gemini Data Loggers Ltd, Chichester, UK) was placed on the surface and covered by a reflective lid secured by plastic mesh and pegs. Adjacent to the lid, a WTD meter was inserted (see below). The instruments were covered by a metal mesh cage which was pegged at the bottom and folded at the top to prevent sheep damage and allow easy access. Circular areas for repeated methane (CH_4), net ecosystem exchange (NEE) and soil respiration (SR) measurements were chosen in each plot (Figure 2.2) and marked with metal pegs. A 1 m x 1 m sub-plot was marked in each plot in a different corner to that of the WTD meter (Figure 2.2).

2.2.2.1 WTD meters

Within the metal mesh cage on each plot (see Figure 2.2), a peat core of 1 m depth (or less if the bedrock was reached) was removed using a stainless steel 5 cm x 5 cm box corer and a 3 cm wide plastic tube was inserted to prevent infilling. A WTD meter (WT-HR 1000, TruTrack, New Zealand) was placed inside this tube so that the zero-line on the meter was flush with the peat surface.

During mowing (see below), the weight of the tractors compacted the peat by about 7-8 cm which also pushed the plastic tubing in the WTD meter holes down. The surrounding peat then sprung back, leaving the tubes buried. Additionally, the drainage holes near the bottom of some WTD meters had become blocked with peat, causing erroneous readings. Therefore, it was deemed necessary to re-core all WTD meter holes to both remove peat build up at the bottom and to retrieve the plastic tubing.

The box corer was used to remove a core which included the original plastic tube. The peat was separated from the tube and the tube was reinserted into the hole so that its top was flush with the peat surface. Before being replaced, additional holes were drilled into the outer

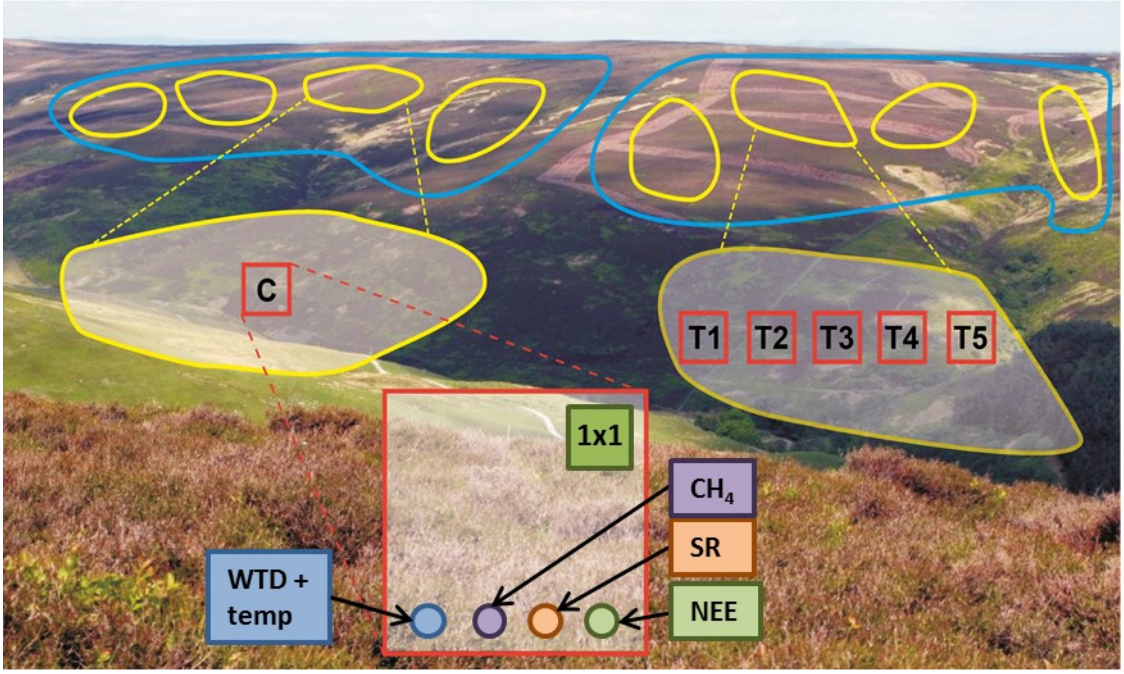


Figure 2.2 Schematic diagram of a typical site layout of the two sub-catchments (blue outline) and four blocks (yellow outline) within each.

Each plot (red outline) is 5 m x 5 m. C plots are in the burning sub-catchment and represent burnt plots (FI). T1-T5 are plots in the mowing sub-catchment and represent mown plots with brash left (LB), mown plots with brash removed (BR), mown plots with the brash left and *Sphagnum* propagules added (LB+Sph), mown plots with the brash removed and *Sphagnum* propagules added (BR+Sph) and plots left uncut as a no management ("do nothing") control (DN). Within each plot is a corner 1 m x 1 m sub-plot (green square), a circle for repeated CH_4 measurements (purple circle), a circle for repeated soil respiration measurements (orange circle), a circle for repeated NEE measurements (green circle) and a mesh cage containing a WTD meter and temperature logger (blue circle).

tube of the WTD meters so drainage was possible even if the bottom holes became reblocked with peat.

2.2.2.2 Preparing the NEE, CH_4 and SR patches

Directly behind each CH_4 peg on a plot, the moss surface was removed from a 20 cm diameter circle which contained no vascular plants. This created an indentation which enabled exact re-location as well as removing the surface autotrophic C fluxes. Dense overhanging vascular plants were clipped back to allow access. During field visits, any plants growing within the circles were removed prior to measurements.

A 30 cm circle was selected for the NEE measurements on each plot. These areas included sufficient *Calluna* stems to be deemed representative of the whole plot and were demarcated only by the pegs (i.e. no indent was made).

Areas for SR measurements were similar to those for CH_4 measurements in that areas without vascular plant shoots were chosen. A 15 cm circle of the moss surface was removed, providing an indent and removing autotrophic fluxes, and any overhanging vegetation was clipped back. Similarly, plant regrowth was removed as necessary.

2.2.3 Management implementation

Site manipulation by management was designed to mimic a 10 year burn rotation. On maps, the sub-catchments were split into patches of approximately 0.3 ha. All plots within a block were included within the same 0.3 ha patch. In the business-as-usual burning sub-catchments, 20% of these patches were designated as areas for burning in spring 2013 and in the mowing sub-catchments, 20% of the patches were designated for mowing in spring 2013. All patches containing plots were included in these burnt and mown areas. A further 20% of each sub-catchment was designated for either burning or mowing (according to sub-catchment) in spring 2015.

The areas identified for burning and mowing were identified on the sites using handheld GPS units (eTrex 8, Garmin, Olathe, KS, USA) and were marked out on the sites with bamboo canes. All WTD meters and temperature loggers were temporarily removed prior to burning and mowing in 2013 to prevent heat or tractor damage.

2.2.3.1 Burning

Burning was undertaken by the local gamekeeper at each site (see Table 2.1 for dates) who was instructed to burn as he usually would. This resulted in some slight differences in burning processes between the sites. However, where possible, fires at all sites were lit at the downhill edge of the marked areas on dry days with a gentle breeze to fan the flames uphill (to slow the spread) and were beaten out with paddles at the uphill edge.

At Nidderdale, each patch was mown around before the fires were set to act as a fire break. There were four people present to set and control the fires in 2013 and two in 2015. At Mossdale in 2013, only the gamekeeper and one other were present to set and control the fires whereas three people were present to tend the fires in 2015. At Whitendale, six people were present to set and control the fires in 2013 and three people in 2015.

2.2.3.2 Mowing

All mesh cages and corner posts were removed and laid outside the marked mowing areas in line with the holes to enable easier relocation of the plots. Coloured duct tape was placed in the post and WTD meter holes to further facilitate this. Pegs on the CH_4, SR and NEE patches were pushed into the peat until almost level with the surface. Despite being within mown blocks (see Figure 2.2), DN plots were not mown, with an unmown buffer zone of approximately 1 m left around the edges.

Mowing was undertaken by the gamekeeper at Nidderdale, by Dalefoot Compost (contractor) at Mossdale and by Dinsdales Moorland Services (contractor) at Whitendale (see Table 2.1 for dates). The tractors used were all fitted with double tyres to reduce compaction of the peat and used only a single pass to cut and chop the vegetation. At Nidderdale, a circular rotating flail, set to a height of 15 cm, was used to cut the *Calluna*. At Mossdale, a rotating cylindrical cutter with a cutting height of 14 cm was used and at Whitendale, a similar cylindrical cutter also with a cutting height of 14 cm was used.

Once mown, the plot corner posts were reinserted. Where the thickness of brash made it impossible to relocate the holes, and/or the coloured tape had been pulled out and deposited elsewhere by the mowers, posts were placed in approximately the correct location, defined by the other plot markers. On all plots, at least one corner post hole was found. All WTD meter holes and Rhizon samplers were relocated. The CH_4, NEE and SR pegs were relocated using a metal detector.

Brash was removed from the BR and BR+Sph plots by raking and from the CH_4, NEE and SR patches on these plots by hand (see Table 2.1 for dates). On LB and LB+Sph plots, care was taken that brash was distributed on the CH_4, NEE and SR patches and inside the metal mesh cage in a manner representing brash distribution across the plot. All brash was left on the mown areas outside the plots.

Table 2.1 Dates of each management or site set-up activity at each site.
See text for details of what each activity involved.

Management/set up activity	**Nidderdale**	**Mossdale**	**Whitendale**
CH_4, NEE and SR patch set up	24th July 2012	26th July 2012	25th July 2012
Burning	5th March 2013	1st March 2013	21st February 2013
	10th & 14th April 2015	19th March 2015	18th March 2015
Mowing	11th April 2013	10th April 2013	7th March 2013
	13th January 2015	31st March 2015	13th & 14th March 2015
Brash removal from plots	11th April 2013	10th April 2013	18th April 2013
Sphagnum pellet addition	25th March 2014	25th March 2014	26th March 2014

2.2.3.3 Sphagnum addition

Sphagnum was added by means of pellets (BeadaMoss, Micropropagation Services, Loughborough, UK; see Table 2.1 for dates). The BeadaMoss pellets consisted of fragments or "propagules" of a single *Sphagnum* species encased in a water gel coating, which protected the *Sphagnum* fragments from desiccation until the moss has established. Pellets containing *Sphagnum capillifolium*, *S. papillosum* and *S. palustre* were used in equal amounts.

For each BR+Sph and LB+Sph plot, a quadrat was placed over the 1 m x 1 m corner sub-plot which subdivided it into 25 equal squares. Thirty-three BeadaMoss pellets of each species were added to the sub-plot, with each quadrat square receiving at least one pellet of each species. The remainder of each 5 m x 5 m plot was divided into 1 m strips and the *Sphagnum* pellets were applied to each strip separately, at a rate of approximately 100 pellets per 1 m^2, by shaking a pot from side to side to prevent pellets from clumping and sticking together.

2.2.4 Gas flux measurements

The NEE, CH_4 and SR fluxes at a single site were always measured on the same day as each other (see Table 2.2 for dates) in order to reduce climate variations between sites in a single measurement set.

2.2.4.1 NEE flux measurements

A custom built clear Perspex chamber (Biology Mechanical Workshop, University of York, UK) with an internal diameter of 29.5 cm and a height of 20 cm, connected to an infrared gas analyser (IRGA; Model 8100, Li-Cor, Lincoln, NE, USA), was used for NEE measurements. All plants which were rooted within the NEE circle were bundled together, a PAR sensor (QS5 – PAR Quantum Sensor, Delta-T Devices, Cambridge, UK) was positioned within the NEE circle so that it would not be covered by vegetation or shadows and the chamber was carefully placed over the stems and sensor. On plots where the vegetation was taller than 20 cm (all plots in the pre-management period and DN plots throughout), an extra collar of the same clear Perspex and either 20 or 40 cm tall (depending on the vegetation height) was placed over the vegetation with the chamber placed on top and taped around to seal the join. A temperature sensor (Therm 30K OHM@25C, part number: 434-08943, Li-Cor, Lincoln, NE, USA) connected to the IRGA was inserted to 5 cm depth next to the chamber and the chamber was sealed to the atmosphere by means of wet *Sphagnum* moss being tucked around the base.

The CO_2 concentration within the chamber was measured every second (s) for 90 s. These measurements were made in more than 90% of the total PAR ("Full Light" measurement; trials

Table 2.2 Dates of net ecosystem exchange, CH_4 and soil respiration flux measurements for each site, which were always measured at a single site on the same day as each other.

Nidderdale	**Mossdale**	**Whitendale**
24th July 2012	26th July 2012	25th July 2012
9th October 2012	10th October 2012	12th October 2012
4th December 2012	5th December 2012	11th December 2012
25th June 2013	26th June 2013	27th June 2013
17th July 2013	18th July 2013	19th July 2013
2nd September 2013	3rd September 2013	4th September 2013
26th November 2013	27th November 2013	28th November 2013
8th April 2014	9th April 2014	10th April 2014
23rd June 2014	24th June 2014	25th June 2014
8th September 2014	9th September 2014	10th September 2014
10th November 2014	11th November 2014	12th November 2014
10th March 2015	11th March 2015	12th March 2015
30th June 2015	1st July 2015	2nd July 2015
18th August 2015	19th August 2015	20th August 2015
25th November 2015	8th December 2015	4th December 2015

prior to this study determined that the amount of light reflected by the Perspex of the chamber was less than 10%; A. Heinemeyer, unpublished data). Without removing the chamber, a shading mesh was placed over the chamber ("30% Light" measurement; on average 30% of total light penetrated the chamber) and CO_2 concentrations recorded for another 90 s. Depending on the light conditions and amount of vegetation in the chamber, a second shading mesh was placed over the first ("10% Light" measurement; on average 10% of total light penetrated the chamber) and another 90 s flux was recorded. For the final 90 s flux, a custom made cover (Environment Department, University of York, UK) was placed over the chamber, blocking out all light (ecosystem respiration or "R_{eco}" measurement). The *Sphagnum* moss seal was removed from plots after measurements to prevent establishment on the NEE circles and to avoid excess relocation around the site.

2.2.4.1.1 NEE flux measurements chamber volume correction

NEE measurements necessitated including plants within the chamber. As the volume of the chamber used is important in calculating the CO_2 flux (Holland *et al.*, 1999), plants with large volumes would reduce the chamber volume and may result in incorrect fluxes. Therefore, plant volumes were estimated in the field and these estimates were validated in the laboratory. The aims were to verify whether including plant volumes in NEE flux calculations was necessary and, if so, whether volume estimates made in the field could be used as proxy for volume measurements, without the need for destructive sampling.

2.2.4.1.2 NEE flux measurements chamber volume correction - methods

During NEE measurements in October 2012, the largest NEE chamber extension (see chamber description in Section 2.2.4.1) was used on all plots, meaning that the chamber had a total height of 60 cm and a volume of 39.6 L. The volume of *Calluna* was estimated as a percentage of the chamber volume to the nearest 5%. Shortly before burning and mowing in spring 2013, all plants within the NEE measurement circles were cut at the stem bases, bagged and sealed.

Stems were cut so that the *Calluna* from each NEE circle fitted as compactly as possible into its bag. Using tongs, a bag was slowly submerged in a 20 L bucket, which was filled to the brim with water and inside a larger container. The bags were mainly sealed but one corner was left open to allow air to escape as it was forced up by the water pressure. The water displaced by the sample was measured and the bucket refilled. An empty bag was also measured five times in the same manner but using a 1 L beaker. The average of this was subtracted from each sample to give the *Calluna* volume.

The LiCor Viewer software was used to derive the CO_2 fluxes from the most linear 60 s portion (Li-Cor Biosciences, 2007) of each NEE measurement under each light condition. For all 2012 NEE measurements and all NEE measurements on DN plots, the measured *Calluna* volume was subtracted from the chamber volume. All CO_2 fluxes were adjusted for (corrected) chamber volume and collar surface area and all fluxes were expressed in µmol CO_2 m^{-2} s^{-1}. To determine whether plant volume correction for chamber volume was necessary, all 2012 NEE fluxes were also calculated using the original (i.e. ignoring the plants) chamber volume.

A paired Student's t-test (using the function "t.test" in the R "stats" package; R Core Team, 2016) comparing the corrected and uncorrected 2012 NEE fluxes was used to determine whether subtracting the plant volume from the chamber volume significantly affected the NEE fluxes. A linear regression model test (employing the function "lm" in the R "stats" package; (R Core Team, 2016) was used to determine the relationship between the estimated percentage volume of *Calluna* within the chamber and the measured volume. Separate linear regressions were also used on the same data which had been split by site.

2.2.4.1.3 NEE flux measurements chamber volume correction - results and discussion

The difference between NEE fluxes corrected for *Calluna* volume and uncorrected fluxes ranged from -0.59 µmol CO_2 m^{-2} s^{-1} to 0.76 µmol CO_2 m^{-2} s^{-1} with a mean of 0.04 µmol CO_2 m^{-2} s^{-1}. There was a significant difference between the corrected and uncorrected fluxes (t_{791} = 10.00, $p < 0.0001$). The estimated percentage of chamber volume occupied by *Calluna* ranged from 10% to 65% with a mean of 33%. The percentage of the chamber volume which was actually occupied by *Calluna* ranged from 0.93% to 6.54% with a mean of 2.73%, which was approximately 12 times less than the estimated percentage volume. Mossdale had the greatest plant volume on average (1329 cm^3) and Nidderdale had the smallest (942 cm^3). There was a significant linear relationship between the estimated and measured volumes across the sites ($R^2 = 0.60$, $p < 0.0001$). There was also a significant linear relationship between estimated and measured volumes at all three sites but the strength of the relationship was weakest at Nidderdale ($R^2 = 0.33$, $p < 0.0001$), stronger at Mossdale ($R^2 = 0.63$, $p < 0.0001$) and strongest at Whitendale ($R^2 = 0.73$, $p < 0.0001$).

The results indicate that plant volumes should be incorporated into NEE flux calculations as they can make a small but significant difference to the fluxes. The larger the NEE fluxes and the larger the *Calluna* plants are in relation to the chamber, the greater the absolute change in NEE fluxes. This inclusion would be particularly important if NEE fluxes are being upscaled as any errors in flux calculations would be multiplied. Although there was a 12-fold difference between the estimated and measured *Calluna* volumes, the difference was relatively consistent. The different strengths of the relationship between measured and estimated volumes between sites is likely to be due to observers becoming more consistent at estimating volumes with practice; volumes at Nidderdale were estimated on the first day of a three day field campaign, those at Mossdale on the second day and those at Whitendale on the third. Therefore, with a little practice, non-destructive field estimations of *Calluna* plant volumes, using a correction factor, are likely to be sufficiently accurate to improve NEE flux calculations.

Here the NEE fluxes were corrected for only the 2012 and DN fluxes due to mowing and burning removing the majority of the *Calluna* biomass from the plots meaning that most plants were estimated to take up less than 5% of the chamber volume during post-management NEE measurements. Assuming that the magnitude of difference between percentage estimation in the field and true *Calluna* volume was similar in other years and for smaller plants, this would mean that the *Calluna* would have filled a maximum of 1.25% of the chamber (the 20 cm tall chamber was mostly used post-management) during post-management measurements on any managed plot, mostly substantially less. This method only took *Calluna* plant volume into account. Given that using these *Calluna* volumes resulted in significantly different NEE fluxes, in future, investigation into whether volumes of other plants, including moss, affect flux calculations is warranted.

2.2.4.2 CH_4 flux measurements

CH_4 fluxes were measured using two different methods. All CH_4 measurements in 2012 and 2013 were made using cover-boxes (a modification on the static chamber method described in Livingston & Hutchinson, 1995) from which gas samples were withdrawn at set time points. These samples were then analysed for CH_4 concentrations. CH_4 measurements from and including June 2014 were measured in real time using an Ultraportable Greenhouse Gas Analyser (UGGA; Model 915-0011, Los Gatos Research, Inc., San Jose, CA, USA).

The cover-boxes comprised a 10 cm tall collar and 15 cm tall chamber, both of which were 20 cm in diameter and made of uPVC pipe (Plumb Center, Wolseley UK Ltd, Leamington Spa, UK). The chambers were topped with circular pieces of uPVC which were glued in place. The chambers were insulated with reflective wadding to minimise any internal temperature change (internal chamber temperatures were monitored periodically and, even on hot days, changed by less than 3°C during the whole closure period). The end of a 2 m length of vacuum tubing (Tygon Formulation R-3603 Tubing, Part number AAC00002, Saint-Gobain Performance Plastics, Akron, OH, USA) was pushed through a rubber bung (SubaSeal No. 25, Sigma-Aldrich, St Louis, MO, USA) which was secured in a small hole drilled through the top of each chamber.

The non-chamber end of the tubing was knotted to create a closed system when the chamber and collar were sealed together.

All plots in a pair of blocks were measured simultaneously. Collars were inserted into the indents created in the CH_4 patches by moss removal. Chambers were placed on top and sealed by means of a 10 cm wide rubber band rolled over the join. Wet *Sphagnum* moss was packed around the base of the collars to create an airtight seal. Gas samples were extracted 5, 15, 25 and 50 minutes after the chambers were sealed by inserting the hypodermic needle (Microlance 0.5 mm x 25 mm, Becton Dickinson & Company Limited, Drogheda, Ireland) of a 20 ml syringe into the tubing above the knot, flushing the syringe three times to equilibrate the gas in the tubing with that in the chamber and injecting the sample into a pre-evacuated 12 ml vial (Exetainer 839W, Labco Ltd, High Wycombe, UK).

The gas samples were stored at ambient temperature and analysed within one month. Gas chromatography flame ionisation detection (GC-FID; AutoSystem XL Gas Chromatograph, Perkin Elmer Arnel, Waltham, MA, USA) was used to quantify CO_2, CH_4 and N_2O concentrations in each vial, aided by a 60-space custom built carousel (Biology Mechanical Workshop, University of York, UK). Blanks (pure nitrogen), standards (a reference gas containing 10 ppm N_2O, 100 ppm CH_4, 500 ppm CO_2, BOC Gases, Guildford, UK) and air (ambient air) samples were used to calibrate results.

The UGGA was connected to a modified (a pressure vent was added in the chamber top) cover box chamber with two sections of tubing (Bev-a-line IV, Thermoplastic Processes, Inc., Georgetown, DE, USA) creating to create a closed system. The chamber was placed gently onto the CH_4 circle of a plot and sealed around with wet *Sphagnum* to obtain an airtight seal. A tablet (Google Nexus, Google Inc., Mountain View, CA, USA) was used to view the flux in real time. On plots where fluxes spiked and then dropped suddenly, the chamber was removed, vented and replaced as these measurements indicated release of a CH_4 bubble, probably caused by chamber placement disturbance, not a true flux. Fluxes were measured over a maximum of 5 minutes.

For the CH_4 measurements taken using cover boxes, fluxes were derived by regressing the five CH_4 concentrations against the time points the samples were withdrawn from the chambers and the change in CH_4 was calculated. Similarly, for measurements using the UGGA, fluxes were derived by regressing the most linear 90 s section of the measurements over time and calculating the increase in CH_4. With both sets of measurements, the flux was discarded and recorded as zero if the R^2 value of the linear slope was less than 0.5. Whilst this R^2 value is low, this was due to some very low CH_4 fluxes meaning that measurement variability was very large. All fluxes were also assessed by eye to verify the linear trend. The chamber volume and collar surface area were used to adjust all CH_4 fluxes (Holland *et al.*, 1999) and they were expressed in nmol CH_4 m^{-2} s^{-1}.

2.2.4.3 SR flux measurements

For SR flux measurements, the IRGA was connected to a 10 cm automated survey chamber (Model 8100-102, Li-Cor, Lincoln, NE, USA). A 10 cm diameter, 5 cm tall uPVC collar (Plumb Center, Wolseley UK Ltd, Leamington Spa, UK) with a bevelled bottom edge was placed firmly (i.e. in full contact with the soil but without cutting sub-surface roots) in the centre of the SR circle with the survey chamber on top. The CO_2 concentration in the chamber was measured every second for 45 seconds.

The LiCor Viewer software was used to derive the CO_2 fluxes from the most linear 30 s portion, based on the R^2 value, of each measurement (Li-Cor Biosciences, 2007). The chamber volume and collar surface area were used to express all CO_2 fluxes in µmol CO_2 m^{-2} s^{-1}.

2.2.5 DOC and POC measurements

Stream water samples were collected monthly between July 2012 and December 2015 from the v-notch weirs on all six sub-catchments. Water samples were collected in pre-rinsed polypropylene bottles (Nalgene, Thermo Scientific, Rochester, NY, USA) directly from the outflow of the weirs. All samples were stored in the dark at 4°C within 24 hours of collection and processed within one month.

Particulate organic matter was separated from a 500 ml subsample of stream water by filtering under vacuum through a pre-ashed (combusted in a muffle furnace for 2 hours at 550°C) and weighed 0.7 µm glass-fiber filter (Whatman glass microfiber filters, Grade GF/F, 47 mm diameter, Sigma-Aldrich, Dorset, UK). Filters were dried overnight in an oven at 105°C, and re-weighed to determine the amount of particulate matter. Filter papers were combusted in a muffle furnace at 375°C for 16 hours following Ball (1964). Samples were cooled and reweighed to determine loss on ignition (LOI) which was used to calculate POC (see Ball (1964) for details).

The filtered stream water samples were refiltered through Rhizon samplers to ensure consistent C fractions were sampled. The DOC concentrations were determined using a total carbon analyser (either LiquiTOC or vario TOC cube, Elementar Analysensysteme GmbH, Hanau, Germany; due to technical reasons, it was not possible to use the same analyser for all samples). Prior to analysis, samples were acidified and sparged with oxygen to remove any inorganic carbon. A five-point calibration was determined with a sodium carbonate and potassium hydrogen phthalate (SC/KHP) solution and standards of 50 ppm SC/KHP were regularly analysed during a machine run to reduce machine drift and errors. All samples were analysed in at least duplicate. Both DOC and POC concentrations were expressed as mg C L^{-1}.

2.2.6 Data analysis

2.2.6.1 Stream flow rate calculations

The height of the water over flowing over each v-notch weir was measured during each site visit. The WTDs recorded by the logger in the pool upstream of each flow weir were corrected (due to some gradually sinking into the pool base over time) using these heights. The instantaneous stream flow rate, Q, was calculated using the form:

$$Q = 4.28 \times Ce \times \tan\frac{\theta}{2} \times (H + k)^{\frac{5}{2}} \qquad \text{Eq.2.1}$$

where Ce is the effective discharge coefficient, θ is the angle of the v-notch in radians, H is the measured head over the weir (i.e. the corrected WTD) in feet and k is the head correction factor (Bengtson, 2010).

The effective discharge coefficient, Ce, was calculated using Eq.2.2 and the head correction factor, k, was calculated using Eq.2.3:

$$\mathrm{Ce}{=}0.61\text{-}\left(8.7\mathrm{x}10\text{-}4{\times}\theta\right){+}\left(6.1{\times}10^{-6}{\times}\theta^{2}\right) \qquad \text{Eq.2.2}$$

$$\mathrm{k}{=}0.014\text{-}\left(3.4\mathrm{x}10\text{-}4{\times}\theta\right){+}\left(3.3{\times}10^{-6}{\times}\theta^{2}\right)\text{-}\left(1.1{\times}10^{-8}{\times}\theta^{3}\right) \qquad \text{Eq.2.3}$$

where θ is the angle of the v-notch in degrees (Bengtson, 2010). The stream flow rates were expressed in L h^{-1}.

2.2.6.2 Statistical analyses

All statistical analyses were carried out in R version 3.3.1 (R Core Team, 2016) unless otherwise stated. Following Zuur *et al.* (2009), residuals were plotted against fitted values and visually assessed for normality and homogeneity of variance. Where values are quoted, these represent the mean (± 95% confidence intervals). The critical p value chosen for significance was 0.05.

Linear mixed effects models employing the "lmer" function from the "lmerTest" package (Kuznetsova *et al.*, 2016) were used to test for management and site effects on the Full Light and R_{eco} fluxes, CH_4 and SR fluxes and DOC and POC concentrations. Due to producing many small fluxes (i.e. close to 0) and very few large fluxes, Full Light NEE, R_{eco}, CH_4 and SR data were square-root transformed for analysis. The managements, sites and time period (either pre-management, i.e. before management implementation, or post-management, i.e. after management implementation) were used as fixed effects, as were the interactions between them. The month in which measurements were made was also included as a fixed effect as were appropriate environmental variables; PAR and soil temperature (Tsoil) were included in the Full Light NEE model, Tsoil in the R_{eco} and SR models, Tsoil and WTD in the CH_4 model and the daily stream water export in the DOC and POC models. A random intercept was included for each model, with a nested structure of blocks in sites (to account for spatial heterogeneity) in years (to account for repeated measurements).

Following the 10-step protocol in section 5.10 of Zuur *et al.* (2009), variables were dropped stepwise from each linear mixed effects model and the log-likelihood ratio and AIC value were used to assess whether a variable should be dropped or kept in the model. For the final models, the “satterthwaite” option was used to calculate the denominator degrees of freedom as the time periods resulted in an unbalanced design (Spilke *et al.*, 2005). Where significant interactions were found, the “glht” function with the “Tukey” option from the “multcomp” package (Hothorn *et al.*, 2008) was used to compare groups within the interaction terms.

2.2.6.3 Upscaling NEE flux measurements

The NEE fluxes were upscaled for FI, LB and DN managements for each site, due to these being the three main managements across the catchments. A more detailed explanation is given in Appendix A, along with example figures and calculations, but is briefly explained here. Light response curves were constructed separately for each management at each site for each set of NEE measurements (i.e. a curve was modelled for FI measurements at Nidderdale in July 2012, a separate curve for FI measurements at Nidderdale for October 2012, etc.) , using the form:

$$\mathrm{CO_2\ flux}=\frac{\mathrm{P_{max}}\times\mathrm{PAR}}{\mathrm{PAR}+\mathrm{K_m}}+\mathrm{R_{eco}} \qquad \text{Eq.2.4}$$

where CO_2 flux is the modelled CO_2 flux at a particular light level, P_{max} is the maximum CO_2 uptake of the curve, PAR is the amount of light in $\mu mol\ m^{-2}\ s^{-1}$, K_m is a calculated constant and R_{eco} is the modelled maximum CO_2 release (equivalent to the R_{eco} measurement with the dark chamber cover). Following Brown (2001), P_{max}, K_m and R_{eco} were calculated using the Solver function in Excel (Microsoft, 2010), which was set to maximise the R^2 of the modelled curve through the measured data points (see Figure A.1 in Appendix A).

The calculated P_{max} and R_{eco} values for each site and management combination were separately regressed against the average chamber temperatures recorded during NEE measurements, giving a linear equation for the P_{max} relationship with temperature and an exponential equation for the R_{eco} temperature relationship (see Figure A.2). Monthly averages of PAR were calculated from the hourly measured AWS recordings and these were regressed by site for each year against the K_m values. This produced linear equations, for which the intercept was set to zero, for each year-site-management regression (see Figure A.3).

The hourly air temperatures recorded by the AWS were used in the regression-derived equations to calculate P_{max} and R_{eco} on an hourly basis to derive the hourly maximum C uptake and C release, respectively, for the DN, FI and LB managements. Likewise, the equation derived from the regression of K_m and PAR was used with the average monthly PAR measurements from the AWS to calculate a value of K_m for each month of each year for each site and management combination. These values were used in Eq.2.4 to derive the net hourly C flux (NEE) for each of the three managements at each of the three sites for each of the four years and were summed to derive monthly (see Figure A.4) and yearly fluxes. The measured NEE fluxes were compared to the modelled NEE fluxes to check that the model was adequate to be used to upscale the fluxes (Appendix A). Fluxes were converted from µmol CO_2 m^{-2} s^{-1} to g C m^{-2} y^{-1}.

2.2.6.4 Upscaling CH_4 flux measurements

The CH_4 fluxes were upscaled for FI, LB and DN managements, due to these being the three main managements across the catchments. CH_4 fluxes were upscaled using time only as they showed no relationship with any environmental variable. Each CH_4 flux was converted from nmol CH_4 m^{-2} y^{-1} to g C m^{-2} y^{-1} using the molecular weight of CH_4. Fluxes were then averaged across managements and sites within years.

2.2.6.5 Upscaling DOC and POC measurements

DOC and POC exports were upscaled for each sub-catchment at each site. DOC and POC concentrations were converted from mg C L^{-1} to g C m^{-3}. As only one DOC and one POC concentration measurement was available for each month, it was assumed that these concentrations represented the average concentrations for that month. Therefore, monthly DOC and POC concentrations were multiplied by the total monthly water loss of the sub-catchment and summed to express DOC and POC export in g C m^{-2} y^{-1}.

2.2.6.6 NECB calculation

For the site NECBs in 2012, all the measurements for NEE, CH_4, DOC and POC were averaged across the three managements which were upscaled as this period was before management implementation. In 2013, 20% of each sub-catchment was mown and burnt respectively, leaving 80% of the entire catchment unmanaged. Therefore, NEE and CH_4 were averaged across managements proportionally for each site, i.e.:

$$\text{Average site NEE}=(0.8\times\text{DN NEE})+(0.1\times\text{FI NEE})+(0.1\times\text{LB NEE}) \qquad \text{Eq.2.5}$$

where DN NEE is the upscaled NEE flux for the DN management at a site, FI NEE is the upscaled NEE flux for the FI management and LB NEE is the upscaled NEE flux for the LB management.

DOC and POC exports were averaged across the two sub-catchments of a site to derive the site DOC and POC exports. This meant that the three main management types were all incorporated in the same proportions as used for NEE and CH_4 due to each stream receiving runoff from the whole sub-catchment, which contained unmanaged areas. For 2015, the same principle was applied to calculating the site NECBs but an additional 20% of each sub-catchment was managed meaning 60% of the whole of each catchment was unmanaged with 20% burnt and 20% mown.

For the management NECBs, the NEE and CH_4 fluxes were averaged for each management across the three sites. Similarly, the DOC and POC exports for the FI and LB managements were averaged across the three sites. As there was no DN sub-catchment, the average of the FI and LB DOC and POC exports were used for the DN management DOC and POC exports, as much of each sub-catchment was unmanaged.

2.3 Results

The different site approaches to burning and mowing described in Methods resulted in slightly different outcomes at each site. At Nidderdale, burnt areas received even and consistent burns which were all contained within the designated areas but were surrounded by a narrow (2-3 m) mown strip. On mown areas, the cutter left large piles of brash in some places with other areas barely covered. As the brash dried, it was distributed more evenly by the wind (although this was the case on all sites).

At Mossdale, one fire in 2013 (which contained a plot) moved faster than expected, spreading out of the designated area and burning into the moss layer in places. All burnt areas at Mossdale visually appeared more thoroughly burnt (shorter stick was left and more of the moss was blackened) than at the other sites. The mowing at Mossdale produced the finest brash.

At Whitendale, some fires did not burn well in 2013 due to partial snow cover which left large amounts of stick and much of the leaf litter on the ground. In a few cases, *Calluna* plants were effectively singed rather than burnt, some even retaining a few leaves. Fires burnt more thoroughly in 2015. The brash left on the mown areas at Whitendale was much coarser (2-5 cm long) than that at the other two sites. Additionally, two areas due to be burnt at Whitendale in 2015 were accidentally mown before burning. Therefore, the areas designated for burning were moved so the mown areas were not included. This resulted in the full 20% of the burnt catchment being put to flames but there was also an additional 0.6 ha of mown *Calluna* within the catchment. However, these mown areas were on the periphery of the burnt catchment and did not include any plots, making it unlikely that any C results were greatly affected.

2.3.1 NEE flux measurements

The Full Light NEE flux measurements ranged from -19.91 to 5.96 µmol CO_2 m^{-2} s^{-1} with an average of 0.74 µmol CO_2 m^{-2} s^{-1} (negative values represent CO_2 uptake) and the R_{eco} fluxes were between 0.03 and 15.64 µmol CO_2 m^{-2} s^{-1} with a mean of 2.72 µmol CO_2 m^{-2} s^{-1}. During Full Light measurements, the PAR ranged from 15 to 1951 µmol m^{-2} s^{-1} with an average of 531 µmol m^{-2} s^{-1}. Soil temperatures were very similar between the pairs of Full Light and R_{eco} measurements (less than 0.5°C).

There was a significant interaction between managements and time period for both Full Light and R_{eco} NEE fluxes ($F_{5, 988} = 12.34$, $p < 0.0001$ and $F_{5, 991} = 12.52$, $p < 0.0001$, respectively). There were no significant differences in 2012 under either light condition (Figures 2.3 and 2.4). Post-management, DN plots took up significantly more CO_2 than any other management under Full Light conditions (Figure 2.3; $p < 0.001$ for all) and emitted significantly more CO_2 during R_{eco} fluxes (Figure 2.4; $p < 0.001$ for all). On average across the post-management period, FI and BR plots lost CO_2 in Full Light, resulting in BR+Sph plots showing significantly lower fluxes than both of these managements (Figure 2.3; $p < 0.01$ for both) and LB+Sph plots having significantly lower fluxes than FI plots (Figure 2.3; $p < 0.01$). Conversely, BR+Sph plots had higher R_{eco} CO_2 fluxes than FI and BR plots (Figure 2.4; $p < 0.01$ for both) and LB+Sph plots had higher fluxes than FI plots (Figure 2.4; $p < 0.01$). LB plots also emitted significantly more CO_2 than FI plots during R_{eco} measurements (Figure 2.4; $p < 0.001$).

Both Full Light and R_{eco} NEE fluxes differed significantly between sites ($F_{2, 5} = 11.38$, $p = 0.0131$ and $F_{2, 47} = 7.57$, $p = 0.0014$, respectively), with Mossdale having the highest CO_2 uptake in Full Light conditions and greatest CO_2 loss during R_{eco} measurements (Table 2.3). Nidderdale showed the smallest uptake of CO_2 under Full Light conditions and the lowest CO_2 loss during R_{eco} measurements.

There was also a significant three-way interaction between management, time period and site under both NEE conditions ($F_{10, 988} = 1.90$, $p = 0.0411$ and $F_{10, 991} = 2.29$, $p = 0.0117$ for Full Light and R_{eco} NEE measurements, respectively). There were no significant differences pre-management. At Nidderdale, DN plots had significantly lower CO_2 fluxes than any other management in Full Light and higher during R_{eco} measurements (Figures 2.5 and 2.6; $p < 0.001$ for all). The same was true at Mossdale, apart from FI plots also showing lower R_{eco} fluxes than LB and BR+Sph plots (Figure 2.6; $p < 0.001$ for both). At Whitendale, plots under DN management only showed greater CO_2 uptake under Full Light conditions, and greater CO_2 release during R_{eco} measurements, than plots under FI, LB and BR managements (Figures 2.5 and 2.6; $p < 0.001$ for all). Similarly, FI plots took up less CO_2 during Full Light measurements but lost less CO_2 during R_{eco} measurements than LB+Sph and BR+Sph plots (Figures 2.5 and 2.6; $p < 0.001$ for all). BR plots also emitted significantly less CO_2 during R_{eco} measurements than LB+Sph and BR+Sph plots (Figure 2.6; $p < 0.01$) and LB plots also lost significantly less than LB+Sph plots (Figure 2.6; $p < 0.04$).

PAR had a non-linear effect on the Full Light fluxes (Table 2.4). The negative PAR coefficient and the smaller positive PAR^2 coefficient together demonstrate that an increase in PAR increased CO_2 uptake but by a smaller amount than the previous increment. Likewise, soil temperature had a similar non-linear effect on R_{eco} fluxes (Table 2.4). Here the linear Tsoil coefficient was positive and the $Tsoil^2$ coefficient was negative, demonstrating that with every unit increase in temperature, the increase in CO_2 flux declined. Soil temperature also significantly affected Full Light NEE fluxes (Table 2.4) although the overall direction of the effect was unclear due to increasing temperature causing both greater uptake and release of CO_2. Despite the inclusion of both PAR and soil temperature in the analysis, the month in which measurements were taken also significantly affected both the Full Light NEE and R_{eco} fluxes (Table 2.4), suggesting that instantaneous light levels and soil temperatures were not the only factors influencing the CO_2 fluxes.

2.3.2 SR flux measurements

SR fluxes ranged from 0.05 to 10.22 µmol CO_2 m^{-2} s^{-1} with a mean of 1.56 µmol CO_2 m^{-2} s^{-1}. There was no significant interaction between management and time period ($F_{5, 992} = 1.84$, p =

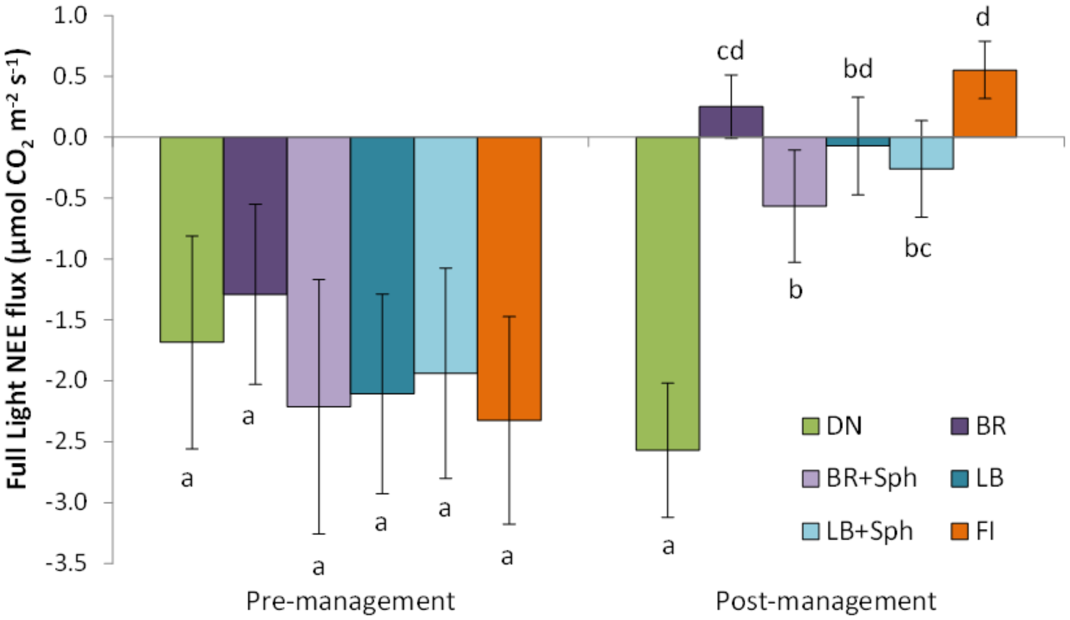


Figure 2.3 Means (± 95% confidence intervals) of Full Light net ecosystem exchange fluxes of all sites combined for the pre- and post-management periods.

Management codes are used where DN represents unmanaged, FI represents burnt, BR represents mown plots with the brash removed, LB represents mown plots with the brash left, BR+Sph represents mown plots with the brash removed and *Sphagnum* propagules added and LB+Sph represents mown plots with the brash left and *Sphagnum* propagules added. Different letters within each time period indicate significant differences between managements.

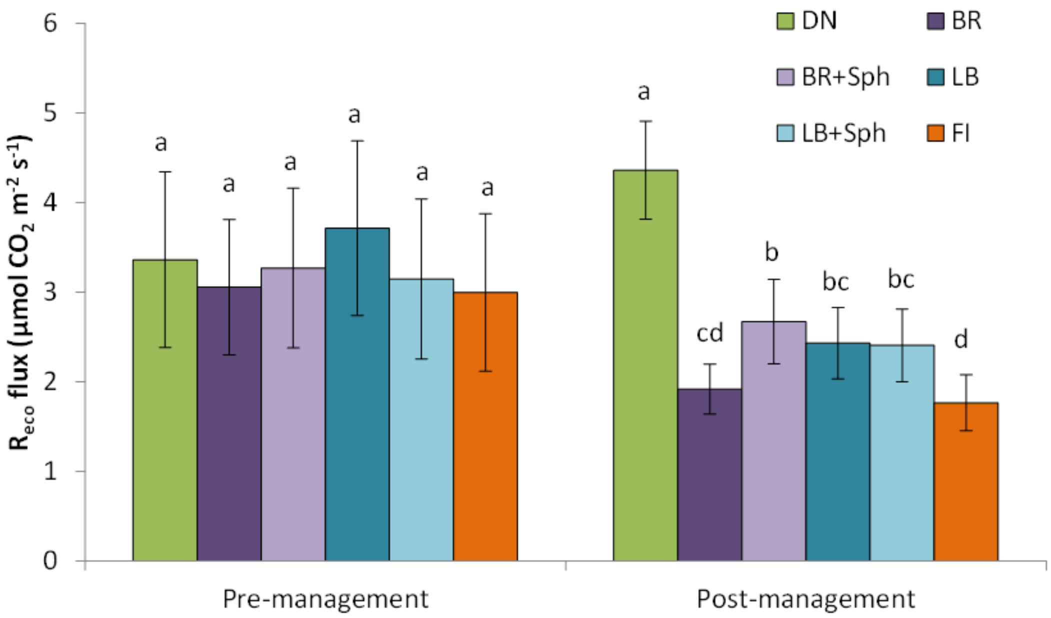


Figure 2.4 Means (± 95% confidence intervals) of the R_{eco} component of the net ecosystem exchange fluxes of all sites combined for the pre- and post-management periods. Management codes are used where DN represents unmanaged, FI represents burnt, BR represents mown plots with the brash removed, LB represents mown plots with the brash left, BR+Sph represents mown plots with the brash removed and *Sphagnum* propagules added and LB+Sph represents mown plots with the brash left and *Sphagnum* propagules added. Different letters within each time period indicate significant differences between managements.

Table 2.3 Means (± 95% confidence intervals) of measured gas fluxes and water concentrations for each site across years.

Values in bold indicate significant differences between sites.

Type of measurement	**Nidderdale**	**Mossdale**	**Whitendale**
Full Light NEE (µmol CO_2 m^{-2} s^{-1})	**-0.31 ± 0.24**	**-1.16 ± 0.33**	**-0.75 ± 0.26**
R_{eco} (µmol CO_2 m^{-2} s^{-1})	**2.51 ± 0.25**	**2.96 ± 0.31**	**2.70 ± 0.27**
SR (µmol CO_2 m^{-2} s^{-1})	1.53 ± 0.14	1.80 ± 0.18	1.35 ± 0.13
CH_4 (nmol CH_4 m^{-2} s^{-1})	21.59 ± 10.54	112.17 ± 42.47	25.95 ± 8.32
DOC concentration (mg C L^{-1})	**26.59 ± 3.57**	**26.00 ± 3.40**	**18.36 ± 2.44**
POC concentration (mg C L^{-1})	**2.84 ± 0.51**	**1.56 ± 0.36**	**2.13 ± 0.74**

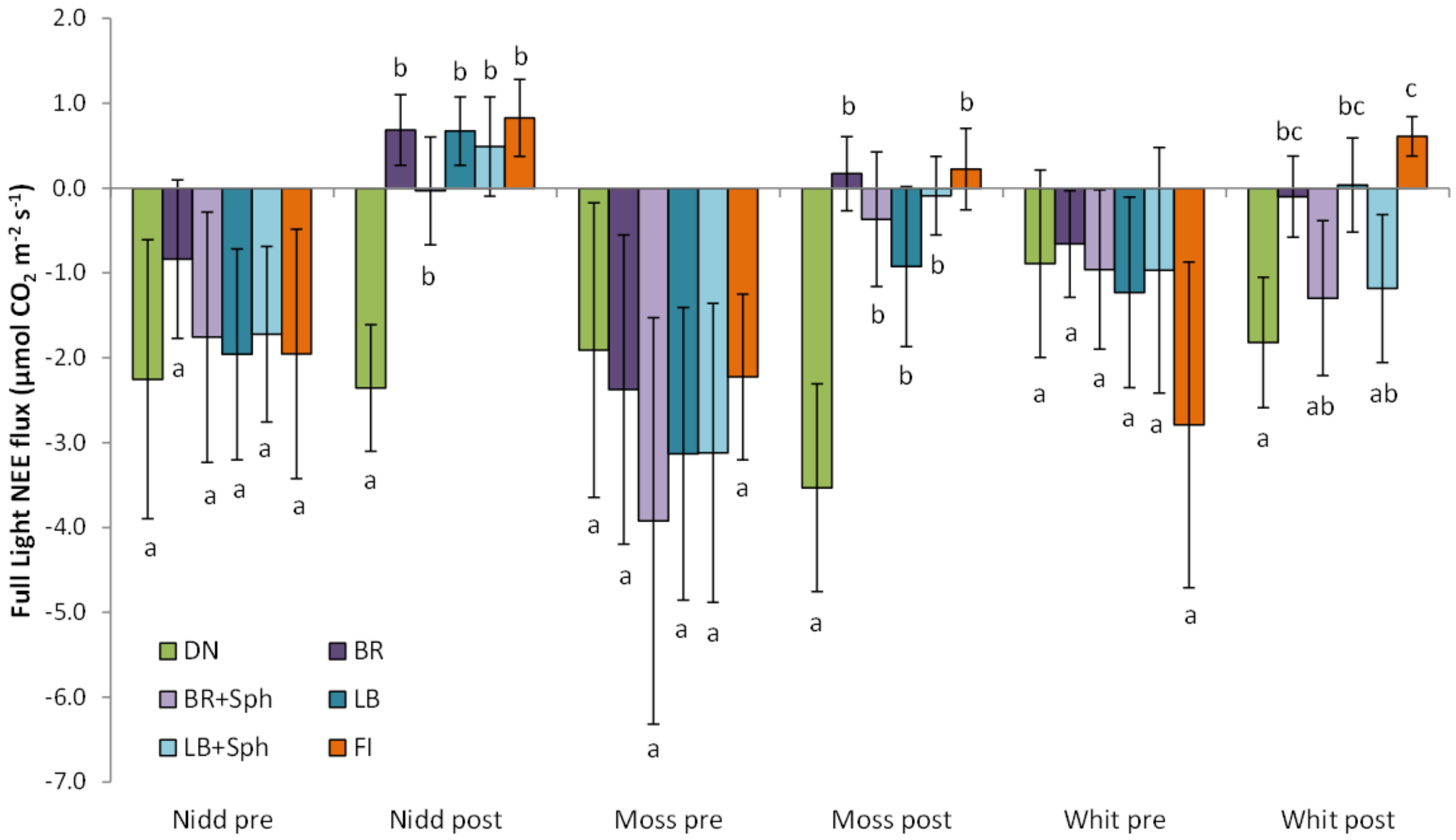


Figure 2.5 Means (± 95% confidence intervals) of Full Light net ecosystem exchange fluxes of each site for the pre- and post-management periods. Management codes are used where DN represents unmanaged, FI represents burnt, BR represents mown plots with the brash removed, LB represents mown plots with the brash left, BR+Sph represents mown plots with the brash removed and *Sphagnum* propagules added and LB+Sph represents mown plots with the brash left and *Sphagnum* propagules added. Different letters within each time period indicate significant differences between managements.

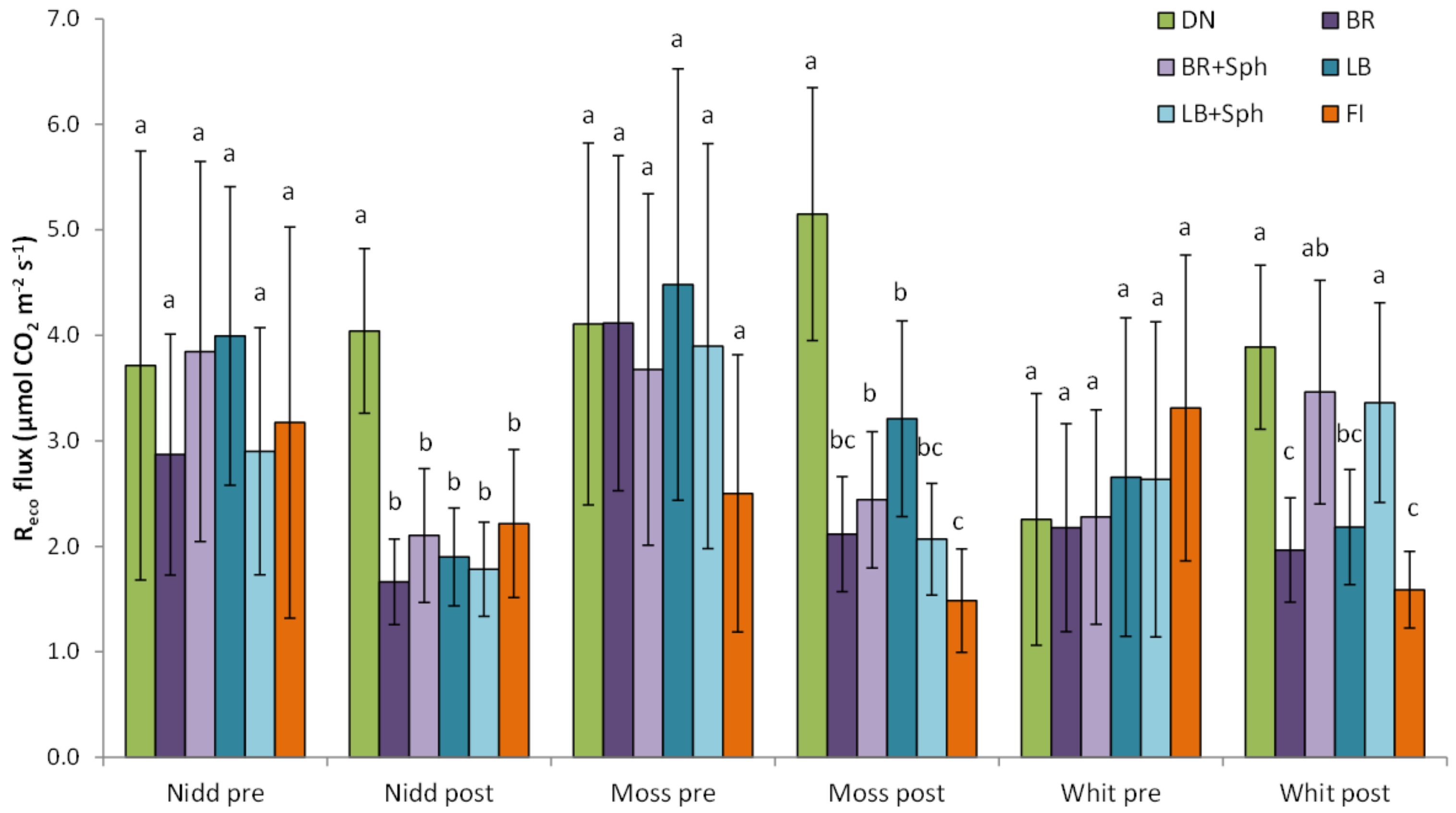


Figure 2.6 Means (± 95% confidence intervals) of the R_{eco} component of net ecosystem exchange fluxes of each site for the pre- and post-management periods. Management codes are used where DN represents unmanaged, FI represents burnt, BR represents mown plots with the brash removed, LB represents mown plots with the brash left, BR+Sph represents mown plots with the brash removed and *Sphagnum* propagules added and LB+Sph represents mown plots with the brash left and *Sphagnum* propagules added. Different letters within each time period indicate significant differences between managements.

0.10). On average, Mossdale had the highest SR and Whitendale the lowest (Table 2.3) but these differences were not significant ($F_{2, 4} = 3.28$, $p = 0.14$), nor was there a significant interaction between management, time period and site ($F_{10, 992} = 0.74$, $p = 0.68$).

Tsoil ranged from -1.4°C to 35.8°C. SR fluxes showed a significant positive non-linear relationship with Tsoil (Table 2.4). As with the NEE fluxes, the month during which measurements were taken also significantly affected the SR flux (Table 2.4), with greater fluxes occurring in summer months, particularly July.

2.3.3 CH_4 flux measurements

The CH_4 fluxes were very variable, ranging from -137.6 to 4203 nmol CH_4 m^{-2} s^{-1}. The mean flux was 53.2 nmol CH_4 m^{-2} s^{-1}, although over 28% of the fluxes were 0 nmol CH_4 m^{-2} s^{-1} meaning that the median flux was only 2.0 nmol CH_4 m^{-2} s^{-1}. There was no significant interaction between management and time period ($F_{5, 1036} = 0.58$, $p = 0.72$). On average, Mossdale released substantially more CH_4 than either Nidderdale or Whitendale (Table 2.3) but this difference was not significant ($F_{2, 6} = 2.93$, $p = 0.14$), nor was there a significant interaction between management, time period and site ($F_{10, 1036} = 0.76$, $p = 0.66$).

The CH_4 fluxes were negatively, but not significantly, affected by WTD (i.e. as the water table dropped further below the peat surface, CH_4 fluxes decreased; Table 2.4). However, as with NEE and SR fluxes, the month of measurement significantly affected the CH_4 fluxes (Table 2.4), with greatest fluxes in August.

2.3.4 DOC and POC measurements

It was not possible to determine either DOC or POC concentrations at Nidderdale or Mossdale in July 2013 as the streams were too dry. There were an additional seven samples from which it was not possible to determine POC as the water volumes collected were not sufficient, due to dry or partially frozen streams. The DOC concentrations in the stream water ranged from 3.9 to 87.5 mg C L^{-1} across sites and averaged 23.6 mg C L^{-1}. The POC concentrations were much lower, ranging from 0.2 to 28.0 mg C L^{-1} with an average of 2.2 mg C L^{-1}. The daily average stream flow on days which water samples were taken ranged from 0.2 to 132000 L h^{-1} with a mean of 14468 L h^{-1}.

There was a significant interaction between management and time period for both DOC and POC concentration ($F_{1, 120} = 7.74$, $p = 0.0063$ and $F_{1, 146} = 13.18$, $p = 0.0047$, respectively). There was only a significant difference in DOC concentration before management implementation (Figure 2.7; $p < 0.001$) with the DOC concentration in the burnt catchment remaining relatively

Table 2.4 Results from linear mixed effects models between each C measurement and its explanatory variables.

Only explanatory variables which assessment of the log-likelihood ratio (used after dropping variables stepwise; see Section 2.2.6.2) determined as explaining sufficient variation are shown. Measurement types followed by (sqrt) were square-root transformed before being used in the models. Variables followed by ^{2} were squared before being used in the models.

Type of measurement	**Explanatory variable**	**Coefficient**	**df (numerator, denominator)**	**F-value**	**p-value**
Full Light NEE (sqrt)	PAR	-0.0026	1, 859	81.46	**<0.0001**
	PAR^2	1.3×10^{-6}	1, 942	54.99	**<0.0001**
	Tsoil	0.0484	1, 893	35.47	**<0.0001**
	Month	-	8, 788	37.24	**<0.0001**
R_{eco} (sqrt)	Tsoil	0.0600	1, 1032	32.96	**<0.0001**
	Tsoil^2	-0.0008	1, 1029	11.00	**0.0009**
	Month	-	8, 1011	25.76	**<0.0001**
Soil respiration (sqrt)	Tsoil^2	0.0008	1, 842	186.98	**<0.0001**
	Month	-	8, 920	69.94	**<0.0001**
CH_4 (sqrt)	WTD^2	-0.0002	1, 980	2.27	0.13
	Month	-	8, 1037	28.31	**<0.0001**
DOC concentration	Daily stream flow	-0.0673	1, 125	1.70	0.19
	Month	-	11, 27	1.85	0.09
POC concentration	Daily stream flow	0.0019	1, 26	0.06	0.82
	Month	-	11, 9	5.66	**0.0082**

stable over time and that in the mown catchment increasing from pre- to post- management. The opposite was true for POC concentrations where concentrations from the mown catchment remained relatively similar but those from the burnt catchment were significantly lower after management implementation than those from the mown catchment (Figure 2.8; $p < 0.001$) but were slightly higher before.

Both DOC and POC concentrations were significantly different between sites ($F_{2, 80} = 21.56$, $p < 0.0001$ and $F_{2, 151} = 7.56$, $p = 0.0007$, respectively). Nidderdale had the highest DOC and POC concentrations, whilst Whitendale showed the lowest DOC concentrations and Mossdale the lowest POC concentrations (Table 2.3). There was no significant interaction between management, time period and site for either DOC or POC concentrations ($F_{2, 118} = 1.31$, $p = 0.27$ and $F_{2, 140} = 0.24$, $p = 0.79$, respectively).

Despite DOC and POC being carried in the stream water, the average daily stream flow did not significantly affect DOC or POC concentrations (Table 2.4). Both DOC and POC concentrations were highest in July. POC concentrations were significantly affected by month whereas DOC concentrations were not (Table 2.4).

2.3.5 NECBs

From the component C fluxes and exports, it was possible to determine the NECB for each site and for three management regimes (FI, LB and DN). The site NECBs indicate that on average over the four years of measurements, Nidderdale was a net source of C, whilst Mossdale acted as a net sink of C and Whitendale was virtually in equilibrium (Table 2.5). This was not the case for all three sites in every year. Nidderdale consistently acted as a net source of C, although the amount lost varied year on year, with more than five times as much C emitted in 2015 as in 2013 (Table 2.5). Mossdale acted as a very strong C sink in 2013, and to a lesser extent in 2014, compared to either of the other sites in any year (Table 2.5). However, this site became a strong C source in 2015, losing more C than gained the previous year. Whitendale lost C in two years and gained C in two years, including gaining in 2015 when both Nidderdale and Mossdale showed a net loss of C (Table 2.5).

The NEE fluxes at Mossdale were consistently negative, meaning that CO_2 uptake via photosynthesis outweighed CO_2 loss by respiration, whereas respiration was greater than photosynthesis at Nidderdale in 2013 and 2015, with an average overall NEE C loss across years, and at Whitendale in 2012 and 2014 (Table 2.5). On average, the largest C loss at Nidderdale and Whitendale was via DOC export in stream water, whereas at Mossdale C loss from CH_4 emissions was greater that from DOC export (Table 2.5). However, the largest C

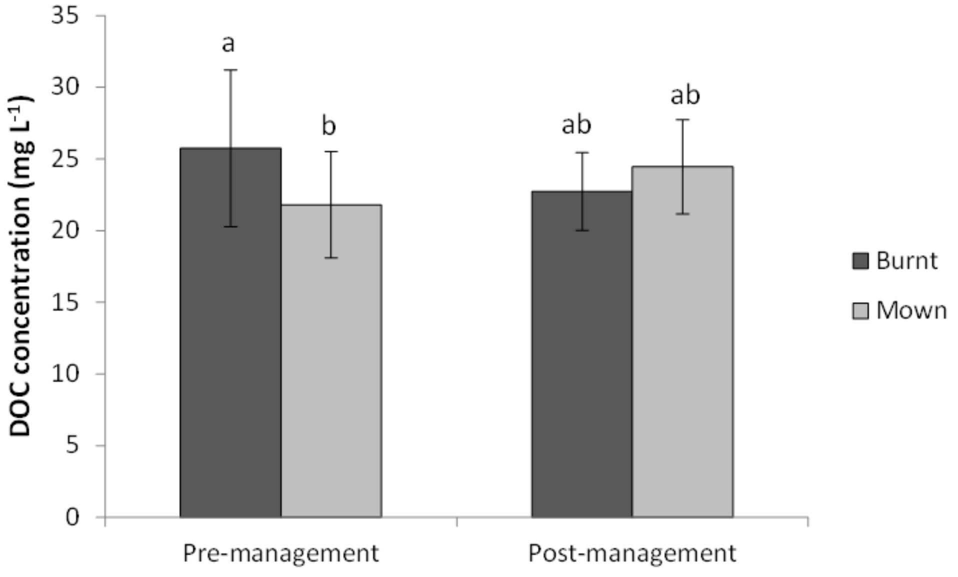


Figure 2.7 Means (± 95% confidence intervals) of dissolved organic carbon concentrations for the burnt and mown catchments of all sites combined for the pre- and post-management periods. Different letters indicate significant differences between management and time period interaction.

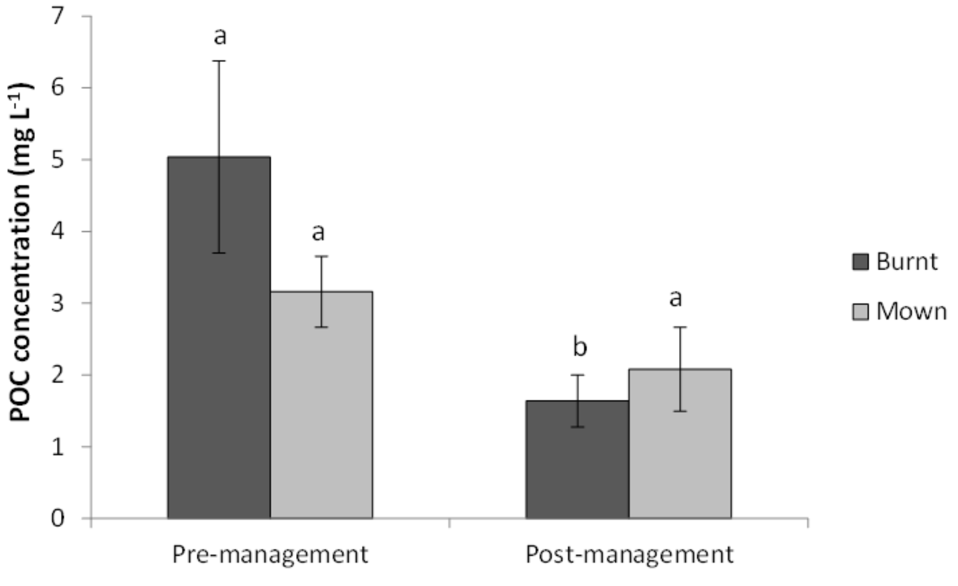


Figure 2.8 Means (± 95% confidence intervals) of particulate organic carbon concentrations for the burnt and mown catchments of all sites combined for the pre- and post-management periods. Different letters indicate significant differences between management and time period interaction.

Table 2.5 The net ecosystem C balance (NECB) at Nidderdale, Mossdale and Whitendale for 2012-2015.

Net ecosystem exchange (NEE) fluxes , CH_4 fluxes, dissolved organic C (DOC) export and particulate organic C (POC) export were upscaled to yearly site values (g C m^{-2} y^{-1}) and summed to derive NECB. All NECB components were proportionally averaged across managements accordingly (see NECB calculation in Methods for details). Values in bold indicate the longer-term 4-year means of the site NECBs and of each C component.

Site	**Year**	**NEE**	**CH_4**	**DOC**	**POC**	**NECB**
Nidderdale	2012	-29.43	1.30	45.19	9.62	26.69
	2013	0.57	1.10	13.27	1.69	16.63
	2014	-10.09	10.77	26.74	2.15	29.57
	2015	61.89	4.83	17.98	2.50	87.19
	4-year mean	**5.73**	**4.50**	**25.80**	**3.99**	**40.02**
Mossdale	2012	-76.26	7.60	41.97	4.68	-22.01
	2013	-317.07	5.66	19.30	0.64	-291.47
	2014	-187.07	35.98	31.98	0.65	-118.46
	2015	-2.12	110.23	27.51	1.42	137.04
	4-year mean	**-145.63**	**39.87**	**30.19**	**1.85**	**-73.72**
Whitendale	2012	7.72	1.26	36.50	6.00	51.49
	2013	-86.63	1.00	11.71	1.81	-72.11
	2014	53.73	2.95	26.50	1.26	83.69
	2015	-100.70	17.92	18.56	2.28	-61.94
	4-year mean	**-31.47**	**5.60**	**23.32**	**2.84**	**0.28**

source at each site was not the same every year. In 2012 and 2013, DOC export represented the largest C loss at all sites but CH_4 effluxes released more C at Mossdale in 2014 and 2015, and the NEE flux released most C at Nidderdale in 2015 and Whitendale in 2014 (Table 2.5). On average, POC represented the smallest return of C to the atmosphere at all sites but C loss from POC export was greater than that from CH_4 release at Nidderdale and Whitendale in 2012 and 2013 (Table 2.5).

The management NECBs demonstrate that over the three years after management implementation, both the burnt and mown areas acted as C sources whereas the unmanaged areas acted as C sinks (Table 2.6). Interestingly, all three of the management groups which were upscaled also acted as small C sources in 2012 (Table 2.6), which was before management was carried out. Whilst both burnt and mown areas consistently lost C across years, unmanaged areas strongly took up C in 2013, gained a moderate amount of C in 2014 and showed only a very small net gain of C in 2015 (Table 2.6).

In the pre-management year, the annual NEE flux of all three management groups was negative (Table 2.6), indicating that the vegetation was taking up more C than the systems were losing. This was consistently the case in all years for the unmanaged areas, whereas the NEE measurements on burnt and mown areas showed a net C loss in the post-management years (Table 2.6). Interestingly, the burnt NEE fluxes were highest in 2013, the year in which burning took place, and decreased in the subsequent two years whereas mown NEE fluxes were a lot lower in 2013 than either 2014 or 2015 (Table 2.6). The largest return of C to the atmosphere from unmanaged areas was via CH_4 effluxes but was via DOC export for burnt and mown areas (Table 2.6). However, this was not consistent, with mown and unmanaged areas losing more C as CH_4 than DOC in 2015 (Table 2.6). On average, POC export represented the smallest C loss for all managements, although C loss via POC export was greater than C loss through CH_4 effluxes for all three managements in 2012 and for mown areas in 2013 (Table 2.6).

2.4 Discussion

There was no attempt made to reconcile the differences in burning and mowing methods and outcomes between the sites as it was deemed that the variation probably encompassed the range of burning and mowing techniques across Northern England. Therefore, any results emerging consistently from the burnt and mown areas across all sites were likely to be directly attributable to the management itself and results where all site values were grouped together are likely to be applicable to other sites.

Table 2.6 The net ecosystem C balance (NECB) for burnt, mown and unmanaged areas for 2012-2015.

Net ecosystem exchange (NEE), CH_4, dissolved organic C (DOC) and particulate organic C (POC) were upscaled to yearly management values (g C m^{-2} y^{-1}) and summed to derive NECB. All NECB components were averaged across sites. The DOC and POC components for unmanaged areas are the averages of values for burnt and mown areas. Values in bold indicate the 3-year post-management (2013-2015) means of the management NECBs and of each C component.

Management	Year	NEE	CH_4	DOC	POC	NECB
Burnt (FI)	2012	-31.72	2.93	39.23	7.03	17.47
	2013	143.47	1.80	15.24	1.13	161.19
	2014	126.07	20.25	26.69	1.53	174.54
	2015	74.74	13.56	21.29	1.83	111.42
	3-year mean	**114.76**	**11.72**	**21.07**	**1.50**	**149.05**
Mown (LB)	2012	-18.44	0.74	43.21	6.51	32.02
	2013	79.76	0.99	14.28	1.63	96.66
	2014	138.96	28.04	30.12	1.18	198.30
	2015	129.36	21.73	21.41	2.30	174.79
	3-year mean	**116.03**	**16.92**	**21.94**	**1.70**	**156.59**
Unmanaged (DN)	2012	-47.80	6.49	41.22	6.77	6.68
	2013	-195.88	2.94	14.76	1.38	-176.79
	2014	-92.89	14.36	28.41	1.35	-48.77
	2015	-90.77	62.11	21.35	2.07	-5.24
	3-year mean	**-126.51**	**26.47**	**21.50**	**1.60**	**-76.94**

2.4.1 CO_2 fluxes

The management types which showed high CO_2 uptake during Full Light flux measurements also showed high CO_2 release during R_{eco} flux measurements (Figures 2.3 and 2.4). This effect is likely due to the size of the plants, particularly as the DN plots showed both the greatest drawdown and release of CO_2 in Full Light and dark (R_{eco}) conditions respectively. Larger plants usually host more leaves, and hence should have a greater photosynthetic capacity, which would explain the greater CO_2 uptake during Full Light conditions. Larger plants also are likely to produce more respiration, not only from their leaves and roots, but also from decomposition of leaf and root litter, which is likely to be greater beneath larger plants (Brown & MacFadyen, 1969).

Interestingly, there was no significant difference in SR fluxes between managements. Although the lack of a management effect is likely to be because of the removal of the aboveground vegetation, the SR fluxes still contained litter decomposition (except on the BR and BR+Sph plots) and belowground autotrophic respiration from plant roots spreading below the cleared SR circle. Given the lack of difference in SR fluxes between managements and that SR fluxes were substantially lower than R_{eco} fluxes (Table 2.3), this suggests that it is the aboveground part of the plants which have the greatest influence on the CO_2 fluxes. Dixon *et al.* (2015) demonstrated that NEE fluxes were best explained by the height of the *Calluna* plants on blanket bogs dominated by *Calluna* in the South Pennines and Peak District, which would support this suggestion. However, Dixon *et al.* (2015) concluded that, where *Calluna* was dominant, the NEE flux would almost always result in a net loss of CO_2 and that this loss would increase with *Calluna* height. In the present study, the difference between the average post-management DN Full Light and R_{eco} fluxes was 1.79 μmol CO_2 m^{-2} s^{-1}, which was smaller than the difference between the equivalent averages for any other management (compare Figures 2.3 and 2.4). This suggests that the net CO_2 loss does not necessarily increase when taller *Calluna* plants are present. Additionally, the NEE component of the NECB should all be positive if the results of Dixon *et al.* (2015) were applicable in this study. This was not the case with only the burnt and mown areas showing positive fluxes, even in 2013, despite any *Calluna* regrowth being extremely short (see Chapter 3). The difference between the present study and that of Dixon *et al.* (2015) could lie in the area studied: their study was conducted in the South Pennines and Peak District which have become virtually devoid of *Sphagnum* mosses due to historic air pollution, whereas all sites in this study possessed some *Sphagnum*, as well as *Eriophorum*, which would have contributed to C drawdown by photosynthesis. Alternatively, or additionally, Dixon *et al.* (2015) inserted their collars into the peat by up to 5 cm, probably severing some surface roots and enhancing decomposition, whereas collars in the present study were only placed on the surface.

It is possible that a difference in temperature caused the differences in NEE fluxes between sites (Table 2.3), as temperature had a significant effect on both NEE fluxes (Table 2.4), although, as the difference in annual average temperature between the three sites is only 0.6°C, it is unlikely that it was temperature alone. As PAR also had a significant effect on NEE fluxes, site differences could have been caused by different light levels occurring during measurements. However, Nidderdale received most light on average (data not shown) and took up least CO_2 during Full Light measurements (Table 2.4), making this an unlikely cause. Plant size may also be a contributing factor to the site differences as Mossdale had both the largest plants (greatest volume) and the highest CO_2 uptake and loss for Full Light and R_{eco} fluxes, respectively (Table 2.3). The substantially higher cover of *Sphagnum* mosses at Mossdale compared to the other two sites (see Chapter 3) may have also contributed to Mossdale having the highest Full Light NEE fluxes, as *Sphagnum*-dominated peat has been shown to release less CO_2 than peat dominated by other species (Dunn *et al.*, 2015). Whilst high *Sphagnum* cover does not explain why Mossdale released most CO_2 in the dark, the greater size of the *Calluna* plants may have offset the presence of *Sphagnum*. However, as the site NEE fluxes were compared across managements, it is likely that the differences in management techniques between the sites also accounted for some of the measured difference in the fluxes.

This is emphasised by the three-way interactions between site, management and time period. The absence of significant differences in NEE fluxes before management implementation gives credence to the post-management differences occurring as a direct consequence of the managements. Nidderdale had the most uniform management and indeed there were only differences between DN NEE fluxes (under both light conditions) and NEE fluxes of all other managements; there were no differences between any mown or burnt NEE fluxes. Mossdale and Whitendale had less uniform burns and, accordingly, some FI NEE fluxes differed from NEE fluxes of some of the mowing managements. Interestingly, both managements which included *Sphagnum* addition at Whitendale took up nearly as much CO_2 as DN plots during Full Light measurements and lost nearly as much through R_{eco}. Whilst this may have been due to these plots regenerating more rapidly than other plots by chance, particularly since this was not observed at Mossdale or Nidderdale, it hints at some *Sphagnum* establishment and growth. There was, however, no noticeable increase in *Sphagnum* cover on the LB+Sph or BR+Sph plots on any site.

Perhaps of greatest note, is that plots under FI management were the only areas to consistently lose CO_2 during Full Light NEE measurements across the post-management period (Figure 2.5). As Mossdale appeared to have the most thorough burns and Whitendale the least, it might be expected that Mossdale FI plots would lose more C than Whitendale FI plots. This was not the case, with the opposite being true. Ward *et al.* (2012) found no differences in NEE fluxes between burnt and unburnt areas of *Calluna*-dominated blanket bog at Moor House National Nature Reserve but showed that burning increased the transfer rate of newly fixed C below ground. As Mossdale was more thoroughly burnt, there were fewer plants present which were capable of assimilating C compared to Whitendale FI plots, meaning that belowground respiration was likely to be lower.

Despite not showing significantly different Full Light NEE fluxes from all other managements when viewed across all sites (Figure 2.3), the consistent C loss from FI plots shows that the vegetation was slower to recover and regenerate following burning than mowing (FI plots had more unvegetated ground than any other management; see Chapter 3). However, the NECB showed that the burnt areas actually lost slightly less C on average over the three years than the mown areas, largely due to the C lost from the NEE component of the NECB decreasing every year following burning whereas the C lost via NEE in the mown areas increased. Although it is not possible to compare the mown NEE fluxes with other studies as, to the author's knowledge, there are none on peatlands, the trajectory of the C loss from NEE on the burnt and mown areas suggests that over a longer time period, the C losses from mown areas could be substantially greater than from the burnt areas. This could be because, although *Calluna* regeneration is slower after fire than after cutting (see Chapter 3), new growth is more vigorous and will overtake *Calluna* regrowth of mown areas. Alternatively, vegetation other than *Calluna* may also have contributed to the differences in NEE fluxes as burning has been shown to significantly affect other peatland species (Harris *et al.*, 2011), particularly bryophytes (Burch, 2008).

2.4.2 CH_4 fluxes

Vegetation has also been shown to have a strong association with CH_4 fluxes (Couwenberg *et al.*, 2011; Gray *et al.*, 2013; Lai *et al.*, 2014). Although the areas on which the CH_4 fluxes were measured had had the surface vegetation removed, the belowground plant system was not directly disturbed and vegetation removal was only from a small (20 cm diameter) circle, meaning that the vegetation - and management - was still expected to have influenced these measurement areas. All measurement areas in burnt and mown plots received burnt material and brash, respectively, in a manner similar to that of the rest of the plot. Additionally, management of moorland vegetation can alter the structure of the soil microbial community (Ward *et al.*, 2012), which could plausibly affect the CH_4 dynamics. Therefore, as both burning and mowing greatly altered the surface vegetation around the measurement areas, it was expected that this would also alter CH_4 fluxes but there was no significant differences between managements. This is in contrast to the findings of Ward *et al.* (2007) who measured lower CH_4 fluxes on burnt compared to unburnt plots. To the author's knowledge, there are no studies comparing CH_4 emissions on blanket bogs which have been managed by mowing. However, CH_4 emissions from the different mowing managements at all sites spanned such a wide range of values, including the lowest CH_4 flux being measured from a BR+Sph plot and the highest from a BR plot (both at Mossdale), which therefore encompassed all DN and FI values, it appears that mowing did not affect CH_4 fluxes, at least, not consistently.

A possible reason for this could be not the vegetation removal itself, but that the removal of vegetation lowered the surface of some of the measurement circles, causing waterlogging. Higher WTDs and standing water create conditions conducive to CH_4 formation (Lai *et al.*, 2014), yet it was observed that waterlogged areas did not always produce the highest CH_4 fluxes and some of the highest fluxes came from measurement areas which were not waterlogged at all. This suggests that the waterlogging caused by vegetation removal is unlikely to have greatly elevated the CH_4 fluxes.

Further to this, Mossdale showed substantially higher CH_4 fluxes than Nidderdale and Whitendale, was generally established to be the wettest site (i.e. higher precipitation and WTDs, often with areas of standing water) and therefore WTD was deemed to be the most likely factor influencing CH_4 fluxes. However, although WTD^2 was included in the linear mixed model, it did not have a significant effect on CH_4 fluxes again suggesting that waterlogging is unlikely to have had a great effect on the CH_4 fluxes. Soil temperature was also initially included in the linear mixed model but did not explain sufficient variation in the CH_4 fluxes to be included in the final model. It is surprising that neither temperature nor WTD showed a significant effect on CH_4 fluxes, since the link between these in wetlands is well established (Liblik *et al.*, 1997; Hargreaves & Fowler, 1998; MacDonald *et al.*, 1998; Lai *et al.*, 2014).

Interestingly, Ward *et al.* (2007) also did not find a significant effect of WTD on CH_4 fluxes in their study, which was also conducted on a northern England blanket bog which was dominated by *Calluna*. Therefore, a long term effect of high *Calluna* cover, regardless of whether *Calluna* shoots are present during measurements, may be to alter the relationship between WTD and CH_4 fluxes. This is particularly pertinent since peatlands typically are a net source of CH_4 (Clymo & Pearce, 1995; Hargreaves & Fowler, 1998; Ward *et al.*, 2007; Gray *et* *al.*, 2013) whereas some net CH_4 oxidation was observed in this study (negative CH_4 fluxes), suggesting alterations in the peatland system. As the month of measurement was the only variable tested to exhibit a significant effect on CH_4 fluxes and fluxes were highest by far in August, when plant growth rates are typically all high, an increase in root exudates of labile C for methanogenesis, combined with interaction between plants, temperature and WTD may help to explain the CH_4 fluxes observed.

Part of the reason that the CH_4 fluxes between managements and sites did not show significant differences could be due to the large number of fluxes which were recorded as zero, although these null fluxes were well distributed between the managements and sites. It is important to note however, that a flux recorded as zero did not necessarily mean that there was no CH_4 production or oxidation; in most cases, it was the result of a very small flux from which the variation was too high to produce the required R^2 value, but in a few cases, it was due to a non-linear flux. Additionally, measurements made with the UGGA resulted in higher average CH_4 fluxes overall than those made with cover boxes, which would appear to suggest a mismatch between the two approaches. However, the discrepancy was not due to the difference in measurement methods (the two methods were comparable to one another when deployed one after another on the same areas; A. Heinemeyer, pers. comm.), it was due to the difference in measurement method resolution: the UGGA recorded CH_4 concentrations approximately every 2 seconds whereas the cover boxes produced five time points over 50 minutes. This resulted in far fewer fluxes being discarded and recorded as zero from the UGGA than cover box method (52 over 7 full sets of measurements compared to 271 over 8 full sets of measurements). Therefore, it is likely that there is some error associated with the average CH_4 fluxes and, more importantly, with the upscaled CH_4 fluxes. Although it is difficult to quantify the magnitude and direction of this error, it is likely to be small.

In contrast to the large proportion of CH_4 fluxes recorded as zero, there were some exceptionally high fluxes, including two over 4000 nmol CH_4 m^{-2} s^{-1}. In the dataset incorporating nearly 5000 chamber measurements of CH_4 fluxes complied by Levy *et al.* (2012) from 21 sites across the UK, the highest flux is over an order of magnitude smaller. However, Levy *et al.* (2012) set 200 nmol CH_4 m^{-2} s^{-1} as an arbitrary threshold and assumed measurements over this were due to measurement error or ebullition.

High CH_4 measurements were not excluded from the dataset in the present study for a number of reasons. Whilst it is possible that the extreme values recorded were as a result of ebullition, the majority of CH_4 fluxes which were greater than 200 nmol CH_4 m^{-2} s^{-1} - of which there were only 58 out of the 1116 recorded CH_4 fluxes across the four years - were measured with the UGGA. When using the UGGA, episodic ebullition events (bubbles) were detected on site where a rapid increase in CH_4 emission was followed by a rapid decrease and these measurements were repeated, thereby greatly reducing the probability that ebullition events were recorded. However, steady ebullition could have produced a linear flux during the five minute chamber closure period which would not have been detected as such. The use of boardwalks (e.g. as in Cooper *et al.*, 2014) may have reduced the likelihood that walking close to the plots facilitated the ebullition of CH_4 but boardwalks were not used, partly due to logistics and partly due to the potential of boardwalks to alter or affect surrounding vegetation (e.g. Lindsay & Ross, 1993). Additionally, steady ebullition may not have been as a result of movement around the plots forcing CH_4 out; changes in air pressure or WTD can also release CH_4 stored within the peat matrix (Glaser *et al.*, 2004; Tokida *et al.*, 2007). By including these potential ebullition events, the average CH_4 fluxes may be higher than most previously published but may actually be closer to the real fluxes, as small chambers deployed periodically usually miss recording ebullition (see Baird *et al.* (2009) for a discussion of measuring episodic ebullition with static chambers), which can represent a substantial contribution to the total CH_4 flux (Tokida *et al.*, 2007).

Although the highest values are substantially higher than previously published values, they are of the same order of magnitude as the maximum 'hotspot' values as those in Fenner *et al.* (2011), who recorded values up to ~1000 nmol CH_4 m^{-2} s^{-1} on a rewetted peatland. Cooper *et al.* (2014) also observed that rewetted peatland sites had 'hotspot' areas, where CH_4 emissions greatly increased in some areas but not others. Whilst the peatlands in this study were not undergoing rewetting, they have a history of management meaning they are not pristine peatlands and therefore may function in different ways, potentially similar to rewetted peatlands. In a study investigating effects of management, Ward *et al.* (2007) noted that CH_4 emissions were higher on grazed areas compared to ungrazed, but could not find a reason to explain why. Similarly, Dinsmore *et al.* (2009) found 0.5% of their study catchment was responsible for 12% of its emissions but this did not always relate to rush or sedge dominated areas. These studies all point to large variability in CH_4 fluxes over small scales with the dominant factors controlling the fluxes being unclear. Excluding high CH_4 measurements from the NECB almost certainly underestimates the true amount of C lost or gained from a peatland. The plots in this study were not measured for CH_4 before being selected. If plots on superficially similar ground can produce such a wide range of CH_4 fluxes, then it is highly likely that there are other areas across the catchments also producing a similar, perhaps even wider, range of values. For these reasons, the very high CH_4 fluxes measured in this study were not only included in the analysis of instantaneous site and management fluxes, but were also included in the yearly NECB calculations. Additionally, as the only factor which showed a significant influence on the CH_4 fluxes was the month of measurement, the fluxes were upscaled using time only as it was not clear whether any other variable would be appropriate to use on these sites. Therefore, this incorporated the assumption that the whole of each site was similar to the *Calluna* dominated areas measured, but all sub-catchments contained areas dominated by rushes or sedges, usually by streams and ditches, which often produce higher CH_4 emissions than the rest of a site (Evans *et al.*, 2015). Although there appeared to be no relationship between sedge cover and CH_4 fluxes (data not shown), it is possible that sedges contributed to some of the highest CH_4 fluxes.

2.4.3 DOC and POC concentrations and exports

The significant difference in DOC concentrations between the burning- and mowing-designated catchments pre-management combined with the absence of a difference post-management (Figure 2.7) suggests that, if there was any true management effect on the DOC concentrations, this was smaller than the natural difference between the sub-catchments. However, as the POC concentrations followed the same pattern (Figure 2.8), and the post-management difference was significant between burnt and mown areas, management may have impacted upon the DOC concentrations, albeit only weakly. If this were the case, given that the burnt sub-catchments produced higher DOC and POC concentrations pre-management and lower concentrations post-management than the mown sub-catchments, this suggests that burning caused lower DOC and POC concentrations than mowing.

Although there are very few, if any, studies which specifically assess the effect of mowing peatland vegetation on DOC and POC concentrations, there have been a number investigating the effects of burning, many of which focus on sites in northern England. In a review of the impacts of burning on DOC, Holden *et al.* (2012) noted that, across catchment-scale studies, burning appeared to cause an increase in water colour, and hence probably DOC concentrations, although it was not always possible to disentangle the effect of burning from the high *Calluna* cover on the areas which were burnt. Nevertheless, Yallop & Clutterbuck (2009) observed higher DOC concentrations in areas where burning caused bare peat and Clutterbuck & Yallop (2010) related an increase in humic coloured DOC to the level of moorland burning in six catchments. The results in the present study contradict these correlative analyses, with both DOC and POC concentrations in the stream water from burnt sub-catchments being lower post-management than pre-management. As DOC concentrations from mown sub-catchments were slightly higher post-management and POC concentrations only slightly lower than pre-management, this suggests that mowing may be detrimental to water quality. This is of particular importance to water companies, for whom higher DOC concentrations can pose treatment problems (Singer, 1999; Clay *et al.*, 2012).

A possible reason for the difference between the DOC concentrations from mown and burnt catchments could be related to nutrient release. Monitoring of water chemistry at Blue Lough in Northern Ireland, both before and after a large wildfire, revealed a sharp increase in nitrate concentration post-fire which caused a drop in pH and DOC concentration (Evans *et al.*, 2016). The prescribed burning in the present study probably produced a similar response to the wildfire at Blue Lough whereas mowing probably resulted in more nutrients being retained in the brash and preventing a large change in pH - over time, more nutrients may be released from the brash which could alter pH and hence DOC concentrations.

In terms of the peatland NECB however, the concentrations of DOC and POC in the stream water are not necessarily important; instead, it is the total export of DOC and POC which matters. When considered in the context of global C cycling, it is the ultimate fate of the exported C which is most important. There is evidence to show that much of the DOC and POC exported from peatlands in stream water is decomposed to CO_2 and CH_4 downstream and released to the atmosphere (Billett *et al.*, 2004; Worrall & Moody, 2014), meaning that DOC and POC export from peatland should be considered as C loss in the same way as the terrestrial gas fluxes. The DOC and POC exports from the burnt and mown sub-catchments are remarkably similar (Table 2.6), despite the differences in concentrations. It is not possible to conclusively state that whether management in general affects DOC and POC exports, due to the paired sub-catchment approach meaning that there were no unmanaged sub-catchments available from which to sample. However, although it should be noted that less than half of each sub-catchment had actually been subject to management by the end of 2015, the similarity between the sub-catchment DOC and POC exports suggests that neither management had a more detrimental or beneficial effect than the other on aquatic C losses.

In contrast, there was a much greater difference in both DOC and POC concentrations (Table 2.3) and exports (Table 2.5) between the sites. Specifically, Whitendale showed much lower DOC concentrations and exports than the other two sites and the same was true with POC at Mossdale. As the daily stream flow had little effect on either DOC or POC concentration, it is unlikely that differences in rainfall and runoff between the sites caused these differences. However, the lower DOC concentrations and exports could be related to the lower cover of *Calluna* (see Chapter 3) as high *Calluna* cover is associated with higher DOC concentrations (Vestgarden *et al.*, 2010; Armstrong *et al.*, 2012; Dunn *et al.*, 2015). This might also partially explain why DOC exports were so much lower at all three sites post-management (Table 2.5) because substantial amounts of *Calluna* had been removed from all sub-catchments. Similarly, as *Sphagnum* cover was substantially higher at Mossdale than at the other two sites (see Chapter 3), the water flow across the peat may have been slower, reducing erosion and hence POC concentrations and exports (Evans *et al.*, 2014). However, this does not explain the substantially lower POC concentrations and exports from all sites and management post-management as there were no changes in *Sphagnum* cover (see Chapter 3). Interestingly, DOC concentration was the only C measurement on which the month of measurement did not have a significant effect. However, as both DOC and POC concentrations were highest in July, it is likely that DOC and POC release were affected either by greater activity of plants and soil organisms (Briones *et al.*, 2010; Wild *et al.*, 2016) or by the warmer and drier conditions (Freeman *et al.*, 2001a). As the sites are in the same region of northern England and therefore receive similar weather, the most likely explanation for the observed differences in DOC and POC concentrations and exports between the sites is a difference in plant composition and growth, and the associated belowground assemblage.

2.4.4 NECBs

The site NECBs indicate that, over the four years of the study, one site was a C sink, one was a C source and the third was practically C neutral. It is interesting that the three sites, which were all superficially similar at the start of the study and were all managed in the same ways throughout the study, should produce three very different outcomes. Just as pertinent, none of the site NECBs are consistent between years, and year is not necessarily a predictor of the magnitude nor direction of the overall C flux. For example, the only year in which Mossdale lost C - and this loss was substantial (Table 2.5) - was 2015, with Nidderdale also showing its greatest C loss in the same year, whereas Whitendale took up more C in 2015 than it had lost in 2012. Given that all three sites are located in north-west England and are therefore subject to similar climatic conditions, and that all three sites are *Calluna* dominated, the opposite direction of the NECBs for different sites in the same years suggests that there are likely to be unmeasured or even unknown factors influencing the C dynamics on these peatlands.

Annual variability in the NECB has been recorded elsewhere. Dinsmore *et al.* (2010) calculated that a lowland peatland in Scotland took up an average of 69.5 g C m^{-2} y^{-1}. Whilst the site was a sink for both years used in their study and averaged -28 g C m^{-2} y^{-1} over a 10 year period (Helfter *et al.*, 2015), an earlier study (Billett *et al.*, 2004) found that the same site lost 8.3 g C m^{-2} y^{-1}. Whilst there were some methodological differences between the two shorter term studies, the primary difference was the size of the NEE fluxes. This is also the case in this study with the NEE fluxes showing the greatest variability of any component of the NECB for all three sites. Other studies have demonstrated a large variability in NEE between years (Lafleur *et al.*, 2003; Roulet *et al.*, 2007; Ward *et al.*, 2007; Worrall *et al.*, 2009) but none of these measured the NECB at more than one site, meaning that much of the inter-annual variability was attributed to changes in the climate whereas, in this study, climate appears less likely to be the sole cause of the variation. One potential reason for the NEE balance for Mossdale in 2015 being close to neutral could be due to damage of the *Calluna* plants by either heather beetle (*Lochmaea suturalis* (Thomson)) or *Phytophthora* species. It was noted that substantial areas of *Calluna* were browned or reddened and there is evidence showing *Calluna* dieback following infestation by either heather beetle (Scandrett & Gimingham, 1991) or *Phytophthora* species (Orlikowski *et al.*, 2004), thus decreasing photosynthesis and CO_2 uptake. However, it was not determined whether heather beetles or *Phytophthora* species were responsible for this discolouration of *Calluna*, nor whether this was the specific cause of the reduction in C uptake during NEE. Given the C uptake via NEE was over 100 times lower at Mossdale in 2015 compared to 2013, more research into the causes of NEE variability and the impacts of heather beetle and *Phytophthora* damage is needed.

Conversely to most other studies, DOC export did not always represent the largest C loss at all sites in all years. This is because some of the CH_4 fluxes recorded in this study were an order of magnitude higher than those recorded or calculated in C budgets in other studies. Dinsmore *et al.* (2010) calculated C losses via CH_4 to be less than 0.5 g C m^{-2} y^{-1}, although they did acknowledge that these values were low for a UK peatland. However, higher values of 2.7 mg CH_4 m^{-2} h^{-1} measured in Caithness using an eddy co-variance system (Hargreaves & Fowler, 1998), and of 3.5 mg CH_4 m^{-2} h^{-1} measured at Moor House (Ward *et al.*, 2007), are still at the lower end of those recorded in this study. Even average 'hotspot' CH_4 fluxes of 2.2 mg CH_4 m^{-2} h^{-1} from gullies at Moor House (McNamara *et al.*, 2008) and of 8.2 mg CH_4 m^{-2} h^{-1} from ditches in Wales (Cooper *et al.*, 2014) are substantially lower than the 2015 average (12.6 mg CH_4 m^{-2} h^{-1}) at Mossdale.

These higher CH_4 values were prevalent across all sites and managements in 2014 and 2015 when the UGGA was used for measurements. However, as previously mentioned, the measurement methods used were comparable to each other so it is unlikely that method alone caused the high variability and high CH_4 emissions. Additionally, Mossdale lost over 7 g C m^{-2} y^{-1} via CH_4 in 2012 when only cover boxes were used, which is substantially higher than the 2015 CH_4 efflux from Nidderdale or the 2014 loss from Whitendale (Table 2.5). Therefore, as with NEE, factors such as climate and change in vegetation and microbial assemblages may have played a role in causing the high inter-annual and inter-site variability of the CH_4 fluxes.

Alternatively, all CH_4 fluxes were measured using small static chambers, regardless of the measurement method. Static chambers are a sensitive method of measurement but are prone to a host of problems, including pressure effects, flux inhibition through high concentration build-ups, leaks and spatial variability of gas fluxes (Denmead, 2008). Therefore, the chambers used in this study, not just for CH_4 fluxes but also for NEE fluxes, may have caused errors in the measurements. Measurement errors or bias related to spatial variability of fluxes are most likely in this study, especially given the wide range of fluxes on superficially similar plots. If the measurement circles had higher or lower fluxes compared to the rest of the plot, these differences would have been multiplied when the annual fluxes were calculated. Techniques such as eddy covariance solve many of the problems associated with static chambers (Denmead, 2008), although these are usually costly methods and present the problem of obtaining reliable results from smaller areas of interest (Baird *et al.*, 2009), such as the different management areas. Whilst the measurement methods may have introduced errors, all plots were measured in the same way which reduces the chance that a particular site or management accumulated more errors than any other.

The NECB for the three different managements also showed considerable inter-annual variability, partially as they were calculated using measurements from all sites. However, it is clear that management also affected the NECB. All three managements were small C sources in the pre-management year (Table 2.6). Although the unmanaged areas lost least C in 2012, the consistency with which these areas took up CO_2 via NEE post-management, compared to the consistency and magnitude with which the burnt and mown areas lost C through NEE fluxes, strongly suggests that the DN management was most beneficial in terms of the peatland NECB.

This is in direct contrast to the findings of Ward *et al.* (2007) who found that areas at Moor House which were burnt had a more negative NEE flux (i.e. took up more C) than unburnt areas. However, although the burnt areas were on a 10 year burn rotation, which is comparable to this study, the plots were measured nine years into the cycle, whereas this study currently only extends three years into the burn cycle. Therefore it is likely that the vegetation was much more established on the burnt Moor House plots and possibly the *Calluna* was starting to degenerate on the unburnt plots, whereas the *Calluna* on the burnt plots in this study was still very short and at fairly low cover (see Chapter 3). A study by Clay *et al.* (2015) investigated more recent burns but also showed burning appeared to increase C uptake, with young burn scars (1-6 years since burning) tending to have a negative NEE flux. Nonetheless, when other C losses were included, Clay *et al.* (2015) demonstrated that all ages of burn caused C release, which agrees with this study. Additionally, Garnett *et al.* (2000) used spheroidal carbonaceous particles as a marker in the peat to calculate that areas on a 10 year burn cycle had an average reduced sequestration rate of 73 g C m^{-2} y^{-1} after three burn cycles compared to unburnt areas. If reduced C sequestration is taken to mean C loss, this value is much closer to the annual C loss calculated for burnt areas in the present study.

It is not possible to compare the mown NECB to literature values as, to the author's knowledge, this is the first C budget calculated for UK peatlands under a rotation mowing regime. It is, however, possible to compare to the NECB for burnt areas. The most striking feature is the similarity between the annual burnt and mown NECBs (Table 2.6). The CH_4, DOC and POC values all follow a similar yearly pattern. The main difference is that, after management implementation, C loss via NEE from the mown areas was lowest directly following mowing and increased thereafter, whereas that from burnt areas was highest after burning and C loss declined over the following two years. It is not possible to tell from only three years of post-management data what the likely trajectory of the NEE fluxes will be, although C loss from NEE on both burnt and mown areas was lower in 2015 than 2014, hinting that vegetation was beginning to recover and take up C.

Based on these values, it appears that burning is slightly more beneficial for the peatlands in terms of C sequestration than mowing. However, no measurements were taken during management implementation. For mowing, there should not have been any additional C loss to the usual fluxes as the brash was left (only BR and BR+Sph plots had brash removed and these mowing management variants were not upscaled). For burning, the majority of the standing plant biomass was pyrolysed, although a small amount of this remained as charcoal, and there may also have been some peat lost in the fires. The latter was not possible to quantify but, from measuring standing biomass on plots before burning (see Chapter 3), 587 (± 155) g C m^{-2} of *Calluna* was burnt, with only about 7 g C of that biomass turned into charcoal (see Chapter 4). Therefore, for a 10 year burn cycle, an additional 58 g C m^{-2} y^{-1} should be added to the NECB for burnt areas. Although biomass was not lost via mowing, tractors were used to carry out the mowing and therefore the amount of C released from the fuel used should also be accounted for. Based on fuel usage figures provided by the gamekeepers and contractors, average emissions for a 10 year management cycle from fuel usage were 14.1 g C m^{-2} y^{-1} for mowing and 1.9 g C m^{-2} y^{-1} for burning (butane was used to start the fires and a fire break was cut using a tractor at Nidderdale in 2013; A. Heinemeyer, pers. comm.). This meant that for the first three years following management implementation, burnt areas lost more C than mown areas (209 g C m^{-2} y^{-1} and 171 g C m^{-2} y^{-1}, respectively).

2.4.5 Uncertainties and limitations

There is great uncertainty associated with upscaling gas fluxes from small static chambers to the landscape scale (Fox *et al.*, 2008). This is particularly pertinent in this study due to the large variations in flux measurements even when sampled on the same day and under similar conditions. As already discussed, this variation could mean that measurement circles had higher or lower fluxes than other areas of the plots, potentially giving rise to errors. Static chambers are also host to a range of other problems which may have also introduced measurement errors. Additionally, the landscape was heterogeneous but all plots were focussed on areas which had a high cover of *Calluna* in 2012, meaning that when fluxes were upscaled, it was assumed that the fluxes from the plots were representative of the whole site or management, which is not necessarily the case. Nevertheless, the NECBs were calculated similarly across all sites and managements and therefore it is likely that any error created in assuming homogeneity between plot and landscape when upscaling chamber measurements was similar across catchments, thus justifying comparison between the sites and managements.

One factor which was not always consistent between managements was the amount of *Calluna* in the chamber during measurements. Whilst fluxes were corrected for the differences in volumes (see Section 2.2.4.1), it was sometimes difficult to place the PAR sensor inside the chamber without it being shaded by branches in areas where *Calluna* was very tall and dense. This was very similar between the plots on a site pre-management but this problem was removed from all but DN plots post-management, as mowing and burning greatly reduced *Calluna* height and density. Therefore, for DN plots, PAR measurements may have been slightly lower than actual PAR levels meaning that upscaled NEE fluxes may have overestimated the CO_2 uptake. However, given the huge difference in post-management NEE fluxes between the managed and unmanaged plots, it is highly unlikely that any shading of the PAR sensor would alter the conclusion that managed areas lose far more C than unmanaged areas.

Despite the streams collecting water from the whole of each sub-catchment and therefore stream DOC and POC not being subject to the same uncertainties with upscaling as chamber measurements, the management DOC and POC exports included water from areas under different managements. Both burnt and mown sub-catchments had areas (over half the sub-catchment in total) which had not been burnt or mown, meaning that monitoring would need to continue for longer than the full 10 year rotation in order to measure the effects of only burning or mowing. Additionally, the unmanaged DOC and POC exports were estimated from the burnt and mown sub-catchments, although this is actually likely to be more accurate due to this being the dominant management type across the catchments throughout the study.

This study did not quantify all the C inputs and losses of the peatland system. DOC inputs from precipitation were not measured or estimated, nor were dissolved inorganic carbon (DIC), dissolved CO_2 or dissolved CH_4, which are all C species exported in stream water. However, DIC and dissolved CH_4 exports tend to be very small, usually smaller than POC exports (Worrall *et al.*, 2003b; Billett *et al.*, 2004; Dinsmore *et al.*, 2010), thus only adding a few grams extra to the annual NECB. Similarly, the DOC inputs from precipitation tend to be very small (Worrall *et al.*, 2003b; Neal *et al.*, 2005) and therefore may cancel out, or even exceed, the DIC and dissolved CH_4 losses. Although DOC usually represents the largest aquatic C export, there is increasing evidence that dissolved CO_2 in stream water can be an important peatland C loss (Hope *et al.*, 2001; Dinsmore *et al.*, 2010). As there was little variation in DOC exports and one of the main aims of this study was to compare the effects of different managements on C fluxes, it is likely that the dissolved CO_2 export also was similar between managements. This is because DOC and POC in the stream contribute to the dissolved CO_2 (Worrall & Moody, 2014) and therefore it is reasonable to expect their concentrations to be related, although there is some debate as to the sources contributing to dissolved CO_2 and therefore whether it should be included at all in the NECB (Billett *et al.*, 2015). Nonetheless, it is acknowledged that C loss in the NECBs presented here may be underestimated by between 2 g C m^{-2} y^{-1} (Worrall *et al.*, 2003b) and 23 g C m^{-2} y^{-1} (Billett *et al.*, 2015), although these values would not change any site or management NECB shown here to be a C sink to a C source.

2.4.6 Conclusions

The site NECBs presented here demonstrate that peatlands managed as grouse moors can represent either a C source or a C sink. Moreover, a single site may not consistently sequester or release C every year, mainly due to variability in NEE, and similar sites may not necessarily follow the same yearly pattern as one another. This is an important consideration given that most studies on peatlands usually consider a single site and often measurements are only made over the course of a couple of years at most. Additionally, CH_4 fluxes made a greater contribution to the NECB in some years and at some sites than DOC exports did, highlighting both the huge variability in these fluxes and the lack of knowledge of peatland C fluxes and the factors influencing them. Gaining long-term datasets of peatland NECB across a number of sites is thus a necessity in order to fully understand the C dynamics of peatlands, particularly those which are likely to be subject to disturbances such as management, and to decipher the controls on the annual variation.

Both the plot level C fluxes and the upscaled management NECBs show that DN management was the most beneficial for the peatlands in terms of C sequestration and, out of the three managements which were upscaled, was the only one to show a net gain of C. There was very little difference in the NECBs of burnt and mown areas, although there appeared to be differences in the time taken for the system to respond, suggesting that management by either method had a similar effect on the peatland C dynamics. When the loss of the plant biomass was taken into account, mowing appeared to be a slightly more favourable option to burning even when tractor fuel consumption was considered. In order to fully assess whether this is the case long-term and whether C uptake declines as vegetation ages on DN areas, the effects of management on the peatland NECB need determining over at least one full 10 year management rotation.

Grouse moors use management to encourage new shoots for grouse to eat. Although new shoots can grow from adventitious rooting of prostrate stems (MacDonald *et al.*, 1995), younger *Calluna* is thought to be more nutritious (Moss, 1967; Savory, 1978). Therefore, if the aim was to increase C sequestration - or at least minimise C loss - whilst still maintain a healthy grouse population, ceasing all forms of management may place these two objectives at odds with one another. There is also the possibility that stopping all management could cause an increased fuel load, which risks increasing wildfire frequency and intensity (Allen *et al.*, 2013), although this may depend upon the moisture content of the peat and on the vegetation present. *Sphagnum* mosses can aid water storage in the peat (Bain *et al.*, 2011; Evans *et al.*, 2014) and therefore management which encourages *Sphagnum* could help to solve both the problem of an increased fuel load and a lack of new shoots by increasing peat moisture content and encouraging regeneration by adventitious rooting. Furthermore, photosynthesis is the only means by which a peatland can take up C, and *Calluna* quantity and quality is of utmost importance to the grouse for which the moors are currently managed, meaning that vegetation dynamics should also be taken into account when considering the benefits and drawbacks of the different management options.

3 Vegetation Matters: Comparing the vegetation dynamics on three UK peatlands under alternative grouse moor managements

3.1 Introduction

Boreal and subarctic peatlands contain over one third of the world's total soil C store(Gorham, 1991; Turunen *et al.*, 2002) and are mainly composed of the dead remains of *Sphagnum* mosses (Bain *et al.*, 2011). Bryophytes, including *Sphagnum*, grow from the tip as the base dies (Glime, 2007), allowing layers of dead vegetation to build up (Clymo, 1992). A combination of the large empty hyaline cells in *Sphagnum* (Lindsay, 2010) and the low hydraulic conductivity of the amorphous dead matter (Ingram, 1982) creates and maintains high water table depths (WTDs) and anaerobic conditions. This lack of oxygen retards decomposition, thus creating layers of semi-decomposed vegetation which constitute peat.

In the UK, much of the peat is found in the uplands in the form of blanket bog, which began forming after the end of the last ice age between 8,000 and 10,000 years ago as a result of a wetter climate (Charman, 2002). Changes in the climate alter the water balance of peatlands (Mauquoy *et al.*, 2002), causing a shift in the assemblage of *Sphagnum* species, all of which have different growth and decomposition rates, hence altering peat accumulation rates (Belyea & Malmer, 2004).

The wide array of hydrological conditions under which *Sphagnum* species thrive means that peatlands are relatively resilient to changes in the climate. However, *Sphagnum* mosses are wetland species meaning that there are concerns that anthropogenic climate change may negatively affect peatlands (e.g. Gorham, 1991). There is extensive evidence that drainage by humans can substantially lower the water table (see Holden *et al.* (2004) for a review), increasing oxygen ingress and hence decomposition (Freeman *et al.*, 2001b). The predicted decrease in summer precipitation, combined with rising temperatures (Murphy *et al.*, 2009), is expected to have similar effects.

Blanket bogs support unique assemblages of plants (Thompson *et al.*, 1995) and the vegetation composition can give an indication of the condition of a bog (Natural England, 2010), as each species requires a different set of hydrological conditions. *Eriophorum* species, which also contribute to peat formation (Bain *et al.*, 2011), and *Sphagnum* species can occupy a wide range of WTDs (depending on the specific species) whilst rushes, sundews (*Drosera* species) and bogbean (*Menyanthes trifoliata*) tend to be found only in wetter areas and dwarf shrubs including bilberry (*Vaccinium myrtillus*),crowberry (*Empetrum nigrum*), ling heather (*Calluna vulgaris*) and cross-leaved heather (*Erica tetralix*) tend to dominate drier areas (Lindsay, 2010). According to a report in 2010 (Natural England, 2010) on the state of English peatlands, over 50% of blanket bogs did not support peat forming vegetation and the majority displayed signs of damage. Given the size of the C store and the rarity of this habitat, as well as its importance in regulating both water quality and quantity (Freeman *et al.*, 2001a; Holden *et al.*, 2007a; Armstrong *et al.*, 2012; Evans *et al.*, 2014), conservation of and restoration to actively growing peatlands which can regulate their own water tables is crucial, in order to avoid exacerbating climate change by C release (Dorrepaal *et al.*, 2009) and to preserve the breeding habitats of rare birds (Carroll *et al.*, 2011).

As well as drainage and climate change threatening the stability of the long-term storage and accumulation of C in blanket bogs, burning also alters the WTD and species composition of peatlands. Although areas of the English uplands have been subject to periodic burning for centuries to improve sheep grazing (Simmons, 2003), a rise in the popularity of grouse shooting 100-200 years ago saw an intensification in burning which still continues, with the area of new burns in the uplands almost doubling between the 1970s and 2000 (Yallop *et al.*, 2006). Wildfires are a natural phenomenon on peatlands but the prescribed burning associated with grouse management occurs much more frequently (Allen *et al.*, 2013), usually on an 8-25 year rotation (Clay *et al.*, 2015). Therefore, although *Sphagnum* mosses are capable of recovery following infrequent burning, regular exposure to fire causes damage and drying (Holden *et al.*, 2007a), which can increase fire intensity (Turetsky *et al.*, 2011). This can damage and remove other vegetation (Holden *et al.*, 2007a), leading to bare ground, erosion and C loss (Evans *et al.*, 2006, 2014).

Burning tends to lead to *Calluna* dominance (although if an incorrect rotation is chosen for the prevailing conditions, *Eriophorum vaginatum* or *Molinia caerulea* can dominate; Grant *et al.*, 1963; Hobbs, 1984; Lee *et al.*, 2013), which is ultimately the aim, as *Calluna* is the main food source for red grouse (*Lagopus lagopus scoticus* (Latham)). However, *Calluna* has a high rate of evapotranspiration (Worrall *et al.*, 2007) which also dries the peat, reducing *Sphagnum* growth and recovery (Campeau & Rochefort, 1996). Additionally, although burning can initially increase the cover of species other than *Calluna* (Harris *et al.*, 2011), when *Calluna* plants mature, the canopy closes over and this can severely reduce the amount of light reaching the ground (Gimingham, 1960), ultimately reducing species diversity (Harris *et al.*, 2011).

Burning is not only undertaken to increase the cover of *Calluna* but also to remove old growth and encourage new shoots. Whilst this is believed to be necessary on drier areas, *Calluna* growing on deep wet peat can regenerate naturally by layering (i.e. adventitious rooting) of stems (MacDonald *et al.*, 1995), bringing the necessity of burning for regeneration into question. Indeed, government guidelines recommend against burning on areas where peat is deeper than 50 cm (Defra, 2007), although this advice is not always heeded, with an estimated 30% of blanket bogs being burnt (Natural England, 2010). However, burning removes dead litter and unproductive woody growth, which reduces the risk of wildfire occurrence and intensity (Albertson *et al.*, 2010; Allen *et al.*, 2013). Additionally, it has long been advocated that burning produces more nutritious *Calluna* shoots by releasing the nutrients from the old growth and making them available for the new plants (Lovat, 1911; Picozzi, 1968).

Both nitrogen (N) and phosphorus (P) are important nutrients for red grouse (Moss, 1969, 1972), particularly for chicks (Savory, 1977) and breeding hens (Moss *et al.*, 1975). There is, in fact, evidence that grouse selectively feed on *Calluna* with a high N and P content (Moss, 1972, 1977) and this selection is even more pronounced in chicks than adults (Savory, 1977). As grouse also prefer to consume *Calluna* shoots from plants between two and eight years old (Savory, 1978), this suggests management is necessary to encourage a constant supply of relatively young *Calluna* if the aim is to encourage grouse.

However, there are methods of management other than burning, such as mowing, although relatively little is known about the effects of mowing on vegetation. For *Calluna*, there is evidence showing that regeneration after cutting is very similar to that after burning in terms of height and cover, with the main differences lying in the season of management (Miller & Miles, 1970) and in the proportions of vegetative regeneration and seed germination (Liepert *et al.*, 1993). Mowing may also be less damaging to other vegetation, especially *Sphagnum* mosses, than burning as the brash left behind may hold moisture and prevent the peat surface drying out, as well as potentially being incorporated into the peat. Although large quantities of brash may increase the risk of wildfire, this could be removed and sold for restoration work elsewhere. However, mowing can necessitate buying expensive machinery or paying subcontractors and there are concerns that the weight of a tractor on deep bogs could compact or damage the peat.

This study aimed to assess the effects of different types of *Calluna* management on the vegetation dynamics on the blanket bogs in northern England. Changes in vegetation composition, *Calluna* height, standing biomass, leaf area index (LAI) and nutrient contents were investigated over four years on areas which had been burnt or mown. The effects of leaving or removing brash which had been generated by mowing, as well as the effects of adding *Sphagnum* fragments after burning or mowing were also assessed. Additionally, the validity of assessing vegetation composition from photographs was determined. It was hypothesised that mowing would result in greater *Sphagnum* cover and less bare ground than burning, but that there would not be any difference in *Calluna* cover, height, biomass and LAI between mown and burnt areas. Burnt areas were expected to have *Calluna* with a higher nutrient than mown or unmanaged areas.

3.2 Methods

3.2.1 Study sites and site set-up

Three sites, all located in north-west England, were surveyed (Figure 3.1). The sites were Nidderdale, Mossdale and Whitendale, which are all described in full in Section 2.2.1. The set-up of the site was identical to that described in Section 2.2.2 (Figure 3.2), with the exception that there was an additional plot with added *Sphagnum* propagules (see Section 2.2.3.3 for details of *Sphagnum* addition) in every block within the burnt sub-catchment. Therefore, in the burning (FI) sub-catchment, each block contained two plots; FI plots were solely burnt and FI+Sph plots were burnt with *Sphagnum* propagules added. In the mown catchment, each block contained five plots; LB plots were mown with the brash left, BR plots were mown with the brash removed, LB+Sph plots were mown with the brash left and *Sphagnum* propagules added, BR+Sph plots were mown with brash removed and *Sphagnum* propagules added and DN plots were left uncut as the no management control. Details of burning, mowing and *Sphagnum* addition are given in Section 2.2.3. All plots were 5 m x 5 m and were marked out with wooden corner posts. A 1 m x 1 m sub-plot was marked out in the corner of each plot (Figure 3.2) with bamboo canes.

3.2.2 Vegetation surveys

3.2.2.1 1 m x 1 m and 5 m x 5 m field surveys

Vegetation surveys were conducted annually at all three sites on consecutive days between 2012 and 2015 in either September or October (see Table 3.1 for dates) due to logistical reasons. The 1 m x 1 m sub-plots and 5 m x 5 m plots were assessed on each occasion. A 1 m^2 quadrat split into 25 equal squares was placed over 1 m x 1 m sub-plot during the surveys to aid estimation of percentage cover. The 1 m^2 quadrat was left in place during the survey of the 5 m x 5 m plot to give guidance for percentage estimation.

All plants were identified to the species level and their percentage cover and that of bare ground and brash were visually estimated. As there was a substantial moss layer beneath the

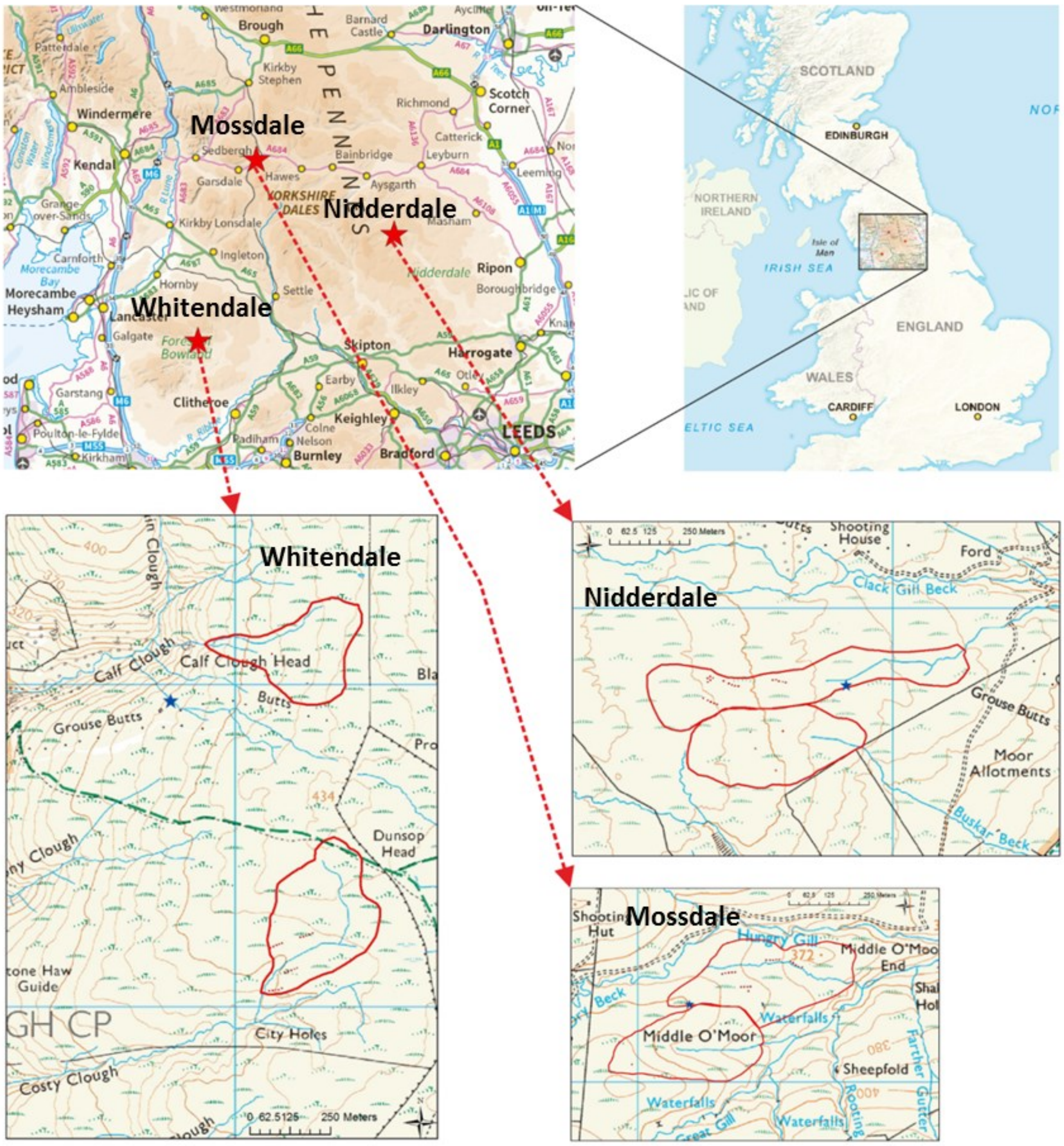


Figure 3.1 Location of the three study sites in north-west England (top maps, red stars). The catchment boundaries (thick red lines) and weather station (blue star) are detailed in the lower maps (from left star to right star) at Whitendale, Mossdale and Nidderdale.

Rights statement: MiniScale® [TIFF geospatial data], Scale 1:1000000, Tiles: GB, Updated: 3 December 2015, Ordnance Survey (GB), Using: EDINA Digimap Ordnance Survey Service, http://digimap.edina.ac.uk, Downloaded: 2016-09-09 14:35:01.73

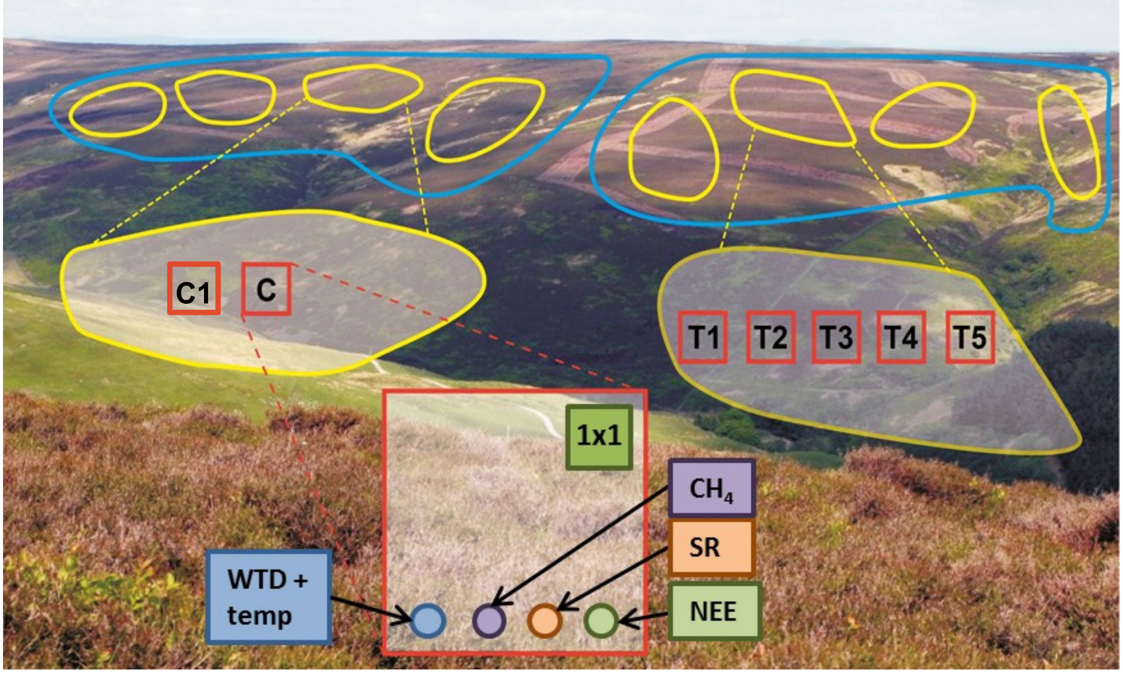


Figure 3.2 Schematic diagram of a typical site layout of the two sub-catchments (blue outline) and four blocks (yellow outline) within each.

Each plot (red outline) is 5 m x 5 m. C plots are in the burning sub-catchment and represent burnt plots (FI) and the additional C1 plots are burnt plots with added *Sphagnum* propagules (FI+Sph). T1-T5 are plots in the mowing sub-catchment and represent mown plots with brash left (LB), mown plots with brash removed (BR), mown plots with the brash left and *Sphagnum* propagules added (LB+Sph), mown plots with the brash removed and *Sphagnum* propagules added (BR+Sph) and plots left uncut as a no management ("do nothing") control (DN). Within each plot is a corner 1 m x 1 m sub-plot (green square), a circle for repeated CH_4 measurements (purple circle), a circle for repeated soil respiration measurements (orange circle), a circle for repeated NEE measurements (green circle) and a mesh cage containing a WTD meter and temperature logger (blue circle).

Table 3.1 Dates of vegetation surveys and *Calluna* plant collection at each site, see text for details of activities.

Pre-management *Calluna* plants were collected on different dates in the burnt (FI) and mown (LB) sub-catchments.

Activity	**Nidderdale**	**Mossdale**	**Whitendale**
Vegetation surveys	29th October 2012	30th October 2012	31st October 2012
	30th September 2013	1st October 2013	2nd October 2013
	15th September 2014	16th September 2014	17th September 2014
	14th September 2015	15th September 2015	16th September 2015
Pre-management *Calluna* plant collection	5th March 2013 (FI)	1st March 2013 (FI)	21st February 2013 (FI)
	11th April 2013 (LB)	9th April 2013 (LB)	7th March 2013 (LB)
Post-management *Calluna* plant collection	18th August 2015	19th August 2015	20th August 2015
Additional *Calluna* plant collection	17th July 2013	18th July 2013	19th July 2013

vascular plants particularly pre-management, the overstorey and understorey were recorded separately. Here the overstorey is taken to mean that which can be seen when viewed from above. Overstorey cover of all species totalled 100%, understorey cover was less than or equal to 100% and total cover therefore was between 100 and 200% as no plot had more than two layers of vegetation. Brash and bare ground cover was included in the overstorey cover where living vegetation was absent. However, in the understorey layer, brash was only recorded if it represented whole dead plants (i.e. litter was not included) and bare ground was not recorded due to some vascular plants being so dense they formed both over- and understorey. All surveys were conducted by the same three observers.

National vegetation classification (NVC) categories were determined for each management type at each site in 2012 and 2015 (pre- and post-management) using MAVIS software (DART Computing & Smart, 2014).

3.2.2.2 Photo resurveys

A photo of each plot was taken during each survey to enable comparison of percentage cover between on the ground estimates and aerial images. On the 1 m x 1 m plots, a digital camera with a rotatable screen (Canon E600 with a 18-55 mm lens, Canon, Tokyo, Japan) was held directly above the plot to take the photograph. On the 5 m x 5 m plots, a GoPro camera (Hero3, GoPro Inc., San Mateo, CA, USA) was attached to a custom-adapted (Biology Workshops, University of York) window cleaning pole, which was extendable to 5 m, and raised over the plots. A smartphone app (GoPro Camera Suite, CameraSuite.org, Guntramsdorf, Germany) was used to remotely trigger the sensor and to ensure the photograph encompassed all four corner posts.

For the 1 m x 1 m plot photos, reassessment of percentage cover was aided by the quadrat dividers. Percentage cover guides (Terry & Chilingar, 1955; Owens & Sergy, 1994) were used to reassess the 5 m x 5 m plot photos. Only the overstorey vegetation was reassessed, as photographs could not capture vegetation or ground beneath this layer. The vegetation was grouped into plant functional types (PFTs) as individual species identification was not reliable, especially on the 5 m x 5 m plots. The groups were *Calluna*, *Eriophorum*, *Sphagnum* species, non-*Sphagnum* mosses, bare ground, brash/dead/burnt material and other species. Where it was not possible to distinguish between *Sphagnum* and other mosses, it was recorded as non-*Sphagnum* moss.

3.2.3 Measuring *Calluna* standing biomass, height and LAI

3.2.3.1 Collecting Calluna

Pre-management *Calluna* plants were cut from the 29 cm diameter circles used for net ecosystem exchange (NEE) measurements (see Section 2.2.4.1.2) before mowing and burning were carried out (see Table 3.1 for dates). Post-management, the *Calluna* plants were cut from a patch the same size as the NEE circle where the *Calluna* cover was representative of that across the plot (Table 3.1). The slight difference in location was because pre-management the plants could be cut directly from the NEE patches as these were scheduled to be burnt or mown, whereas NEE flux monitoring was ongoing when post-management plants were cut. All plants were cut with secateurs as close to the stem bases at the peat surface as possible to gather all the aboveground *Calluna* biomass (resulting in some stems being cut below the moss layer). Plants from each plot were bagged separately and the bags sealed to prevent water loss.

3.2.3.2 Percentage cover and height of Calluna

The percentage cover of *Calluna* was assessed on each 1 m x 1 m and 5 m x 5 m plot during the vegetation field surveys in each year meaning that the cover values for the 2012 and 2015 surveys were approximately the cover on the plots when the pre- and post-management samples were cut, respectively. *Calluna* height was measured in five places on each plot during the vegetation surveys and was averaged for each plot in each year.

For the *Calluna* cut post management, stems were photographed from above when arranged on a 30 cm diameter flower board and percentage cover was estimated using the same guides as for the photo resurveys (Terry & Chilingar, 1955; Owens & Sergy, 1994). The height of the *Calluna* cut post-management was measured in five places whilst on the flower board and averaged.

Calluna heights less than or equal to 3 cm were classed as having germinated from seed within the past year due to the observation that most of the regenerating shoots grew from woody stems at least 3-4 cm tall. Heights of 4 cm or more were assumed to be either regrowth from stems existing before management implementation or *Calluna* plants germinated from seed in a previous year. Percentage germination was determined for each plot in each year according to these height classes.

3.2.3.3 Fresh, air-dry and oven-dry weights

Samples were split into ‘leafy’ and ‘woody’ portions and weighed. Leaves which were not grey-brown and desiccated (i.e. were likely to have been alive within the past year) were included in the ‘leafy’ portion: this was effectively the photosynthetic portion of the plants which had been active during the majority of the NEE measurement campaigns (see Chapter 2 for NEE measurement details, dates and results).

The ‘leafy’ and ‘woody’ portions of each sample were left to air-dry fully (for at least 5 days) after which each portion was re-weighed. Subsamples of approximately 1 g air-dried ‘leafy’ material and 3-4 g air-dried ‘woody’ material were weighed out from each sample. These were stored in paper bags to prevent moisture absorption. The subsamples were dried in an oven at 65°C until constant weight was achieved. On removal from the oven, the subsamples were cooled in a desiccator and re-weighed.

3.2.3.4 Leaf area index (LAI)

Before oven-drying, each ‘leafy’ subsample was spread out in a single layer in a clear Perspex tray and scanned on an Epson Perfection 4870 scanner (Epson America, Inc., Long Beach, CA, USA). Images were analysed using WinRhizo 1995 software (Régent Instruments Inc., Sainte-Foy, Québec, Canada) set to TWAIN interface and calibrated for use with leaf area. Some subsamples were split into two and the areas summed to avoid leaves overlapping in the scan area (10 cm x 15 cm). Images generated during the scans were checked manually to ensure detection of all leaves.

3.2.3.5 Correcting LAI for water loss

As most samples were collected within a short period of time, it was not possible to process all *Calluna* immediately following cutting. Whilst samples were processed as soon as possible, it took a month to fully separate and weigh them all. Additionally, as soon as a bag was opened to separate the sample into ‘leafy’ and ‘woody’, the *Calluna* began drying out, lost weight and the leaves shrank. Therefore, additional samples were taken from all three sites (see Table 3.1 for dates) to obtain correction factors for fresh leaf area to calculate LAI.

Samples were double bagged and sealed immediately following cutting to ensure minimal moisture loss. All samples were weighed on 23rd July 2013 before bags were unsealed. To obtain full fresh sample weights, bag weights were subtracted once plants had been air-dried. Each sample was unsealed briefly to remove three ~1 g subsamples of ‘leafy’ material which were immediately weighed on a fine balance and scanned to obtain fresh leaf area as before (see Section 3.2.3.4). All subsamples were left 4-6 days to air-dry before being re-weighed and re-scanned. Subsamples were oven-dried at 65°C until a constant weight was achieved as before for direct comparison between these correction samples and the actual plot samples.

3.2.4 Plant nutrient content

3.2.4.1 Acid digests

The oven dried 'leafy' *Calluna* subsamples from the NEE plots were ground in a ball mill. Approximately 0.5 g of each ground subsample was weighed on a four point balance and placed in a Kjedahl tube with 10 ml of 70% nitric acid (AnalaR NORMAPUR® grade, VWR International LLC, Radnor, PA, USA). A glass marble was placed on top of each tube and tubes were left overnight. For each block (18 tubes), there was a 'blank' consisting of only nitric acid (i.e. without the *Calluna* material). The following morning, the tubes were heated by increasing the temperature by 10°C every 15 minutes in a heating block until 60°C was reached. Tubes were left at 60°C for 3 hours then heated to 110°C using the same incremental method. After a further 6 hours, the tubes were removed from the heating blocks and left to cool overnight.

A small quantity (5-10 ml) of ultra-pure deionised water was added to each tube and swirled to mix. Each sample was separately filtered through a hardened ashless filter paper (125 mm diameter, No. 540, Whatman, GE Healthcare Life Sciences, Little Chalfont, UK) into a centrifuge tube. The marble and Kjedahl tube were also rinsed into the filter paper and the filter paper was rinsed around with ultra-pure water. The samples were then re-filtered through clean filter papers into volumetric flasks and each sample made up to 100 ml with ultra-pure water. Samples were stored in clean centrifuge tubes at room temperature. Acid digests of the pre-management *Calluna* were carried out between 13th and 28th May 2015 in three separate batches and post-management *Calluna* samples were digested between 14th and 30th October 2015, also in three batches.

3.2.4.2 ICP elemental analysis

All samples were diluted by half to run in an inductively coupled plasma mass spectrometer (ICP; iCAP 7000 Series ICP spectrometer, Thermo Scientific, Waltham, MA, USA), with 10 ml of sample mixed with 10 ml of ultra-pure water in clean centrifuge tubes. Blanks and washes were both nitric acid, which was diluted to the same concentration as that in the samples, and two washes were run after every 12 samples. A certified reference material (Birch leaf Standard, CatNo. B2166, Elemental Microanalysis Ltd, Okehampton, UK) was also run between the two washes. Element concentrations were calibrated using 0.5, 1, 2, 5, 10 and 20 ppm concentrations of a multi-element standard (CertipurR, Merck KGaA, Darmstadt, Germany), containing K, Na, Ca, Mg, Fe, Al, Mn, Zn, Cu and Pb, which was made up in a nitric acid matrix. Phosphorus was similarly calibrated using 0.5, 1, 2, 5 and 10 ppm concentrations of a phosphorus standard containing H_3PO_4 (CertipurR, Merck KGaA, Darmstadt, Germany). Argon was used as the carrier gas. Pre-management samples were run in the ICP on 3rd June 2015 and post-management samples on 4th November 2015. Many of the Pb concentrations were below the machine limit of detection, resulting in negative concentrations being recorded. Therefore, Pb was excluded from further analyses.

3.2.4.3 C:N analysis

Approximately 50 mg of each ground oven dried 'leafy' *Calluna* subsample taken from the NEE plots was accurately weighed on a 4 point balance and folded into a tin foil cup (Art-No. 05 000 429, Elementar Analysensysteme GmbH, Hanau, Germany) to form a tight ball. The samples were analysed using the "Plant500" method in a C:N analyser (vario Macro, Elementar Analysensysteme GmbH, Hanau, Germany). Standards were glutamic acid and the results were factored according to the standards. For the pre-management *Calluna*, C:N analysis was carried out between 7th May and 18th June 2015. For the post-management *Calluna*, the C:N analysis was carried out between 9th November and 2nd December 2015.

3.2.5 Data analysis

There was no visual evidence of successful establishment of *Sphagnum* from the Beadmoss pellets (see Sections 3.2.1 and 2.2.3.3 for details of *Sphagnum* pellet addition). Additionally, *Sphagnum* propagules were only added to relevant plots in 2014 whereas burning and mowing were carried out in 2013.Therefore, for the purposes of analysis, any plots to which *Sphagnum* was added were combined with the other plots of the same management (i.e. FI+Sph and FI plots were grouped, LB+Sph and LB plots were grouped, and BR+Sph and BR plots were grouped). This resulted in four management groups - burning (FI), mowing with the brash left (LB), mowing with brash removed (BR) and the unmanaged control (DN) - meaning that, across sites, there were 12 DN replicates and 24 FI, LB and BR replicates.

All statistical analyses were carried out in R version 3.3.1 (R Core Team, 2016). Following Zuur *et al.* (2009), residuals were plotted against fitted values and visually assessed for normality and homogeneity of variance. Where a transformation was used on the data, residuals of the transformed data were assessed. Where values are quoted, these represent the mean (± 95% confidence intervals). The critical p value chosen for significance was 0.05.

3.2.5.1 Vegetation surveys - species richness and diversity

Species richness and diversity were calculated for each plot in each year at both plot sizes. Shannon's H index was used for diversity and was calculated using the "diversity" function ("vegan" package"; Oksanen *et al.*, 2016). The exponential was taken of each number returned by the diversity function to convert these values to the effective number of species, i.e. the number of equally common species, which can be compared more clearly. Species richness was calculated as the average number of species per management per year at both plot sizes using "specnumber" ("vegan" package; Oksanen *et al.*, 2016).

Linear mixed models employing the "lmer" function from the "lmerTest" package (Kuznetsova *et al.*, 2016) were used separately on the diversity and species richness values. The fixed effects in the model were management, time period ('pre-management' = 2012 and 'post-management' = 2013-5), site, survey scale (i.e. plot size) and the interactions between these. A random intercept was included for each model, with a nested structure of blocks in sites (to account for spatial heterogeneity) in years (to account for repeated measurements).

Following the 10-step protocol in section 5.10 of Zuur *et al.* (2009), variables were dropped stepwise from each linear mixed effects model and the log-likelihood ratio and AIC value were used to assess whether a variable should be dropped or kept in the model. For the final models, the "satterthwaite" option was used to calculate the denominator degrees of freedom of the F statistics because the different lengths of the time periods caused an unbalanced design (Spilke *et al.*, 2005). Where differences were significant, the "glht" function with the "Tukey" option from the "multcomp" package (Hothorn *et al.*, 2008) was used to determine between which groups the differences occurred.

3.2.5.2 Vegetation surveys - percentage cover

Burnt material was combined with brash/dead *Calluna* to create a single group to prevent burnt matter becoming the dominant "species" which separated burnt plots from the other plots. To simplify the analysis, only total percentage cover data from the 5 m x 5 m plots were used. The percentage cover data of all species (including bare ground and brash/dead/burnt material) were transformed using the Hellinger's distance option of the "decostand" function in the "vegan" package (Oksanen *et al.*, 2016). The Hellinger transformation was used as it removed problems arising from plots having more than 100% cover recorded in total, without altering the weighting given to rare or abundant species (Legendre & Gallagher, 2001).

Redundancy analysis (RDA) is an ordination technique in which the ordination is constrained by the variables (Kindt & Coe, 2005). RDA was run on the Hellinger transformed vegetation matrix using the “rda” function of the “vegan” package (Oksanen *et al.*, 2016) to assess the effect of management on the vegetation composition. As the site and block in which the plots were located and the year of the survey were likely to influence the vegetation cover, these variables were also applied to the RDA to assess their effect on the vegetation matrix. However, although forward selection (using the “forward.sel” function in the “packfor” package; Dray, 2013) showed all these variables to be significant in the same model, the RDA was run separately for each variable (four models in total) in order to assess the effects of each variable more clearly. Almost all 2012 (pre-management) observations had high *Calluna* cover, resulting in them having nearly identical RDA scores to DN plots from post-management years, which considerably lowered the amount of variation the model explained. Pre-management data were therefore excluded from the final analysis to demonstrate the impacts of each management more clearly.

To facilitate interpretation, the function “cascadeKM” using the Calinski-Harabasz criterion was used to determine an appropriate number of groups formed by k-means clustering. This was visually checked using the “kmeans” function. The function “ordihull” was used to add polygons according to the k-groups onto the RDA. These functions were all from the “vegan” package (Oksanen *et al.*, 2016).

RDA identifies the main drivers separating plots from each other and k-means partitioning enables the identification of groups amongst the observations. However, neither allows for direct testing of specific variables between groups. Therefore, the results of the RDA were useful in aiding selection of species to investigate further. Eight main species were identified by the RDA and used for further testing. Additionally, all *Sphagnum* species, other than *S. fallax* which was one of the eight chosen, were summed and tested as an extra ‘species’ (there were too many zeros to test each species separately).

Linear mixed models were implemented as described for species richness and diversity (Section 3.2.5.1) with the following exceptions. The Hellinger transformed species percentage cover data were used to test the effect of management for each of the identified species in turn. The fixed effects were management and time period, and the interaction between them. As *Calluna* and *E. vaginatum* were the dominant plants and *Sphagnum* species are arguably the most important on a peatland, site was also used as a fixed effect for these three models to determine whether the site-wise differences in management implementation and climatic conditions affected the changes in plant cover over time more than the managements themselves. This would then indicate whether these management responses could be expected in general across other sites or were site specific.

3.2.5.3 Photo resurveys

As the photo resurvey data was neither normally distributed nor were the variances equal, either as a whole or when split by plot size or PFT, and as the field and photo surveys were paired by plot in each year, a Wilcoxon signed rank test was used, which employed the "wilcox.test" function with the "paired" option in the "stats" package (R Core Team, 2016). The test was used on the full dataset to determine whether the percentage cover values differed between the two methods and also when the data was split by plot size and by PFT to see whether these influenced the method of surveying.

3.2.5.4 Calluna standing biomass, height and LAI

The oven-dried subsample weights were divided by the air-dried subsample weights and multiplied by the full air-dried weights to obtain full sample oven-dried biomass for each NEE flux chamber area. 'Leafy' and 'woody' portions were calculated separately. As the *Calluna* cut from the chamber areas was only from a very small area of the plot, upscaling merely by multiplying the biomass over the full plot area was not appropriate, particularly post-management when *Calluna* cover and height was more variable. Therefore the biomass on the 5 m x 5 m plots was calculated for the post-management period by the following equation:

$$Plot\ biomass = \frac{BioCh}{AreaCh} \times \frac{\%CoverCh}{\%CoverPl} \times \frac{HtCh}{HtPl} \times AreaPl \qquad \text{Eq.3.1}$$

where Plot biomass is the calculated *Calluna* biomass on the plot in g, BioCh is the biomass of the *Calluna* cut from the chamber area in g, AreaCh is the area the chamber covers in cm^2, %CoverCh is the *Calluna* percentage cover in the chamber area, %CoverPl is the *Calluna* percentage cover in the plot, HtCh is the average height of the *Calluna* from the chamber area in cm, HtPl is the average height of the *Calluna* from the plot in cm and AreaPl is the area of the plot in cm^2.

Plot biomass could not be calculated in the same way for the pre-management period because no measurements were made in the pre-management period of percentage cover of *Calluna* in the chamber, height of *Calluna* in the chamber or height of *Calluna* on the 5 m x 5 m plots. However, as *Calluna* cover was more uniform in the pre-management period and the cut *Calluna* mostly filled the chamber, the amount of C lost during burning on the 1 m x 1 m FI sub-plots was calculated as:

$$Calluna\ C = \frac{BioCh}{AreaCh} \times \%CoverPl \times AreaPl \times \%C \qquad \text{Eq.3.2}$$

Where *Calluna* C is the calculated amount of C contained within the *Calluna* plants in g C m^{-2} and %C was the percentage of C contained within the *Calluna* leaves.

Correction factors were calculated for leaf area by dividing the fresh leaf area of the additional subsamples by the air-dried leaf area of the same sample. The air-dried leaf area of the *Calluna* subsamples from the NEE circles was multiplied by this correction factor to obtain the fresh leaf area and upscaled to the total leaf area in the chamber using the ratio of oven-dried to fresh weight of the additional samples to obtain the fresh weights of the NEE samples. Each NEE patch covered 660.5 cm^2 of ground (29 cm diameter circles) and LAI was calculated by dividing total leaf area of each sample by this value.

As the *Calluna* data were not normally distributed nor did the residuals show homogeneity of variance when fitted to linear/parametric models, Kruskal-Wallis tests were employed, using the “kruskal.test” function of the “stats” package (R Core Team, 2016), to investigate differences between managements. These tests were run separately on the ‘leafy’ to ‘woody’ ratios of the total oven-dried material, LAI, heather height for 1 m x 1 m plots, percentage of plants germinated and biomass in the chambers. Where significant results were detected, Dunn’s post hoc test (“posthoc.kruskal.dunn.test” from the “PMCMR” package; Pohlert, 2014) was used to determine which managements differed.

3.2.5.5 Plant nutrient content

All elemental concentrations were calibrated using the appropriate standards (phosphorus or multi-element) and converted from ppm to µg g^{-1} dry material or percentage of dry material (whichever was most appropriate for the concentrations) using sample dry weight and dilution concentration. All values which appeared to be produced as a result of machine error (i.e. were negative or apparently devoid of a particular element) were removed. Additionally, one LB post-treatment sample from Nidderdale was missing and was therefore excluded from all analyses. This meant the number of replicates from each group was not the same for all elements.

Linear mixed models were implemented as described for species richness and diversity (Section 3.2.5.1) with the following exceptions. The time periods, managements and sites were used as fixed effects in the mixed model. The only random effect used was the block the plots were in as there was only one measurement post-management.

3.3 Results

3.3.1 Vegetation field surveys

Overall, the MAVIS software classified all plots at all sites in 2012 and 2015 as the NVC category M19a, which is the *Erica tetralix* subcommunity of the *Calluna vulgaris – Eriophorum vaginatum* blanket mire community.

In total, 77 species, including 13 different species of *Sphagnum*, were found across the three sites during the four survey years. Some species were found only at one site during one year whereas others were present at all sites throughout. The species richness differed significantly between survey scales ($F_{1, 612}$ = 552.99, $p < 0.001$), with the 5 m x 5 m plots hosting 14.1 species on average compared to 9.0 species on 1 m x 1 m plots (Figure 3.3). There was also a significant interaction between site and scale ($F_{2, 612}$ = 7.10, p = <0.001), with Nidderdale having fewest species on both 1 m x 1 m sub-plots and 5 m x 5 m plots (7.0 and 11.0, respectively), Whitendale more (9.4 and 15.1, respectively) and Mossdale the most (10.6 and 16.0, respectively). There was no significant interaction between management and time period ($F_{3, 612}$ = 1.95, p = 0.12) although the species richness increased slightly on all managements over time.

The Shannon's H diversity index was not significantly different between the survey scales ($F_{1, 611}$ = 3.70, p = 0.06), but was between the sites ($F_{2, 611}$ = 71.92, $p < 0.001$), with Nidderdale having the lowest diversity. There was a significant interaction between management and time period ($F_{3, 611}$ = 4.98, p = 0.002). The diversity increased significantly from the pre-management to the post-management period on both the FI ($p < 0.001$) and LB (p = 0.008) plots, with FI plots having significantly lower diversity than BR and LB plots ($p < 0.03$ for both) in the pre- but not post-management period (Figure 3.4). There was no significant interaction between management, site and period ($F_{6, 586}$ = 1.04, p = 0.40).

When management was used as the constraining variable in the RDA, 18.9% of the overall variability of the Hellinger-transformed vegetation matrix (excluding 2012 data) was explained (adjusted R^2 = 0.19, $F_{3, 248}$ = 20.54, $p < 0.001$). The first axis separated plots which were dominated by brash/dead/burnt material from those dominated by *Calluna* (RDA1 of Figure 3.5). The second gradient separated observations with a high cover of *Hypnum jutlandicum* from those with a high cover of *Eriophorum vaginatum* and, to a lesser extent, *Sphagnum fallax* (RDA2 of Figure 3.5). The k-means partitioning satisfactorily divided the 252 observations into three groups ($F_{2, 249}$ = 70.00, $p < 0.001$). These groups, when plotted over the

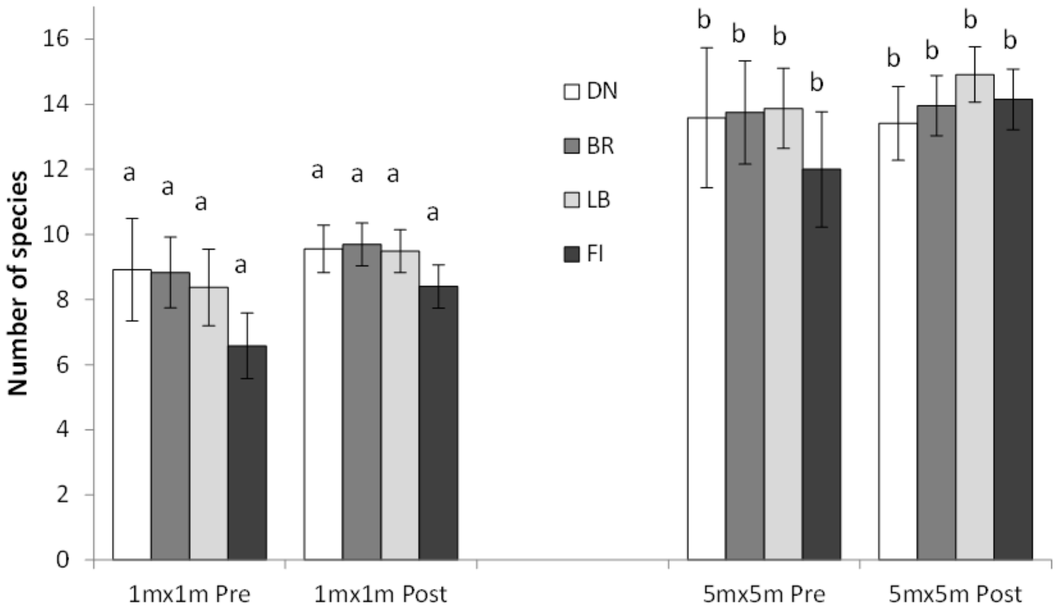


Figure 3.3 Mean (± 95% confidence intervals of the mean) of the species richness (i.e. number of species) for each management group in each year split by plot size.

Management codes are used where DN represents unmanaged, FI represents burnt, BR represents mown plots with the brash removed and LB represents mown plots with the brash left. Different letters within each time period indicate significant differences between managements.

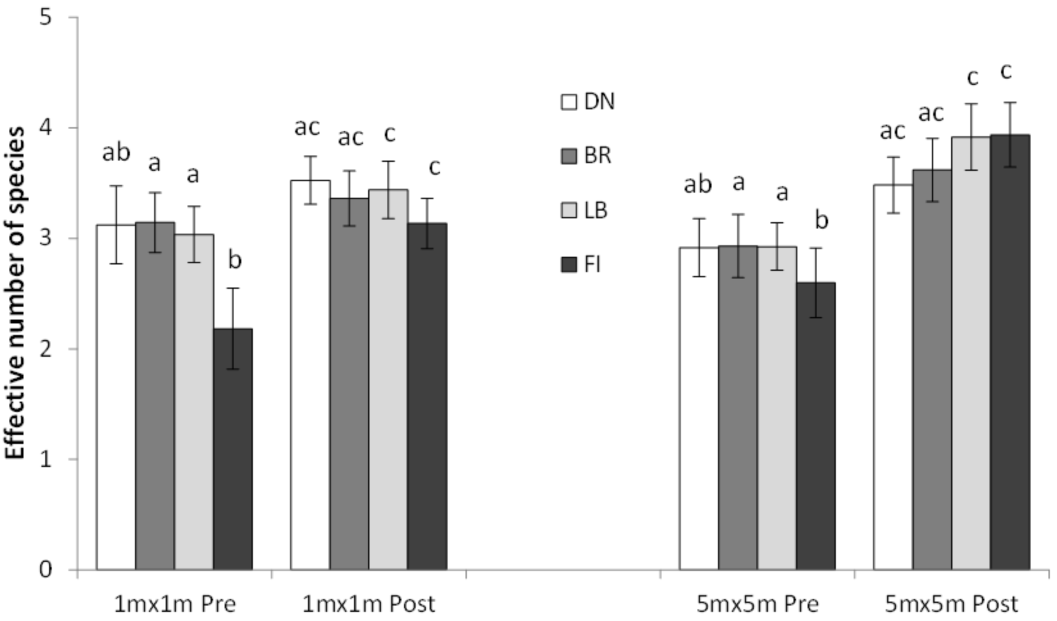


Figure 3.4 Mean (± 95% confidence intervals of the mean) of the effective number of species, derived by taking the exponential of the Shannon H index, for each management group in each year split by plot size.

Management codes are used where DN represents unmanaged, FI represents burnt, BR represents mown plots with the brash removed and LB represents mown plots with the brash left. Different letters within each time period indicate significant differences between managements.

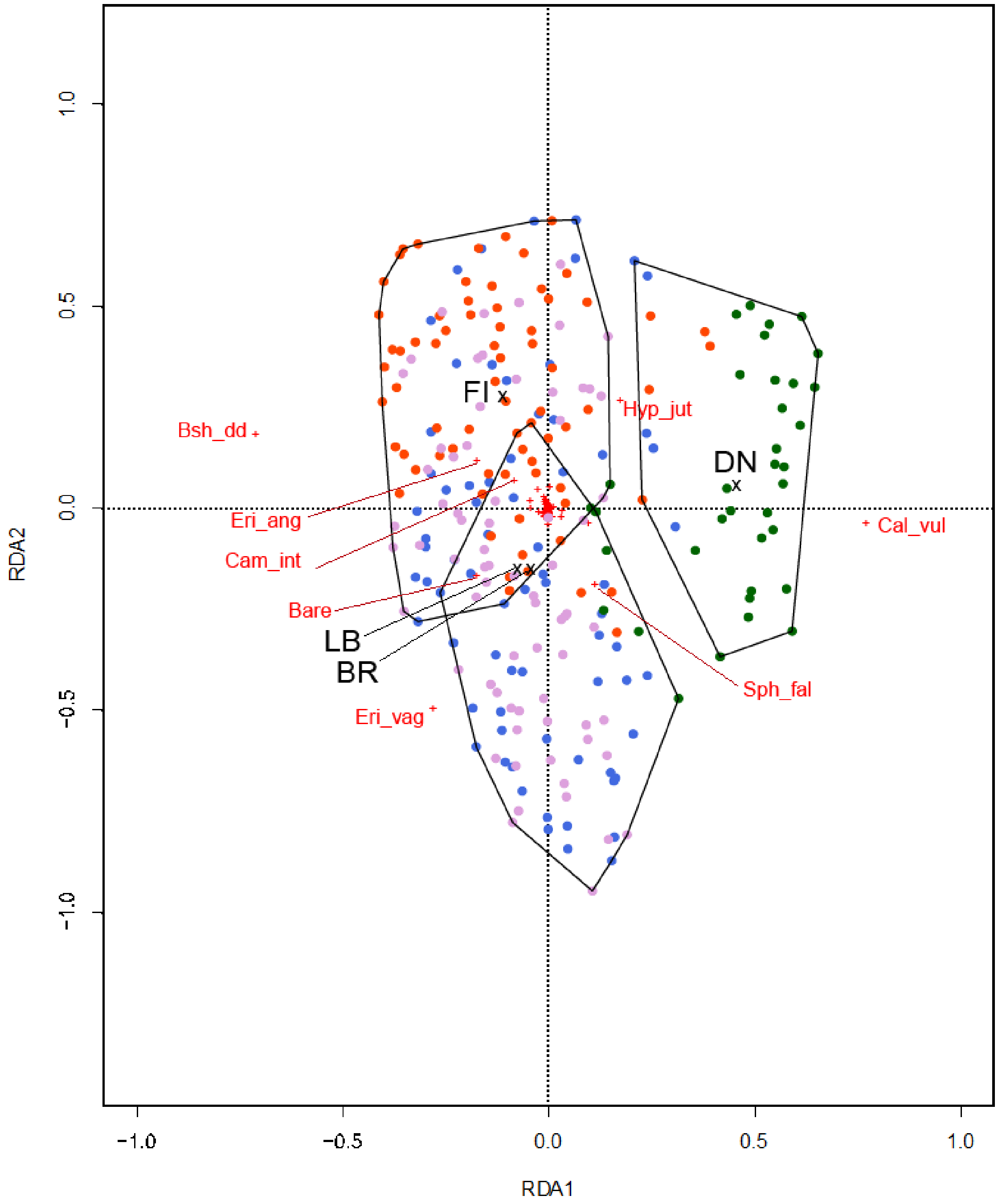


Figure 3.5 Redundancy analysis (RDA) of vegetation composition in 2013, 2014 and 2015 (i.e. post-management) with management as the constraining variable.

Black crosses represent the centroids of the management groups where DN represents unmanaged, FI represents burnt, BR represents mown plots with the brash removed and LB represents mown plots with the brash left. Red crosses represent the positions of individual species. The eight most influential are labelled with the first three letters of the genus name and species name (for plant species; Bsh_dd is brash/dead/burnt material and Bare is bare ground). Coloured dots represent the position of each individual plot in a given year where dark green is for DN, orange is for FI, blue is for BR and pink is for LB. The groups assigned by k-means partitioning are shown by the polygons.

RDA graph, coincided closely with the centroids of the management groups (see Figure 3.5), effectively creating a burnt, a mown and an unmanaged polygon. These polygons show that *Calluna* was the most closely associated species with the 'unmanaged polygon', *E. vaginatum* was with the 'mown polygon' and brash/dead/burnt material was with the 'burnt polygon'. Moreover, when the observations were coloured by their actual management, 83% of the DN observations fitted into the 'unmanaged polygon', 82% of the FI plots fitted into the 'burnt polygon' (or were in the small overlap) and 58% of each of the BR and LB observations fitted into the 'mown polygon' (or were in the small overlap).

When year was used as the constraining variable for the RDA, it explained 8.9% of the variance of the vegetation matrix (Appendix B; adjusted $R^2 = 0.09$, $F_{2, 249} = 13.33$, $p < 0.001$). The first axis explained most of the variability (92.5%) and plots generally moved from brash/dead/burnt material in 2013 which were both on the far left to *Calluna* and *E. vaginatum* on the right in 2015. Most DN plots remained on the right-hand side for all years. This RDA indicated that the main change between years was that plots which had been burnt or mown regained vegetation.

The RDA incorporating site as the constraining variable explained 12.4% of the variability of the transformed vegetation matrix (Appendix B; adjusted $R^2 = 0.12$, $F_{2, 249} = 18.74$, $p < 0.001$). The first axis separated Mossdale, which was most closely associated with *S. fallax* and *S. capillifolium*, from the other two which were associated with *H. jutlandicum*. The second axis separated Nidderdale, which had more *Calluna*, from Whitendale, which had more *E. vaginatum* and *Vaccinium myrtillus*.

The blocks to which the plots were allocated also explained a small (3.7%) but significant (Appendix B; adjusted $R^2 = 0.04$, $F_{3, 248} = 4.20$, $p < 0.001$) amount of the variability of the matrix when used as the constraining variable of the RDA. However, the species were very clustered at the centre and it was not clear which species were associated with which blocks.

The eight most influential species/groups identified by the RDA and chosen for further analysis were *Calluna*, brash/dead/burnt material, *H. jutlandicum*, *E. vaginatum*, *E. angustifolium*, *S. fallax*, bare ground and *Campylopus introflexus*. Additionally, all *Sphagnum* species (excluding *S. fallax*) were summed and analysed as a single group. Of these nine species/groups, *Calluna*, *E. vaginatum*, bare ground and brash/dead/burnt material showed significant interactions between management and time period (see Table 3.2 for linear mixed model results). Only *E. vaginatum* showed any significant differences in the pre-management period with LB plots having significantly higher cover than FI plots (Figure 3.6B; $p = 0.025$). Percentage cover of *E. vaginatum* increased significantly from the pre-management to post-management period on

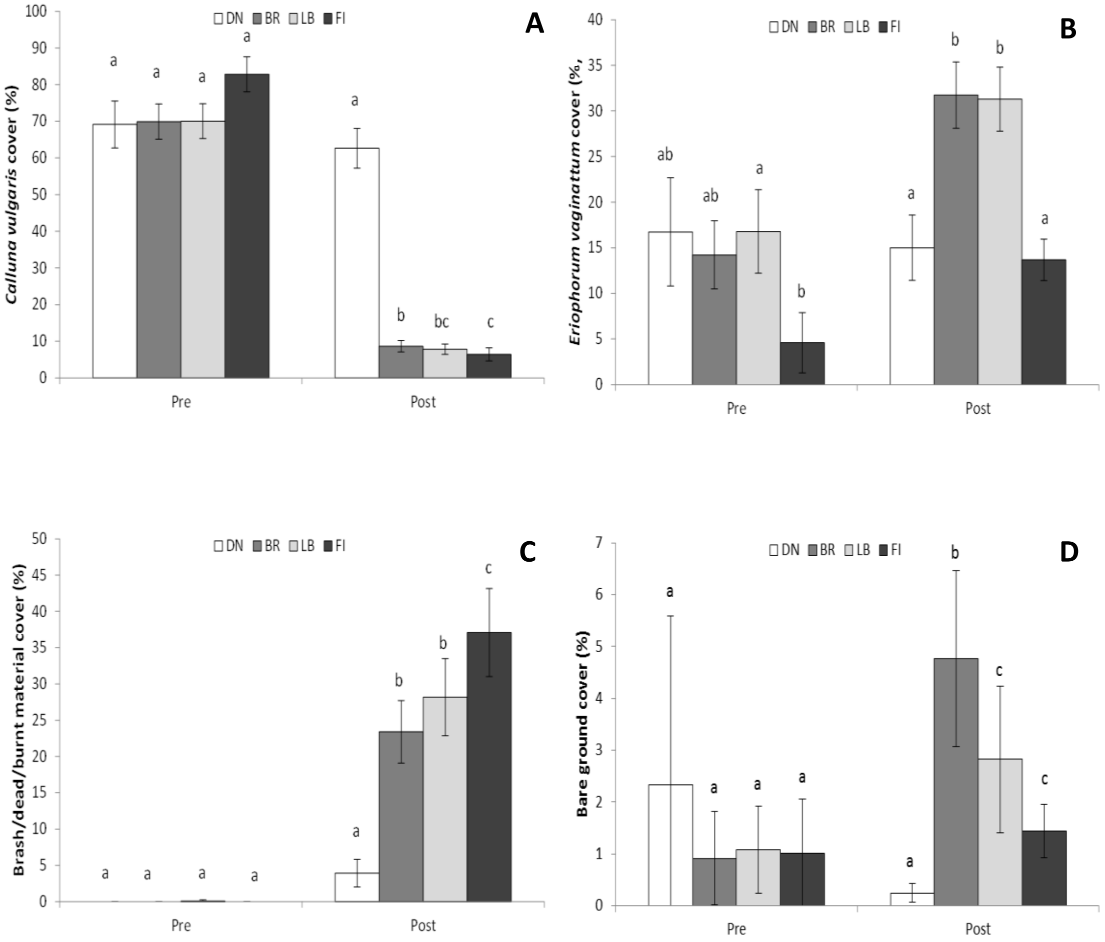


Figure 3.6 Mean (± 95% confidence intervals of the mean) percentage cover of A) *Calluna vulgaris*, B) *Eriophorum vaginatum*, C) brash/dead/burnt material and D) bare ground for each management group in the pre- (2012) and post-management (2013-5) periods for the 5 m x 5 m plots.

Management codes are used where DN represents unmanaged, FI represents burnt, BR represents mown plots with the brash removed and LB represents mown plots with the brash left. Different lower case letters within each time period indicate significant differences between managements.

Table 3.2 Results from linear mixed effects models of the effect of interaction between management and time period (pre- and post-management) for each vegetation species. For each model, the F value, the p value and the Satterthwaite approximation of the denominator degrees of freedom (df), are given. The numerator degrees of freedom = 3 for all models. Results of post-hoc tests for pairwise comparisons of the managements are also given, where DN is unmanaged, BR is brash removed, LB is left brash and FI is burnt. Only post-hoc results from the post-management period are shown (there were no significant differences pre-management). Significant values are shown in bold.

Species	**F value**	**p value**	**df**	**DN to BR**	**DN to LB**	**DN to FI**	**BR to LB**	**BR to FI**	**LB to FI**
Calluna vulgaris	42.62	**<0.001**	271	**<0.001**	**<0.001**	**<0.001**	1.00	**0.013**	0.10
Brash/dead/ burnt material	14.97	**<0.001**	272	**<0.001**	**<0.001**	**<0.001**	0.80	**<0.001**	**0.001**
Hypnum jutlandicum	2.70	0.05	270	-	-	-	-	-	-
Eriophorum vaginatum	5.32	**<0.001**	295	**<0.001**	**<0.001**	0.73	0.98	**<0.001**	**<0.001**
Eriophorum angustifolium	1.45	0.23	272	-	-	-	-	-	-
Sphagnum fallax	0.30	0.83	270	-	-	-	-	-	-
Bare ground	8.67	**<0.001**	271	**<0.001**	**<0.001**	**0.002**	**0.013**	**<0.001**	0.11
Campylopus introflexus	1.83	0.14	272	-	-	-	-	-	-
All *Sphagnum* spp.	0.54	0.66	297	-	-	-	-	-	-

BR and LB plots ($p < 0.011$) but not on FI or DN plots (Figure 3.6B; $p > 0.05$). This resulted in BR and LB plots having significantly higher *E. vaginatum* cover than DN and FI plots post-management (Table 3.2; Figure 3.6B). DN plots had significantly higher *Calluna* cover and significantly lower cover of brash/dead/burnt material and bare ground than the other managements (Table 3.2; Figures 3.6A, 3.6B and 3.6C). BR plots also had marginally but significantly more *Calluna* than FI plots (Table 3.2; Figure 3.6A). There was also significantly higher cover of brash/dead/burnt material on FI plots compared to BR and LB plots (Table 3.2; Figure 3.6A) whereas BR plots had significantly more bare ground than LB and FI plots (Table 3.2; Figure 3.6A).

Nidderdale had higher *Calluna* cover across all plots post-management than the other two sites (significant interaction between site and period; $F_{2, 295} = 4.98$, $p = 0.007$) but there was no significant interaction between management, period and site ($F_{6, 295} = 1.60$, $p = 0.15$), despite *Calluna* cover at Whitendale almost halving on DN plots due to frost damage over the winter of 2012/13. There was a significant different in *E. vaginatum* cover between sites ($F_{2, 295} = 14.26$, $p < 0.001$), with Whitendale having the highest cover, but no significant interaction between management, period and site ($F_{6, 295} = 0.67$, $p = 0.68$). Likewise, *Sphagnum* cover was significantly different between sites ($F_{2, 297} = 275.67$, $p < 0.001$), with Mossdale having the most *Sphagnum*, but no significant interaction between management, period and site ($F_{6, 297} = 0.94$, $p = 0.47$). Interestingly, Nidderdale had the most *Sphagnum* species recorded (11 species) despite having lowest cover (1.5%), whilst Mossdale had the fewest (8 species) but by far the highest cover (26.8%). Whitendale had low *Sphagnum* cover (1.7%) with 10 species recorded.

3.3.2 Photo resurveys

There were 84 photos for which *Sphagnum* and non-*Sphagnum* moss could not be distinguished out of a total of 570 photos which contained some form of moss, meaning less than 15% of moss was unclassified. Although field and photo survey percentage cover estimates appeared similar (Table 3.3), there was a significant difference between them ($V_{2393} = 1509200$, $p = 0.022$). When the data was split by the plot size, the percentage cover estimates between field and photo surveys were significantly different for the 5 m x 5 m plots ($V_{1138} = 354210$, $p = 0.006$) but not for the 1 m x 1 m plots ($V_{1255} = 404060$, $p = 0.44$). There was a significant difference between field and photo estimates for all species groups ($p < 0.02$ for all) but neither estimate was consistently higher for all categories (Table 3.3). Overall, there was a tendency for groups with low percentage covers to be underestimated in the photos, as plants were too small to see, and groups with higher percentage cover to be underestimated in the field, due to the viewing angle of the observer.

Table 3.3 Mean percentage cover of *Calluna*, *Eriophorum*, *Sphagnum*, non-*Sphagnum* mosses, bare ground, brash/dead/ burnt material and other species determined from the field and photo surveys split by plot size.

Species group	**1 m x 1 m field survey**	**1 m x 1 m photo survey**	**5 m x 5 m field survey**	**5 m x 5 m photo survey**
Calluna vulgaris	26.7	27.2	15.7	15.1
Eriophorum spp.	22.4	23.5	29.6	30.8
Sphagnum spp.	6.0	5.2	5.1	4.0
Non-*Sphagnum* moss	20.1	16.2	19.9	16.9
Brash/dead/burnt	2.9	2.6	2.6	2.9
Bare ground	21.1	24.5	26.1	29.9
Other spp.	1.0	0.7	1.2	0.3

3.3.3 *Calluna* standing biomass, height and LAI

The average 'leafy' to 'woody' ratio (i.e. grams of 'leafy' material per gram 'woody' material) was over five times higher post-management than pre-management period. The 'leafy' to 'woody' ratio was only significantly different between managements after management implementation (Figure 3.7; $\chi^2_3 = 30.10$, $p < 0.001$), with DN plots having substantially lower ratios than any other management ($p < 0.001$ for all). LAI was higher overall in the pre-management period and showed no differences between managements in this period (Figure 3.7; $\chi^2_3 = 0.76$, $p = 0.86$). Similarly to the 'leafy' to 'woody' ratio, LAI was significantly different post-management ($\chi^2_3 = 28.74$, $p < 0.001$) with DN plots having higher LAIs than the other managements (Figure 3.7; $p < 0.001$ for all).

Calluna was shortest in 2013 directly after mowing and burning and height increased slightly thereafter. *Calluna* height was only different between managements in the post-management period on both the 1 m x 1 m sub-plots (Figure 3.8; $\chi^2_3 = 30.52$, $p < 0.001$) and 5 m x 5 m plots (Figure 3.8; $\chi^2_3 = 124.37$, $p < 0.001$). On both plot sizes, DN plots consistently had significantly taller *Calluna* than other plots (Figure 3.8; $p < 0.001$ for all). On 5 m x 5 m plots, *Calluna* was also significantly shorter on FI plots than on LB and BR plots (Figure 3.8; $p < 0.001$ for all).

No *Calluna* was classed as germinating from seed in 2012 nor did any germinate on DN plots in any year (all plants were >4 cm). The percentage of *Calluna* plants which were classed as germinated was highest in 2013 and decreased thereafter (Figure 3.9). There were significant differences in percentage of germinated *Calluna* plants measured on different managements on both the 1 m x 1 m sub-plots (Figure 3.9; $\chi^2_3 = 46.89$, $p < 0.001$) and 5 m x 5 m plots (Figure 3.9; $\chi^2_3 = 50.39$, $p < 0.001$). On both plot sizes, DN plots had significantly lower germination than the other managements and FI plots had significantly higher germination than LB plots (Figure 3.9; $p < 0.04$ for all). On 5 m x 5 m plots, FI plots also had a significantly higher proportion of *Calluna* germinated from seed than BR plots (Figure 3.9; $p < 0.001$).

On average, the biomass of the *Calluna* cut from the chambers pre-management was 88.8 (± 11.0) g and did not differ significantly between managements (Figure 3.7; $\chi^2_3 = 0.89$, $p = 0.83$). Post-management, the average *Calluna* biomass cut from the chamber-sized circles on DN plots was 97.0 (± 24.9) g which was significantly higher than the 6.0 (± 1.4) g cut from burnt and mown plots (Figure 3.7; $\chi^2_3 = 29.65$, $p < 0.001$). When post-management *Calluna* biomass was scaled up to the full plot sizes, there was 9737 (± 2890) g on the 5 m x 5 m DN plots and an average of 639 (± 130) g on the BR, LB and FI plots (these managements were combined as values were very similar). On average, the pre-management FI plots contained 1129 (± 297) g *Calluna* biomass m^{-2}. The C content of the corresponding 'leafy' material was 52.3 (± 0.1) %

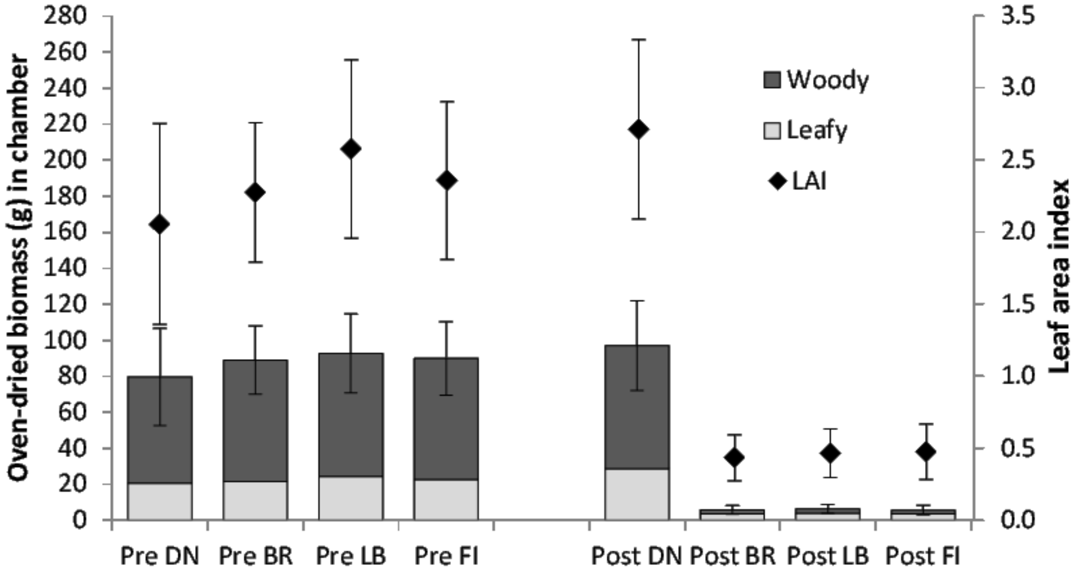


Figure 3.7 Mean (± 95% confidence intervals of the mean) of the biomass (split into 'leafy' and 'woody' biomass, represented by pale and dark grey bars respectively) and leaf area index (black diamonds) of the *Calluna* cut from the net ecosystem exchange circles (covering an area of 660 cm^2) for each management group in the pre- (2012) and post-management (2015) periods.

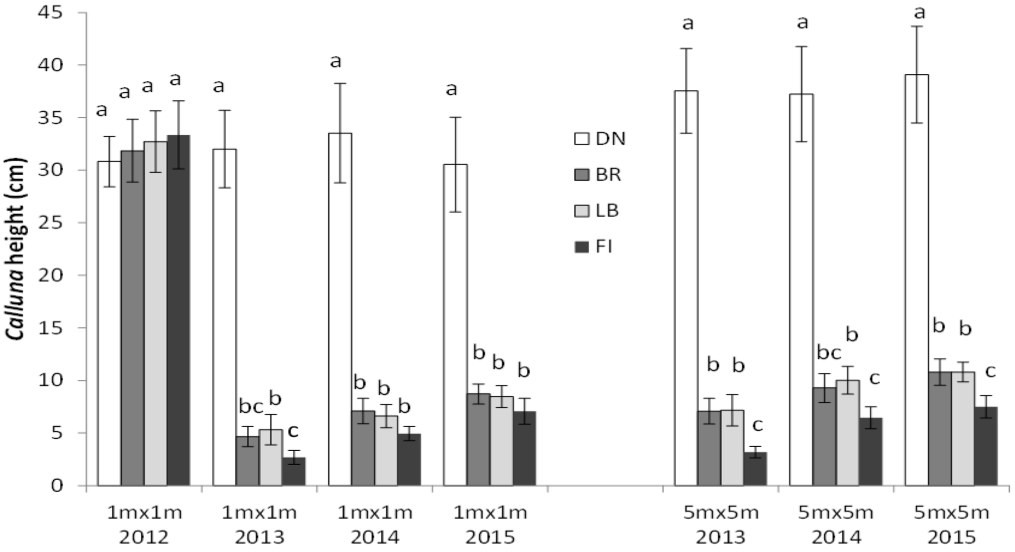


Figure 3.8 Mean (± 95% confidence intervals of the mean) of *Calluna* height for each management group by year.

Management codes are used where DN represents unmanaged, FI represents burnt, BR represents mown plots with the brash removed and LB represents mown plots with the brash left. Different lower case letters within each year of each survey size indicate significant differences between managements.

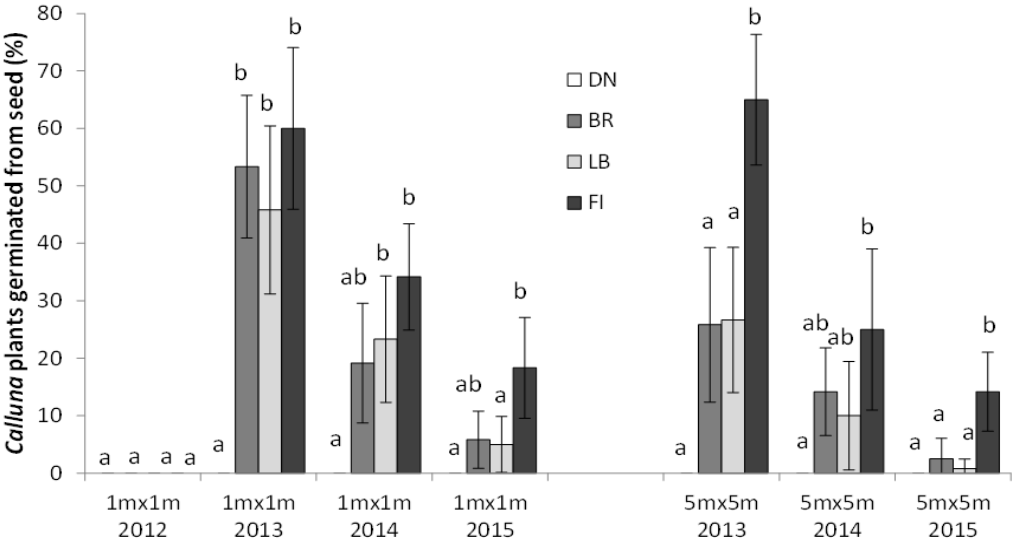


Figure 3.9 Mean (± 95% confidence intervals of the mean) of percentage of *Calluna* plants germinated from seed (i.e. were < 3 cm tall) for each management group by year.

Management codes are used where DN represents unmanaged, FI represents burnt, BR represents mown plots with the brash removed and LB represents mown plots with the brash left. Different lower case letters within each year of each survey size indicate significant differences between managements.

and was assumed to be similar or greater in 'woody' material. This meant that 587 (± 155) g C m^{-2} was lost on average during burning.

3.3.4 Plant nutrient content

Nutrient concentrations were mainly higher at all sites after management implementation than before (see Table C.1 in Appendix C for minimum maximum and average values). Concentrations of N, K, Na, Ca, Fe, Al, Mn, Zn and Cu in *Calluna* were significantly different between sites (see Table 3.4 for p values), with Mossdale having the lowest and Whitendale the highest concentrations of N, Fe, Al and Cu. Mossdale also had the lowest overall concentration of Zn in its *Calluna* but Nidderdale had the highest. Whitendale had the lowest amount of Ca and Mn in its *Calluna* with Mossdale and Nidderdale having similar amounts. Mossdale had highest amounts of K and Na, particularly pre-management, and Nidderdale had the least. Despite these differences between sites, only Zn showed a difference between sites in the pre- and post-management periods ($F_{6, 116} = 1.81$, $p = 0.004$; Mossdale had significantly lower content than the other two sites in the post-management period) and there were no elements for which the concentrations in *Calluna* differed significantly between managements within a site in the different time periods (see Table 3.4).

Nutrient concentrations were more similar between managements before management implementation than after (see Table C.2 in Appendix C for minimum maximum and average values). Concentrations of N, P, K, Na, Mg, Al, Mn and Cu were significantly different in *Calluna* plants between managements but only in the post-management period (see Table 3.4 for p values). There were no significant differences between managements for Na and Cu in the post-management period ($p > 0.05$ for all). DN plots had significantly lower concentrations of N, P, K, Mg and Mn than all other managements (Figure 3.10; see Table 3.5 for p values) and significantly higher concentrations of Al than LB and FI plots. There was no significant difference in N, P, Mg, Al and Mn concentrations between BR, LB and FI plots but FI plots had significantly higher *Calluna* K concentrations than BR or LB plots (Figure 3.10C; see Table 3.5 for p values). The only element which showed a significant interaction between management, time period and site was Na (Figure 3.10D; see Table 3.5 for p values) but the post-hoc test revealed that only FI and DN plots differed pre-management ($p < 0.001$).

3.4 Discussion

Due to logistical reasons, it was not possible to conduct the 2012 vegetation survey until October. This was not ideal as plants usually begin to senesce and die back by early September, meaning that it is possible that the cover of some species, particularly grasses and

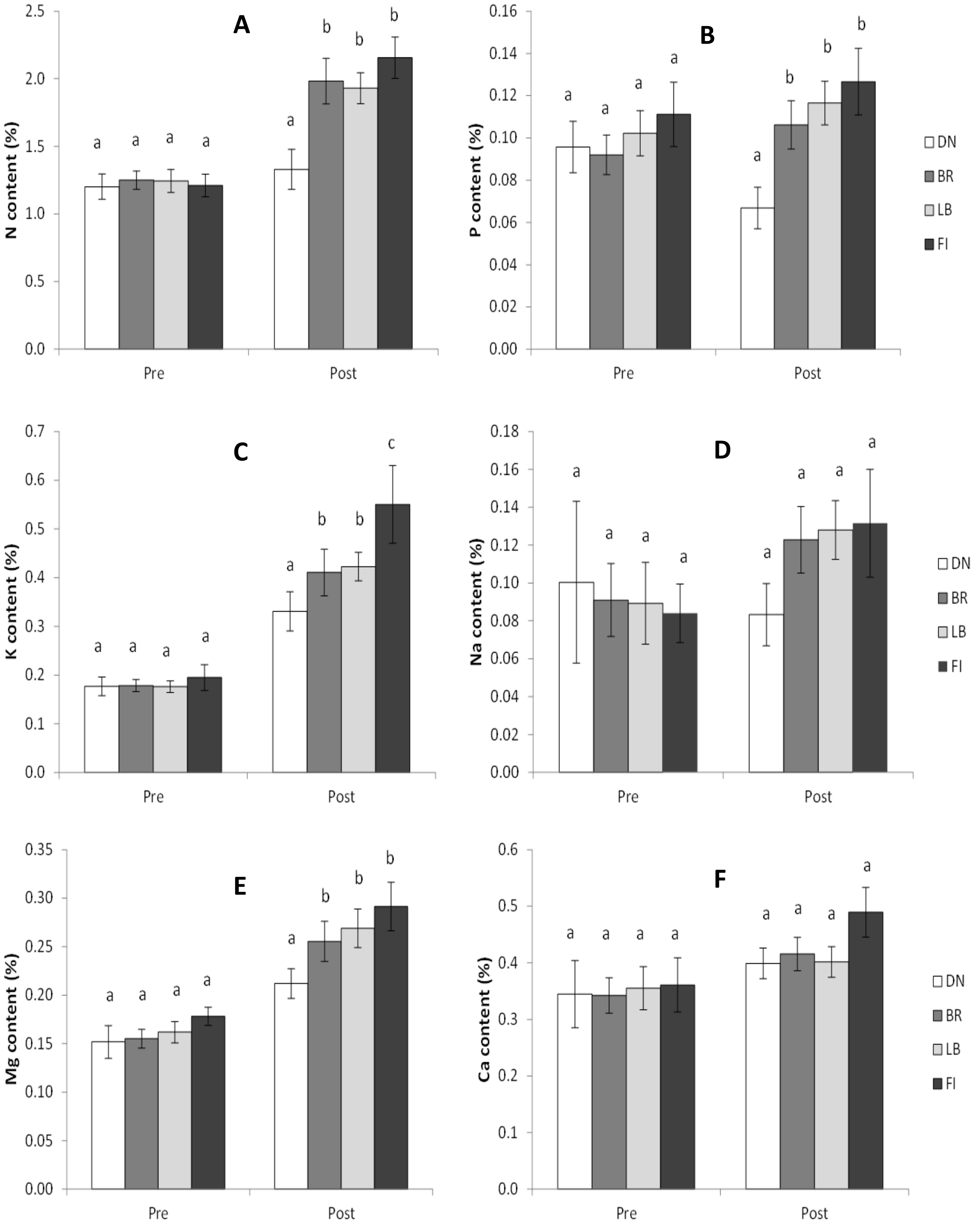
Table 3.4 Results from linear mixed effects models investigating differences in *Calluna* nutrient content between the four managements in the pre- and post-management periods (numerator degrees of freedom = 3) and between the four managements in each of the three sites in each period (numerator degrees of freedom = 6).
For each model, the F value, the p value and the Satterthwaite approximation of the denominator degrees of freedom (df) are given. Significant values are shown in bold.

Element	Management: Period interaction		Management: Period: Site interaction		Site		Model df
	F value	P value	F value	P value	F value	P value	
N	12.28	**<0.001**	0.46	0.83	12.43	**<0.001**	119
P	5.09	**0.002**	0.94	0.47	2.70	0.07	115
K	8.06	**<0.001**	1.47	0.19	3.91	**0.023**	116
Na	3.76	**0.013**	2.51	**0.026**	12.25	**<0.001**	119
Ca	2.18	0.10	0.66	0.68	8.31	**<0.001**	116
Mg	3.00	**0.034**	1.06	0.39	1.89	0.16	115
Fe	1.44	0.23	1.63	0.15	9.85	**<0.001**	115
Al	3.69	**0.014**	2.05	0.06	8.88	**<0.001**	119
Mn	21.22	**<0.001**	0.78	0.59	3.60	**0.030**	119
Zn	2.68	0.05	2.06	0.06	18.59	**<0.001**	116
Cu	3.70	**0.012**	1.24	0.29	9.05	**<0.001**	299

Table 3.5 Results of post-hoc tests for pairwise comparisons of elemental concentrations between the managements are given, where DN is unmanaged, BR is brash removed, LB is left brash and FI is burnt.

Only post-hoc results from the post-management period are shown. Significant values are shown in bold.

Element	DN to BR	DN to LB	DN to FI	BR to LB	BR to FI	LB to FI
N	**<0.001**	**<0.001**	**<0.001**	1.00	0.40	0.12
P	**<0.001**	**<0.001**	**<0.001**	0.84	0.26	0.93
K	**0.036**	**0.009**	**<0.001**	1.00	**<0.001**	**<0.001**
Mg	**0.005**	**<0.001**	**<0.001**	0.90	0.09	0.65
Al	0.06	**0.009**	**0.031**	1.00	1.00	1.00
Mn	**<0.001**	**<0.001**	**<0.001**	1.00	0.55	0.46


A
N content (%)
0.0
0.5
1.0
1.5
2.0
2.5
Pre
Post
a a a a
a b b b
B
P content (%)
0.00
0.02
0.04
0.06
0.08
0.10
0.12
0.14
0.16
Pre
Post
a a a a
a b b b
☐ DN
▩ BR
☐ LB
■ FI
C
K content (%)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Pre
Post
a a a a
a b b c
D
Na content (%)
0.00
0.02
0.04
0.06
0.08
0.10
0.12
0.14
0.16
0.18
Pre
Post
a a a a
a a a a
☐ DN
▩ BR
☐ LB
■ FI
E
Mg content (%)
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.35
Pre
Post
a a a a
a b b b
F
Ca content (%)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Pre
Post
a a a a
a a a a
☐ DN
▩ BR
☐ LB
■ FI

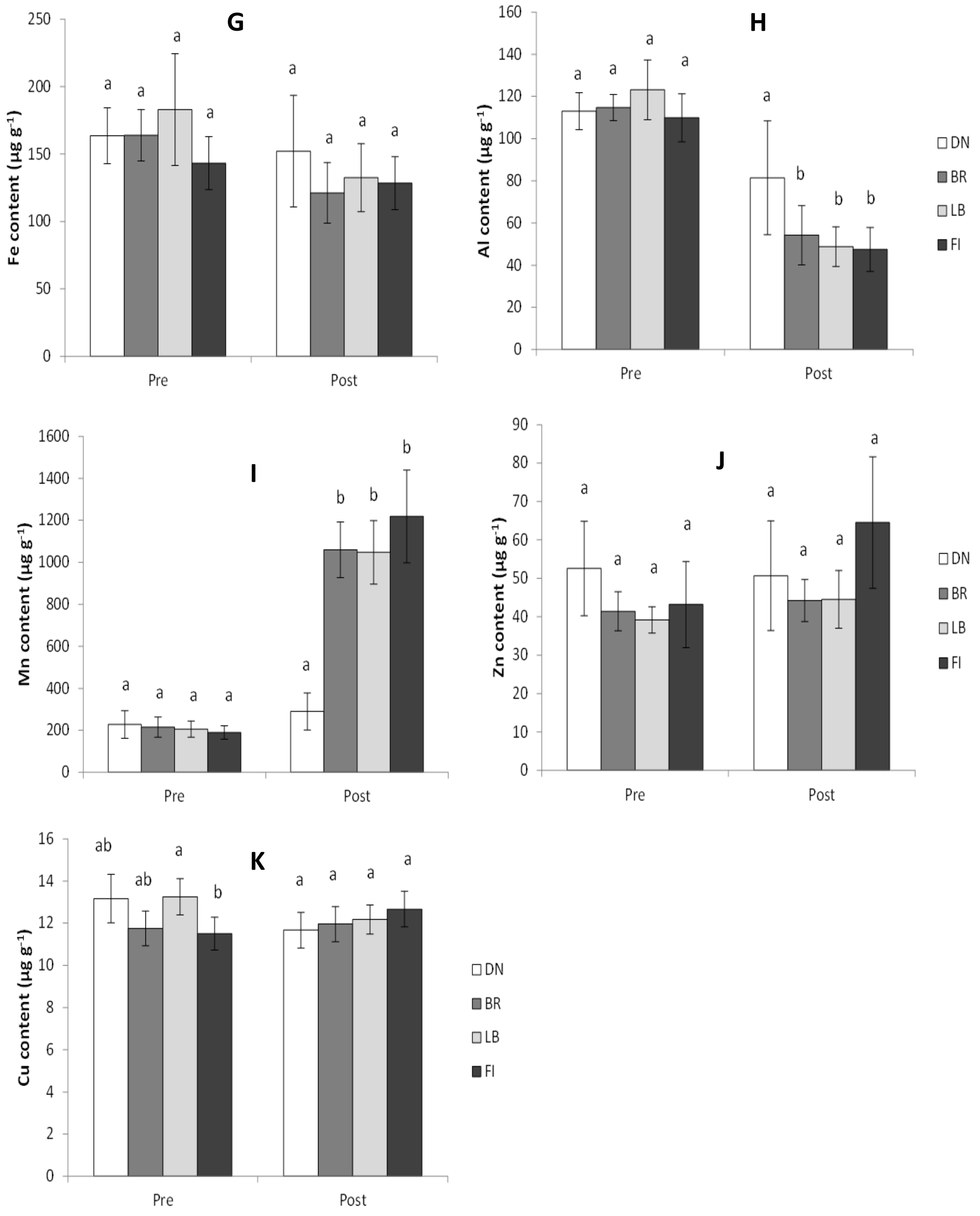


Figure 3.10 Mean (± 95% confidence intervals of the mean) of A) N content, B) P content, C) K content, D) Na content, E) Mg content, F) Ca content, G) Fe content, H) Al content, I) Mn content, J) Zn content and K) Cu content of *Calluna* for each management group in the pre- (2012) and post-management (2015) periods.

Management codes are used where DN represents unmanaged, FI represents burnt, BR represents mown plots with the brash removed and LB represents mown plots with the brash left. Different lower case letters within each time period indicate significant differences between managements.

sedges, may have been underestimated, or that a few species may not have been recorded. The subsequent vegetation surveys were conducted during late September to maintain consistency between the years and all plots were surveyed each year within a three day period. Therefore, any plant cover or species richness errors made due to plant dieback are likely to be consistent across sites, managements and years, warranting direct comparison. Additionally, incidental observations made of the vegetation at sites during other measurement occasions (see Chapter 2) suggest that cover values are unlikely to be substantially different if the surveys were conducted during the summer months.

3.4.1 Species richness and diversity

All management groups at all three sites both before and after management implementation were classified as the *Erica tetralix* subcommunity of the *Calluna vulgaris – Eriophorum vaginatum* blanket mire community (NVC sub-group M19a). This both confirmed that the sites still supported a blanket bog vegetation community and that the sites were very similar to one another. The result also suggested that the species composition in all managements was similar.

The species richness confirms that management had little impact on the number of species (Figure 3.3). The Shannon's diversity index indicated that there was a small management effect on the effective number of species (Figure 3.4), i.e. a change in the number and evenness of species in the plant community. However, most of the significant differences in species diversity occurred between the management groups before burning and mowing. Despite this, FI plots had significantly higher diversity post-management than pre-management and no longer had lower diversity than LB or BR plots, suggesting that burning did increase species diversity more than any other management (Figure 3.3). This finding is supported by Harris *et al.* (2011) who concluded that prescribed (i.e. regular and controlled) burning was needed to maintain diversity. They also showed that there was an immediate (1-10 years) increase in species numbers following burning. There was a slight increase in species richness from pre- to post-management for all managements apart from the 5 m x 5 m DN plots (Figure 3.3). Given that species diversity also increased from pre- to post-management, this suggests that the removal of the dominant *Calluna* resulted in more light and space for understorey plants to grow (Grace & Woolhouse, 1973), leading to a more even species composition. The slight increase in number of species on 1 m x 1 m DN sub-plots may have been due to observers becoming more experienced at searching for species over time and therefore may not have been a true increase. Alternatively, the substantial decrease in *Calluna* cover on Whitendale DN plots due to frost damage during the winter of 2012/13 may have contributed to the increase in species diversity on DN plots (Figure 3.4) and enabled additional species to colonise.

Regardless of the decline in living *Calluna* at Whitendale, *Calluna* at all sites was over 30 cm tall at the start of the study and DN plots maintained this height throughout (Figure 3.8). However, Harris *et al.* (2011) concluded that *Calluna* should be burnt before reaching 25 cm in height as other species in areas where *Calluna* was over 40 cm tall had restricted growth. Therefore, there should have been very few species on any plot in 2012 and on DN plots throughout the study, with far higher species richness on post-management burnt and mown plots. This was not the case (Figure 3.3). It could be that the *Calluna* on all sites had a sufficiently open structure (see MacDonald *et al.* (1995) for a description of different *Calluna* growth forms) before management implementation to allow sufficient light to penetrate for photosynthesis in the understorey (Grace & Woolhouse, 1973) leading to greater productivity and species richness (Hector *et al.*, 1999). A longer study would be needed to elucidate whether species richness and diversity declined on the DN plots as *Calluna* height increased and whether species richness increased on the burnt and mown plots.

Both species richness and diversity were significantly different between sites. This could be seen to contradict the finding that all three sites were classified as the same NVC. However, the NVC only uses a “constancy value” between 1 and 5 for each species (see MAVIS user guide; DART Computing & Smart, 2014) meaning that each class is relatively broad. Nevertheless, the differences in species richness and diversity between sites indicate that the sites were not as similar as they first appeared. Mossdale had the highest diversity and richness and visually appeared the least heavily managed (there were large areas without *Calluna*, although no plots were located in these areas, as well as areas with a *Sphagnum* carpet and with no obvious haggs or areas without peat), whilst Nidderdale had the lowest richness and diversity and appeared the most intensively managed (there was an obvious burn pattern across the wider site, not just the study catchment, and rocks showed through the peat in places at the downslope end of the catchment). This suggests that management by burning may result in a decrease in species richness but only over a longer period of time than this study covers. However, Mossdale was also the wettest site (mean annual precipitation (MAP) of 2115 mm) and Nidderdale the driest site (MAP of 1651 mm), meaning that climate may play a role in regulating species richness and diversity on blanket bogs. Without further research, it is not possible to conclusively state whether climate or management intensity is the greater driver of species richness and diversity.

3.4.2 Vegetation composition

In contrast to the similarities in species diversity and richness, the species composition changed over time in some managements. The RDA, combined with the k-means polygons, showed that the burnt, mown and uncut groups each had a major and minor factor separating them with another two factors in the overlap between the burnt and mown groups (Figure 3.5). Given that RDAs usually use many variables to attempt to explain changes or differences in vegetation cover (e.g. Field *et al.*, 2014; González & Rochefort, 2014), it is remarkable that managements alone, especially when combined across sites and years, explained nearly 20% of the variability of the vegetation composition. Additionally, this was greater than the variability explained by site (12.4%), year (8.9%) and block (3.7%). Contrary to the NVC results, this strongly suggests that management was instrumental in driving changes in species composition. Considering that a burnt and a mown polygon were clearly identified, these changes were not solely due to a reduction in *Calluna*. Other factors such as climate and landscape features (e.g. slope, aspect, etc.) may also have influenced the vegetation cover but are far more likely to have acted across all plots on a site, regardless of management.

It is however not necessarily the number nor evenness of species, nor what drives species composition which ultimately matters for a bog: it is which species are affected that matters most. As peat represents a vast and stable C store (Gorham, 1991) and is largely composed of and maintained by *Sphagnum* moss (Bain *et al.*, 2011), *Sphagnum* species are arguably the most important group of plants on blanket bogs. It is generally thought that burning retards *Sphagnum* growth, as burning can dry the peat (Holden *et al.*, 2014), and there is evidence that frequent burning can reduce *Sphagnum* cover and C uptake (Kuhry, 1994). Additionally, the high *Calluna* cover encouraged by burning can increase evapotranspiration, also drying the peat (Worrall *et al.*, 2007), which can reduce *Sphagnum* growth and recovery (Campeau & Rochefort, 1996).

Surprisingly, the results of this study did not show a negative impact of burning on total *Sphagnum* cover. Admittedly, *S. fallax*, which was the only *Sphagnum* species showing influence in the RDA (Figure 3.5) and had lower cover on FI plots than any other plots post-management, but FI plots also had lowest cover of this species pre-management and there was a small increase in *S. fallax* cover after burning. Additionally, when the cover of all *Sphagnum* species (excluding *S. fallax*) was combined, *Sphagnum* cover was relatively constant across periods in all managements. By chance, FI plots had less *Sphagnum* cover than DN, BR or LB plots before management implementation and this cover was maintained even three years after burning took place. However, longer term monitoring is required to fully assess the effects of burning on *Sphagnum* cover and to determine whether the brash on LB plots enhanced *Sphagnum* growth by protecting *Sphagnum* fragments and plants from desiccation.

It is interesting to note that there was an inverse relationship between the number of *Sphagnum* species and the total cover of *Sphagnum*. Mossdale had much higher *Sphagnum* percentage cover than the other two sites but only 8 species and Nidderdale had the lowest cover but 11 species. The difference in the cover of *Sphagnum* species is likely to be related to moisture since Mossdale was the wettest site (MAP of 2115 mm) and Nidderdale the driest (MAP of 1651 mm). This theory is supported by Campeau & Rochefort (1996) who found that all except one (which was not found on any site in the present study) of the *Sphagnum* species they investigated had greatly increased cover in wetter conditions. The difference in number of species may be related to the type of habitat each species prefers since not all species were found at all sites. For example, *S. tenellum* is usually found on bare peaty ground or well drained wet heaths (Amphlett & Payne, 2010a) and this species only occurred at Nidderdale, probably because the other sites were too wet or because Nidderdale was more disturbed. Additionally, Breeuwer *et al.* (2009) found that *S. cuspidatum* and *S. magellanicum* responded conversely to different water table regimes, perhaps explaining why both these species were only found in localised areas in the present study. However, *S. fallax* was found at all sites. This species inhabits a wide range of habitats (Amphlett & Payne, 2010b) which may explain its distribution and why it appeared unaffected by management (Table 3.2). Due to the low cover of the other *Sphagnum* species, which necessitated grouping them for analysis, it is possible that individual *Sphagnum* species did respond differently to the various managements, but that these differences were not detectable at such low cover.

Regardless, retaining *Sphagnum* is important for blanket bogs. Dunn *et al.* (2015) showed that areas of bog dominated by *Sphagnum* mosses (unspecified mixture) were more beneficial for C storage than either *Juncus effusus* or *Calluna*, as the peat directly beneath released less CO_2, CH_4 and DOC. Although in the present study these C fluxes were not specifically measured on *Sphagnum*-dominated ground, Mossdale took up more C than the other two sites (see Chapter 2) and had greater *Sphagnum* cover. High *Sphagnum* cover is also very beneficial in terms of water storage and can help to regulate flood waters (Bain *et al.*, 2011; Evans *et al.*, 2014), as well as being associated with lower DOC concentrations in stream water (Vestgarden *et al.*, 2010; Armstrong *et al.*, 2012). Ultimately, choosing a management which promotes and maintains *Sphagnum* cover and growth will be beneficial for the hydrology and C balance of a blanket bog (Gorham, 1991; Orwin & Ostle, 2012; Dunn *et al.*, 2015), but further study is needed in order to determine whether any management assessed here will satisfy these requirements.

E. vaginatum and *E. angustifolium* are also typical bog species although their importance on and benefits for a bog are not as clear as those of *Sphagnum* mosses. On the one hand, *Eriophorum* species can take up substantial amounts of C (Bortoluzzi *et al.*, 2006), can contribute to peat formation (Crowe *et al.*, 2008; Bain *et al.*, 2011) and rapidly colonise bare peat after disturbance (Crowe *et al.*, 2008), thereby reducing runoff and increasing water retention time in the peat (Grayson *et al.*, 2010) which could therefore benefit *Sphagnum* recolonisation. On the other hand, *E. vaginatum* can form dense tussocks, which may block out light beneath, and has aerenchyma which facilitate CH_4 release (e.g. Greenup *et al.*, 2000; Fenner *et al.*, 2011; Cooper *et al.*, 2014) as well as aerating the peat, which may accelerate decomposition (Freeman *et al.*, 2001b). It is therefore unclear as to whether *Eriophorum* species are beneficial for the C balance of a peatland or not, since these species may both contribute to C accumulation and stimulate C release. As *Eriophorum* species are typically found on peatlands which have a net uptake of C (e.g. Roulet *et al.*, 2007; Nilsson *et al.*, 2008), it is likely that the C accumulation aspects outweigh the C release aspects.

In this study, the majority of plots contained *E. vaginatum* both before and after management implementation, with some plots containing *E. angustifolium* at a much lower cover. Whitendale had more *Eriophorum* species than either of the other sites, probably largely due to this site having least *Calluna*, which was generally dominant pre-management. *E. vaginatum* was the only species for which there was a significant difference in species cover between managements in the pre-management period with FI plots having lower cover than LB plots. However, although *E. vaginatum* cover increased on both FI and LB plots following management (Figure 3.6B), the much greater increase on LB plots, which was matched by the increase on BR plots, strongly suggests that mowing encouraged *E. vaginatum*.

Previous studies (Hobbs, 1984; Lee *et al.*, 2013) have found that *E. vaginatum* dominated when burning was on a short (10 year) rotation. Although it appears no studies have specifically investigated the effects of mowing on *Eriophorum* species, Milligan *et al.* (2004) demonstrated that cutting reduced cover of *Molinia caerulea*, a moorland grass which often grows in tussocks. Therefore, it was unexpected that BR and LB plots had higher *E. vaginatum* cover than FI plots, especially since it was observed during mowing that the blades removed the tops of many existing *E. vaginatum* tussocks. However, *E. vaginatum* cover did increase on FI plots following management (Figure 3.6B), as did *E. angustifolium* cover, although the latter not significantly so.

The high *Calluna* cover observed at all sites pre-management (Figure 3.6A) is probably as a result of the historic burning. At Mossdale, there is evidence in the peat of a large and sustained increase in charcoal fragments over the last 200 years (McCarroll *et al.*, 2015) which is probably mirrored in other sites across England, including at Nidderdale and Whitendale (Simmons, 2003; Yallop *et al.*, 2006). The slight decrease in *Calluna* cover on DN plots from pre- to post-management (Figure 3.6A) was almost entirely attributable to Whitendale where living *Calluna* cover more than halved on some plots over the winter of 2012-3 due to damage by frost. There was additionally some decrease in *Calluna* at Mossdale in 2014-5 which was either caused by heather beetles (*Lochmaea suturalis* (Thomson)), which can damage *Calluna* (Scandrett & Gimingham, 1991), or by *Phytophthora* species which cause shoot death (Orlikowski *et al.*, 2004).

Calluna is managed on moorlands in order to encourage new growth for red grouse to eat and burning has been advocated as the most effective method for at least a century (Lovat, 1911). Therefore, whilst *Calluna* cover was expected to be significantly lower on burnt and mown plots compared to DN plots in the post-management period, what was unexpected was that FI plots also had significantly lower cover than BR plots and substantially, if not significantly, lower cover than LB plots (Table 3.2; Figure 3.6A). This suggests that mowing may be more beneficial for grouse than burning, at least in the first few years. This is in contrast to the findings of Liepert *et al.* (1993), who found no difference in *Calluna* cover between cutting and burning, and of Cotton and Hale (1994), who concluded that *Calluna* recovery on areas cut by a flail lagged behind that of *Calluna* on burnt areas by about a year. Here, the difference may lie in the monitoring period as Cotton & Hale (1994) did not begin surveying vegetation cover until five years after treatments were carried out; in this study, the most recent survey (2015) was only two and a half years after management implementation.

However, Kayll and Gimingham (1965) assessed vegetative regrowth (i.e. production of shoots from existing stems) of *Calluna* plants two months after burning and cutting and found greater regeneration on cut plants which agrees with the present study. Miller & Miles (1970) found that autumn burning caused more prolific regeneration than spring burning with the opposite being true for cut *Calluna*; regeneration was better after spring than autumn cutting. All management in this study was carried out in spring so direct comparison is not possible. However, *Calluna* regeneration on FI plots at Whitendale was slightly higher than that on both LB and BR plots. As Miller & Miles (1970) concluded that the damper conditions in autumn protected the *Calluna* stem bases from excess heat and as Whitendale was burnt when snow was lying, this suggests that conditions at the time of burning may be important. Further study is required to determine whether mowing at particular times of year benefit species other than *Calluna*, as well as to assess whether regeneration on FI plots is likely to outperform

Calluna growth on BR and LB plots in the future, making monitoring over a full management cycle vital.

None of the other plant species chosen for further analysis following the RDA showed significant differences between managements (Table 3.2). However, *Campylopus introflexus* is an invasive species (Richards, 1963), which has the potential to influence the dynamics of other species, in that it has been shown to suppress *Calluna* seed germination (Equihua & Usher, 1993). Although not significantly different, *C. introflexus* cover was higher on BR and LB plots post-management compared to DN plots and substantially higher on FI plots. The suppressive ability of *C. introflexus* on *Calluna* regeneration therefore appears to provide an explanation for the lower *Calluna* cover on FI plots (Figure 3.6A). However, *Calluna* regeneration from seed germination was higher on the FI plots than any other plots, suggesting that either *C. introflexus* did not have had a suppressive effect or that this effect was counteracted by fire increasing the germination rate (Mallik & Gimingham, 1985). Additionally, (Equihua & Usher, 1993) showed that seeds which did germinate on *C. introflexus* carpets produced plants which grew taller. This was not the case in the present study as FI plots had significantly shorter *Calluna* than the other managements (Figure 3.8). The lack of an effect of *C. introflexus* on *Calluna* height and germination could be because, although there was more *C. introflexus* on FI plots than any other plots post-management, the cover still averaged only 3%. As *C. introflexus* is a pioneer species of bare ground (Rothero, 2010), more frequent burning could encourage higher cover which may then impact negatively upon *Calluna* dynamics. On the other hand, rapid colonisation of bare ground by *C. introflexus* could alter surface roughness and slow down water flow (Grayson *et al.*, 2010) which may in turn aid *Sphagnum* recolonization on the wetter ground (Campeau & Rochefort, 1996), benefitting the hydrology and C store of the peat. Further investigation is required to determine the longer term effects of increases in *C. introflexus* on managed peatlands. The higher cover of *C. introflexus* on FI plots may partially explain the lower amount of bare ground on these plots post-management compared to BR and, to a lesser extent, LB plots. Amount of bare ground is related to both peat erosion (Evans *et al.*, 2006) and high loss of particulate organic C (POC) via streams (Evans *et al.*, 2014). Evans *et al.* (2014) showed that the POC flux was linearly related to the percentage cover of bare peat, where areas with 100% bare ground could lose up to 500 g C m^{-2} yr^{-1}. Although in this study, there were no plots with 100% bare ground, the higher amount of bare ground on BR plots potentially means that removing brash after mowing could have negative effects for the C balance of the underlying peat.

However, as vegetated ground reduces overland water flow in comparison to bare ground (Holden *et al.*, 2008; Grayson *et al.*, 2010), the substantial amount of ground covered by brash/dead/burnt material should probably be taken into account in the context of erosion and C loss as, although this would have altered surface roughness, much of this was underlain by bare ground. When bare ground and brash/dead/burnt material cover estimates were combined, BR and LB plots had lower cover of non-vegetated ground (28% and 31%, respectively) than FI plots (39%). There was only a slight difference in DOC and POC concentrations measured from the burnt and mown sub-catchment streams (see Chapter 2) but, as the brash/dead/burnt material decomposes and vegetation recolonises bare ground, these differences may become more pronounced. A longer study would be needed to determine whether this is the case.

3.4.3 Photo resurveys

There was a significant difference between field and photo estimates of the seven cover groups (Table 3.3). Given that both methods involved surveying by eye, it is likely that human error partially contributed to some of the differences. However, only the 5 m x 5 m plots differed in their cover estimates. This was mainly due to the photo resolution being too low to accurately distinguish between small species and species at low cover, which was particularly relevant for *Calluna* directly following management and for Other species, which were usually less than 3% in total and often partially hidden under other vegetation. Given that the estimates made of cover in the 1 m x 1 m photo surveys were similar to those made in the field, there is real potential to apply this method to engage landowners in habitat monitoring as well as producing scientifically meaningful data.

Since many landowners and gamekeepers are largely interested in producing grouse and keeping traditional practices such as burning alive, they may not understand or feel engaged with scientific monitoring. However, if a monitoring method is simple, they may be persuaded to conduct a trial on their land, even if just to assess *Calluna*. One of the main reasons why the photo resurveys were conducted by eye rather than employing a digital method to quantify vegetation cover (e.g. pixel spectral classification; Carleer & Wolff, 2004) was because the photos can be easily obtained using a camera or smartphone and easily analysed by comparing to percentage cover charts, or simply comparing photos over time, without the need for any specialised software or even a computer.

There are two main drawbacks to surveying vegetation using photos. Firstly, it is not possible to identify all species to the species level, which includes most mosses and liverworts. In principle, this would not be a problem as the primary use would be quantifying *Calluna* and typical bog species cover. Secondly, and more importantly, it is only possible to identify and quantify species to 100% cover. Many moss species, including *Sphagnum*, grow mainly amongst or beneath the main canopy meaning that it is likely that moss cover would frequently be underestimated. A potential solution could be to take photographs not only from above but also from different angles around the sides of a plot. Although the primary interest of gamekeepers would be to establish the speed and vigour of *Calluna* regrowth, the same photos could be collated and assessed by conservation or academic organisations for changes in *Eriophorum* and *Sphagnum* cover, especially since *Sphagnum* was distinguishable from other mosses in more than 85% of the photos. Additionally, Peichl *et al.* (2014) showed that photos taken with a point-and-shoot digital camera could be used to assess vegetation phenology by colour analysis and related to the C dynamics.

3.4.4 *Calluna* standing biomass, height and LAI

Classifying *Calluna* plants into ‘leafy’ and ‘woody’ portions required some subjectivity, especially with young *Calluna* where most stems, even the more rigid lignified ones, were green. However, any errors in material classification were likely to have been consistent for plants across all plots.

Calluna on DN plots had a far lower ‘leafy’ to ‘woody’ ratio than the BR, LB or FI plots post-management. This was due to the *Calluna* being older and therefore without as much growth vigour (Gimingham, 1975) as the younger plants, as well as possessing longer and thicker lignified stems; although some plants on burnt and mown plots regrew from old stems, these were much shorter having been burnt or cut almost to the ground. A higher ‘leafy’ to ’woody’ ratio may seem beneficial for grouse but the quantity of *Calluna* leaves was more than seven times greater on DN plots than any other management. The benefit of management however, was that most of the unproductive woody growth was removed, lowering the potential fuel load and reducing the risk of wildfires (Allen *et al.*, 2013).

Additionally, management significantly reduced the LAI (Figure 3.7) which opened up the canopy, allowing more light to penetrate to the moss layer; whilst this may have induced a growth response, this would have only been in moss height as the cover values did not exhibit much change. Typically, LAI values at Moor House National Nature Reserve (NNR), a much-studied experimental bog with areas managed by burning, were between 1 and 2 (Heal & Perkins, 1978), which were low compared to the post-management DN plots (2.71) and high compared to the other managements (0.43 to 0.47). Given that much of the *Calluna* on BR, LB and FI plots was removed by management, the low LAI with leaves covering just under half the ground was unsurprising. Compared to the values in Heal & Perkins (1978), these plots actually showed a relatively rapid recovery of *Calluna* since LAI was determined less than three years after management. The high and relatively stable LAI on the DN plots suggests that the productivity of the *Calluna* leaves was in balance with the loss of leaves. It also indicates that the canopy was densely closed, possibly meaning that the upper layers of the canopy were blocking out the light for the layers beneath (Grace & Woolhouse, 1973). This is unlikely to be beneficial to plants beneath the canopy such as *Sphagnum* mosses (Aerts *et al.*, 1990), suggesting that the management approach of doing nothing (i.e. the DN management), is unlikely to be useful long term to increase C accumulation or moisture retention. However, there is evidence to suggest that *Calluna* on wetter bogs can regenerate by layering (MacDonald *et al.*, 1995) whereby vegetative trailing stems root whilst the older plant dies back (Forrest, 1971). Additionally, once *Calluna* reaches an age of about 30-40 years, gaps often develop in the canopy (Gimingham, 1975) which may then allow re-establishment of an understorey. Based on the stable LAI, the *Calluna* on DN plots appeared not to have reached this stage but further study would be required to determine whether gaps appeared in the *Calluna* canopy in future, as this may negate or lessen the need for management in wetter areas.

It is of interest that, although there were no differences in LAI or the ‘leafy’ to ’woody’ ratio between BR, LB and FI plots, there were differences in height. FI plots had shorter plants than LB and BR plots in all years at both survey scales (Figure 3.8) despite not all differences being statistically significant. This may be related to the percentage of plants which germinated from seed as opposed to re-growing from the original stem as FI plots had the highest proportions (Figure 3.9). Liepert *et al.* (1993) also found that burnt areas had more *Calluna* seed germination whereas mown areas had more vegetative regrowth. However, their results varied depending on the age of the *Calluna* before management. Similarly, Miller & Miles (1970) and Hobbs & Gimingham (1984) found that *Calluna* re-growing from existing stems grew with more vigour from stems which were 6-10 years old than any other age, regardless of whether they had been cut or burnt. What neither study determined was whether this would be the case for repeated management cycles or whether the growth rate would decline with each cycle. The age of *Calluna* in the current study was unknown and was assumed to be similar across sites but was estimated to be 15-20 years old given its height. This estimated age may explain the high germination rates (up to 100% of *Calluna* measured on some plots) and the relatively low proportion of vegetatively regenerating *Calluna* in 2013 (Figure 3.9).

Mallik & Gimingham (1985) showed that *Calluna* seeds germinate better after fire. The maximum germination from any fire-treated seeds was 76%, compared to their control which had 58% germination. Although the results in the present study show that FI plots had a higher proportion of *Calluna* growing from seed than BR and LB plots (Figure 3.9), there was still substantial seedling establishment on mown plots. Additionally, when taking into account the higher percentage cover of *Calluna* on mown plots compared to burnt (Figure 3.6A), the actual number of plants growing from seed is likely to have been similar. Mallik & Gimingham (1985) reported that ground temperatures should not exceed 100°C to reduce risk of killing seeds. It may be that burning exceeded these temperatures on some FI plots, killing seeds and lowering germination. Given how low this maximum temperature suggested by Mallik & Gimingham (1985) is and the comparable germination rates observed on BR and LB plots compared to FI plots, mowing may produce more consistent results in terms of *Calluna* germination and regrowth, thereby benefitting grouse.

In terms of C dynamics, the amount of regrowth and the amount of biomass lost is more important than the method of regrowth. Although only the C content of the 'leafy' material was measured, it was assumed that the 'woody' material had a similar or greater C content as wood contains lignin which is C rich. Any underestimate in C content of the 'woody' components however may have been cancelled out by not including biomass of other plants present on the FI plots in the estimate of C lost through burning. Additionally, some charred material and ash was left on the plots, meaning burning did not release all the biomass C (Allen, 1964). Regardless of the precise amount, the figure of 587 g C m^{-2} in the *Calluna* biomass on the FI plots is probably fairly representative of the total amount of C lost. This represents a substantial amount when compared to the annual C budgets (see Chapter 2). However, there may also have been some C loss from the brash on the mown plots as this decomposed but this loss is less immediate and some brash may be overgrown by plants and become incorporated into the peat. Further investigation is required into the ultimate fate of the brash.

Moor House NNR is classified as M19b in the NVC system (Rodwell, 1991; Ward *et al.*, 2007) and all three sites in this study classed as M19a. Therefore, the main vegetation communities are comparable and all are blanket mires in the north west of England. It was therefore surprising that the biomass of *Calluna* recorded in this study was not comparable. Forrest (1971) recorded values of 665 g m^{-2} dry *Calluna* biomass on an area of Moor House which had not been burnt for 30 years. These values were approximately half as much as those for the pre-management values presented in this study, although it should be noted that the *Calluna* had probably been burnt more recently than 30 years before the pre-management samples were cut. A more recent estimate by Ward *et al.* (2007) found that unburnt areas held five times less biomass than the DN plots. Furthermore, the biomass calculated for FI plots three years after burning was almost the same as that recorded by Ward *et al.* (2007) at Moor House nine years into a 10 year burning cycle. As Moor House is the most studied blanket bog in the UK, there is the assumption that it is representative of all *Calluna*-dominated blanket bogs in the UK. The large differences in *Calluna* biomass suggest otherwise as there was little difference in the biomass recorded at the three sites in this study. However, this study could contain errors generated by sampling *Calluna* from only a small chamber area on each plot and multiplying up to the plot size using the percentage cover.

For red grouse, the biomass gained is far more important than the amount lost or retained since *Calluna* is their main food source (Wilson & Leslie, 1911; Jenkins *et al.*, 1963) and older *Calluna* is "valueless as food for grouse" (Wilson & Leslie, 1911) compared to the bright green new shoots. Unfortunately, although tags were attached to *Calluna* stems at all sites, it was not possible to directly derive growth rates due to the majority of these tags being eaten by sheep. However, there was an increase of almost 300 g m^{-2} *Calluna* biomass between pre- and post-management DN plots which could be taken as the growth rate over the three years. The burnt and mown plots produced less than half the amount the DN plots did but similar amounts to each other (121 g m^{-2} for FI plots; 112 g m^{-2} for BR plots and 124 g m^{-2} for LB plots; see Figure 3.7). This agrees with the study by Liepert *et al.* (1993) in the North York Moors National Park, which also found that burnt and cut areas produced similar amounts of *Calluna*, although their values were an order of magnitude smaller after the same number of growing seasons. However, Liepert *et al.* (1993) determined the regenerating biomass by a combination of harvesting along a transect and counting density shoots in a small quadrat which may account for some of the differences. In contrast, values from a study in Scotland estimated a year's growth to be slightly more than the three years of growth recorded here, although this was based on additional shoot production of *Calluna* which was already at least five years old. For grouse however, it is not just the quantity of biomass which matters, it is also the quality.

3.4.5 Plant nutrient content

Moss (1967) noted that there was no change in chemical composition of *Calluna* over 6 years old. However, Moss (1967) also showed that the nutrient content of the *Calluna* varied with the season, regardless of age, although there were not consistent seasonal changes. As seasonal variability is probably due to climatic conditions in the locality, this could at least partially explain some of the differences in the *Calluna* nutrient content between sites. It may also explain the small differences in *Calluna* nutrient content between pre- and post-management DN plots.

The most striking revelation shown through measuring the plant nutrient content of *Calluna* was that, of the six elements which differed significantly between managements (excluding Na and Cu which had no post-management differences), five of these (N, P, Mg, Al and Mn) did not show any significant differences between the burnt (FI) and mown (BR and LB) managements post-management (Tables 3.4 and 3.5). Additionally, N, P, K, Mg and Mn had significantly lower content in *Calluna* from DN plots than from the managed plots. Although there were higher Ca concentrations in *Calluna* plants on FI plots, they were not significantly higher and reflected the slightly higher pre-management concentrations (Figure 3.10F). The drop in P content of *Calluna* on DN plots in the post-management period (Figure 3.10B) may be as a result of variation between plants selected in the two periods, an effect of season, or it may be that the *Calluna* age affected P uptake (Moss, 1969). If the latter was the case, it may not be advisable to leave *Calluna* completely unmanaged if grouse production is a concern. Additionally, Savory (1978) showed that grouse preferred to eat *Calluna* between two and eight years old and, from the results shown here, management is more likely to provide this.

Estimates of the amount of *Calluna* eaten by red grouse range from 63 g d^{-1} for wild cocks to 100 g d^{-1} for wild laying hens (Savory, 1974). The only element for which the *Calluna* differed significantly between burnt and mown plots was K. Laying hens require higher amounts of some elements due to the nutrients being used in the creation of eggs (Jenkins *et al.*, 1965). A wild grouse during egg laying retains (i.e. requires) up to 160 mg K d^{-1} (Moss, 1977). Therefore, even though *Calluna* from the FI managed plots had significantly more K in than *Calluna* from the BR management, a grouse eating from the BR management plots would only need to eat up to 39 g of *Calluna* each day to satisfy its K requirements. Even eating *Calluna* from DN plots, which had significantly lower concentrations than all the other managements, the grouse would only require 48 g of *Calluna* per day. This shows that even grouse eating only 63 g *Calluna* d^{-1} would easily consume the necessary amount of K, regardless of the management.

Likewise, using the maximum values required by a laying hen (which are assumed to be the maximum amounts required and may also be instrumental in breeding success; Jenkins *et al.*, 1965) reported by Moss (1977) for each element, *Calluna* from any management would satisfy the hen's N, Na, Mg and Ca requirements. DN plots had lower concentrations of all these elements but even so, a laying hen which solely fed on unmanaged areas would at most require 50 g of *Calluna* to satisfy its N requirements, 31 g for Na, 11 g for Mg and 80 g for Ca. For P, a hen would require 129 g of *Calluna* if solely feeding on DN plots, which is substantially greater than the upper estimate of dry matter consumed per day. However, 68 g, 81 g and 74 g of *Calluna* would be require to meet P requirements if feeding was solely on FI, BR and LB plots respectively, all of which are within the range of *Calluna* consumed per day. This suggests that some form of intervention management is required to recycle some of the P from older plants and allow new growth to use it.

There is evidence that red grouse selectively consume plants with higher N and P contents (Moss, 1972, 1977) and this selection is even more pronounced in chicks than adults (Savory, 1977). Chicks selected *Calluna* with an average of 2.32% N and 0.25% P (Savory, 1977). These values are much higher than the average values on any management here, although seven plots (out of the 72) contained more N than this. However, chicks are likely to only eat the very newest tips (Savory, 1977) and the material analysed for burnt and mown plots contained a mixture of leaves representing three years of growth. Also, the post-management *Calluna* was cut in August whereas pre-management *Calluna* was cut in early spring, which likely affected the content of some nutrients (Moss, 1967), although should not have affected the differences between managements within a period. Additionally, although *Calluna* is the main component of the red grouse's diet, both chicks and adults eat other plants and some insects (Savory, 1977). Where available, *Vaccinium myrtillius* L. is sought after, which has a higher P content and usually begin growing earlier in spring than *Calluna* (Moss, 1972). Few studies on red grouse nutrition have been conducted on moors with high *Eriophorum* cover, or if they have, the nutrient content of *Eriophorum* has not been considered. However, female capercaillie (*Tetrao urogallus*) and to some extent willow grouse (*Lagopus lagopus*), the latter of which is very closely related to the red grouse, have been shown to select high-N and -P foods, including the flower buds of *Eriophorum vaginatum* (Pulliainen & Tunkkari, 1991). Therefore, it might be worth land managers considering the range and cover of species other than *Calluna* when considering management options to benefit their grouse populations.

Post-management, differences in Na, Ca, Fe, Zn and Cu were present between the various managements to a greater or lesser extent but none was significantly different (Figure 3.10). Although these elements are important components of diet, different managements do not appear to produce large or consistent effects on most of them and therefore no particular management should be selected on the basis that it can control the content of any of these elements in *Calluna*. The 3- to 4-fold increase in Mn content however should be considered, especially since lack of Mn can cause breeding and development problems in poultry and pheasants (National Research Council, 1994), although as with N and P, it appears that it is management in general which is required to elevate Mn concentrations rather than specifically mowing or burning. Given that N and, especially, P are considered to be the most important nutrients for red grouse (Moss, 1969, 1972, 1977; Savory, 1977), this suggests that, with regards to red grouse nutrition, there is no reason to prefer either burning or mowing as a method of *Calluna* management.

3.4.6 Conclusions

There are many aspects of vegetation which have been considered here with regard to different types of *Calluna* management. The managements did not affect the species richness or diversity (Figures 3.3 and 3.4) and the only difference seen in 'leafy' to 'woody' ratios and LAI of *Calluna* plants (Figure 3.7) and the biomass of *Calluna* (Figure 3.7) was to be expected since the unmanaged plots differed from the managed. Similarly, DN plots had taller *Calluna* due to this not being cut or burnt, although the FI plots had shorter than BR or LB plots (Figure 3.8), which seemed to be as a result of a higher proportion of plants growing from seed after burning (Figure 3.9).

However, there were differences in the cover of *Calluna*, *E. vaginatum*, bare ground and brash/dead/burnt material between the managements (Figure 3.6). From a grouse shooting perspective, *Calluna* cover is the most important since this is the main food source of red grouse. It was therefore surprising that BR plots had significantly higher *Calluna* cover than FI plots, and LB plots also had higher cover than FI plots, which neared significance (Table 3.2), given that burning is usually advocated as the best form of management for grouse. The higher cover of *E. vaginatum* on mown plots regardless of brash removal was less surprising since it is a typical bog plant and mowing is thought to dry the peat less than burning. Although there were no differences in *Sphagnum* cover between managements, in the longer term, *E. vaginatum* may provide sheltered and damper areas for *Sphagnum* plants to grow, but further monitoring and research are required to determine whether this is the case. The higher amount of bare ground on BR plots is probably explained by the lower cover of brash/dead/burnt material through the removal of the mown and mulched material, which may still be detrimental for water retention and increase surface runoff, thereby causing erosion of the peat. Overall however, the FI plots had a lower cover of vegetated ground. Of the six elements which showed differences between the managements, the only difference for five of these was between DN plots and managed plots. Although K was higher in *Calluna* from burnt rather than mown plots, there was still sufficient K for grouse, even during egg laying.

Overall, in terms of C storage, mowing the *Calluna* and leaving the brash in place (LB management) appeared to offer the most benefits, as removing brash resulted in higher amounts of bare ground (BR plots), burning resulted in lower cover of vegetated ground and a large loss of C from biomass (FI plots), and no management resulted in lower cover of *E. vaginatum* (DN plots). In terms of benefits to grouse, *Calluna* on unmanaged plots had lower concentrations of the most important nutrients for grouse (N and P) and therefore may have detrimental effects on the population. In terms of nutrient content of *Calluna*, there is no advantage to having *Calluna* with a higher K content and therefore burning need not be preferred over mowing. Taking into account the cover and height of *Calluna*, mowing with brash removal (BR) is most productive, although there is little difference if the brash is not removed (LB) and this brash may be beneficial longer term with regard to nutrient cycling and water retention. Additionally, the higher *E. vaginatum* cover on mown plots increases the amount of an extra P-rich food source which the grouse may utilise. Although vegetation dynamics were only assessed for the first three years of the 10 year management cycle, overall, if the aim is to increase C storage whilst maintaining a grouse population which offers a shootable surplus, the LB management appears to hold the most benefits. If the aim is solely to increase C storage, the DN management may prove beneficial in terms of having the greatest standing biomass and least bare ground, although further monitoring is required to determine the longer term effects of all types of management on *Sphagnum* cover and diversity.

4 Getting to the root of the matter: can ericoid fungi break down recalcitrant organic carbon compounds?

4.1 Introduction

Ericoid fungi can form mycorrhizal symbioses with ericaceous species, such as *Calluna vulgaris*, or exist as 'free-living' fungi in the soil. When in a mycorrhizal association, they help the plant to acquire nutrients from the soil and receive C from the plant in return (Read, 1991): this benefits the growth of both plant and fungus. Ericoid fungi have saprotrophic properties and it has been demonstrated that they have the capability to break down structural and recalcitrant components in plant litter and soil including cellulose (Varma & Bonfante, 1994), hemicellulose (Burke & Cairney, 1998), polyphenols (Varma & Bonfante, 1994) and lignin (Haselwandter *et al.*, 1990), amongst others. This suggests that even when they are not in mycorrhizal associations, they help to cycle and release nutrients which can aid plant growth, thereby reducing the susceptibility of the peat to erosion (Evans *et al.*, 2014).

Likewise, burning can accelerate plant regeneration (Mahmood *et al.*, 2003), as the residue left behind has a higher content of available nutrients than the soil or unburnt litter. However, burning can also release waxes or bitumens which partially waterproof the surface (Clymo & Gore, 1983), increasing surface runoff and dissolved organic carbon (DOC) release. It is therefore unclear as to the overall effect that burning has on water quality because, although implicated in increasing DOC concentrations (Clutterbuck & Yallop, 2010), burning does not necessarily cause consistent increases in DOC or water colour (Holden *et al.*, 2012).

Additionally, as burning is mainly only used on grouse moors in the UK, this cannot explain the increase in the amount of DOC in, and the water colour of, streams flowing from many peat-covered catchments since at least 1990 across the northern hemisphere (Stoddard *et al.*, 2003; Skjelkvåle *et al.*, 2005) and at least 1962 in the UK (Worrall *et al.*, 2003a). Explanations for this long term trend include droughts (Worrall & Burt, 2004), increasing temperatures (Freeman *et al.*, 2001a; Worrall *et al.*, 2004), and recovery from acidification as a result of decreasing nitrate and sulphate deposition (Stoddard *et al.*, 2003; Evans *et al.*, 2005; Monteith *et al.*, 2007).

This long-term increase in water colour is concerning for water companies, which must abide by regulations to provide water without colour that is safe for human consumption (Defra, 2016). The main cause of colouration is the humic substances which constitute the more hydrophobic components of DOC. Humic substances largely comprise humic acids, which are dark brown to black, and fulvic acids, which are pale brown to yellow (Thurman, 1985). DOC also contains non-coloured substances, consisting mainly of simple hydrophilic compounds such as carbohydrates, fats, proteins and waxes, which are more easily broken down by microorganisms so have a shorter residence time than the humic substances (Schnitzer & Khan, 1972; Thurman, 1985).

DOC is removed from water in treatment plants by adding an amount of coagulant which varies with the quantity and colour of the DOC in the water. However, whilst this removes the darker humic acids fairly easily, thus reducing the water colour, it is harder to remove the fulvic acids and non-coloured substances (Worrall & Burt, 2009). If these substances remain in the water at high concentrations, the chlorination process used to disinfect drinking water can result in the formation of disinfection by-products, such as trihalomethanes and haloacetic acids, which are believed to be carcinogenic (Singer, 1999; Clay *et al.*, 2012). In both moving and static water bodies in Scotland, Dawson *et al.* (2009) found a reduction in the proportion of humic substances in DOC. This is reflected in the long-term increase in the amount of coagulant needed to be added to water per unit of colour (Worrall & Burt, 2009), suggesting that the proportions of fulvic acids and non-coloured substances are indeed increasing. This provides a greater and more expensive challenge to the water companies.

Much of the DOC, which is an important component in peatland C budgets (Roulet *et al.*, 2007; Nilsson *et al.*, 2008; Dinsmore *et al.*, 2010), that is washed out of catchments decomposes to CO_2 and CH_4 further downstream (Billett *et al.*, 2004; Worrall & Moody, 2014). Increasing DOC concentrations are therefore likely to also increase the downstream gaseous evolutions which, combined with CO_2 and CH_4 emissions directly from the peat, could accelerate climate change and impose negative feedbacks (Davidson & Janssens, 2006).

Climate scenarios for the UK predict hotter temperatures and a decrease in summer rainfall (Murphy *et al.*, 2009), which are likely to cause lower peatland water tables. It has been demonstrated both under drier conditions, which allow greater oxygen ingress (Freeman *et al.*, 2001b), and warmer conditions (Freeman *et al.*, 2001a), that the enzyme phenol oxidase becomes more active. This enzyme removes phenolic compounds, which are known to inhibit other enzymes and microbes, thus enabling an increase in biodegradation (Freeman *et al.*, 2001b) and potentially increasing both DOC and CO_2 release.

A changing climate is also likely to cause shifts in plant assemblages, which on northern peatlands will result in a decline in mosses and other bryophytes to the benefit of vascular plants (Gallego-Sala & Prentice, 2013). It has been suggested that this is linked to the release of labile C compounds from vascular plants into the soil (Bragazza *et al.*, 2013). Indeed, there are a number of studies demonstrating the ability of vascular plants to prime decomposition of older soil C (Fontaine *et al.*, 2007; Hartley *et al.*, 2012; Lindén *et al.*, 2013; Wild *et al.*, 2016).

As evidenced in Chapter 3, *Calluna vulgaris* is the most common vascular plant found on grouse moors, due to management encouraging regeneration and germination. There is growing evidence showing that *Calluna* is associated with elevated DOC concentrations (Vestgarden *et al.*, 2010; Armstrong *et al.*, 2012) as well as studies demonstrating the priming and loss of ancient C by *Calluna* plants (Walker *et al.*, 2016). Wetter peatlands tend to produce high CH_4 emissions but relatively low CO_2 emissions compared to other soils due to high WTDs excluding many aerobic processes (Lai, 2009). *Calluna* however, has a high transpiration rate so can reduce water tables and dry out peat (Worrall *et al.*, 2007), shifting decomposition from anaerobic to aerobic (Freeman *et al.*, 2001b), which could explain the higher DOC concentrations and CO_2 emissions associated with *Calluna* plants.

However, much of the organic matter in both the peat (Bosatta & Ågren, 1999) and the charcoal created from burning (Woolf *et al.*, 2010) is assumed to be stable and recalcitrant meaning it is unlikely that *Calluna* plants themselves greatly affect it. Crucially therefore, ericoid mycorrhizas, whether in association with *Calluna* roots or not, may utilise their saprotrophic abilities to break down either peat or charcoal, or both, and therefore be at least partially responsible for the observed increase in DOC production and water colour (Worrall *et al.*, 2003a, 2004; Clutterbuck & Yallop, 2010; Armstrong *et al.*, 2012). Additionally, given the evidence that *Calluna* plants prime decomposition of ancient C (Walker *et al.*, 2016), it may not be solely bacteria which are primed, but ericoid mycorrhizas which cause the increase in soil respiration.

There are three main methods used to determine how much respiration each ecosystem components contributes: physically partitioning components in an otherwise intact system, usually by excluding roots; separating and measuring components individually and summing the fluxes; and using stable (^{13}C) and radioactive(^{14}C) C isotopes (Hanson *et al.*, 2000). The first two options introduce an element of disturbance, the latter more than the former, resulting in measurements which do not necessarily reflect those of the original ecosystem or its component parts. Isotopic methods circumnavigate these problems (Hanson *et al.*, 2000).

The use of C isotopes has been instrumental in the partitioning of autotrophic plant respiration and heterotrophic respiration that has been stimulated by plant addition (Hahn *et al.*, 2006). Components enriched in ^{13}C (Wild *et al.*, 2016) or ^{14}C (Haselwandter *et al.*, 1990) can be added to intact or laboratory systems, for which both the component and system isotopic signatures are known, and proportional respiration contributions can be derived from the signature of the evolved C. Alternatively, the natural isotopic gradient, measured in %Modern (which is a relative measure with the baseline being 100 %Modern in 1950), can be used. Due to atomic bomb testing in the mid-20th century releasing a pulse of ^{14}C (bomb peak ^{14}C) to the atmosphere, C fixed by photosynthesis since the 1960s has an elevated ^{14}C content, with C enrichment of approximately 190 %Modern occurring in the mid-1960s (Levin *et al.*, 2008) and falling to a contemporary level of about 103 %Modern. In contrast, as peat accumulates over millennia, the basal peat is relatively depleted in ^{14}C compared to the upper layers (Borren *et al.*, 2004) due to the exponential decay of ^{14}C. The peat profile therefore represents a continuum of ^{14}C enrichment, with the exception of C fixed since the 1960s, which can be coupled with mass balance approaches to partition respiration into recently derived CO_2, usually assumed to be that from plants, and older CO_2 from soil respiration (Hardie *et al.*, 2009; Walker *et al.*, 2016).

Here, a pot experiment, which enabled manipulation of ecosystem components, was used to monitor CO_2 and CH_4 fluxes and DOC concentrations. This was coupled with ^{14}C measurements to partition the effects of ericoid fungi, *Calluna* plants and charcoal on DOC and CO_2 fluxes, with the aim of establishing whether the presence of ericoid fungi affected decomposition, and hence DOC and CO_2 production, by decomposing charcoal, old organic matter in the peat or both. Specifically, the hypotheses tested were that ericoid mycorrhizal presence within *Calluna* roots would a) increase DOC production and CO_2 fluxes, b) alter DOC composition and c) increase the age of DOC and respired CO_2. Additionally, that these decomposition effects would d) differ between a single ericoid fungus (*Hymenoscyphus ericae*) and a natural mixed community and e) pots with free-living fungi (i.e. no plant) would also affect DOC and CO_2 production rates.

4.2 Methods

4.2.1 Peat preparation

Peat was collected between 1 and 2 m from the top of a peat hagg in the Peak District, which was expected to have a minimum age of 3000 years based on evidence from (Tallis, 1991). This was to avoid problems associated with bomb-peak C ages (Evans *et al.*, 2007) and to provide a strong contrasting age against any recently produced C (e.g. from plant root exudates). Living roots were removed and pieces of peat with a diameter more than about 3 cm were broken up. Plastic boxes (64 L capacity; Really Useful Storage Boxes, London), lined with polythene sacks, were filled with peat to a depth of 30 cm. Filled boxes were gamma-irradiated at 34.5 kGy (Bradford Synergy Health PLC, Bradford). Although a dose of 10 kGy should have been sufficient to destroy the filamentous fungi (Parker & Vincent, 1981), 34.5 kGy was the only available dose and increased the chance that all fungal spores were rendered inviable. Both autoclaving and microwaving were considered as sterilisation methods but were deemed impractical for the quantity of peat required (see Trevors (1996) for details of appropriate weights and layer thicknesses required for adequate sterilisation). Additionally, autoclaving releases more nitrates, ammonium and soluble organic matter than gamma-irradiation (Salonius *et al.*, 1967) and can destroy the soil structure (Trevors, 1996). In order to reduce the impact gamma-irradiation had on the peat, the soil was air-dried before irradiating to reduce the release of radiation-induced soluble organic matter as much as possible (Salonius *et al.*, 1967), which involved mixing to remove moisture. This mixing also homogenised the peat which was necessary to obtain a consistent average age throughout.

The sterile peat was rehydrated by being submerged in deionised water for 2 weeks in a laboratory environment to reduce the risk of contamination by fungal spores. The peat was drained in a 24 cm tinned mesh sieve (Kitchen Craft, Birmingham) and lumps were further broken up to smaller than 2 cm in diameter. Every sieve full of peat was also rinsed with fresh deionised water to wash out excess DOC caused by the gamma-irradiation process (Genney *et al.*, 2000) before peat was placed into plant pots. Finer peat fragments were retrieved by filtering through pieces of cotton cloth.

4.2.2 Pot preparation

Forty eight 25 cm diameter and 22 cm tall PVC pots (ref: 101; LBS Horticulture Ltd, Colne, UK), forty eight 32 cm diameter by 4 cm tall saucers (ref: SAU 019; LBS Horticulture Ltd, Colne, UK) ninety six 11 cm diameter 3 cm tall uPVC collars (Plumb Center, Wolseley UK Ltd, Leamington Spa, UK) were wiped with a 7.5% calcium hypochlorite solution (Technical grade $CaCl_2O_2$, Sigma-Aldrich Company Ltd., Dorset, UK) and rinsed five times with deionised water to sterilise them. Pieces of 1 µm nylon mesh (Normesh Limited, Oldham) were glued over the pot drainage holes (2 cm by 4 cm) with Bostik All Purpose Glue (Bostik Ltd, Stafford) and sealed around the edges with non-toxic aquarium silicone sealant (Everbuild Building Products Ltd, Leeds).

Pots were filled in batches of 12 with the sterile washed peat. Filled pots were placed in the saucers, which were filled with deionised water (pH adjusted to 3.6). This simulated a WTD in the pots of -18 cm, which was chosen as it was deemed to represent a typical summer WTD on a blanket bog managed by burning (the WTDs on all three sites studied in Chapters 2 and 3 frequently recorded WTDs below -18 cm between late spring and early autumn). Additionally, lower WTDs tend to cause increased decomposition due to more aerobic conditions (e.g.

Frolking *et al.*, 2011) and it was hoped this would help to provide sufficient C release (in both water and air) for radiocarbon analysis. A pre-soaked Rhizon soil moisture sampler (pore size 0.15 µm, Rhizosphere Research Products B.V., Wageningen, Netherlands) was inserted through a hole drilled 18 cm from the top of each pot (so it was just above the WTD) and sealed in place with the aquarium silicone sealant. For the top of each pot, a pair of sterile collars was glued together with a 26 cm diameter circle of the 1 µm nylon mesh sandwiched between. All joins were sealed with aquarium silicone sealant (see Figure 4.1 for schematic of full pot set-up).

4.2.3 Pre-treatment measurements

Water samples were collected twice from each pot during a five week period (see Table 4.1 for dates) by attaching 50 ml luer-lock syringes to the Rhizon samplers. The syringes were held open with a retainer to create a vacuum. The DOC concentrations were determined using a total carbon analyser (LiquiTOC, Elementar Analysensysteme GmbH, Hanau, Germany). Prior to analysis, samples were acidified and sparged with oxygen to remove any inorganic carbon. A five-point calibration was determined with a sodium carbonate and potassium hydrogen phthalate (SC/KHP) solution and standards of 50 ppm SC/KHP were regularly analysed during a machine run to reduce machine drift and errors. All samples were analysed in duplicate. The absorbency of the water samples was measured in a 1 cm wide quartz cell at 254, 400, 465 and 665 nm (Abs_{254}, Abs_{400}, Abs_{465} and Abs_{665}) using an ultra-violet spectrophotometer (Lambda 25 UV-Vis spectrophotometer, PerkinElmer Ltd, Beaconsfield, UK), with a blank (deionised water) reading subtracted from each sample.

An infrared gas analyser (IRGA; Model 8100, Li-Cor, Lincoln, NE, USA) and an Ultraportable Greenhouse Gas Analyser (UGGA; Model 915-0011, Los Gatos Research, Inc., San Jose, CA, USA) were connected in sequence to a 10 cm automated survey chamber (Model 8100-102, Li-Cor, Lincoln, NE, USA) to allow for simultaneous CO_2 and CH_4 measurements. Although the UGGA is able to measure both CO_2 and CH_4, the IRGA was connected in order to enable the chamber to be raised and lowered, thus pinpointing the exact measurement periods, which aided derivation of the fluxes. The chamber was placed over the top collar, which had been pressed onto the peat surface, and fluxes measured for a 90 s period on four occasions during a three week period (see Table 4.1).

On 29th January 2015, all pots were weighed to the nearest gram during the gas measurements, having been watered to excess with pH-adjusted (pH 3.6) deionised water 12 hours before. The offset from the top of the pot to the peat surface was also measured to the nearest half centimetre. On 30th January, a teaspoonful of peat was removed from the

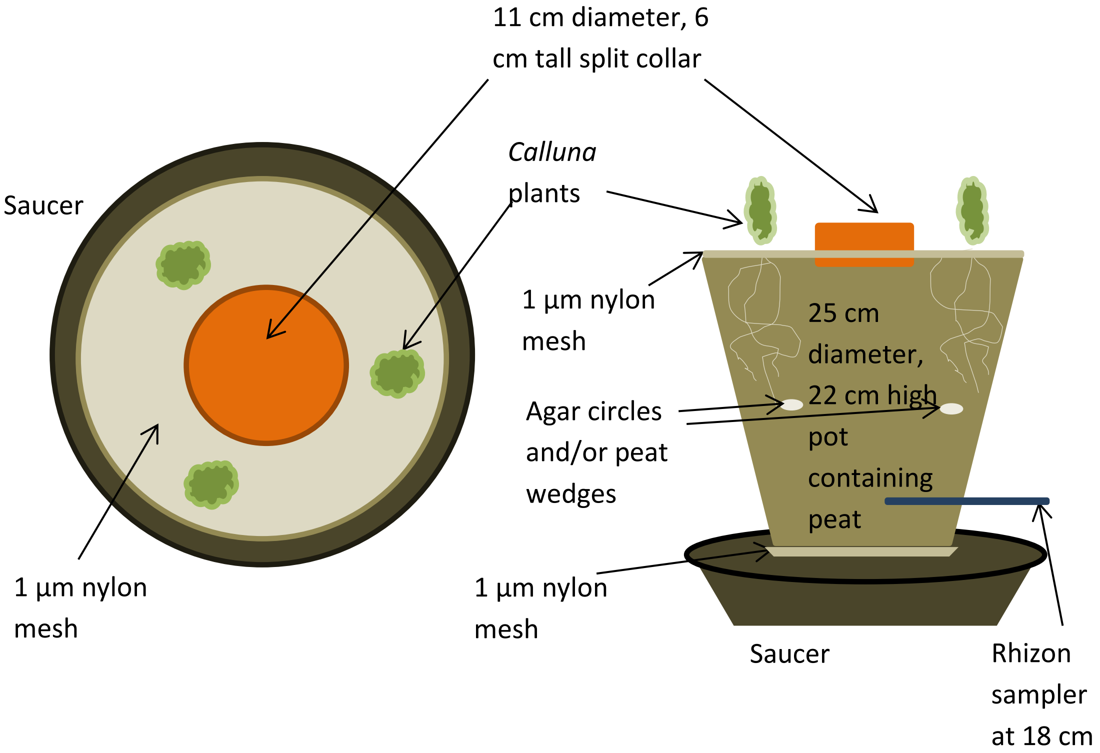


Figure 4.1 Schematic of a full pot set-up.

The diagram on the left shows a pot as viewed from above. The diagram on the right shows a cross-section of a pot viewed from the side. All pieces of mesh, Rhizon samplers and collars were glued and sealed around to prevent fungal spore entry. Not all pots contained *Calluna* plants and all pots had either agar, agar inoculated with *H. ericae* culture or agar and non-sterile peat wedges buried below the peat surface (see Table 4.2 and text for treatments).

Table 4.1 Dates (all in 2015) when plant pots were measured for CO_2 and CH_4 and when water samples were collected from the pots.
Water samples were tested for DOC and absorbency at various wavelengths (see text) with one month of collection. No CH_4 samples were collected for ^{14}C analysis.

Measurement set	**CO_2 measurements**	**CH_4 measurements**	**Water samples**
Pre-treatment measurements (all 2015)	22nd January	22nd January	
	29th January	29th January	19th January
	30th January	30th January	11th February
	5th February	5th February	
Post-treatment measurements (all 2015)	12th August	12th August	12th August
	13th October	13th October	13th October
	6th November	6th November	9th November
	10th November	10th November	13th November
	19th November	19th November	19th November
^{14}C sample collection (all 2015)	14th October*	-	Continuous multiple collections between 20th and 26th October
	15th–16th October		
	19th October		

*No CO_2 sample collection for radiocarbon analysis was made on 14th October; the CO_2 fluxes measured on this date were used in the mass balance equations.

subsurface of each pot, weighed and placed in a foil tray in an oven at 80°C until a stable weight was reached. The water content was calculated from the wet and dry peat weights for each pot and the dry weight for each pot calculated.

4.2.4 Making charcoal

On 3rd July 2014, all *Calluna* plants (which were 30-40 cm tall) were cut at the base from a 5 m x 1 m patch at Whitendale. On 31st July, the air-dried *Calluna* plants were burnt on a clean brick barbeque pit, with the burnt *Calluna* caught underneath in a metal tray lined with aluminium foil. The burnt *Calluna* residue was stored in air-tight plastic containers at ambient temperature. Although this burnt residue is referred to as charcoal throughout the rest of this thesis, it should be noted that the residue is not solely charcoal; it is likely a mixture of ash and charcoal (see Section 4.4 for further details).

4.2.5 Culturing ericoid mycorrhizas

Due to its extensive use in laboratory trials, *Hymenoscyphus ericae* (Read) Korf and Kernam (Strain He 101; supplied by Dr JR Leake, University of Sheffield) was chosen as the single ericoid mycorrhiza fungus. The fungus was cultured on Modified Melin Norkrans agar (MMN) media acidified to pH 4.7 with 10%HCl and containing 50 mg $CaCl.2H_2O$, 25 mg NaCl, 155 mg $MgSO_4.7H_2O$, 250 mg $(NH_4)_2HPO_4$, 500 mg KH_2PO_4, 7.2 mg $FeCl_3.6H_2O$, 1 mg thiamine, 2.5 g d-glucose, 10 g malt extract and 15 g agar per litre. The fungal plates were stored at 4°C to slow growth.

4.2.6 Growing *Calluna* plants

Seed trays and propagator lids were sterilised with 7.5% calcium hypochlorite solution, in the same manner as the pots and saucers were (Section 4.2.2). Each tray was filled with sterilised coarse sand. The sand was sterilised by microwaving when saturated with deionised water in a 900W microwave for 4 min kg^{-1} sand, as this was deemed quickest and most cost-effective for killing fungal spores (Ferriss, 1984).

Stem and heel cuttings were taken from young (less than one year old) *Calluna* plants (Cheviot Trees, Berwick-upon-Tweed, UK). The lower leaves were stripped off and cuttings were immediately placed in deionised water to prevent desiccation. The cuttings were sterilised in 3.25% calcium hypochlorite solution for 5 minutes then rinsed five times in autoclaved (121°C for 15 minutes) deionised water.

The cuttings were planted into the sterilised wet sand with the bottom end of each cutting dipped into rooting powder (Doff Portland Ltd, Nottingham, UK). Cuttings were watered in with half-strength ericaceous feed (containing 24% total N, 12% P_2O_5, 8% K_2O, 2% MgO, 0.02% B, 0.01% Cu, 0.2% Fe, 0.02% Mn, 0.002% Mo and 0.05% Zn; Chempak, Ipswich, UK) mixed with deionised water and covered with the sterilised propagator lids. Trays were placed inside a growth cabinet (Sanyo MLR-352, Sanyo Electric Co., Ltd., Tokyo, Japan) with a 16 hour light (at 18°C)/8 hour dark (at 14°C) cycle. The light source was provided from the sides by white fluorescent tubes with an average light level of 150 µmol m^{-2} s^{-1}. The day length was reduced by 2 hours per week in the month prior to removal from the cabinet and temperature was also lowered: the final settings were 10 hours light (at 12°C)/14 hours dark (at 10°C). Sand was kept moist by regular addition of deionised water. Half-strength ericaceous feed was added once every three weeks.

4.2.7 Treatment set-up

The pre-treatment measurements were used to partition the pots into four blocks. The pre-treatment DOC concentrations showed a pattern which corresponded to the four batches used to fill the pots. No such patterns were observed in the CO_2 or CH_4 fluxes. Therefore, four blocks were defined as the four batches in which the pots were filled.

Treatments were administered between 6th March and 14th April 2015 and randomly allocated to one pot per block. Each pot received either *H. ericae* fungal culture (H), a wedge of non-sterile peat to introduce a mixed natural fungal and microbial community (M) or sterile agar, and either *Calluna* plants (C), or not, and charcoal (B), or not. This produced a fully crossed replicated design of 12 treatments. Treatment codes from Table 4.2 will be used henceforth. Where a treatment component is generically referred to, the component code parts not referred to will be represented by X, e.g. XXB represents all pots with charcoal, XC- represents all pots with *Calluna* plants and no charcoal.

Burning has been used for grouse moor management since at least the 1850s (Lovat, 1911) and many moors manage on a 10-20 year cycle (Grant *et al.*, 2012). The *Calluna* from the 5 m x 1 m patch produced 88 g of charcoal. As the surface area of each pot was 490 cm^2, the 3.5 g (± 0.012 g) of charcoal added to each XXB pot was the equivalent of about 4-5 burns, simulating a site managed by burning over the past 50-100 years. The charcoal was spread evenly across the peat surface and roughly mixed into the top ~5 cm.

The *H. ericae* culture was added to the relevant pots by means of punching out approximately 1 cm diameter circles of agar from the growing edges of the culture and burying these about

Table 4.2 Codes used for the 12 pot treatments and the components of each pot treatment.

Treatment Code	Treatment Components
---	Peat only (and sterile agar)
-C-	*Calluna* plants (and sterile agar)
--B	Burnt material/charcoal (and sterile agar)
-CB	*Calluna* plants and burnt material/charcoal (and sterile agar)
H--	*H. ericae* fungal culture
HC-	*H. ericae* fungal culture and *Calluna* plants
H-B	*H. ericae* fungal culture and burnt material/charcoal
HCB	*H. ericae* fungal culture, *Calluna* plants and burnt material/charcoal
M--	Non-sterile peat wedges
MC-	Non-sterile peat wedges and *Calluna* plants
M-B	Non-sterile peat wedges and burnt material/charcoal
MCB	Non-sterile peat wedges, *Calluna* plants and burnt material/charcoal

5 cm below the peat surface. Three circles were added to each pot, evenly spaced round the edge. All pots without *H. ericae* culture addition (including MXX pots) received similar sized circles of sterile MMN media agar in the equivalent places. Non-sterile peat wedges of approximately 3 cm x 1 cm x 1 cm were cut from the root zone of a *Calluna*-covered peat monolith from Mossdale and inserted in the peat to a similar depth as the agar circles.

A single tray of *Calluna* plants was initially used for all relevant pots in a block. Plants were carefully separated and visually sorted by size into three groups based on root size. Three small slits were cut in the mesh circles. The slits were between the pot edge and collar and corresponded to the buried agar locations. One plant was pushed through each slit meaning each pot received one plant from each size group. *Calluna* plants were fixed in the mesh by sealing both sides of the slit around the stem with non-toxic aquarium silicone sealant. Once dry, the central collar was pushed into the peat in the centre of each pot and the peat packed around the base to ensure a seal. The roots of the three attached plants were buried directly next to the agar/fungal circles or peat wedges, placing the growing roots in the vicinity of the fungal mycelium. All pots, including those without plants, received 500 ml of full-strength ericaceous feed. The mesh circles were then glued to the pot edges and sealed with silicone sealant to prevent contamination from fungal spores.

Pots were kept in an unheated greenhouse (heaters automatically switched on only when the greenhouse air temperature dropped below 6°C) and watered by filling the central collars with deionised water, acidified to pH 3.6 with hydrochloric acid. Once every three weeks, half strength ericaceous feed was used instead of water until plants were fully established and new shoots appeared. Some plants did not establish in the pots. On 30th April 2015, 11 dead *Calluna* plants were replaced with live ones. To reduce the disturbance to the established plants, new plants were sealed through a slit in a 2 cm x 2 cm piece of the 1 µm nylon mesh using a similar method to the initial planting. Dead plants were removed from the pots and new plants were immediately pushed through the holes and roots buried in the peat. The extra piece of mesh was glued to the mesh circle and sealed around. All pots were moved outside to a sheltered courtyard on 29th June 2015. Due to colder temperatures, pots were returned to the unheated greenhouse on 3rd November 2015.

4.2.8 Pot measurements

Five sets of water sample were collected from the Rhizon samplers in all pots post-treatment over three months (Table 4.1). The collection procedure and method of measuring absorbency were identical to those used before treatments were added (see “Pre-treatment measurements” above). The DOC concentrations were also measured using the same method but were made using a different total carbon analyser (vario TOC cube, Elementar Analysensysteme GmbH, Hanau, Germany).

The CO_2 and CH_4 fluxes were measured in parallel five times over three months (Table 4.1). The methods and equipment were identical to those described in "Pre-treatment measurements" (see above), apart from flux measurements ranging between 2 and 5 minutes in length due to lower fluxes in cooler weather. The CO_2 fluxes were also measured over 5 minute periods prior to ^{14}C sampling (see next Section).

Soil moisture content was monitored and maintained at 75% (± 5%) by regular weighing of pots and watering with pH-adjusted (pH 3.6) deionised water. Pots were watered through the mesh in the central collars and water was removed from the saucers of any overweight pots to aid drainage. This was to remove soil moisture as a factor in explaining any measured differences between treatments.

4.2.9 ^{14}C sampling

Not all treatments could be sampled for ^{14}C analysis due to funding reasons. As MXX treatments were expected to exhibit similar effects to HXX treatments, it seemed prudent to only assess one form of fungal addition. HXX was chosen as it was the more controlled fungal introduction and therefore the fungal component fluxes from these pots were less likely to include other potentially confounding component fluxes, such as peatland bacterial contributions. The selected treatments were ---, --B, H--, HC- and HCB, as this combination enabled ages of all components to be derived. Three replicates were chosen for each treatment based on blocks. However, due to total plant death before sampling in two HCB replicates, a MCB pot was used for one replicate. All selected pots were arranged randomly on an electric blanket for the entire collection period to facilitate respiration.

When sampling for ^{14}C analysis, it is important to prevent contamination by atmospheric CO_2. As such, 26 cm diameter circles were cut from plastic vacuum storage bags to fit over the mesh on top of the pots, with a hole in centre so the central collar was not covered. These were sealed into place with the silicone sealant. For XCX pots, the plastic circles were slit to sit around the stems and sealed in place. Custom built 20 cm long and 10 cm diameter uPVC chambers (Biology Mechanical Workshop, University of York, UK) were fixed over the central collars in the pots by means of thick rubber bands to create an airtight seal. Each chamber had a male and female auto-shutoff coupling (Colder Products Company, St Paul, MN, USA) glued into holes 4 cm from the bottom and 4 cm from the top of the chamber, respectively.

An established molecular sieve sampling system (MS^3; see Hardie *et al.* (2005) and Garnett & Murray (2013) for full details) was used to collect samples from ^{14}C analysis. The only modification to the system was that the IRGA used here contained an integral pump with an adjustable flow rate, negating the need for a pump in sequence. This reduced the number of connections and lengths of tubing where potential leaks could occur. The MS^3 was coupled to each chamber in succession and the chamber air was passed through the soda lime cartridge at 3 L min^{-1} for 3.5 minutes to remove atmospheric CO_2. This scrubbed the chamber air approximately five times and caused measured CO_2 concentrations to fall below 10 ppm. Scrubbed chambers were left to build up respired CO_2, with concentrations periodically checked. After 28-33 hours (exact time depended on the pot), the chamber air was forced through a zeolite molecular sieve cartridge (type 13X, 1.6 mm pellets, Sigma-Aldrich, Dorset, UK) at 500 ml min^{-1} to capture the CO_2. Collection was terminated when the CO_2 concentrations in the chamber dropped below 500 ppm to reduce the risk of atmospheric CO_2 contamination.

As there was insufficient CO_2 retrieved from the first sampling event (based on the measured chamber CO_2 concentrations during CO_2 capture), a second collection was made on the same molecular sieve cartridges. To prevent plant roots becoming oxygen starved due to the plastic covers on the mesh, there was a two day gap after CO_2 collection before the chambers were resealed, during which the plastic covers were removed. For the second collection period, the plastic covers were resealed, chambers rescrubbed and left for 6-9 hours to allow respired CO_2 to accumulate before collection. Two pots required a third collection event.

The DOC samples for ^{14}C analysis were collected by attaching acid-washed 50 ml luer-lock syringes to the pot Rhizon samplers. Syringes were held open with a retainer to create a vacuum. Syringes were placed inside cardboard tubes during collection to prevent photo-degradation of the DOC. Once full, syringes were emptied into acid-washed bottles (Nalgene, Thermo Scientific, Rochester, NY, USA) through pre-ashed, pre-rinsed (with deionised water) 0.7 µm glass-fiber filter (Whatman glass microfiber filters, Grade GF/F, 25 mm diameter, Sigma-Aldrich, Dorset, UK) and reset on the same Rhizon sampler. The DOC concentrations from 13th October 2015 were used to calculate the minimum water volume required to obtain sufficient DOC for ^{14}C analysis and appropriately sized samples were taken. Bottled samples were stored at 4°C in the dark.

The molecular sieve cartridges and DOC samples, along with three peat samples and a charcoal sample which were obtained before treatment addition, were sent to the NERC Radiocarbon Facility (East Kilbride, UK). The CO_2 was thermally retrieved (500°C), dried and cryogenically purified. The DOC was retrieved by rotary evaporation, freeze-drying and hydrolysis in hydrochloric acid, and combusted in an elemental analyser (Costech Instruments) for conversion to CO_2. The peat samples were heated with CuO in a sealed quartz tube and recovered as CO_2.

Each sample was split into subsamples. One of each subsample was analysed for $^{13}C/^{12}C$ ratio on a dual-inlet isotope ratio mass spectrometer (VG Optima, UK) and expressed ‰ relative to the Vienna PDB reference standard. Another subsample was converted to graphite by Fe/Zn reduction and analysed for ^{14}C by accelerator mass spectrometry at the Scottish Universities Environment Research Centre (SUERC, East Kilbride, UK).

4.2.10 Data analysis

All data manipulation was performed in Microsoft Excel and all statistical analyses were undertaken in R version 3.3.1 (R Core Team, 2016) unless otherwise stated. Following Zuur *et al.* (2009), residuals were plotted against fitted values and visually assessed for normality and homogeneity of variance. Where values are quoted, these represent the mean (± 95% confidence intervals). The critical p value chosen for significance was 0.05.

4.2.10.1 Pot measurements (pre- and post-treatment)

Raw DOC concentrations were corrected for machine drift using the standards and blank samples. All absorbency values were standardised to absorbance units per metre (m^{-1}) by multiplying the cell length by the appropriate value (here 100). Abs_{254} was divided by the weight-adjusted (see below) DOC concentration to obtain specific ultra-violet absorbency ($SUVA_{254}$) values and expressed in L mgC^{-1} m^{-1} kg dry $soil^{-1}$. $SUVA_{254}$ is often used by water companies as a proxy for the aromaticity of DOC and to determine the need for or amounts of enhanced coagulation and softening prior to treatment (Weishaar *et al.*, 2003). Water colour was expressed in Hazen units by multiplying Abs_{400} by 12, following (Watts *et al.*, 2001). The relative proportions of fulvic to humic acids were expressed as E4/E6 ratios (Thurman, 1985) by dividing Abs_{465} by Abs_{665}.

The LiCor Viewer software was used to derive the CO_2 fluxes from the most linear 50 s portion of each measurement. Similarly, CH_4 fluxes were derived by regressing the most linear 30-60 s section of each measurement over time and calculating the increase in CH_4 s^{-1}. With CH_4, the flux was discarded and recorded as zero if the linear relationship gave $R^2 < 0.4$ (there were no such problems for CO_2). Whilst this R^2value is low, this was due to very low CH_4 fluxes meaning that measurement variability was very large. All fluxes were also assessed by eye to verify the linear trend.

All weight-dependent values were adjusted to compensate for the different amounts of peat in each pot using:

$$V_{corr} = \frac{V}{P_{DW}} \qquad \text{Eq.4.1}$$

where V is the pot CO_2 or CH_4 flux or DOC concentration, P_{DW} is the dry weight of peat in the pot in kg and V_{corr} is V per kg of dry peat.

4.2.10.2 ^{14}C processing

Following convention (Stuiver & Polach, 1977), all ^{14}C data were normalised to -25‰ $\delta^{13}C$ to correct for mass-dependent isotopic fractionation and were expressed as %Modern relative to the activity of the NBS Oxalic Acid international radiocarbon standard. One --B replicate was removed from both the $^{14}CO_2$ and $DO^{14}C$ analyses due to producing unrealistically high values (i.e. values of 110.99 and 111.81 %Modern, which were substantially higher than both the peat and charcoal components, suggesting significant pot contamination from a bomb-peak C source).

A multi-component isotope mass balance approach, based on the two- and three-component mass balance approaches used by Hardie *et al.* (2009), was employed to derive the fluxes and isotopic concentrations of each pot component. The full equation was:

$$D_E F_E = D_P F_P + D_H F_H + D_C F_C + D_B F_B \qquad \text{Eq.4.2}$$

where *D* represents the average isotopic concentration (^{14}C %modern) and *F* the average flux (either DOC or CO_2) kg dry soil^{-1} (see Eq.4.1) apportioned to each component. *E* represents the concentration or flux from the whole ‘pot ecosystem’, *P* represents that from the peat component, *H* that from the *H. ericae* fungus component (or natural mixed fungal community in one case), *C* that from the *Calluna* root component and *B* that from the burnt material/charcoal. The CO_2 fluxes used were measured less than 24 hours prior to CO_2 collection for radiocarbon analysis (Table 4.1) and the DOC concentrations used were those measured in the water samples taken for ^{14}C analysis. For pots only containing some components, appropriate simpler mass balance equations were used. It was assumed that F_E from the --- pots represented the F_P in all other pots meaning that:

$$F_H = F_E - F_P \qquad \text{Eq.4.3}$$

where F_E represented the average flux of the H-- pots. The isotopic concentration of the *H. ericae* fungal component was calculated using:

$$D_H = \frac{D_E F_E - D_P F_P}{F_H} \qquad \text{Eq.4.4}$$

where D_E represented the average isotopic concentration of the H-- pots. Similarly, D_B and F_B were calculated using Eq. 4.3 and 4.4 but substituting D_B for D_H and F_B for F_H and using D_E and F_E from the --B pots. As the -C- pots were not sampled for ^{14}C, the *Calluna* component flux and isotopic concentration were calculated using:

$$F_C = F_E(HC -) - F_E(H - -) \qquad \text{Eq.4.5}$$

and

$$D_C = \frac{D_E(HC-)F_E(HC-) - D_E(H--)F_E(H--)}{F_C} \qquad \text{Eq.4.6}$$

where D_E(HC-) and D_E(H--) represent the average isotopic concentrations from HC- and H-- pots, respectively, and F_E(HC-) and F_E(H--) represent the average fluxes from HC- and H-- pots, respectively. Similarly, D_B and F_B were calculated using Eq. 4.5 and 4.6 but substituting D_B for D_C, F_B for F_C, D_E(HCB) and F_E(HCB) for D_E(HC-) and F_E(HC-), and D_E(HC-) and F_E(HC-) for D_E(H--) and F_E(H--).

The component ages were determined using:

$$Years\ BP = -8033 \ln \frac{D}{100} \qquad \text{Eq.4.7}$$

where 'Years BP' is the radiocarbon age in years before present, where 0 years BP = AD 1950, and 8033 represents the mean lifetime of ^{14}C (Stuiver & Polach, 1977). Any samples or components for which the ^{14}C content was >100 %Modern, radiocarbon ages were derived using data from Levin *et al.* (2008) (see Hardie *et al.* (2009) for details).

4.2.10.3 Statistical analysis

Linear mixed effects models employing the "lmer" function from the "lmerTest" package (Kuznetsova *et al.*, 2016) were used to test for treatment effects on the CO_2 and CH_4 fluxes, DOC concentrations, $SUVA_{254}$ values, Hazen units, E4/E6 ratios and ecosystem $^{14}CO_2$ and ecosystem $DO^{14}C$ content. The treatment, the pre-treatment/post-treatment period and interaction between them were the fixed effects (except for the $^{14}CO_2$ and $DO^{14}C$ content which were only measured post-treatment). For all tests apart from $^{14}CO_2$ and $DO^{14}C$ content, random terms were included for pot (as a repeated measure) and block. For $^{14}CO_2$ and $DO^{14}C$ content, the block was the random term.

Following the 10-step protocol in section 5.10 of Zuur *et al.* (2009), models were checked to determine whether a variable should be kept by removing variables stepwise from each linear mixed effects model and assessing the log-likelihood ratio and AIC value. The “glht” function with the “Tukey” option from the “multcomp” package (Hothorn *et al.*, 2008) was used to determine between which treatments significant differences occurred.

Linear regression tests (employing the function “lm” in the R “stats” package; R Core Team, 2016) were used to determine whether there was a relationship between the DOC concentrations and any of the measured water quality indicators (Abs_{254}, Abs_{400}, Abs_{465} and Abs_{665}). Separate linear regressions were used for each wavelength in each period (pre- and post-treatment).

4.3 Results

4.3.1 Water measurements

The DOC concentrations in the soil pore water of the pots averaged 99.2 mgC L^{-1} kg dry $soil^{-1}$ before treatment addition, which was significantly higher ($F_{1,3} = 173.77$, $p = 0.0009$) than the post-treatment average of 20.7 mgC L^{-1} kg dry $soil^{-1}$. However, the DOC concentrations did not differ significantly between treatments either pre- or post-treatment ($F_{11,34} = 0.78$, $p = 0.66$; Table 4.3).

Similarly, there was no significant interaction in $SUVA_{254}$ between treatment and period ($F_{11,46} = 0.85$, $p = 0.59$; Table 4.3). In contrast, $SUVA_{254}$ was significantly higher post-treatment ($F_{1,32} = 422.28$, $p < 0.0001$), with an average of 7.2 L mgC^{-1} m^{-1} kg dry $soil^{-1}$ compared to 2.0 L mgC^{-1} m^{-1} kg dry $soil^{-1}$ pre-treatment.

The colour of the water samples ranged from almost clear to tea-brown which measured 63 to 773 Hazen units, with an average of 270 Hazen. The E4/E6 ratios were between 0.99 and 5.16 with a mean of 2.44. Although both Hazen units and E4/E6 ratios were slightly higher post-treatment, these increases were not significant ($F_{1,3} = 1.72$, $p = 0.28$ and $F_{1,3} = 5.52$, $p = 0.10$, respectively). There was also no significant interaction between the periods and the treatments ($F_{11,60} = 0.68$, $p = 0.75$ and $F_{11,48} = 0.53$, $p = 0.87$, respectively; Table 4.3).

There was no significant relationship between DOC concentration and absorbance at any wavelength pre-treatment ($R_2 < 0.01$, $p > 0.18$ for all). Post-treatment, there was a significant linear relationship between DOC concentration and absorbance at all wavelengths measured. The relationship was strongest between DOC concentration and Abs_{254} ($R_2 = 0.76$, $p < 0.0001$)

Table 4.3 Pot treatment averages in the pre- and post-treatment periods of the DOC concentrations, $SUVA_{254}$ values, Hazen units, E4/E6 ratios and CH_4 fluxes. Numbers in brackets are 95% confidence intervals. Treatment codes are explained in Table 4.2.

Treatment	DOC concentration (mgC L^{-1} kg dry $soil^{-1}$)		$SUVA_{254}$ (L mgC^{-1} m^{-1} kg dry $soil^{-1}$)		Hazen units		E4/E6 ratio		CH_4 flux (nmol m^{-2} s^{-1} kg dry $soil^{-1}$)	
	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post
HCB	96.94 (±14.23)	14.62 (±2.50)	2.13 (±0.60)	6.89 (±1.37)	231.45 (±25.40)	204.24 (±53.02)	1.97 (±0.20)	2.20 (±0.41)	0.005 (±0.010)	-0.014 (±0.027)
HC-	102.71 (±11.93)	21.78 (±4.93)	1.86 (±0.33)	5.68 (±0.57)	224.33 (±18.63)	227.52 (±53.86)	1.96 (±0.13)	2.24 (±0.36)	-0.018 (±0.034)	0.010 (±0.020)
H-B	101.28 (±12.45)	21.08 (±3.91)	1.93 (±0.43)	6.66 (±0.93)	227.48 (±22.66)	282.52 (±60.35)	1.98 (±0.16)	2.67 (±0.40)	-0.024 (±0.027)	-0.002 (±0.024)
H--	94.88 (±7.70)	20.40 (±2.46)	2.05 (±0.30)	7.12 (±0.81)	236.55 (±25.27)	281.65 (±47.80)	1.98 (±0.13)	2.66 (±0.31)	-0.022 (±0.065)	-0.029 (±0.039)
MCB	108.55 (±12.35)	23.15 (±6.65)	1.70 (±0.41)	6.18 (±0.51)	284.48 (±79.77)	285.59 (±95.03)	1.88 (±0.27)	2.50 (±0.55)	-0.006 (±0.011)	-0.033 (±0.060)
MC-	111.37 (±14.66)	20.07 (±4.68)	1.79 (±0.26)	6.89 (±0.77)	231.98 (±19.29)	268.17 (±60.37)	2.00 (±0.13)	2.59 (±0.40)	0.022 (±0.031)	0
M-B	93.73 (±26.75)	19.81 (±5.42)	2.07 (±0.43)	9.14 (±1.25)	224.40 (±43.19)	365.31 (±86.65)	1.93 (±0.24)	3.10 (±0.49)	0.009 (±0.018)	0
M--	95.20 (±16.68)	19.07 (±4.58)	2.23 (±0.63)	8.02 (±1.11)	233.63 (±19.09)	306.09 (±70.31)	2.04 (±0.15)	2.68 (±0.41)	0.024 (±0.040)	-0.014 (±0.023)
-CB	98.07 (±15.56)	24.98 (±5.84)	2.07 (±0.39)	7.95 (±1.06)	241.73 (±25.90)	343.89 (±74.31)	1.99 (±0.15)	2.99 (±0.45)	-0.041 (±0.071)	0
-C-	93.65 (±10.14)	18.52 (±3.80)	2.13 (±0.35)	7.15 (±0.70)	229.65 (±24.32)	261.90 (±70.42)	1.98 (±0.14)	2.52 (±0.42)	0.001 (±0.028)	0
--B	88.08 (±13.78)	20.04 (±4.18)	2.20 (±0.89)	7.75 (±1.16)	220.43 (±45.59)	253.09 (±38.40)	1.89 (±0.29)	2.45 (±0.24)	-0.004 (±0.034)	-0.006 (±0.011)
---	105.60 (±21.48)	24.63 (±5.88)	2.12 (±0.40)	7.35 (±1.14)	239.49 (±26.88)	312.96 (±56.53)	2.01 (±0.11)	2.87 (±0.36)	0.031 (±0.092)	-0.019 (±0.025)

and became progressively weaker at higher wavelengths (DOC and Abs_{400}: $R_2 = 0.57$, $p < 0.0001$; DOC and Abs_{465}: $R_2 = 0.44$, $p < 0.0001$; DOC and Abs_{665}: $R_2 = 0.17$, $p < 0.0001$).

4.3.2 Gas flux measurements

As with the DOC concentrations, CO_2 fluxes from the pots reduced significantly following treatment addition ($F_{1,370} = 87.77$, $p < 0.0001$; Figure 4.2). There was also a significant interaction between the pre- and post-treatment periods and the treatments ($F_{11,370} = 3.54$, $p < 0.0001$). However, the post-hoc test revealed that this was due to significant differences between treatments in different time periods. Due to the apparent pattern of fluxes post-treatment, with all pots containing *Calluna* plants exhibiting greater CO_2 fluxes than those without (Figure 4.2), the same test using only the post-treatment CO_2 fluxes showed a significant difference between treatments ($F_{11,33} = 2.69$, $p = 0.0138$). Fluxes from HCB and -CB pots were significantly higher than fluxes from --B and --- pots ($p < 0.04$ for all).

The CH_4 fluxes ranged from -0.590 to 0.691 nmol m^{-2} s^{-1} kg dry $soil^{-1}$, although many pots had no discernible CH_4 flux (i.e. the fluxes were 0). The average post-treatment CH_4 flux (-0.009 nmol m^{-2} s^{-1} kg dry $soil^{-1}$) was slightly lower than the average pre-treatment flux (-0.002 nmol m^{-2} s^{-1} kg dry $soil^{-1}$) but there was no significant difference between the two time periods ($F_{1,372} = 0.89$, $p = 0.35$). There was also no significant interaction between treatment and time period ($F_{11,372} = 1.14$, $p = 0.33$; Table 4.3).

4.3.3 ^{14}C measurements

The pot ecosystem CO_2 effluxes differed significantly between the five treatments chosen for radiocarbon analysis ($F_{4,7} = 6.90$, $p = 0.0130$), with the pots containing *Calluna* plants producing significantly higher fluxes than the --- and --B pots ($p < 0.016$ for all; Figure 4.3). The HCB pots also produced significantly higher fluxes than the H-- pots ($p = 0.013$). Similarly, the $^{14}CO_2$ content differed between treatments ($F_{4,9} = 11.73$, $p = 0.0013$), with pots containing *Calluna* showing significantly higher enrichment ($p < 0.045$ for all; Figure 4.3). The MCB pot was included in analysis as if it were a HCB pot, although it was noted that the pot ecosystem $^{14}CO_2$ content was 10 %Modern lower than that of the two HCB pots (74.79 %Modern compared to 84.68 %Modern; see Appendix D for full list of individual pot ecosystem ^{14}C content, publication codes and sample types), equating to a difference of 1000 years.

The presence of charcoal slightly reduced the DOC concentrations, especially when in combination with *Calluna* and mycorrhizal fungi, although there was no significant difference in DOC production between treatments ($F_{4,9} = 0.50$, $p = 0.73$; Figure 4.4). Conversely, the DOC concentrations in the HCB pots contained the highest ^{14}C content. Despite there being

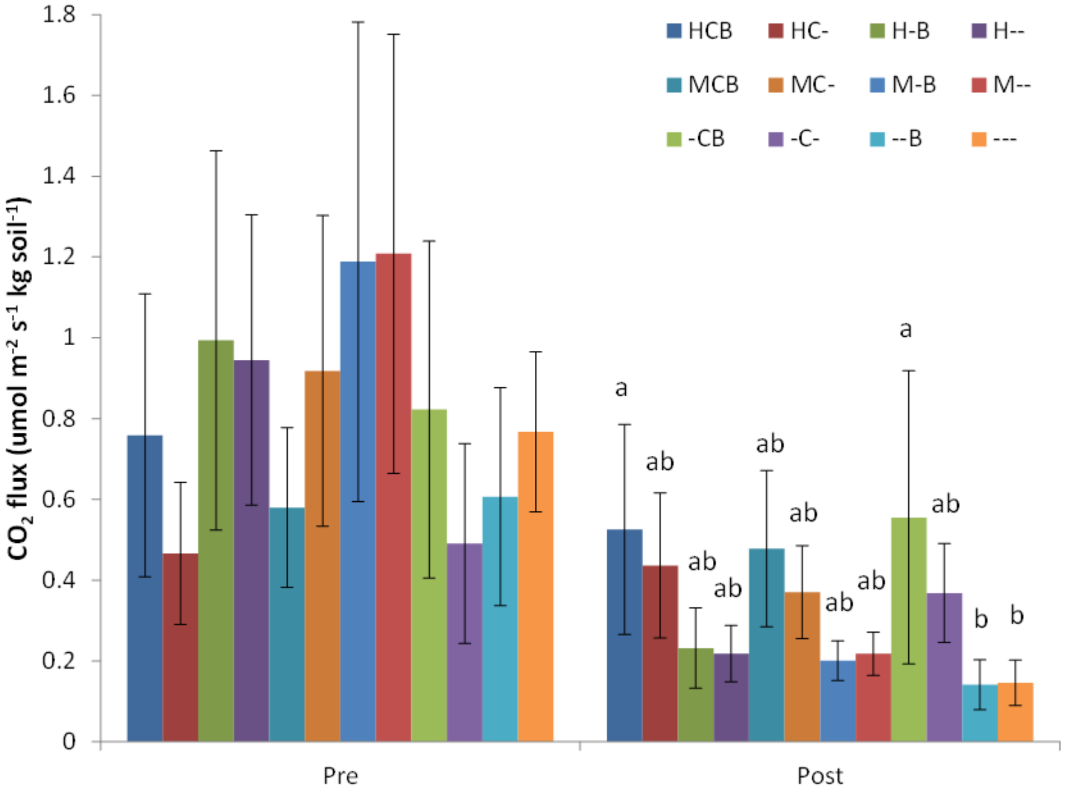


Figure 4.2 Pot treatment averages in the pre- and post-treatment periods of the CO_2 fluxes. Error bars are 95% confidence intervals. Treatment codes are explained in Table 4.2. Different letters indicate significant differences between managements. There were no significant differences post-treatment (all “a”).

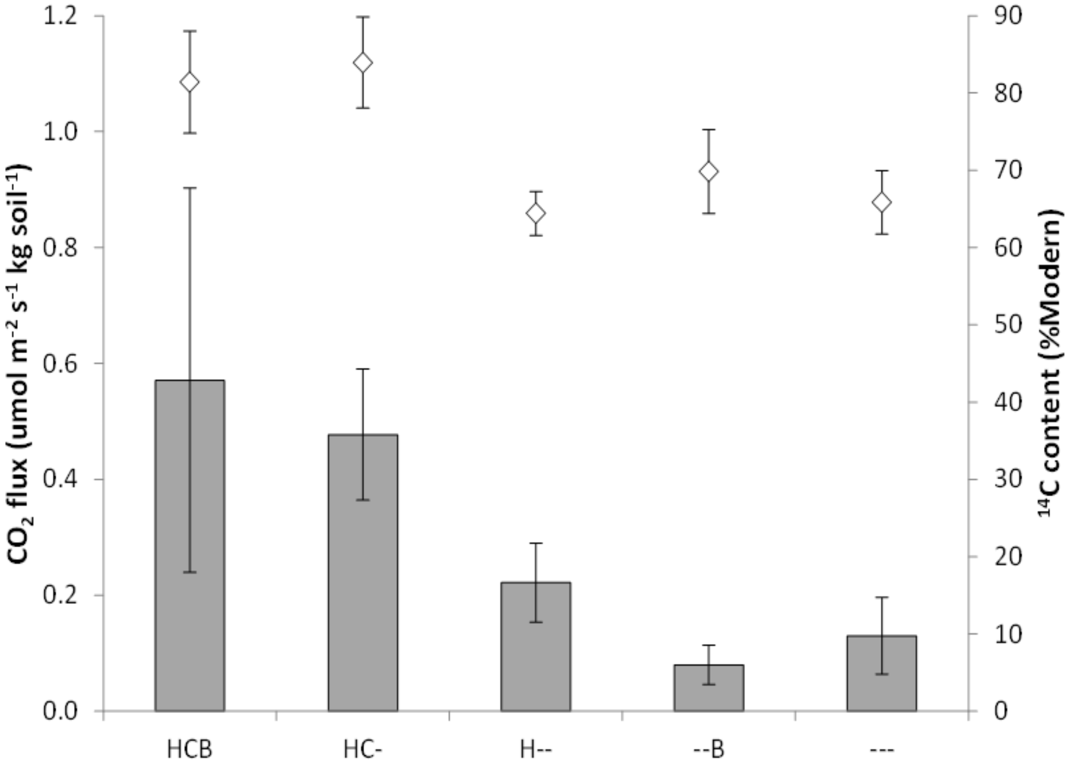


Figure 4.3 Pot treatment averages of the CO_2 fluxes (grey bars), taken the day before radiocarbon sampling, and the ^{14}C content of the CO_2 (white diamonds).

Error bars are 95% confidence intervals. Treatment codes are explained in Table 4.2. Note the different scales on the two axes.

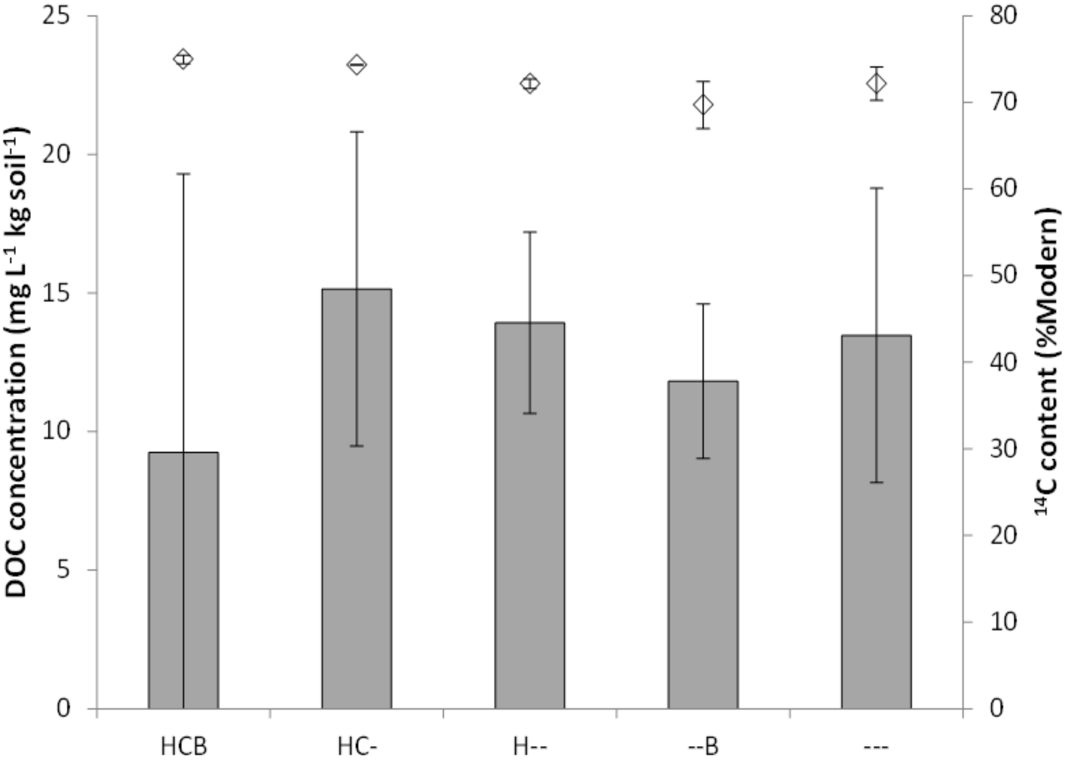


Figure 4.4 Pot treatment averages of the DOC concentrations (grey bars), measured in the water samples taken for radiocarbon sampling, and the ^{14}C content of the DOC (white diamonds).

Error bars are 95% confidence intervals. Treatment codes are explained in Table 4.2. Note the different scales on the two axes.

substantially less variability in the ^{14}C content of DOC than of CO_2, the pot ecosystem DO^{14}C content also differed significantly between treatments ($F_{4,9} = 7.66$, $p = 0.0057$). HCB pots showed significantly more ^{14}C enrichment than --B, H-- and --- pots ($p < 0.035$ for all; Figure 4.4) and HC- pots had a higher DOC ^{14}C content than --B pots ($p < 0.001$; Figure 4.4). There was however no difference in the DO^{14}C content between the MCB pot and the two HCB pots (74.94 %Modern and 74.92 %Modern, respectively; see Appendix D).

The *Calluna*-associated CO_2 flux calculated by the mass balance approach showed that the *Calluna* contributed 45% of the flux in the HCB pots and 54% in the HC- pots. The *Calluna* contribution to the DOC concentration was much smaller, accounting for 13% of the concentration produced by the HCB pots (although this assumes the lower DOC concentration in these pots was entirely caused by the charcoal causing a reduction, see below) and 8% produced by the HC- pots. Similarly, although smaller than the *Calluna* contributions, the *H. ericae* fungal contributions were much smaller to the DOC concentrations than to the CO_2 fluxes, comprising 5% (again assuming concentration reduction by charcoal) and 3% of the HCB and HC- pot DOC concentrations, respectively, and 16% and 19% of the CO_2 fluxes, respectively. Notably, 41% of the CO_2 flux of the H-- pots was attributable to *H. ericae* fungi, despite the fungal DOC contribution to the H-- pots being only 3%.

Due to the combination of treatments chosen for radiocarbon analysis, the charcoal component flux contributions could be calculated in two different ways. When the --B and --- pots were used (Eq.4.3), both the charcoal CO_2 flux and DOC concentration contributions were negative, reducing the flux and concentration by 64% and 12%, respectively, relative to the --- pots. However, when calculated using the HCB and HC- pots (Eq. 4.5), 16% of the CO_2 flux from the HCB pots could be attributed to the charcoal component, although the presence of charcoal reduced the DOC concentration by 39%.

The respired CO_2 from the peat was over 300 years older than the bulk peat sample (3021 ± 91 years old, i.e. 68.66 ± 0.78 %Modern) whereas the DOC was almost 400 years younger (Table 4.4). The mass balance calculations revealed that *Calluna* plant respiration was modern (100.85 %Modern) and *Calluna*-attributable DOC was only 73 years BP (99.10 %Modern). Strikingly, both the *H. ericae* fungal respiration (62.37 %Modern) and the DOC portion attributable to the fungus (71.24 %Modern) were older than the respective peat components by 436 and 101 years, respectively (Table 4.4).

The bulk charcoal sample was modern, with an average age of about 8 years old (approximately from the year 2009; 104.95 ± 0.48 %Modern; 40.9% C content by weight). Due to the combination of dated treatments, the charcoal component contributions could be

Table 4.4 Radiocarbon (^{14}C) ages in years BP and the associated CO_2 and DOC contributions for each treatment component calculated using the mass balance approach.

The first values for the charcoal-induced component were calculated using --B and --- pots and the second using HCB and HC- pots. All values are derived from averages of three pots apart from the first charcoal-induced age and flux which only used two pots in the --B average.

Component	**Radiocarbon age of CO_2 (years BP)**	**Radiocarbon age of DOC (years BP)**	**CO_2 flux (μmol m^{-2} s^{-1} kg dry $soil^{-1}$)**	**DOC concentration (mgC L^{-1} kg dry $soil^{-1}$)**
Peat	3356	2623	0.13	13.46
H. ericae fungus	3792	2724	0.09	0.46
Calluna plants	Modern	73	0.26	1.23
Charcoal	4172 or 3042	865 or 2493	-0.05 or 0.09	-1.65 or -5.91

calculated in two different ways. Using the --B and --- pots (giving the base effect of charcoal addition to peat) produced ages of 4172 and 865 years BP (59.49 and 89.79 %Modern) for CO_2 and DOC respectively, whereas when the HCB and HC- pots were used, the charcoal CO_2 and DOC components were calculated as 3042 and 2493 years BP (68.48 and 73.32 %Modern) respectively. As all calculated charcoal CO_2 and DOC ages are substantially older than the charcoal sample, they cannot be derived directly from the charcoal and therefore should be considered as charcoal-induced component ages (and fluxes). Additionally, since only the latter value for the CO_2 age was calculated using a positive flux (both DOC charcoal-induced component concentrations were negative), these ages should be treated with caution.

4.4 Discussion

4.4.1 Treatment effects on water quality

The five-fold reduction in DOC concentrations from the pre-treatment to post-treatment measurements (Table 4.3) was unexpected as the rehydrated peat was rinsed thoroughly, which should have removed any labile C liberated during gamma-irradiation (Genney *et al.*, 2000). The treatment addition did not cause the observed reduction in DOC concentrations because otherwise the --- pots would have still produced high concentrations post-treatment. It is possible that the labile C was not fully removed through rinsing, with the remainder gradually washing out over time, or oxidising and being released as CO_2. The lack of relationship between DOC concentration and the UV absorbance at any wavelength in the pre-treatment measurements supports the conjecture that the gamma-irradiation procedure disrupted the peat structure, although the strong relationships post-treatment suggest this disruption was temporary.

However, the reduction in DOC concentrations from pre- to post-treatment is likely to be due, at least in part, to the pre-treatment DOC samples being collected when the pots were inside whereas post-treatment DOC samples were collected when pots were either outside or in an unheated greenhouse. The higher temperatures the pots were exposed to pre-treatment would have enhanced decomposition (Freeman *et al.*, 2001a) and hence DOC production. Although the pots were regularly watered throughout the whole experiment, the warm conditions likely caused more transpiration, leading to greater fluctuations in WTD and lower WTDs, which would have also increased oxygen infiltration and decomposition (Freeman *et al.*, 2001b). The peat in all pots probably contained some microorganisms as, although gamma-irradiation should have killed all existing microbes and most spores, the peat was unavoidably exposed to the air during the potting process and so is likely to have gained some sort of microbial assemblage which would enhance decomposition. The change from a low SUVA pre-treatment to a higher SUVA post-treatment also suggests that temperature and lower WTDs played a role in regulating the dissolved organic matter in the water, as microbial activity is higher under warmer and drier conditions which increases the amount of non-coloured hydrophilic components in soil water, leading to lower SUVA (Scott *et al.*, 1998).

Although *Calluna* plants are associated with higher DOC production than other peatland plants (Vestgarden *et al.*, 2010; Armstrong *et al.*, 2012), it has been suggested that areas of bare peat are responsible for higher DOC concentrations than vegetated areas (Yallop & Clutterbuck, 2009), due to greater erosion (Imeson, 1971) and faster runoff (Holden *et al.*, 2008). Therefore, pots without plants were expected to produce more DOC than pots containing plants, yet this was not the case (Table 4.3). This may be due to the mesh covering preventing plant litter input to the planted pots, as litter decomposition products contribute to DOC production (Bragazza *et al.*, 2006). However, plant root exudates would also be expected to contribute to DOC (Billett *et al.*, 2011) but appeared not to here. Although the HCB treatment did produce the lowest average DOC (and was consistently the lowest over time), the -CB pots produced the highest concentrations, meaning that it is unlikely that the difference was caused by the vegetation. It is also unlikely that any differences were caused by either type of fungal inoculation or by charcoal, as there was remarkably little variation between any treatments in relation to DOC and there was no consistency in which treatment components the pots with higher DOC concentrations contained.

There are many possible reasons for this. One is that, as the pots were not on a slope and therefore there was little opportunity for erosion and runoff to occur, the plants had no capacity to alter the DOC export. This is particularly pertinent as DOC concentrations were sampled from the soil pore water rather than from a stream as exported DOC, where surface roughness plays a role in overland flow (Holden *et al.*, 2008) and therefore in the rates at which C is moved and exported. Regardless of the DOC export, the lack of difference in DOC concentrations within the soil between pots containing *Calluna* plants and not, either free-living or mycorrhizal *H. ericae* fungal hyphae or a natural microbial community or neither, or pots containing charcoal or not, suggests that none of the components were instrumental in the production of DOC.

A second possibility is that it was not the quantity of C in the water that differed but the fractions and compounds within the C that differed. Although there were visual differences in the colour of the samples, it appears that this is not the case as there were no significant differences between the treatments in $SUVA_{254}$ or Hazen units or in the E4/E6 ratios, nor did the differences in colour relate consistently to the treatments. This was unexpected as, previously, field studies have recorded differences in E4/E6 ratios (Qassim *et al.*, 2014) and water colour (Wallage & Holden, 2010) between vegetated and unvegetated areas. The absence of a difference also contradicts the hypothesis that the ericoid fungi would alter the DOC composition by breaking down recalcitrant compounds which should remain intact in the non-fungal pots.

$SUVA_{254}$ is related to DOC, in that the DOC concentration is used in its calculation, but it takes into account the chemical composition. Despite $SUVA_{254}$ commonly being used by water companies and being a good indicator of aromaticity (Weishaar *et al.*, 2003), there are suggestions that wavelengths below 300 nm can give noisy signals when used to measure DOC (Grayson & Holden, 2012), which might explain the apparent lack of difference in $SUVA_{254}$ here. However, there was a strong linear relationship between the DOC concentration and Abs_{254} post-treatment suggesting that there was no treatment effect on $SUVA_{254}$. Additionally, given that the relationship between DOC and absorbance was weaker at higher wavelengths, it appears that wavelengths below 300 nm do not necessarily introduce noise. The linear relationship between DOC concentrations and Abs_{400} may explain why the Hazen units were also similar between treatments (Table 4.3).

The E4/E6 ratio represents the relative proportion of fulvic to humic acid, with lower ratios (2 to 5) indicating more mature (i.e. more decomposed) humic acids and higher ratios (8 to 10) containing more of the less mature fulvic acids (Thurman, 1985). As the highest E4/E6 ratio for any pot on any given measurement day was 5.16, this suggests the peat was highly humified, which would be consistent with the fact that the peat was approximately 3000 years old. The higher range of E4/E6 ratios post-treatment (1.14 to 5.16) compared to pre-treatment (0.99 to 2.47) suggests there was some structural disturbance caused by gamma-irradiation which resulted in some of the more highly decomposed fraction being flushed out over time. The XCX pots were expected to have higher E4/E6 ratios due to newly plant-derived compounds mainly contributing fulvic acids (Wallage *et al.*, 2006b). Conversely, if anything, the XCX pots showed slightly (although not significantly) lower E4/E6 ratios than pots without plants.

However, greater proportions of fulvic acids are thought to be associated with higher levels of microbial activity (Wallage *et al.*, 2006b) and, in general, fresh C inputs such as plant root exudates have been shown to stimulate microbial decomposition (Fontaine *et al.*, 2007). Therefore, another possibility as to why there were no observed differences in DOC concentrations is that there were differences in the amount of DOC, or in the composition of the DOC, produced in the different treatments but that these differences were not detected due to conversion of the DOC to gas (either CO_2 or CH_4) shortly after production.

Worrall & Moody (2014) showed a decline in DOC concentrations in stream water of 65% over a 70 h period, with much of the decrease occurring within 10 h of entering the stream. Whilst a large portion of the loss was attributed to photic processes, they demonstrated DOC conversion both to CO_2 (or CH_4) and from labile to more refractory forms (Worrall & Moody, 2014). Although there would have been little, if any, light below the peat surface in the pots and therefore photodegradation of DOC would have been negligible or absent, biodegradation is possible. Wickland *et al.* (2007) measured a 6-15% conversion of soil pore water DOC to CO_2 and a 10-90% of vegetation-litter-derived DOC to CO_2 in a month long dark incubation experiment using water and vegetation samples from Alaskan black spruce forest. As already discussed, the pots did not have litter input, and so are unlikely to have litter-derived DOC, but XCX pots would have received root exudates. Based on the range of biodegradability of both the soil pore DOC and vegetation litter DOC in Wickland *et al.*'s (2007) experiment, the plant or fungal components in the pots may have produced additional DOC to the base rate of production which was decomposed faster than that produced by the peat and released.

Alternatively, the physical and chemical conditions in the pots may have differed between treatments, which may subsequently have altered the quantity and proportions of organic matter in solution. The amounts and fractions of dissolved organic matter in soils are influenced by the soil solution pH and ionic strength (Kipton *et al.*, 1992). Despite the WTD of all pots being kept relatively constant, the presence of plants likely increased transpiration, leading to drier peat which is known to suppress the mobility of DOC (Clark *et al.*, 2005), hence any additional DOC produced by the plants would have remained in the soil and not have been detectable in the soil water. As more of the darker hydrophobic humic acids are released into solution at lower ionic strengths (Kipton *et al.*, 1992), the plants may have taken up (i.e. removed) nutrients supplied by the ericaceous feed from the peat, resulting in a lower ionic strength than in the other pots and causing the lower than expected E4:E6 ratios. Similarly, the ash content of the charcoal component probably added additional nutrients, as ash is used as a fertiliser and can increase the pH of the soil solution (Naylor & Schmidt, 1986), again altering the amount and composition of DOC in the sampled soil pore water. It is therefore possible that, even if the different treatment components did alter the DOC production and composition, these differences were not detected in the water extracted from the peat due to these same components also altering the physico-chemical properties of the peat and preventing or promoting DOC release.

4.4.2 Treatment effects on gas fluxes

The CH_4 results do not support the theory that DOC is broken down into gases, mainly due to the paucity of positive (or indeed negative) CH_4 fluxes, which resulted in no differences between treatments (Table 4.3). This is probably due to the peat in the pots being much drier than on a natural blanket bog, although the WTD was similar to the summer WTDs observed on the three managed peatland sites in Chapters 2 and 3. In part, this dryness is due to a moderately low WTD (18 cm) but also because the gamma-irradiated peat did not fully rehydrate, despite being submerged in water for two weeks. Although CH_4 production can still occur at lower WTDs, it is often outweighed by CH_4 consumption which causes lower net emissions (Sundh *et al.*, 1994). This is likely to have occurred in the pots to produce the very small and negative fluxes.

However, the CO_2 results could support the explanation that additional DOC produced by the different components was rapidly decomposed and released in gaseous form (Figure 4.2). Although only the HCB and -CB pots had significantly higher CO_2 fluxes than --B and --- pots, there is a clear trend within the post-treatment fluxes, with XCB pots showing the highest CO_2 fluxes, followed by the XC- pots and then non-*Calluna* pots having the lowest fluxes. The *Calluna* plants were over two years old by the final set of measurements meaning that the roots systems were well developed, hence the majority of the additional CO_2 from the XCX plots was probably directly attributable to root respiration. However, this does not preclude the possibility that plant exudates or plant-derived DOC encouraged, or primed, microbial activity, increasing the CO_2 emissions and decreasing DOC concentrations. As previously mentioned, the main DOC fractions in plant root exudates are fulvic acids (Wallage *et al.*, 2006b), which are less decomposed (Thurman, 1985) and hence more easily broken down. Combined with the relatively dry soil in the pots, it is highly likely that there was at least some microbial priming by plant-derived DOC, particularly since the aerated conditions caused by the lower soil moisture are likely to have enabled the enzyme phenol oxidase to remove phenolic compounds, which inhibit decomposition processes (Wetzel, 1992), at a faster rate due to increased oxygen infiltration (Freeman *et al.*, 2001b).

Conversely, ericoid fungi do not add C in the same way, due to not being primary producers. It was hypothesised that the fungi, both in mycorrhizal association with the plants and as free-living fungi and both as a single fungal species (*H. ericae*) and as part of a natural mixed community, would break down recalcitrant organic matter, both in the form of peat and charcoal. There is extensive evidence that ericoid fungi can break down lignins and phenolic compounds in controlled laboratory conditions (Haselwandter *et al.*, 1990; Varma & Bonfante, 1994; Bending & Read, 1997; Burke & Cairney, 1998). Whilst not significantly higher, the H-- and M-- pots produced more CO_2 than the --- pots and the H-B and M-B did likewise compared to the --B pots (Figure 4.2). This may be purely by chance, especially since the difference was small, but the effect was observed for all five full sets of CO_2 measurements, suggesting that the fungi's saprotrophic capabilities were being utilised to break down the peat.

The effect was not so clear when *Calluna* plants were present, with -CB pots actually having the highest fluxes (Figure 4.2). It is possible that there was fungal contamination of the soil or plants (which, due to time constraints, it was not possible to verify) but it may instead be that when plants are present, the fungi form mycorrhizal associations and use the more easily accessible plant C inputs for energy, thereby greatly reducing the need to break down C other than that from the plants. Nutrient solution was added to all pots in order to sustain the non-mycorrhizal plants and may have been adequate to meet the plants' needs, meaning that the mycorrhizal plants had little need for the fungi to acquire additional N or P from complexes within the soil. This could explain the lack of difference in the CO_2 fluxes between the non-mycorrhizal and mycorrhizal *Calluna* pots. Alternatively, viewed again from the angle that the plants had sufficient nutrients to not require any additional breakdown from mycorrhizas, it may be that the fungi in the HCX and MCX pots effectively outcompeted the bacteria which were utilising the plant exudates in the -CX pots, meaning that CO_2 fluxes were similar because heterotrophic respiration in all *Calluna* XCX pots was mainly of broken down plant C inputs, albeit respired by different organisms.

The results do not seem to show any consistent effect of charcoal addition. As mentioned in Section 4.2.4, the charcoal was likely a mixture of charcoal and ash. Given that the C content of the charcoal used for ^{14}C analysis was 40.9%, compared to a C content of 52.3% for unburnt *Calluna* plants (see Chapter 3), and there were visible pieces of charred plant material, the proportion of charcoal is likely to be substantial, although this was not determined. Nevertheless, the burnt plant residue would have included at least some ash, which might explain the inconsistent effect of charcoal addition as each pot may have received a different proportion of ash and charcoal, despite being mixed well before distribution.

Ash is typically used as a fertiliser (Naylor & Schmidt, 1986) meaning that all pots with charcoal addition probably had a higher nutrient content than those without. The H-B pots produced very slightly more CO_2 than the H-- pots but the M-B and M-- pots showed the reverse, indicating that the free-living fungi did not break down charcoal, nor did their growth appear to be enhanced by any additional available nutrients the ash added. On average, the XCB pots emitted more CO_2 than the XC- pots suggesting that mycorrhizal fungi may decompose charcoal. Research on biochar, which is essentially charcoal produced under specific conditions, showed that saprophytes and mycorrhizas responded differently to biochar addition (Thies & Rillig, 2009). Therefore, in the presence of plants, ericoid fungal processes may switch from saprophytic to mycorrhizal, thereby altering the fungi's interaction with the charcoal. Additionally, or alternatively, the plants may have utilised any nutrients provided by the ash component of the added burnt residue, either by directly taking the nutrients up or acquiring them via the mycorrhizal fungi, which could therefore have increased plant growth, hence increasing respiration.

The trend of higher CO_2 fluxes from XCB pots compared to XC- pots was not consistent across all sampling dates and, if the assumption that mycorrhizal fungi had no need to break down soil C complexes due to plant C inputs being easier to utilise was true, then it would seem odd for them to switch from plant exudates to breaking down charcoal. This effect was also greater in the non-fungal pots with -CB pots producing more CO_2 than -C- pots. Mahmood *et al.* (2003) observed that the addition of biochar (charcoal) to pine seedlings increased plant growth regardless of mycorrhizal status, which would increase plant respiration. Similarly, (Strandberg & Johansson, 1999) found that growth of *Calluna* plants was higher with fertiliser (N, K or both) whether or not the plants had mycorrhizal associations. Therefore, the difference in CO_2 fluxes between *Calluna* pots with and without charcoal addition is likely to be directly attributable to the charcoal (or nutrients from the ash component) and not the fungi.

4.4.3 Treatment effects on radiocarbon age

The ^{14}C enrichment and calculated ages of both the bulk peat and charcoal samples were consistent with expectations. The estimated peat age of 3000 years BP was encompassed within the error term for the measured peat age, facilitating interpretation of the results because the old age provides a strong contrast against the *Calluna* plants and *H. ericae* culture, which were both grown with access to modern C, and the charcoal, which was approximately eight years old.

Therefore it was surprising that the mass balance revealed that the *H. ericae* culture contributed DOC and CO_2 that was older than the respective ages of the peat DOC and CO_2, despite these being substantially different from one another (Table 4.4). Given that the *H. ericae* fungus was cultured on d-glucose which was believed to be a modern C source, the only reasonable explanation incorporating both the increases in DOC and CO_2 attributed to the fungi (Table 4.4) and the apparently millennial age of the *H. ericae* contribution is that this C came from very old peat. Therefore, despite initially rejecting the hypothesis that the ericoid fungi would increase the DOC concentration by breaking down recalcitrant compounds (see

Section 4.4.1 above), the radiocarbon data instead support this hypothesis, as well as strengthen the rather uncertain suggestion that ericoid fungi also respired peat-derived CO_2.

Previous studies have shown that release of old C occurs in peatlands in the presence of enchytraeid worms (Briones *et al.*, 2010) and that microbes are capable of breaking down old recalcitrant C in a variety of systems (e.g. Bardgett *et al.*, 2007; Fontaine *et al.*, 2007; Wild *et al.*, 2016). However, although postulated by Walker *et al.* (2016) and evidenced under laboratory conditions that ericoid mycorrhizas can break down recalcitrant compounds (see review by Read *et al.*, 2004), it appears that this is the first demonstration that ericoid fungi break down and use recalcitrant ancient peat as a C source. As the WTD in the pot ecosystems was -18 cm and the conditions therefore more represented a drained or heavily managed bog, this conclusion is consistent with the understanding that peat drainage increases peat decomposition (Frolking *et al.*, 2011), and contributes another mechanism to explain it. Investigation under more anaerobic and wetter conditions is needed to further elucidate the role ericoid fungi play in the cycling and breakdown of recalcitrant organic C compounds in peat.

As autotrophs, the *Calluna* plants were expected to add only recently fixed C (atmospheric ^{14}C content was estimated to be approximately 102.76 %Modern at sample collection based on extrapolation of data from Levin *et al.* (2008), as assumed by other ^{14}C mass balance studies, e.g. Gaudinski *et al.*, 2000; Hardie *et al.*, 2009; Walker *et al.*, 2016). This meant the plant C should be substantially more ^{14}C enriched than the peat (which was 68.66 %Modern) and therefore only a relatively small C contribution from the *Calluna* would result in a relatively large change to the average age of the pot. Although only significantly higher than the --B pots, the HC- treatment showed ^{14}C enrichment that was very similar to the HCB pots and higher than either the H-- or --- treatments (Figure 4.4). This suggests that the *Calluna* plants did contribute to DOC production, thereby elevating the $DO^{14}C$ content in the HCX treatments, but this DOC addition was not detected in the water sample analyses.

From the mass balance calculations, it appears that *Calluna* contributed 13% of the DOC produced in the HCB pots. However, HCB pots produced the lowest DOC concentration (Figure 4.4) which potentially means that any one component, or any combination of the three components, could have reduced the DOC concentration relative to the control pots. As the --B treatment also produced less DOC than the --- pots, it was assumed that the lower concentrations measured in the HCB pots were entirely due to the charcoal, since a plant contribution was detected in the $DO^{14}C$ and the HC- pots showed a similar enrichment but a higher DOC concentration.

However, the DOC concentration of the -CB pots (which were not chosen for ^{14}C analysis) exhibited the highest average DOC concentration of any treatment meaning that either the plant contribution in these pots was very high or that charcoal contributed to the DOC release. Alternatively, as previously mentioned, changes in the pH and ionic strength of the soil solution may have altered the amount of DOC released. It is possible that the charcoal component in the -CB pots had a higher ash content than other pots meaning that the pH could have been higher, causing a greater release of DOC (Clark *et al.*, 2005; Evans *et al.*, 2012). Although the plant did not appear larger in the HCB pots compared to the -CB pots, the belowground parts of the plants may have been more well developed, whether because of the mycorrhizal fungi or by chance, and caused increased transpiration, drying the peat. Drier peat induces sulphate release, which decreases pH, thereby decreasing DOC release into the soil solution (Clark *et al.*, 2005). This could explain the lower DOC concentrations from the HCB pots (and the higher concentrations in the -CB pots), whilst still allowing for a plant contribution to the $DO^{14}C$, as a proportion of the plant produced DOC would have been released into the soil solution.

The $DO^{14}C$ content calculated for the *Calluna* component was 99.10 %Modern which equates to an age of 73 years BP, substantially older than the two-year-old plants. This means that the plant contribution contained C from before the peak in bomb-^{14}C as it was 3.66 %Modern lower than the atmospheric concentration estimated during sampling. Hardie *et al.* (2009) similarly discovered that the plant respiration component of their field $^{14}CO_2$ measurements was older than the plants and concluded that the additional older respired C was plant-induced but not directly respired from the plant. Under the reasonable assumption that the *Calluna* plants only added recent fixed C and following the reasoning of Hardie *et al.* (2009), the *Calluna* component age calculated here strongly suggests an element of plant-induced DOC production, i.e. a priming effect. This corroborates with research by Fontaine *et al.* (2007), who demonstrated that fresh plant C inputs primed microbial decomposition of ancient C, and supports the conclusions drawn above from the pot water quality monitoring.

Further to this, the CO_2 fluxes of the HCB pots used for the mass balance approach were significantly higher than all other treatments except HC- and both HCB and HC- pots showed significantly higher ^{14}C enrichment than pots not containing *Calluna* (Figure 4.3). The *Calluna* component ^{14}C enrichment of the CO_2 was 1.91 %Modern less than that expected from the actual age of the plants, again demonstrating that there was *Calluna*-induced respiration of older peat, which agrees with field-based research that specifically showed *Calluna* (as opposed to other peatland vegetation) to exhibit priming effects in peat (Walker *et al.*, 2016). The lower ^{14}C enrichment from the HCX pots of the DOC compared to the ^{14}C enrichment of the CO_2, combined with the high CO_2 fluxes and the apparently smaller amount of priming detected in the $^{14}CO_2$, verifies the assumptions made above that either the plants altered the physico-chemical conditions within the peat to change the amount of DOC released or that much of the plant associated DOC was not detected in the DOC concentration, as it was mineralised and respired as CO_2 by microbes and that the plant C inputs caused microbial priming.

Fridborg *et al.* (1978) demonstrated with plant-tissue culture that activated charcoal adsorbed toxic C compounds, which would be expected to increase microbial activity due to the removal of inhibitory substances. However, both the ages and fluxes of charcoal containing pots showed contradictory effects. The HCB treatment had a lower DOC concentration than the --B pots, suggesting that the charcoal had a greater DOC reduction effect when the mycorrhizal plants were present. Conversely, the charcoal seemed to cause an increase in the CO_2 flux in the presence of mycorrhizal plants but still decreased the flux in relation to the control in the --B pots. Additionally, the charcoal addition alone reduced the DOC age but increased the CO_2 age relative to the control whereas the DOC age was barely affected by charcoal addition to mycorrhizal plants.

There is evidence that soil containing biochar can adsorb nearly 50% more DOC than unamended soil as well as decrease soil respiration by altering enzyme activity and microbial C use efficiency (Jin, 2010). This could explain the charcoal-associated reduction in DOC, both with and without plants, and the lower respiration rate without plants, although it is unclear whether these effects would continue as the charcoal aged or whether any stored DOC would be released over time. Since biochar can have variable effects on mycorrhizas (Warnock *et al.*, 2007) and has been shown to positively affect some ericoid species (Duclos & Fortin, 1983), the increased respiration in the HCB pots could be a combination of the increased fresh C inputs, the removal of inhibitory compounds by charcoal and the increased activity of the mycorrhizal fungi. Whilst this does not address the different ages, the DOC and CO_2 ages from the --B pots are virtually identical (0.15 %Modern difference; Figures 4.3 and 4.4), suggesting that it is the ages of the other pots which vary, and the decrease in age of the $^{14}CO_2$ from HCB pots relative to HC- pots could be a combination of the charcoal removing inhibitory compounds and the *Calluna* adding labile C which enabled the fungi to further break down peat as well as plant compounds.

However, as previously mentioned, not all of the charcoal component was necessarily charcoal; some was probably ash and therefore this may have altered both the pH and ionic strength, causing differences in DOC release, and this effect may have differed when other components were present. Younger C inputs may have had a different hydrophobicity to older C compounds and therefore changes in the pH or soil moisture caused by addition of the charcoal component may have altered the proportional release of these compounds (Scott *et al.*, 1998), causing some of the unexpected age differences between treatments and making the charcoal component appear ancient (Table 4.4).

4.4.4 General caveats and limitations

The aim of this experiment was not to determine the actual age of DOC or CO_2 emissions but to investigate which components formed and released these products and from which sources they were derived. Therefore, the measured ages of the pot ecosystems - and therefore the calculated ages of each component DOC and CO_2 contribution - should not be taken at face value and should only be used relatively to one another. In a peatland, the peat age increases gradually with depth (e.g. McCarroll *et al.*, 2015) whereas the pot ecosystems consisted of only old homogenised peat. If a similar experiment were to be conducted in situ, the ages produced would likely differ due to a large younger layer of C at the peat surface.

Additionally, results for an intact bog may differ slightly due to the peat being wetter and not disturbed. In order to effectively remove fungal spores and sterilise the soil, the drying and gamma-irradiation processes inevitably caused disturbance and resulted in peat which would not fully rehydrate. Therefore, similar field experiments would likely show decreased CO_2 release but may produce consistently positive CH_4 fluxes, which are an important part of peatland C cycling but were largely absent in the pots. It should also be noted that the Rhizon samplers used have a pore size of 0.23 µm, meaning that, although the cut-off for DOC is arbitrary, the DOC results may not be directly comparable with other studies as the standard cut-off is 0.45 µm.

It would be interesting to use runoff or stream DOC since it appears here as though there were no differences in soil pore water DOC concentrations due to some of the DOC produced either being oxidised to CO_2 before it could be measured or held in the solid phase in the soil instead of being released into solution. It is also DOC export which is most important for water companies, as it is this they have to treat, and for peatland C budgets as it is possible that in wetter, more intact peat, soil DOC is cycled as CH_4 or possibly CO_2 below the surface, with very little being released. Alternatively, the wetter conditions could cause greater release of DOC or a change in the proportions of humic substances released, which might help elucidate the effect each component has on DOC production and release. However, the difficulty of excluding ericoid fungi in a field would require careful consideration.

4.4.5 Conclusions

Over the past 50 years, there has been a concerning increase in the amount of DOC and in the colour of the water leaving peat-covered catchments (Monteith *et al.*, 2007). Bragazza *et al.* (2013) suggested that "the quantity and quality of DOC might be controlled by vascular plants through a greater rhizodeposition of labile C compounds". There is also mounting evidence that both warming (Dorrepaal *et al.*, 2009) and certain types of vegetation (Walker *et al.*, 2016) can cause the liberation of old carbon from peatlands which, amongst other pressures such as drainage and burning, casts doubt upon the longevity of peat as a stable long-term C store.

The results in this study strongly suggest that the ericoid mycorrhizal fungus, *H. ericae*, broke down old recalcitrant C compounds in peat and released this C both as DOC and CO_2. This is evidenced by the ages of the *H. ericae* component CO_2 and DOC being older than the base peat component CO_2 and DOC ages. Although the fungal contributions to soil DOC were very low and the contributions to CO_2 were less when plants were present, the function of ericoid fungi in decomposition of recalcitrant organic matter should be considered in the context of peatland C cycling. Given that one of the HCB replicates used in the radiocarbon sampling was actually a MCB pot and yet produced DOC of a very similar age and CO_2 of an older age than the HCB pots, it is likely that the mixed microbial and fungal community broke down more old compounds than the single ericoid fungus.

Despite the heterotrophic component strongly influencing the age of the CO_2 and DOC, the *Calluna* plants had a far greater influence on the quantity of CO_2 and DOC produced, partially due directly to the plant inputs but also because these inputs primed microbial decomposition of older organic matter. In light of the expectation that climate change is expected to increase plant growth, that greater plant growth is associated with a larger priming effect (Hartley *et al.*, 2012) and that *Calluna* appears to exhibit greater priming effects than other peatland vegetation (Walker *et al.*, 2016), these results demonstrate that *Calluna* may threaten the longevity of the peatland C store. Conversely, burning may counteract some of this effect since charcoal made from *Calluna* plants appears to reduce DOC by over a third (Figure 4.4) whilst only increasing CO_2 emissions by about a fifth (Figure 4.3). Additionally, burning reduces *Calluna* cover and fungal biomass but increases plant C uptake and C transfer to soil microbes (Ward *et al.*, 2012). However, at least some of the apparent charcoal effect is likely to be due to the charcoal and ash changing some of the physico-chemical conditions in the peat. This raises the question as to whether the apparent effects of charcoal addition would be the same under a higher WTD and whether these effects would continue as the charcoal aged.

Therefore, there is an urgent need to investigate the seemingly varied effects of charcoal, and its interactions with other vegetation and microbes, as well as the effects of ericoid fungi in the field on peatland C dynamics in order to solve this apparent conundrum.

5 General Discussion

5.1 Summary of findings

This thesis has combined catchment scale field manipulations with smaller scale experiments at both pot and plot level to investigate the impacts of different methods of *Calluna vulgaris* management on the carbon (C) balance and vegetation composition of upland peatlands, and has further explored the relationship between mycorrhizal fungi and *Calluna* in the context of C cycling and water quality.

In Chapter 2, field trials on three *Calluna* dominated blanket bogs in north west England were used to examine the impacts of different methods of grouse moor management on the net ecosystem C balance (NECB) and on the components of the NECB. The traditional practice of rotational burning (FI) was compared to the main alternative of mowing (LB) and to unmanaged control (DN) areas on a catchment scale and was combined with plot scale manipulations involving leaving (LB) or removing (BR) brash and adding *Sphagnum* propagules (LB+Sph and BR+Sph) after mowing. The NECBs calculated for each of the three sites demonstrated that blanket bogs which are managed as grouse moors can act as either a C source or a C sink and that both the strength and direction of the net C transfer between the ecosystem and the atmosphere can vary from year to year. The NECBs calculated for the managements investigated on the catchment scale showed that, once the loss of plant biomass and the C released from tractor fuel was taken into account, areas under FI management lost more C than areas under LB management. The main difference between FI and LB NECBs was the size of the net ecosystem exchange (NEE) in different years, demonstrating that mowing results in a more delayed release of C by more rapid recovery of plants, and making this the first study to provide a C balance for mowing on a blanket bog and comparing this to the C balance for burning. The plot scale measurement showed that there was little difference between the mowing manipulations but confirmed that some mowing managements had significantly different effects than burning on the NEE flux.

Chapter 3 used the same sites and experimental design to assess the impact of four of the different management manipulations (DN, FI, LB and BR) on vegetation composition and on *Calluna* growth and nutrient content. Vegetation surveys showed that FI plots had both lower *Calluna* cover and shorter *Calluna* plants than LB or BR plots, bringing into question the merits of burning for grouse management. Mown areas also had a higher cover of *Eriophorum vaginatum*, a typical bog plant, and more generally had a higher proportion of vegetated ground than FI plots. Leaves from *Calluna* plants on FI, LB and BR plots had a significantly higher content of N, P, K, Mg and Mn than leaves from *Calluna* on DN plots, demonstrating the importance of management in providing nutrient rich shoots for red grouse. There was no difference between nutrient content in *Calluna* leaves from burnt or mown plots, apart from FI plots having a significantly higher K content. Taking into account differences in *Calluna* cover and height, mowing appeared to provide a greater number of nutritious *Calluna* shoots for grouse than burning, as well as encouraging more typical blanket bog vegetation.

In Chapter 4, a pot experiment, in conjunction with ^{14}C measurements of CO_2 and DOC, was used to establish whether ericoid fungi, both when in mycorrhizal association with *Calluna* plants and as free-living fungi, could decompose recalcitrant organic matter. A fully crossed replicated design containing *Calluna* plants, charcoal and ericoid fungi was employed to compare the ability of a single cultured ericoid fungus, *Hymenoscyphus ericae*, to that of a natural mixed microbial community to break down charcoal, peat or both. The radiocarbon dates strongly indicated that the ericoid fungus, *H. ericae*, broke down old recalcitrant C compounds in the peat and released this C as both CO_2 and dissolved organic carbon (DOC). Furthermore, this ability was not restricted to the single cultured fungus, thus providing the first demonstration that ericoid fungi can utilise ancient peat as a C source. The *Calluna* plants caused an increase in both CO_2 and DOC release, due to the plant inputs priming microbial decomposition, whilst the presence of charcoal reduced DOC concentrations whilst only showing a small positive effect on CO_2 release, suggesting that high *Calluna* cover may be detrimental to peatlands but burning may partially mask this effect, at least in the short term.

Collectively, the findings presented in this thesis show that grouse moor management in general can have negative impacts on the C store within the peat when performed on blanket bogs. However, the results also demonstrate that the different types of management have different effects on vegetation, which is the main builder and maintainer of peat, and that not all effects are negative. These findings could inform gamekeepers, land managers, peatland restoration projects and policy of the benefits and drawbacks of management for both red grouse and C storage. In order to fully understand the impacts of *Calluna* management on blanket bogs, a longer monitoring period and further research into some aspects is required. The remainder of this chapter draws together the results and discusses their implications for peatlands and for grouse management, as well as making suggestions of future research areas and needs.

5.2 Impacts of different methods of *Calluna* management on peatlands and C cycling

The results from both field and pot experiments suggested that *Calluna* management could harm the peatland C balance. The field manipulations demonstrated that, over the first three years following management, both burnt and mown areas released more C (Chapter 2) and had a lower proportion of vegetated ground (Chapter 3) than unmanaged areas. The pot experiment demonstrated that the presence of *Calluna* plants, which management is designed to encourage, primed microbial decomposition and resulted in greater CO_2 and DOC release and that ericoid fungi, which are associated with *Calluna*, broke down recalcitrant matter, albeit in rather dry peat (Chapter 4). However, there were also indications that not all managements were necessarily detrimental to all aspects of peatland C. Charcoal created from *Calluna* burning appeared to reduce the DOC loss from the pot ecosystems (Chapter 4) whilst mowing prevented the conversion of approximately 58 g C m^{-2} y^{-1} from *Calluna* plants to CO_2 (*cf*. releasing only 14 g C m^{-2} y^{-1} from tractor fuel during mowing) and encouraged *E. vaginatum* expansion (Chapter 3).

Given that burning has converted all three sites studied here, as well as many others across the UK (Natural England, 2010), from *Sphagnum* dominated blanket bogs to *Calluna* dominated peatlands over 100-200 years (Thompson *et al.*, 1995), returning the sites back to their original vegetation state in order to increase C sequestration would probably take decades to centuries. Simply leaving these ecosystems in their altered state would likely result in degenerate *Calluna*, which is not greatly productive (Gimingham, 1960), and this would increase the fuel load, thereby increasing the risk of wildfire intensity and severity (Albertson *et al.*, 2010), which could ultimately result in a greater C loss than management by burning (Allen *et al.*, 2013). Additionally, this could have negative consequences for breeding waders, as has happened in the Berwyn Special Area for Conservation in Wales (Warren & Baines, 2014).

Thus, it would appear that any change in the state of these peatlands systems would require some form of management intervention. However, despite primarily being used as grouse moors, these areas are still peatlands. This means that in many of the wetter areas there still is a viable cover of *Sphagnum* which could recolonise the peat surface, increasing C sequestration. This process is more likely to happen with little or no management intervention and may still be possible on drier areas of peatland if taller and denser *Calluna* is first removed to reduce water loss via transpiration and allow light down to the moss layer. Although any reduction in *Calluna* is unlikely to be popular either with the shooting community or with the public at large - due to *Calluna* moorland being valued as a habitat for red grouse, amongst other species, and for its aesthetic value (Bonn *et al.*, 2009) - encouraging *Sphagnum* will not necessarily reduce *Calluna* cover as *Calluna* is able to regenerate by layering (MacDonald *et al.*, 1995). Additionally, the quantity of C stored within the peat and the other ecosystem services provided by peatlands are good reasons for wanting to restore and preserve these blanket bogs, regardless of any desire for *Calluna* moorland. There is already recognition that many other activities impacting blanket bogs are not sustainable or beneficial long term and there have been substantial efforts made in some areas to improve conditions and reduce these activities and the impacts they have.

Grip blocking has been implemented across a number of peatlands across the UK, with over €250 million spent on peatland drain blocking since the late 1980s (Armstrong *et al.*, 2009). This has raised water tables in many areas and slowed water flow, allowing *Sphagnum* recolonisation and recovery of other vegetation (Armstrong *et al.*, 2008). This may also provide benefits in terms of water quality by reducing the DOC concentrations in and exports via stream water (Gibson, 2006; Armstrong *et al.*, 2010). There have been calls from the government to phase out peat use for horticultural applications (HM Government, 2011) and a widespread reduction in SO_2 deposition (Fowler *et al.*, 2005), both of which can reduce bare ground and erosion. Additionally, organisations, such as Moors for the Future (www.moorsforthefuture.org.uk), have initiated revegetation across large areas of bare and eroding peat.

The main difference between many of the activities detrimental to blanket bogs and burning is that there is direct evidence of the damage caused and clear links to the activities, e.g. cutting drainage ditches through peat lowers the water table depth (WTD) and causes erosion, whereas the evidence is less clear and sometimes contradictory for burning. There are some studies suggesting a relationship between burning and an increase in DOC production (Clutterbuck & Yallop, 2010), whilst others have observed no effect (Ward *et al.*, 2007) or that burning decreases DOC (Worrall *et al.*, 2007). That two studies on the same sites can find different effects of burning on the same metrics (both Ward *et al.* (2007) and Worrall *et al.* (2007) conducted studies at Moor House National Nature Reserve (NNR)) does not provide impetus to land managers to alter their management practices.

Although the present study did not find differences in the DOC concentrations (Chapter 2) or *Sphagnum* cover (Chapter 3) between areas under burning and unmanaged areas, there were differences in the NECB. Crucially, when taking into account the quantity of C lost by burning the biomass (even when offset by the quantity of diesel combusted by the tractors during mowing), mowing released less C than burning (Chapter 2) and encouraged *E. vaginatum* growth (Chapter 3), which also is a peat forming species (Bain *et al.*, 2011). The effects of these management methods are likely to alter over time as the vegetation community changes and dead matter decomposes. It is possible that the brash on LB plots will release significant amounts of CO_2 as it breaks down, and may also become a source of DOC. Depending on the location and precise method of mowing, this brash could be removed and baled for use in restoration work, especially as this technique is one of the more effective and acceptable methods of grip blocking (Armstrong *et al.*, 2009). However, if the brash provides a nursery environment for *Sphagnum* mosses by increasing the surface roughness and slowing water flow, there is potential for *Sphagnum* to grow over the brash, ultimately integrating it into newly formed peat and storing this C instead.

If the latter is the case, this could have positive and wide ranging implications for the UK and beyond. The storage of C, or in this case the prevention of additional C release, by brash aiding formation of new peat could exert a negative feedback on the climate (opposite to that described by Davidson & Janssens, 2006) by raising the water table, thereby preventing release of C as CO_2 and encouraging CO_2 uptake through more rapid regeneration of peat forming blanket bog species. This in turn could have multiple benefits, cooling the climate, storing water and releasing it more slowly which could prevent flooding, improving water quality and conserving the biodiversity and landscapes people value (Maltby, 2010).

As red grouse are endemic to the British Isles and the UK holds over 75% of the world's *Calluna* moorland (Tallis *et al.*, 1998), it is probably the only country in which peatlands are managed in such an intensive manner and have been for so long. Therefore, extrapolating findings with regards to NECBs (Chapter 2) or vegetation changes (Chapter 3) to other countries may not be directly applicable. However, UK peatlands store over 3 Gt C (Lindsay, 2010; Bain *et al.*, 2011) indicating that there could be substantial changes in global C dynamics should this C store be lost. Additionally, although both the peat material and local climate are very different, large areas of tropical peatlands are burnt to clear vegetation, which can have detrimental effects on the C balance of these areas (Fargione *et al.*, 2008). If the primary aim is to clear vegetation, some links could be drawn from this study.

More pertinently, 70% of the UK's drinking water is derived from surface waters, which mainly come from peat dominated upland catchments (Bain *et al.*, 2011), and the colour of this water has been increasing since at least 1962 (Worrall *et al.*, 2003a), making it more difficult, and hence expensive, for water companies to treat (Clay *et al.*, 2012). Water quality regulations were introduced in 1981 (Drinking Water Directive (80/778/EC)), with later revision of this legislation, shifting the focus from the tap to the environment the water was derived from (Defra, 2016). Although the results in the present study do not show benefits from mowing peatlands compared to burning them in terms of DOC, and in fact may show a slight rise in DOC concentrations (Chapter 2), there may be benefits longer term if the brash left by mowing increased water retention and encouraged greater *Sphagnum* establishment.

Additionally, the revelation that ericoid fungi, which form mycorrhizal associations with *Calluna* roots, are capable of breaking down recalcitrant ancient organic matter and releasing this as DOC (Chapter 4), demonstrates that increased *Calluna* cover, regardless of the method used to encourage it, may be detrimental to water quality. These effects were observed with both mycorrhizal and free-living fungi (Chapter 4), and therefore may occur in pristine peatlands if ericoid fungi function similarly under wet conditions as they do under relatively dry and disturbed conditions, as in the pots. As *Calluna* has a high transpiration rate which can dry the surrounding peat (Worrall *et al.*, 2007), an increase in *Calluna* cover is likely to increase the fungal biomass, leading to more degradation of recalcitrant matter which is likely to increase DOC and POC concentrations in runoff and stream water, especially following heavy rain events. Therefore, as mowing encourages more typical blanket bog species such as *E. vaginatum*, this may counter some of the effects *Calluna* exerts on the WTD, thus preventing the release of the broken down recalcitrant peat from ericoid fungi, enabling the molecules to be recycled by other microbes (e.g. as with CH_4 cycling, Whalen & Reeburgh, 2000) and remain part of the peat complex.

5.3 Implications of different methods of *Calluna* management for landowners and their grouse

A central component of this thesis has been grouse moor management techniques. Therefore, the impacts of these techniques must be considered on the grouse themselves as well as on those who manage the land, or pay for the land to be managed, for grouse. Without the good will and permission of the land owners, new land management techniques cannot be trialled. Likewise, a lack of support from land owners, or a lack of land owner confidence or understanding in the benefits a particular management may offer them, could result in reams of evidence being produced in favour of an alternative without any uptake or adoption. Consultation processes, such as that of Dougill *et al.* (2006) can result in conflicting problems and complexities being addressed by both stakeholders and researchers, but these consultations can take a very long time.

The present study was largely concerned with grouse moor management techniques. Therefore, as grouse eat mainly *Calluna*, the main attempt that this study employed to produce results which land owners and managers could directly relate to, was to consider both the quantity and the quality of the *Calluna* produced as a result of the different management techniques (Chapter 3). Not only was the nutrient content of *Calluna* from burnt and mown areas very similar, but mowing actually increased *Calluna* cover and height in relation to burning. Additionally, mowing increased the cover of *E. vaginatum* which can provide N- and P-rich flower buds in spring (Pulliainen & Tunkkari, 1991), which could prove beneficial to laying hens as these nutrients may be instrumental in breeding success (Jenkins *et al.*, 1965). Should these differences extend beyond the three years after management implementation considered here, this could provide incentive for a widespread adoption of mowing *Calluna* as a technique for managing grouse moors.

There are other features of the study which may engage with land owners and managers, not all being initially planned. Apart from the obvious benefits to drinking water quality and cost that reducing DOC concentrations may have, increasing surface roughness by leaving brash and thus retaining more water can have beneficial effects on certain insect populations. Craneflies (*Diptera*: *Tipulidae*) are an important component of red grouse chick diet and high soil moisture is necessary to produce a high cranefly abundance (Carroll *et al.*, 2011). As the main aim of grouse moors is to produce a shootable surplus of grouse, chick survival is important. The smaller amount of bare ground and the greater cover of *E. vaginatum* on mown areas combined with the layer of brash (Chapter 3) may result in lower evaporation rates from mown areas compared to burnt areas, thus providing craneflies with higher and more stable soil moisture.

An additional, and less expected, outcome of the study which certainly appealed to one land owner relates to the potential that brash from mowing could help to prevent erosion and C loss. Managing moorlands responsibly, whether or not they overlay deep peat is vital for the conservation of soil in which the *Calluna* plants grow. High instability or great loss of this soil is likely to be detrimental to the *Calluna* and, if erosion reaches the bedrock, could ultimately prevent rooting of any plants. Additionally, the vast quantities of C which would be released to the atmosphere as a result of long term severe erosion could accelerate climate change (Davidson & Janssens, 2006). Upon having these links highlighted, this particular land owner who had initially appeared sceptical at best that the study could provide benefit to his grouse moor, became one of the most enthusiastic stakeholders involved in the project (A. Heinemeyer, pers. comm.). It appears that this was as a result of him understanding that the actions he and his land managers undertook to manage the grouse moor today could have profoundly negative consequences for future generations. Therefore, it may be beneficial for any future studies considering the impacts of land management to ensure that all stakeholders are informed of the positive and negative implications of all of the options which are being studied or considered in order to engage them and increase the likelihood that they will heed the outcomes.

However, regardless of whether a land owner or manager is convinced that a particular type of management has more benefits than another, there are other considerations. Many grouse moors in England are run at the margins of financial limits, some even qualifying for subsidies, particularly in the highly degraded Peak District National Park (Dougill *et al.*, 2006). If an estate does not already own a tractor and mowing equipment, a change in management from burning to mowing would require an initial outlay of tens of thousands of pounds. Employing a contractor to mow could be a cheaper alternative, at least short term, but even this may cause the estate to make a net financial loss. Although government subsidy payments could be used as an incentive to alter management practices, this may not prove popular with the public who may not understand the full implications. Alternatives include funding from water companies, restoration carbon offsetting schemes (IUCN Peatland Programme, 2015) or a 'tourist tax' (Bonn *et al.*, 2009).

Instead of paying subsidies as encouragement to change management, there could be tighter regulations with fines imposed if these are not followed. There has been a recent debate held within the British parliament on grouse shooting, in response to a petition calling for a ban on shooting (Vaughan, 2016). Whilst the outcome of this debate is not yet known, there are other petitions calling for a ban on burning following flooding in Hebden Bridge. Given the link between burning, eroding peatlands and flooding (e.g. Worrall *et al.*, 2007), this may mean alternative management practices are considered.

However, whether or not burning is banned outright or the regulations tightened, there are drier areas which may require management to reduce fuel load and prevent wildfires (Allen *et al.*, 2013) but where it is not practical or possible to take a tractor. These areas include steep slopes and ground with a large number of rocks protruding. In these cases, careful burning on long rotation may prove necessary, although cutting small areas by hand to act as a fire break should be considered and encouraged where possible.

5.4 Further considerations

The findings in Chapters 2 and 3 only cover one pre-management year and three years after management implementation. Therefore, any conclusions drawn from the results presented in these studies should take into account the fact that these peatlands have formed over millennia (Charman, 2002) and have been managed over centuries (Holden *et al.*, 2007a); three years is a very short period and it may be decades before the full implications of the management techniques used here are seen. Additionally, the management cycles were designed on a 10 year rotation meaning that monitoring has occurred for less than half the cycle. Although there were different management responses, particularly with regards to vegetation (Chapter 3), there may be further differences in the responses which could lead to a different conclusion long term. Therefore, ideally monitoring should continue with regards to C, water quality and vegetation for at least the next seven years in order to capture the effects of a full management rotation. If regular monitoring is not possible, ensuring commitment from the three sites to continue managing the catchments in the pre-specified way and revisiting the sites to acquire further measurements in 2023 or beyond, would enable any longer term effect to be revealed.

However, this study exhibit advantages over other similar studies and proves a robust basis for statistical analysis. Many studies only take measurements for one or sometimes two years when measuring NECBs (e.g. Ward *et al.*, 2007; Clay *et al.*, 2010; Dinsmore *et al.*, 2010), meaning that annual variation is poorly quantified. The present study encompasses annual variations over four years, which gives more credence to future extrapolation, although further monitoring would be beneficial.

Another advantage is that this manipulative experiment was based on the before-after control-impact (BACI) design, first suggested by Green (1979) as the “optimal impact study design”. One criticism of the BACI approach is that it is usually unreplicated meaning that it is difficult to tell whether a measured feature has changed due to the impact or due to natural variation (Underwood, 1992). However, this problem is usually compounded because the control and impact sites are spatially distant meaning that the sites may be affected by different natural occurrences, such as storms. The present study countered this problem by using three sites, thus providing replication. Each site had two sub-catchments, thus providing both control and impact areas within each site. Although the sites were not located adjacent to one another, the pairs of sub-catchments were. This minimised the chance of random natural events affecting the control without affecting the impact areas, and vice versa. Further, the three-fold replication could be seen to have militated against the probability that natural changes were more variable than the changes caused by management, due to the pre-management year revealing substantial differences between the sites. This therefore emphasises the consistent results arising from each management at all sites, meaning that these results are likely to be applicable to other blanket bog sites managed as grouse moors across England and, perhaps, the rest of the UK.

The pot experiment (Chapter 4) enabled a fully crossed design by manipulation of the components in each pot. Despite the results indicating that for the first time that ericoid fungi break down recalcitrant matter, the peat in the pot ecosystems had been subject to gamma-irradiation and drying, likely altering the structure. As ericoid mycorrhizas typically only extend a few millimetres from roots they have colonised (J. Leake, pers. comm.), partitioning *in situ* is unlikely to be achievable. However, further work into the belowground interactions and processes in blanket bogs, and their responses to disturbance such as management activity, urgently requires further investigation, particularly in light of increasing DOC concentrations (Worrall *et al.*, 2003a) and as climate change is likely to affect bogs, regardless of whether management practices are altered.

5.5 Concluding remarks

The management of blanket bogs provides a great challenge for the future. There is extensive evidence that the vast majority of the UK's blanket bogs are damaged. However, there have been major inroads made into reversing some of the damage caused, particularly with regard to grip blocking to raise water tables. With grouse moors management, there is a growing awareness of the problems but, as yet, very little evidence on alterative options.

This thesis has presented findings which demonstrated that management of *Calluna*-dominated blanket bogs for grouse by burning is not necessarily the best management. In terms of C cycling, mowing resulted in a lower net release of C than burning, largely because more rapid regeneration of both *Calluna* and *E. vaginatum* resulted in a greater C uptake via photosynthesis. The greater cover of *Calluna* and *E. vaginatum* also resulted in less bare ground, which could prevent POC release and erosion, as well as offering a greater quantity of nutritious food for red grouse. The revelation that ericoid mycorrhizas can break down ancient recalcitrant matter in peat, increasing both CO_2 and DOC release, is worrying in a system which is already under much pressure. However, the greater cover of vegetation in mown areas compared to burnt areas may aid *Sphagnum* recovery, slow water flow and raise the water table, preventing much of the DOC produced by the ericoid fungi leaving the catchment.

The three multi-annual NECBs for intensively managed blanket bogs will greatly contribute to the understanding of annual variation in the C dynamics of these systems. The multi-annual NECBs, combined with the vegetation dynamics, for areas under burning, mowing and no management will contribute greatly to the understanding of what the benefits and drawbacks to each of these managements entail. The finding that ericoid fungi break down old recalcitrant matter will enhance understanding of belowground C cycling, as well as raising further questions.

Overall, there is a need to appreciate the many benefits that properly functioning blanket bogs can provide, whilst also recognising that grouse shooting forms a prominent part of upland culture and the rural economy. Whilst this may appear initially to not be possible, the results from this study suggest that, in conjunction with measures such as ditch blocking and in collaboration with the people who own and manage the land, mowing may provide an opportunity to both improve the condition of blanket bogs without negatively impacting upon the grouse on which the shooting community rely.

Appendix A - Upscaling NEE flux measurements to annual budgets

In Chapter 2, the NEE fluxes were upscaled from fluxes measured in the field over 5 minutes across a range of light levels to annual NEE estimates. This was performed separately for the FI, LB and DN managements at each of the three sites. For each measurement date, a light response curve was modelled for each of the three selected managements at each site (i.e. a curve was modelled for FI measurements at Nidderdale in July 2012, a separate curve for FI measurements at Nidderdale for October 2012, etc.), using the equation:

$$CO_2\ \text{flux}=\frac{P_{max}\times PAR}{PAR+K_m}+R_{eco} \qquad \text{Eq.A.1}$$

where CO_2 flux is the modelled CO_2 flux at a particular light level, P_{max} is the maximum CO_2 uptake of the curve, PAR is the amount of light in µmol m^{-2} s^{-1}, K_m is a calculated constant and R_{eco} is the modelled maximum CO_2 release (equivalent to the R_{eco} measurement with the dark chamber cover). Following Brown (2001), P_{max}, K_m and R_{eco} were calculated using the Solver function in Excel (Microsoft, 2010), which was set to maximise the R^2 of the modelled curve through the measured data points (see Figure A.1 for comparison of measured versus modelled light response curves for Nidderdale DN plots in October 2012; Nidderdale DN plots in 2012 will be used as an illustrative example throughout this explanation).

This enabled filling in of all terms except PAR in Eq. A.1. For Nidderdale DN plots in October 2012, this gave the equation:

$$CO_2\ \text{flux}=\frac{-10\times PAR}{PAR+1010}+2.6 \qquad \text{Eq.A.2}$$

There were three set of NEE measurements made in 2012 and four sets in each of the other three years. For each year, the calculated P_{max} values for each site and management combination were regressed against the average air temperature inside the chamber during that measurement set (e.g. the average air temperature in the chamber for all DN plots measured at Nidderdale in October 2012), giving a linear equation (Figure A.2a). Similarly, the calculated R_{eco} values were regressed against the same chamber temperature averages, producing exponential equations (Figure A.2b).

Monthly averages of PAR were calculated from the hourly measured AWS recordings at each site. For each year, the K_m values for each site and management combination were regressed against the monthly PAR measurements for the months in which NEE measurements occurred. This produced a linear equation for which the intercept was set to zero (Figure A.3).

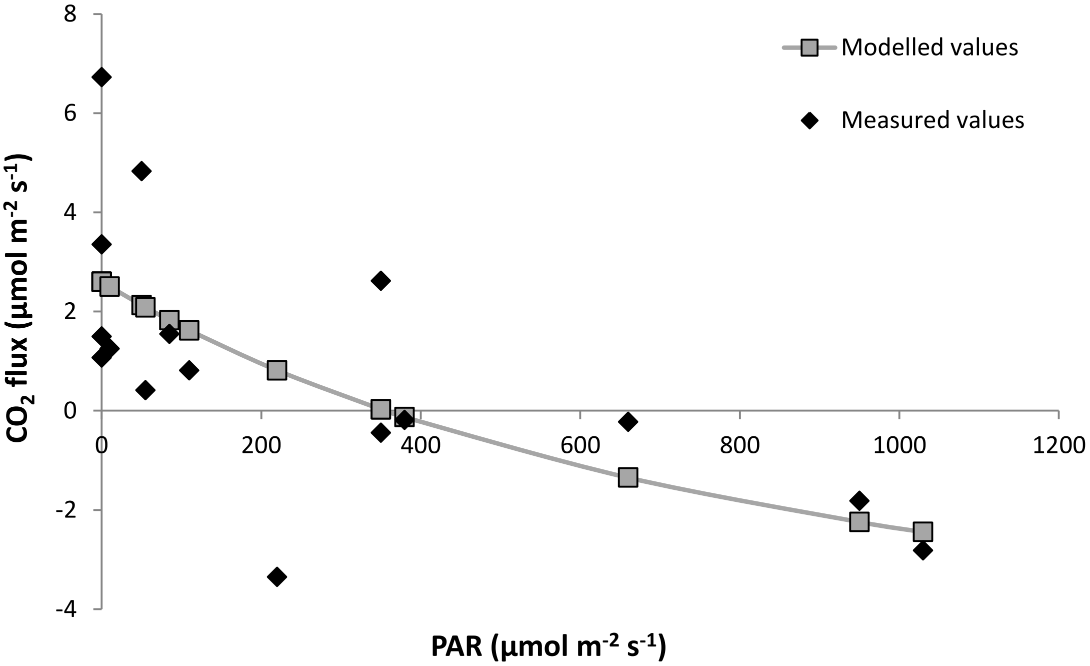


Figure A.1 Comparison of the measured CO_2 fluxes at different PAR levels to the modelled values which were used to construct the light response curve for Nidderdale DN plots in October 2012, and from which the parameters P_{max}, K_m and R_{eco} are derived in Eq. A.1.

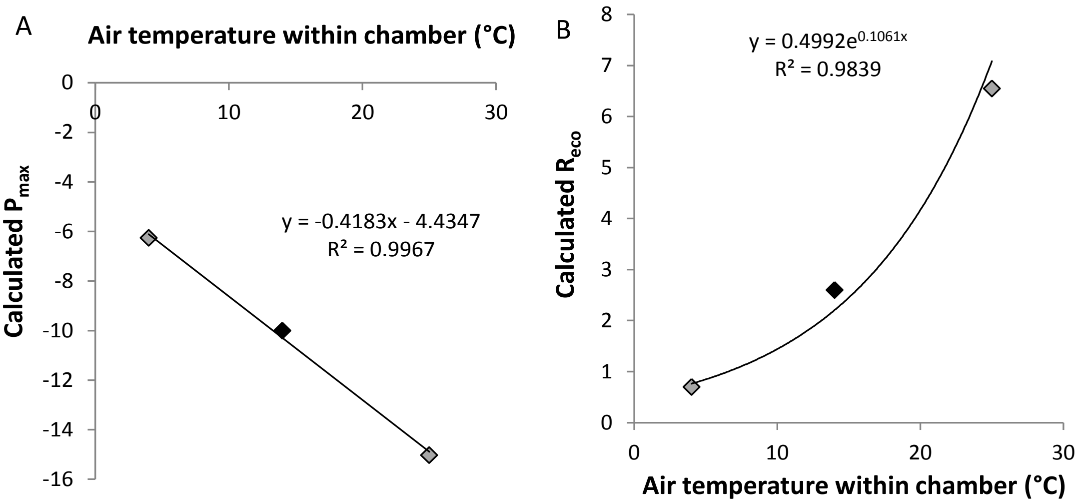


Figure A.2 Regression between chamber air temperature and A) the calculated P_{max} values (linear) and B) the calculated R_{eco} values (exponential) for Nidderdale DN plots in 2012. The points incorporating the calculated P_{max} and R_{eco} values from Eq.A.2 are in black to enable identification. The regression equations are displayed with R^2 values.

Values for R_{eco} (the maximum C release) and P_{max} (the maximum C uptake) were calculated on an hourly basis for each site and management using the equations derived from regression with chamber temperature (Figure A.2), where x was the hourly air temperature recorded by the AWS. Likewise, the equation derived from the regression of K_m and PAR (Figure A.3) was used with the average monthly PAR measurements from the AWS to calculate a value of K_m for each month of each year for each site and management combination.

These values were used in Eq.A.1 to calculate the NEE flux for each hour of each year and for each management within each site. The hourly calculated NEE fluxes were summed to derive the monthly (Figure A.4) and yearly net C budgets. Fluxes were converted from µmol CO_2 m^{-2} s^{-1} to g C m^{-2} y^{-1}.

The modelled NEE fluxes were compared to the measured fluxes in order to validate the accuracy of the annual NEE budgets. The average was taken of the measured NEE fluxes (only the Full Light portion was used as the shaded portions were only needed to fit the light response curves) for each site and management combination on each measurement date. The corresponding modelled fluxes were calculated by taking the average of the hourly calculated values for the period covering the whole measurement period. This was assumed to be the same period for each group of measurements for the same site and management combination. Specifically, the time periods used for Nidderdale were 09.30-13.30 for DN and LB plots and 12.30-15.30 for FI plots, those for Mossdale were 08.30-13.30 for DN and LB plots and 12.30-15.30 for FI plots, and those for Whitendale were 10.30-15.30 for DN and LB plots and 08.30-11.30 for FI plots.

A paired Student's t-test (using the function "t.test" in the R "stats" package; R Core Team, 2016) was used to determine whether the measured NEE fluxes were significantly different from the modelled fluxes. Although modelled fluxes tended to be closer to zero than the measured fluxes were (Figure A.5), there was no significant difference between the measured and modelled NEE fluxes ($t_{134} = 1.64$, $p = 0.1043$). This suggested that the model was adequate to be used to upscale the NEE fluxes.

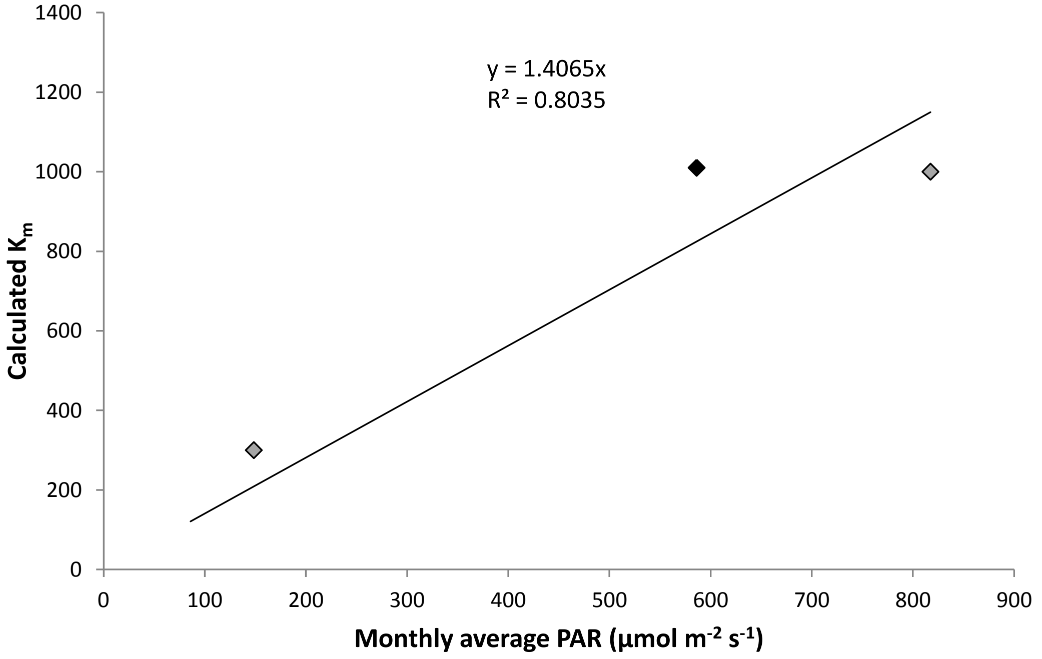


Figure A.3 Linear regression between the calculated K_m values for Nidderdale DN plots in 2012 and the corresponding average monthly PAR measurements.

The points incorporating the calculated K_m values from Eq.A.2 are in black to enable identification. The regression equations are displayed with R^2 values.

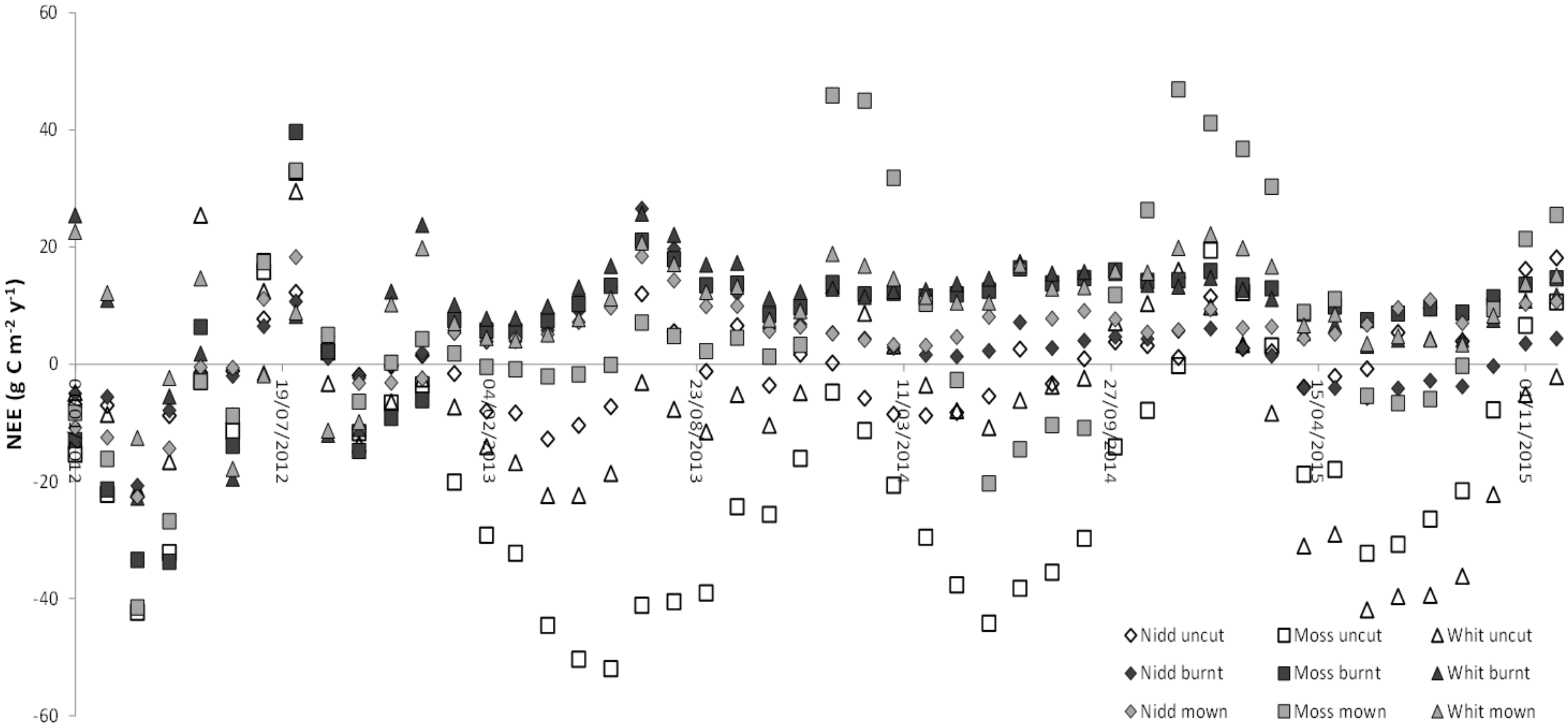


Figure A.4 Monthly modelled NEE fluxes for each of the three upscaled managements (FI, LB and DN) at each of the three sites.

Appendix B - Redundancy analyses using year, site or block as constraining variables

In Chapter 3, redundancy analyses (RDAs) were performed on the vegetation percentage cover data to assess the effects of management on the vegetation composition. As the site and block in which the plots were located and the year of measurement were also expected to affect the vegetation composition, these were applied separately as constraining variables to RDAs. The results of the RDAs using year, site or block as the constraining variable are outlined in Section 3.3.1, shown in Figures B.1-3 and discussed in Section 3.4.2. Although year, site and block are used as the constraining variables in Figures B.1-3, the dots (which represent the position of each individual plot in a given year) are coloured according to management to demonstrate that, whilst year, site and block explain a significant portion of the data in the vegetation matrix, these factors contain plots from all managements.

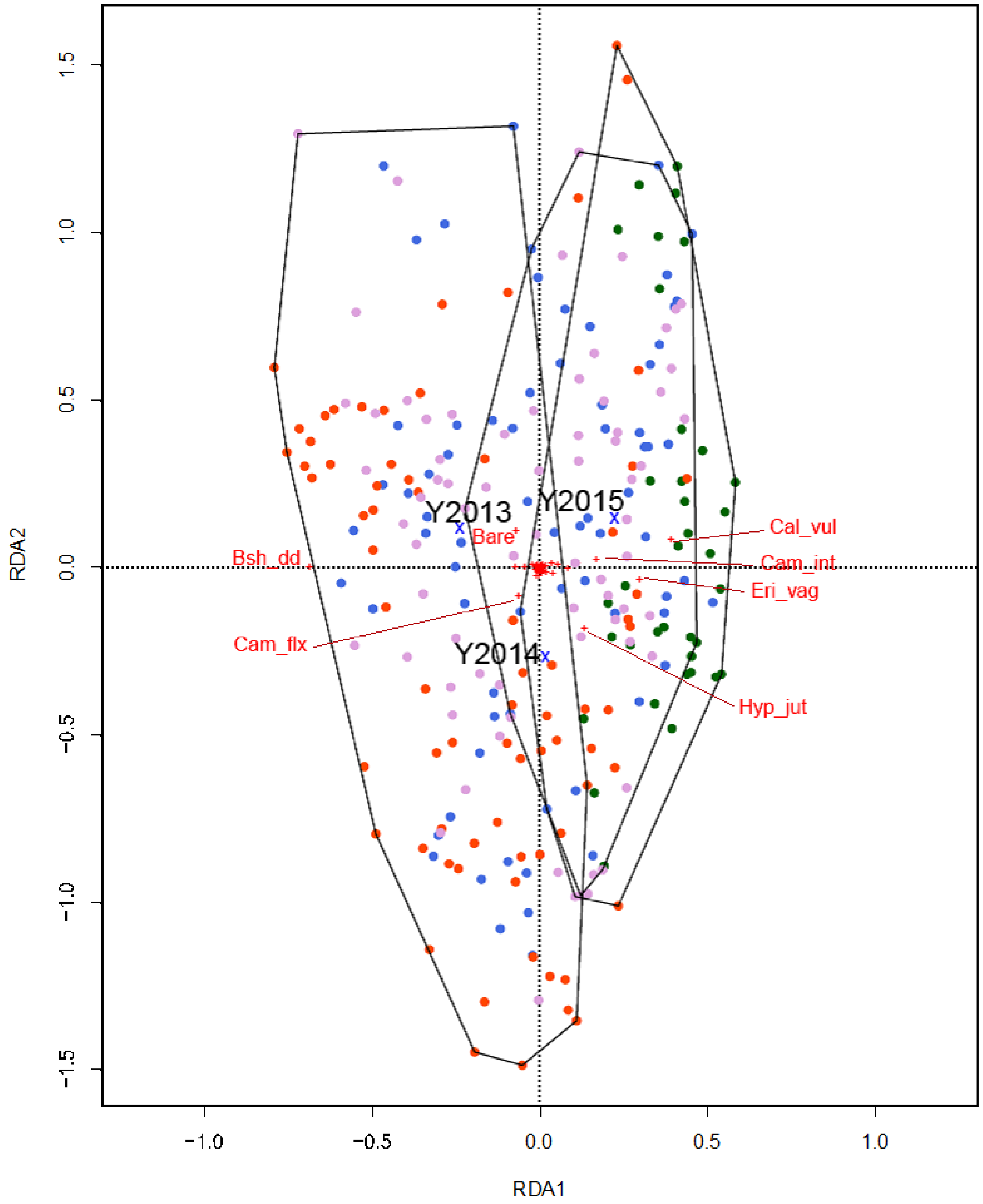


Figure B.1 Redundancy analysis (RDA) of vegetation composition in 2013, 2014 and 2015 (i.e. post-management) with year as the constraining variable.

Blue crosses represent the centroids of the years. Red crosses represent the positions of individual species. The most influential are labelled with the first three letters of the genus name and species name (for plant species; Bsh_dd is brash/dead/burnt material). Coloured dots represent the position of each individual plot in a given year where dark green is for DN managed plots, orange is for FI, blue is for BR and pink is for LB (see Section 3.2.5 for management codes). The groups assigned by k-means partitioning are shown by the polygons.

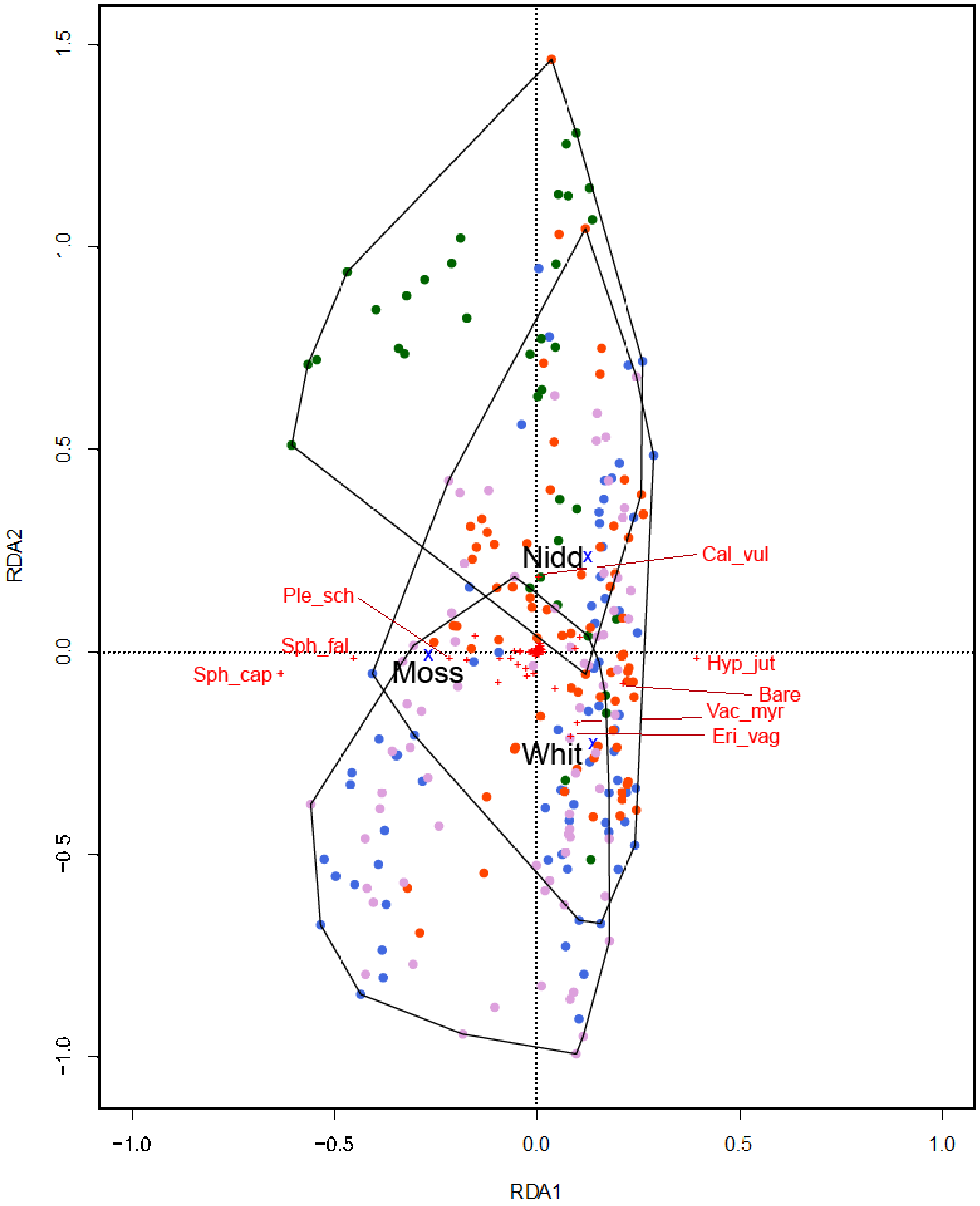


Figure B.2 Redundancy analysis (RDA) of vegetation composition in 2013, 2014 and 2015 (i.e. post-management) with site as the constraining variable.

Blue crosses represent the centroids of the sites. Red crosses represent the positions of individual species. The most influential are labelled with the first three letters of the genus name and species name (for plant species; Bare is bare ground). Coloured dots represent the position of each individual plot in a given year where dark green is for DN managed plots, orange is for FI, blue is for BR and pink is for LB (see Section 3.2.5 for management codes). The groups assigned by k-means partitioning are shown by the polygons.

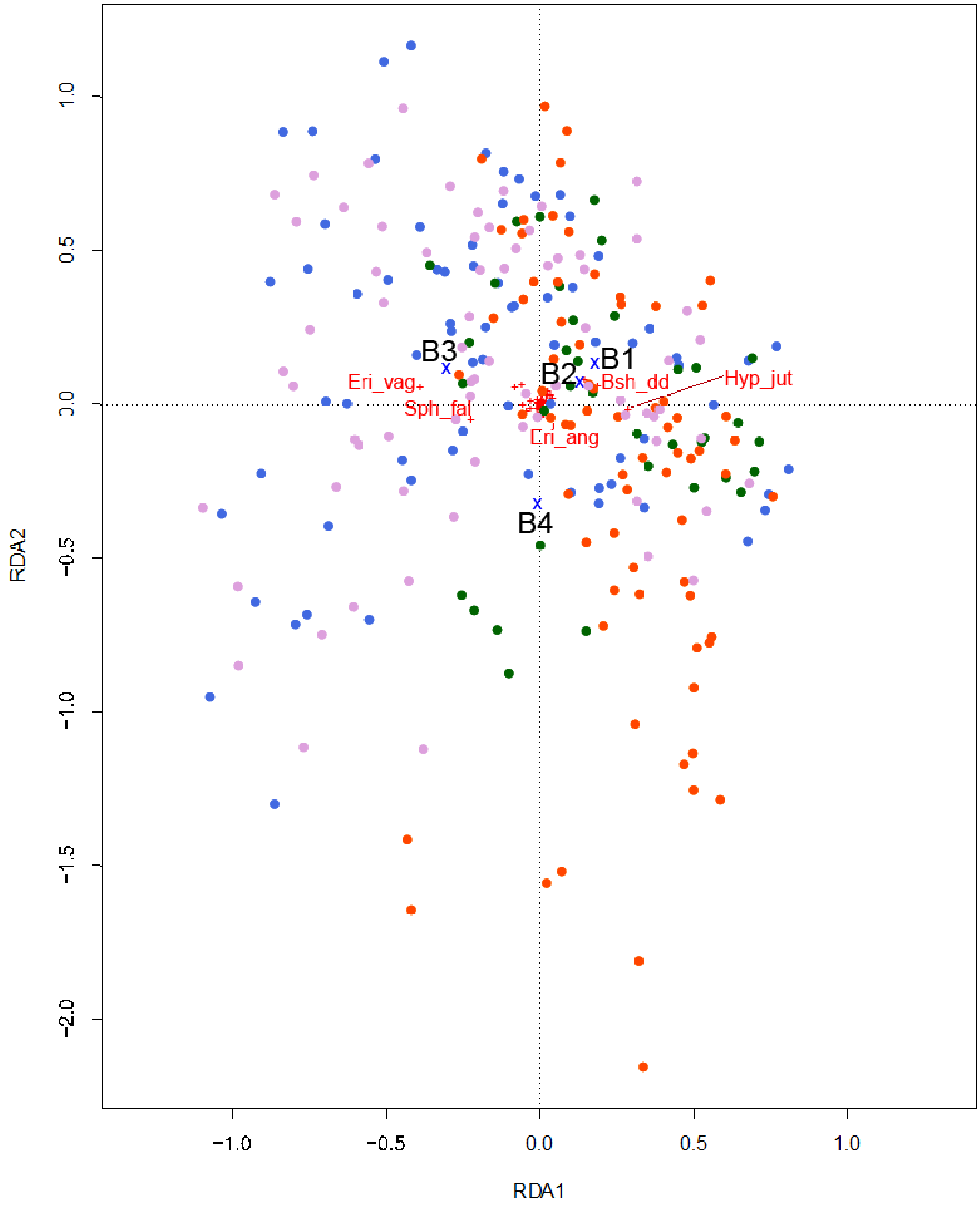


Figure B.3 Redundancy analysis (RDA) of vegetation composition in 2013, 2014 and 2015 (i.e. post-management) with block as the constraining variable.

Blue crosses represent the centroids of the blocks. Red crosses represent the positions of individual species. The most influential are labelled with the first three letters of the genus name and species name (for plant species; Bsh_dd is brash/dead/burnt material). Coloured dots represent the position of each individual plot in a given year where dark green is for DN managed plots, orange is for FI, blue is for BR and pink is for LB (see Section 3.2.5 for management codes). No polygons are shown as the data were too clustered to satisfactorily divide the observations into groups.

Appendix C - Plant nutrient content minimum and maximum values

In Chapter 3, the nutrient content was determined for *Calluna* plants on all plots at all sites during 2012 and 2015, representing the pre- and post-management periods, respectively. Concentrations of 11 different elements were measured in the *Calluna* leaves. These elements were N, P, K, Na, Mg, Ca, Fe, Al, Mn, Zn and Cu. Results of the statistical analysis to determine whether there was a significant difference in concentration of each nutrient on different management and different sites pre- or post-management are detailed in Section 3.3.4. To facilitate interpretation of the results and to allow comparison to other studies, the minimum, maximum and average concentrations of each element for each site in the two time periods are shown in Table C.1 and the same values for each management in the two time periods are shown in Table C.2.

Table C.1 The minimum (min), maximum (max) and average (av) concentrations of each of the 11 elements measured in *Calluna* leaves for each site pre- and post-management. Site abbreviations are used where Nidd is a contraction of Nidderdale, Moss is a contraction of Mossdale and Whit is a contraction of Whitendale. Concentrations are given as percentages (%) for nitrogen (N), phosphorus (P), potassium (K), sodium (Na), magnesium (Mg) and calcium (Ca), and as µg g^{-1} of oven-dried leaf material for iron (Fe), aluminium (Al), manganese (Mn), zinc (Zn) and copper (Cu).

Site and period	Value	%						µg g^{-1}				
		N	P	K	Na	Mg	Ca	Fe	Al	Mn	Zn	Cu
Nidd pre	Min	1.02	0.05	0.12	0.03	0.10	0.18	121	91.5	70.1	28.2	8.71
	Max	1.53	0.15	0.22	0.09	0.22	0.59	214	134	383	106	14.8
	Av	1.23	0.09	0.16	0.05	0.16	0.40	160	108	214	49.8	12.4
Nidd post	Min	1.08	0.04	0.15	0.04	0.12	0.15	47.0	19.1	174	17.3	5.92
	Max	2.82	0.16	0.58	0.24	0.33	0.54	581	134	1753	125	15.3
	Av	1.84	0.10	0.40	0.12	0.25	0.42	155	56.1	899	59.1	12.1
Moss pre	Min	0.95	0.06	0.12	0.06	0.15	0.30	93.6	93.0	68.6	24.4	8.67
	Max	1.22	0.14	0.23	0.31	0.20	0.44	213	156	366	205	13.1
	Av	1.07	0.10	0.19	0.14	0.18	0.38	143	109	211	43.1	11.1
Moss post	Min	0.94	0.04	0.29	0.05	0.18	0.30	74.8	21.7	105	23.9	9.99
	Max	2.92	0.25	0.83	0.21	0.38	0.56	148	190	1900	62.2	15.8
	Av	1.81	0.12	0.46	0.12	0.26	0.40	102	44.1	1122	37.5	12.0
Whit pre	Min	1.18	0.06	0.13	0.04	0.11	0.18	97.2	91.9	54.6	28.2	10.3
	Max	1.75	0.17	0.28	0.13	0.20	0.42	424	249	571	75.2	17.5
	Av	1.41	0.11	0.19	0.08	0.14	0.27	197	133	204	42.1	13.9
Whit post	Min	1.34	0.06	0.24	0.04	0.17	0.26	88.7	34.7	125	30.9	9.73
	Max	2.76	0.17	0.66	0.20	0.35	0.59	356	186	1649	110	16.6
	Av	2.01	0.10	0.41	0.12	0.27	0.44	156	67.4	834	50.5	12.2

Table C.2 The minimum (min), maximum (max) and average (av) concentrations of each of the 11 elements measured in *Calluna* leaves for each managment pre- and post-management. Management codes are used when DN represents unmanaged, BR represents mown plots with the brash removed, LB represents mown plots with the brash left and FI represents burnt. Concentrations are given as percentages (%) for nitrogen (N), phosphorus (P), potassium (K), sodium (Na), magnesium (Mg) and calcium (Ca), and as µg g^{-1} of oven-dried leaf material for iron (Fe), aluminium (Al), manganese (Mn), zinc (Zn) and copper (Cu).

Mgmt and period	Value	%						µg g^{-1}				
		N	P	K	Na	Mg	Ca	Fe	Al	Mn	Zn	Cu
DN pre	Min	0.96	0.06	0.12	0.05	0.11	0.18	116	93.0	54.6	35.3	10.4
	Max	1.51	0.13	0.23	0.31	0.19	0.51	216	145	383	105	16.5
	Av	1.20	0.10	0.18	0.10	0.15	0.34	164	113	227	52.5	13.2
DN post	Min	0.94	0.04	0.24	0.05	0.18	0.33	87.8	35.8	105	30.6	10.1
	Max	1.81	0.10	0.49	0.13	0.26	0.52	344	186	639	110	14.9
	Av	1.33	0.07	0.33	0.08	0.21	0.40	152	81.4	290	50.7	11.7
BR pre	Min	1.02	0.05	0.12	0.03	0.10	0.19	113	95.3	68.6	24.9	8.71
	Max	1.65	0.13	0.24	0.19	0.19	0.51	266	165	571	74.9	16.0
	Av	1.25	0.09	0.18	0.09	0.16	0.34	164	115	215	41.4	11.8
BR post	Min	1.43	0.04	0.15	0.04	0.12	0.15	47.0	19.1	272	17.3	5.92
	Max	2.92	0.15	0.68	0.20	0.32	0.53	356	190	1753	78.9	16.6
	Av	1.98	0.11	0.41	0.12	0.26	0.42	121	54.3	1059	44.2	12.0
LB pre	Min	0.95	0.06	0.13	0.03	0.10	0.18	113	91.5	98.9	24.4	10.0
	Max	1.75	0.15	0.24	0.22	0.22	0.59	424	249	549	50.2	17.5
	Av	1.24	0.10	0.18	0.09	0.16	0.36	183	123	205	39.2	13.3
LB post	Min	1.41	0.07	0.27	0.05	0.17	0.26	74.8	21.7	450	32.0	9.47
	Max	2.55	0.17	0.57	0.21	0.35	0.54	341	118	1900	114	15.8
	Av	1.93	0.12	0.42	0.13	0.27	0.40	132	48.8	1047	44.5	12.2
FI pre	Min	1.04	0.06	0.12	0.05	0.15	0.23	93.6	91.9	78.9	28.2	8.67
	Max	1.52	0.17	0.28	0.13	0.20	0.51	213	156	253	99.7	13.3
	Av	1.21	0.11	0.20	0.08	0.18	0.36	143	110	189	43.2	11.5
FI post	Min	1.62	0.09	0.35	0.06	0.23	0.37	88.7	25.3	644	32.3	10.1
	Max	2.76	0.17	0.83	0.24	0.38	0.59	197	81.8	1875	125	15.0
	Av	2.16	0.13	0.55	0.13	0.29	0.49	128	47.5	1218	64.5	12.7

Appendix D - Raw 14C values and publication codes

In Chapter 4, radiocarbon analyses were performed on 15 CO_2 and 15 DOC samples collected from the pot ecosystems to determine the age of the samples. Additionally, three homogenised peat samples (i.e. containing a mixture of peat from all pots) and one sample of charcoal created from burning *Calluna* plants were also dated. All ^{14}C data were normalised to -25‰ $\delta^{13}C$ to correct for mass-dependent isotopic fractionation and were expressed as %Modern relative to the activity of the NBS Oxalic Acid international radiocarbon standard, following convention (Stuiver & Polach, 1977). The normalised ^{14}C values, the measured $\delta^{13}C$ content and the Scottish Universities Environmental Research Centre (SUERC) publication codes are detailed in Table D.1 for all of the samples sent for radiocarbon dating.

Table D.1 Scottish Universities Environmental Research Centre (SUERC) publication codes and sample types.

The ^{14}C and δ^{13}C content of each sample are shown. Treatment codes refer to the pot treatments, which are laid out in full in Table 4.2.

Publication code	**Sample type**	**Treatment code**	**^{14}C content (%Modern ± 1σ)**	**δ^{13}C content (‰)**
SUERC-64843	CO_2	H--	62.96 ± 0.34	-24.3
SUERC-64844	CO_2	---	61.67 ± 0.34	-24.7
SUERC-64848	CO_2	HCB	83.45 ± 0.39	-26.6
SUERC-64849	CO_2	--B	73.23 ± 0.36	-19.7
SUERC-64850	CO_2	HC-	89.25 ± 0.41	-27.1
SUERC-67911	CO_2	---	68.03 ± 0.35	-19.9
SUERC-67912	CO_2	HC-	83.68 ± 0.37	-27.0
SUERC-67913	CO_2	--B	110.99 ± 0.51	-20.7
SUERC-67917	CO_2	H--	62.97 ± 0.35	-23.9
SUERC-67918	CO_2	HCB	85.91 ± 0.40	-26.8
SUERC-67919	CO_2	---	67.86 ± 0.33	-21.2
SUERC-67920	CO_2	H--	67.31 ± 0.34	-22.3
SUERC-67921	CO_2	HC-	78.84 ± 0.38	-21.9
SUERC-67922	CO_2	--B	66.43 ± 0.35	-24.3
SUERC-67923	CO_2	MCB	74.79 ± 0.37	-26.6
SUERC-65920	DOC	H--	71.57 ± 0.33	-26.5
SUERC-65921	DOC	---	71.80 ± 0.32	-27.0
SUERC-65922	DOC	HCB	75.36 ± 0.33	-26.7
SUERC-65923	DOC	--B	67.99 ± 0.32	-27.7
SUERC-65924	DOC	HC-	74.30 ± 0.33	-25.9
SUERC-67898	DOC	---	74.00 ± 0.34	-26.6
SUERC-67899	DOC	HC-	74.34 ± 0.33	-26.9
SUERC-67900	DOC	--B	111.81 ± 0.49	-27.6
SUERC-67901	DOC	H--	72.53 ± 0.33	-26.8
SUERC-67902	DOC	HCB	74.48 ± 0.34	-26.8
SUERC-67903	DOC	---	70.64 ± 0.33	-27.4
SUERC-67907	DOC	H--	72.25 ± 0.33	-27.3
SUERC-67908	DOC	HC-	74.26 ± 0.34	-26.8
SUERC-67909	DOC	--B	71.38 ± 0.31	-27.0
SUERC-67910	DOC	MCB	74.94 ± 0.33	-27.0
SUERC-65527	Peat	n/a	69.54 ± 0.32	-27.7
SUERC-65528	Peat	n/a	68.06 ± 0.31	-27.8
SUERC-67897	Peat	n/a	68.38 ± 0.32	-27.5
SUERC-68198	Charcoal	n/a	104.95 ± 0.48	-30.2

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