RESTORATION AND RECOVERY OF *SPHAGNUM* ON DEGRADED BLANKET BOG

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DOCTOR OF PHILOSOPHY

2015

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A thesis submitted in partial
fulfilment of the requirements of the
Manchester Metropolitan University for
the degree of Doctor of Philosophy

Division of Biology and Conservation Ecology
School of Science and the Environment
Manchester Metropolitan University

2015

Ever tried. Ever failed.
No matter. Try again.
Fail again. Fail better.

–

Samuel Beckett

Abstract

1. The blanket bogs of the southern Pennines and Peak District are severely degraded, attributed to centuries of poor land management, wildfire and atmospheric pollution. Restoration efforts have focussed on the revegetation of bare and eroding peat surfaces, with considerable success.
2. *Sphagnum* mosses provide the form and function of blanket bog, with their remains making up the majority of the peat body. These species were lost from the region and remain largely absent, despite restoration efforts.
3. As a keystone species of peatlands, their return is essential to the continued provision of ecosystem services derived from these uplands. Hence, their reintroduction is of great importance.
4. Preliminary trials determined *Sphagnum* can be reintroduced to numerous degraded conditions found on blanket peat, with *S. fallax* the best performing species. Water availability was strongly implicated as a significant factor, with drought proving fatal to propagules. In areas of dense vegetation, flailing has the potential to increase establishment, but requires further verification.
5. Growth trials indicated the legacy of atmospheric pollution was still exerting influence upon the growth of *Sphagnum*. Peat from the southern Pennines region was shown to contain elevated concentration of numerous pollutant heavy metals and nutrients. A comparative study of some UK bogs demonstrated the consequences of biogeochemical characteristics, whilst further implicating the importance of water availability in degraded sites.
6. The potential of *Sphagnum* reintroduction to degraded sites was demonstrated, within the constraints of shorter time scales. Over longer periods, with increased experimentation and subsequent monitoring, further understanding will undoubtedly be gathered. It is essential this knowledge is shared, updated and applied by conservation agencies and parties conducting such work.

Acknowledgements

Director of studies:	Simon Caporn
Supervisory team:	Robin Sen
	Matt Bucker
Technical staff:	David McKendry
	Dave Groom
	Sue Hutchinson
	Graham Tinsley
	Amy Hall
	Alistair Battersby
Department colleagues:	Richard Payne
	James Rowson
	Chris Field
	Trish Linton
	Paul Chipman
	David Elliot
	Daphne Lai
Student volunteers:	Martin Kay
	Joshua Riggs
	Anna Keightley
	Wayne Donner
	Kat Sambrooks
	Tom Squires
	Felix Nwaishi
Moors for the Future Partnership:	Rachael Maskill
	Jon Walker
	Brendon Wittram
Micropropagation Services Ltd.:	Neal Wright
	Barbara Wright
Funding:	Manchester Metropolitan University
	Moors for the Future Partnership
	Co-operative Foundation
Collaboration and access:	United Utilities
	Yorkshire Water
	National Trust
Motivation, sanity and coffee:	Family, friends, and everyone along the way

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Chapter 1 – Introduction

1.1 Overview

The blanket bogs of the southern Pennines are arguably the most degraded peatlands within the United Kingdom (Tallis, 1985b). A history of industrial pollution, poor land management and wildfire has ravaged these landscapes, resulting in large swathes of actively eroding moorland, characterised by bare peat surfaces (Holden *et al.*, 2007b), and species-poor vegetation communities. Amid improving air quality and land management reforms, efforts have been made to restore these landscapes to functional, peat-accumulating systems. There has been widespread success in revegetating denuded areas and limiting further peat loss. However, one vital component of these landscapes remains largely absent – *Sphagnum* mosses (Caporn *et al.*, 2006; Carroll *et al.*, 2009). Whilst restoration techniques utilised on lowland raised bogs (e.g. Wheeler & Shaw, 1995) have yielded some success, the upland blanket bogs of northern England present new challenges: a legacy of industrial pollution, severe erosion, disturbed hydrology, and isolated and inaccessible locations. It is these problems which necessitate the research undertaken here. *Sphagnum* provides the very form and function of these peatlands (Tallis, 1998) and so their widespread return is essential to the restoration of blanket bogs.

This Chapter will describe and analyse these ecosystems, along with the causes and impacts of degradation. The focus of this introduction will be on the blanket bogs of the southern Pennines, and does not aim to collate all available knowledge on peatlands, but to highlight the factors of relevance to the research and region described.

1.2 Ombrotrophic mires

1.2.1 Formation and structure

Peat is the partially decomposed remains of plants and forms wherever the rate of growth and subsequent accumulation of organic material is greater than the rate of decay. Peat formation tends to occur in conditions of waterlogging since this drastically reduces the amount of oxygen available to aerobic bacteria; oxygen diffuses through water 10,000 times more slowly than through air (Clymo & Hayward, 1982). Decomposition is therefore effectively limited to anaerobic microorganism species (e.g. Archaea) and pathways, with a greatly reduced rate of mineralisation (Lindsay, 2010). This leads to the net accumulation of semi-decomposed plant remains – peat.

Waterlogging occurs where inputs of water into a system exceed those being lost. This can be due to high levels of precipitation and humidity, and low levels of evapotranspiration and drainage. Peat can be formed from a range of vegetation types, and in temperate and humid climates *Sphagnum* mosses can dominate (Aerts *et al.*, 1992), along with significant contributions from other vegetation types, such as sedges and rushes (Lindsay, 2010). *Sphagnum* exhibits a range of physiological traits which make it resistant to decay, and therefore efficient at forming peat (discussed later in Section 1.3.2).

Ombrotrophic bogs receive almost all their hydrological and nutrient inputs through precipitation (Clymo, 1983). They are diplotelmic (dual-layered) systems (Ingram, 1983), made up of the acrotelm and catotelm (Ivanov, 1981). The acrotelm is the uppermost layer containing the live and recent dead plant material, through which water and oxygen can move freely. The water table usually fluctuates within this region, which can be anywhere up to 75 cm deep (Holden *et al.*, 2011; Lindsay, 1995a; Wallage & Holden, 2011). Due to the penetration of oxygen into this layer, aerobic decomposition has the potential to occur. *Sphagnum* and other mosses differ from vascular plants, growing from an apical region and dying from their base upwards (Lindsay, 2010). The structure of *Sphagnum* begins to break down 10 – 20 cm below the surface as stems and branches collapse (Clymo, 1992). Beyond the acrotelm, and within the zone of permanent waterlogging and anoxia is the catotelm, containing the bulk of the peat (Holden *et al.*, 2011; Lindsay, 1995a; Wallage & Holden, 2011). This is a more uniform colloidal matrix containing identifiable plant remains, through which water moves extremely slowly, effectively isolating the bog from the underlying substrate (Baird *et al.*, 1997; Clymo, 2004).

There are two distinct types of ombrotrophic peatland: raised bog and blanket bog, sharing common traits but differing in some key aspects.

Raised bog

Peat can begin to accumulate where waterlogging occurs due to the features of the landscape and inputs of groundwater. These groundwater-fed peatlands are known as fens. Over time and through shifts in vegetation, the build-up of organic material and peat becomes sufficient to raise the surface above this groundwater influence. *Sphagnum* usually becomes dominant and the peatland takes on a raised, dome-like structure as more material is added to the body of peat, hence the term raised bog (Rydin & Jeglum, 2013). This relies upon sufficient input of water through precipitation and minimal losses through drainage to maintain the hydrology. It is now referred to as a bog since it receives nearly all its nutrient and hydrological inputs through precipitation (ombrotrophic) (Clymo, 1983).

Blanket bog

Blanket bog forms in conditions of high rainfall and humidity, limiting rates of evapotranspiration (O'Connell, 1990). The balance of these parameters is critical to the formation of these ecosystems. Whilst some threshold values exist; e.g. > 1200 mm annual precipitation, > 160 wet days each year, mean annual temperature of < 15 °C for the warmest month, and an excess of 200 mm precipitation over evapotranspiration for the month of April – September (Lindsay *et al.*, 1988; Moore, 1993; Wheeler & Shaw, 1995); there is likely to be significant variation. For example, blanket bog in Wick, Caithness receives ~ 800 mm rainfall each year (Met Office, 2015).

Blanket peat covers 22,500 km^2 of the UK (nearly 8 %) to an average depth of 2 m (Tallis, 1998), reaching 4 – 5 m or more on extensive plateaux (Charman, 2002; Ratcliffe, 1964). Blanket bog is mostly found in the north and west where conditions are wettest and coolest. Scotland contains most of this resource in the UK (Carey *et al.*, 2008). Moving easterly and southerly raises the altitudinal limit from sea level in the Shetlands (Evans & Warburton, 2011), 180 m in Northern Ireland (Cruickshank *et al.*, 1993), 250 m in Wales (Yeo, 1997), and 350 m or more in the southern Pennines (Anderson & Tallis, 1981; Anderson & Yalden, 1981b; Evans & Warburton, 2007).

Blanket peat formation in the UK is likely to be the result of a combination of natural and anthropogenic factors. The uplands have been subjected to thousands of years of human influence, and as such are cultural landscapes influenced by grazing, cutting and burning (Dodgshon & Olsson, 2006; Ratcliffe & Thompson, 1988; Webb, 1986). Much of the uplands would have been forested prior to human intervention some 5,000 – 6,000 years ago (Simmons, 2002, 2003; Tipping *et al.*, 2003), with the only open areas limited to above the climatic tree line, or on very shallow or wet soils (Birks, 1988). When combined with a shift to a wetter climate causing waterlogging (Godwin, 1981), and a reduction in tree cover through wildfire (Robinson, 1983) and wild animal grazing (Simmons, 1975; Yalden, 1996), conditions for peat formation were created. In some instances, blanket bog could therefore be considered a plagioclimax ecosystem.

Blanket bog is defined by the Habitats Directive (EC, 2007) as: “Extensive bog communities or landscapes on flat or sloping ground with poor surface drainage, in oceanic climates with heavy rainfall, characteristic of western and northern Britain and Ireland. In spite of some lateral water flow, blanket bogs are mostly ombrotrophic. They often cover extensive areas with local topographic features supporting distinct communities.” Its name arises from the way the peat drapes itself over the landscape, covering underlying features, resulting in smooth and undulating scenery. Where blanket peat cover is extensive, it may form part of a mire complex, including ombrotrophic and minerotrophic (fen) components (Doyle, 1990, 1997). Peat in these systems accumulates at a rate of 0.07 – 1.2 mm year^{-1} (Chambers, 1984; Tallis, 1995a).

1.2.2 Blanket bog ecology

Since peat forms in waterlogged conditions, the plant species and communities found on blanket bog are those which can tolerate persistently wet conditions. These conditions are beneficial to *Sphagnum* mosses, which dominate these areas (Boudreau & Rochefort, 1998; Buttler *et al.*, 1998; Campeau & Rochefort, 1996; Clymo & Reddaway, 1971; Grosvernier *et al.*, 1997b; Holden *et al.*, 2011; Komulainen *et al.*, 1999; Malmer *et al.*, 1994). Indeed, the blanket peats of northern England were formed from the remains of *Sphagnum affine* and *S. austinii* (previously grouped and termed *S. imbricatum*), with *Eriophorum* spp., dwarf shrubs and other graminoids all contributing variable amounts depending on the prevailing vegetation composition (Chambers *et al.*, 2007a; 2007b; Malmer *et al.*, 1994). Analysis of contemporary peat macrofossils indicates that the vegetation composition was similar to current blanket mire NVC (Rodwell, 1991) communities (Chambers *et al.*, 2007a; 2007b).

Providing a universal description of the vegetation of high-quality blanket bog can be difficult since there is considerable floristic variation across the UK (Ratcliffe, 1977), influenced by a range of factors, such as geographical features and altitude (Tallis, 1998). A consistent feature is the significant abundance of *Sphagnum*, encompassing a number of different NVC communities (M15, M17, M18, M19, etc. (Rodwell, 1991)) alongside sedges such as *Eriophorum* spp. and dwarf shrubs (Johnson & Dunham, 1963; Rawes & Heal, 1978). This indicates the peatland is active – i.e. peat-forming vegetation is growing and material is being transferred to the catotelm (Gunnarson *et al.*, 2008; Malmer *et al.*, 1994).

High quality, active blanket bog shows characteristic surface patterns, following a hummock-hollow structure (Boatman, 1983). This microtopographical gradient runs, from highest to lowest: hummock, high ridge, low ridge, hollow, and pool (Lindsay, 2010). Since intact blanket bogs are characterised by a high, stable water table (5 – 10 cm from the surface) (Holden *et al.*, 2006; 2011; Stewart & Lance, 1991; Wallage & Holden, 2011), these structural differences in height represent a hydrological gradient. Characteristic species occupy these differing niches (Lindsay, 1995b; Lindsay *et al.*, 1988; Ratcliffe & Walker, 1958), with some limited to particular surface structures (Tallis, 1998).

Pristine ombrotrophic bogs are nutrient poor, acidic ecosystems due to their dominance by *Sphagnum* and hydrological regime. The permanent waterlogging of the peat and chemical conditions created by *Sphagnum* drastically reduces rates of mineralisation and therefore nutrient availability (see Section 1.3.2 for details on *Sphagnum*). In ombrotrophic systems all inorganic inputs are from precipitation and air-borne sources (Proctor, 2006). Hence, the composition of bog water is similar to the average composition of rainwater, but is concentrated and modified due to evaporation and ion exchange (Proctor, 1992, 2003, 2006). There is some seasonal variation due to temperature, a direct influence upon evaporation and biological activity (Proctor, 2003). *Sphagnum* acts as an efficient ion exchanger, binding cations and releasing H^+ ions (Anschutz & Gessner, 1954; Ramaut, 1954; Williams & Thompson, 1936). This, along with the release of organic acids from the vegetation (Clymo, 1984; Proctor & Maltby, 1998), leads to an acidic environment with pH < 5, with Cl^- and SO_4^{2-} as the main anions (Wheeler & Proctor, 2000). Plant growth is often limited by phosphorus or nitrogen, or a combination of the two, dependent upon local rates of N deposition (Beltman *et al.*, 1996; Hayati & Proctor, 1991; Proctor, 2006). Due to their development under such stringent conditions, blanket bog hydrology, soils and ecology are very sensitive to small changes in their local environment (Holden *et al.*, 2007b).

1.2.3 Significance of blanket bog

Blanket bogs are relatively common in Britain but are rare within the global context (Tallis, 1995a), with the UK containing perhaps 13 % of the resource worldwide (Tallis, 1998). The total extent of blanket bog worldwide is thought to be 100,000 – 150,000 km^2 (Lindsay *et al.*, 1988; Stroud *et al.*, 1987), with the UK as the largest single contributor (Tallis, 1998), hence they are of international importance (Lindsay, 1993, 1995a; b). They provide the largest extent of unfragmented habitats in the UK, supporting nationally important species such as cloudberry *Rubus chamaemorus*, mountain hare *Lepus timidus*, golden plover *Pluvialis* apricaria, black grouse *Tetrao tetrix*, and hen harrier *Circus cyaneus* (Pearce-Higgins *et al.*, 2009; Stroud *et al.*, 1987; Van der Wal *et al.*, 2011; Yalden, 2009).

Blanket bogs and the uplands have provided humans with a range of benefits throughout history, including seasonal hunting of wild animals during Neolithic times, grazing of livestock and extraction of peat for fuel up until the 16th century (Van der Wal *et al.*, 2011). Over the last century or so, there has been a gradual shift in attitude towards the uplands, and blanket bogs in particular, from barren wasteland and quagmire, to increasing recognition of the beneficial ecosystem services these areas provide for humans (Parkyn *et al.*, 1997).

Perhaps the two most important ecosystem services provided by blanket bog are those relating to carbon and water. These include the provision of high quality drinking water and buffering of storm events, reducing flooding downstream; the uptake and storage of carbon on geological timescales (2010; Bonn *et al.*, 2009); and the regulation of global levels of atmospheric gases (Clymo, 1998; Moore *et al.*, 1998). Their continued provision relies upon the functional state of the bog, featuring an acrotelm layer with a stable water table and abundant *Sphagnum* (Rydin & Jeglum, 2013).

Northern peatlands hold about 450 Gt carbon, around 25 % of total global soil carbon (Gorham, 1991; Moore, 2002), representing around 25 % of all atmospheric carbon in CO_2 (Schlesinger, 1991). Active, peat-forming ecosystems are a net sink of carbon dioxide (Gorham, 1991) and a source of methane, a potent greenhouse gas (Huttunen *et al.*, 2003). Hence, peatlands play an important role in global carbon cycling and concentrations of atmospheric gases (Gorham, 1991; Yu *et al.*, 2010; 2013).

The majority of the UK's drinking water (68 %) comes from surface water sources (DWI, 2008; DWQR, 2008), with most of that from the uplands. For example, the Peak District National Park contains 55 reservoirs supplying surrounding towns and cities. Abstraction licenses total more than 450 billion litres of raw water per year from these catchments (Bonn *et al.*, 2010). High rainfall in the uplands due to orographic enhancement (Malby *et al.*, 2007), together with a peat-covered catchment makes these areas well suited to the provision of drinking water (Evans *et al.*, 1999; Holden & Burt, 2003a; b). In intact condition, deep peat soils and the vegetation communities they support are effective at retaining a proportion of pollutants deposited in these upland areas (Currey *et al.*, 2011), a priority under the EU Water Framework Directive (Van der Wal *et al.*, 2011).

Some ecosystem services are less tangible and more difficult to quantify, such as cultural heritage, human well-being and the provision of leisure activities (Natural England, 2009; SNH, 2008). Tourism and recreation generates substantial income. For example, the Peak District National Park receives 22 million visitors per year, spending £185 million and providing 3,400 jobs (Peak District National Park Visitor Survey, 1998). Van der Wal *et al*. (2011) gives a summary of the ecosystem services provided by blanket bogs and the uplands, and Bonn *et al*. (2010) provides an extensive analysis relevant to the Peak District.

1.3 *Sphagnum* ecology

1.3.1 Species distribution

The keystone species of bogs is *Sphagnum*, a genus of between 150 and 200 species (Isoviita, 1966), including around 100 well-known species of North America and Eurasia, and another 10 – 15 in similar climates of the southern hemisphere (Rydin & Jeglum, 2013). The range of *Sphagnum* extends from the arctic to sub-Antarctic, and whilst most abundant at high latitudes of the northern hemisphere (Gore 1983) there is thought to be substantial diversity in the tropics (Shaw *et al.*, 2003). *Sphagnum*-dominated peatlands can be found in many other regions of the world, including Argentina, Chile, Madagascar, New Zealand, Tasmania (Daniels & Eddy, 1990).

Over the *Sphagnum*-formed, hummock-hollow undulations of the bog surface, there are distinct niches occupied by *Sphagnum* species, separated by vertical distance representing differences in hydrological conditions (Robroek *et al.*, 2007a). The highest parts are the furthest from the water table and therefore the driest, with the lowest areas often submerged. The distribution of *Sphagnum* species is governed by their competitive ability across these niches rather than optimum growing conditions. Species may be capable of growing in a wide range of conditions but can be restricted because of this competition; e.g. *S. papillosum* outcompeting *S. compactum* across much of its range, relegating it to very wet or very dry conditions (Lindsay, 2010). Competitive ability is the result of morphological and physiological constraints (Andrus *et al.*, 1983), with a balance between growth rate, the ability to transport water to the apical zone (capitulum), and the ability to minimise evaporative water loss (Rydin & McDonald, 1985a; b; Rydin *et al.*, 1999; Titus & Wagner, 1984). Environmental factors, such as nutrient and light availability, are also involved (Hayward & Clymo, 1983; Rydin *et al.*, 1999), alongside intraspecific competition for space, light and water (Robroek *et al.*, 2007a). The 34 species found in the UK are separated into six taxonomic sections, with well-defined common niches of growth (Table 1).

Table 1 – Taxonomy of UK *Sphagnum* species (Atherton *et al.*, 2010).

Section	*Sphagnum species*	*Niche*
Acutifolia	*S. capillifolium, S. fimbriatum, S. fuscum, S. girgensohnii, S. molle, S. quinquefarium, S. russowii, S. skyense, S. subnitens, S. warnstorfii*	Hummocks, carpets
Cuspidata	*S. angustifolium, S. balticum, S. cuspidatum, S. fallax, S. flexuosum, S. lindbergii, S. majus, S. pulchrum, S. riparium, S. tenellum*	Aquatic, carpets
Sphagnum	*S. affine, S. austinii, S. magellanicum, S. palustre, S. papillosum*	Low hummocks, carpets
Squarrosa	*S. squarrosum, S. teres*	Flushes
Subsecunda	*S. contortum, S. denticulatum, S. inundatum, S. platyphyllum, S. subsecundum*	Flushes, carpets
Rigida	*S. compactum, S. strictum*	Carpets, hummocks

Sphagnum is classified as a xerophytic hydrophyte – water-loving with adaptations for periodic drought conditions. Its growth requires a consistent supply of water to the capitula, the ability of which varies between species and is thought to be the most important factor in determining their occurrence along hydrological gradients (Andrus, 1986). This is due to varying capabilities of water holding capacity and capillary water transport (Andrus *et al.*, 1983). Hummock species have greater ability in these two key features (Hayward & Clymo, 1982; Ingram, 1983; Luken, 1985; Titus & Wagner, 1984), compared with hollow species, which are usually restricted to zones closer to the water table (Robroek *et al.*, 2007c).

However, hollow species have a higher growth rate than hummock species (Andrus, 1986; Gunnarsson, 2005) and so under favourable hydrological conditions can expand their range beyond their regular habitat (Robroek *et al.*, 2007c). Conversely, hollow species are severely affected by water limitation with some unable to survive drought (Boatman, 1977; Hulme, 1986). Despite this, *Sphagnum* appears able to regenerate from considerable beneath the bog surface (> 30 cm), even from plant material which appears brown and dead (Clymo & Duckett, 1986). Hummock species have a slower growth rate, but a high tolerance to drought and potential to recover subsequently (Clymo, 1973; Titus & Wagner, 1984). However, these relationships can be complex. *S. denticulatum* was shown to survive desiccation well, whilst hummock species such as *S. capillifolium* survived poorly, and with *S. papillosum* shown to be the most sensitive (Clymo & Hayward, 1982). Irrespective of their ecological niche, the greatest productivity of all *Sphagnum* species is found in conditions of high water availability (Clymo & Reddaway, 1971, 1974).

1.3.2 *Sphagnum* properties

Sphagnum forms a large part of many peat deposits (Clymo, 1970) thanks to their biomass production and slow rate of decay (Clymo & Hayward, 1982; Limpens & Berendse, 2003; Moore, 2002; Rydin *et al.*, 1999). The hydrological and hydrochemical conditions of the bog are regulated by *Sphagnum* (Clymo & Hayward, 1982; Rydin *et al.*, 1999; Van der Schaaf, 2002), maintaining conditions which reduce decomposition and favour carbon sequestration (Berendse *et al.*, 2001; Van Breemen, 1995a). *Sphagnum* acidifies its environment through ion exchange, selectively taking up cations (Ca^{2+}, K^{+}, Mg^{2+}) and replacing them with H^{+} ions (Andrus, 1986; Anschutz & Gessner, 1954; Ramaut, 1954; Williams & Thompson, 1936). The maximum ecological amplitude for several *Sphagnum* species was found to be pH 4 – 5, with no significant presence below pH 3.5 (Andrus, 1986; Andrus *et al.*, 1983). Higher pH (up to 7.5) in itself is not detrimental to the growth of *Sphagnum*, however, this increase in pH is often accompanied by an increase in Ca^{2+} which can lead to reduced growth in some species (Clymo & Hayward, 1982).

Mineralisation is further limited by the production of compounds by *Sphagnum* (Verhoeven & Liefveld, 1997). For example, the genus-specific p-hydroxy-β-carboxymethyl-cinnamic acid, and polysaccharide sphagnan greatly reduce the decay of *Sphagnum* and neighbouring plants (Bartsch & Moore, 1985; Børsheim *et al.*, 2001; Clymo & Hayward, 1982; Painter, 1991; Verhoeven & Toth, 1995). This acidic, waterlogged and hostile environment produces extremely slow rates of decay and a net increase in accumulated plant material, and therefore, carbon. *Sphagnum* species sequester more carbon in temperate and northern ecosystems than any other group of plants (Berendse *et al.*, 2001; Van Breemen, 1995a).

1.4 Drivers of blanket bog degradation

1.4.1 Overview

Blanket bogs are viewed as sensitive ecosystems which can be destabilised by a change in number of factors (Tallis, 1998), the majority of which are the result of human activities, whether direct or indirect. These communities have developed over thousands of years, and on similar timescales are able to adapt to changes in prevailing conditions (Lindsay, 2010). However, the rapid changes in conditions brought about by man are potentially beyond the capacity of these ecosystems to adapt (Holden *et al.*, 2007b). These changes and activities can be obvious: e.g. the burning of vegetation to promote particular species, or the removal of peat for fuel. However, others can be more indirect: e.g. the emission of pollutants from industry, or an increase in greenhouse gases and shifts in climate. The extent of UK blanket bog is estimated to have declined by 44 % (from 0.3 % to < 0.2 % absolute aerial cover) between the 1940s and 1980s (Van der Wal *et al.*, 2011), with 3,500 km^2 classified as degraded (Tallis, 1998).

Prior to the Industrial Revolution, erosion features were present on blanket bogs (Tallis, 1997a), however, these did not extend to the landscape-scale devastation seen in the upland areas of northern England. Current erosion patterns are the result of combined natural and anthropogenic factors over the last 1,000 years (Tallis, 1987), resulting in the most degraded blanket bogs in the country (Tallis, 1985b). Widespread erosion and loss of vegetation cover with consequent increased degradation appears to coincide with the onset of the Industrial Revolution, particularly in the southern Pennines (Tallis, 1964, 1987). Many areas of the southern Pennines were, and remain to be, in unfavourable condition (JNCC, 2009), due to large areas of eroding bare peat, species-poor vegetation communities and the widespread absence of *Sphagnum*. Stratigraphic analysis shows *Sphagnum* formed a substantial component of the vegetation and was present as recently as 250 years ago (Conlan, 1991; Conway, 1954; Montgomery & Shimwell, 1985; Tallis, 1964).

The region has suffered from a legacy of intensive grazing, atmospheric pollution deposition and a series of wildfires (McMorrow *et al.*, 2009). This has led to large-scale degradation with extensive bare peat areas, widespread gully erosion covering up to 34 % of plateaux (Evans & Lindsay, 2010), increased soil acidity (pH between 2.9 and 3.5), severely elevated heavy metal concentrations (Rothwell *et al.*, 2005b) and very low water tables (> 300 mm below surface in eroded areas (Allott *et al.*, 2009)). Areas unaffected by erosion with continuous vegetation are characterised by high cover of cotton grasses and heather (NVC M19 and M20 (Rodwell, 1991)). The species-poor community *Eriophorum angustifolium* blanket bog (M20) (Crowe *et al.*, 2008), and the *E. angustifolium* sub-community (M20a) are distinguished where some species have declined due to aerial pollution (Ferguson *et al.*, 1978) and land management (Phillips *et al.*, 1981), namely *Sphagnum* and associated species. The loss of *Sphagnum* has been attributed to the successive and combined effects of fire and atmospheric pollution (Tallis, 1964). Figure 1 shows a typically degraded blanket bog landscape in the southern Pennine region, displaying degraded features outlined here.

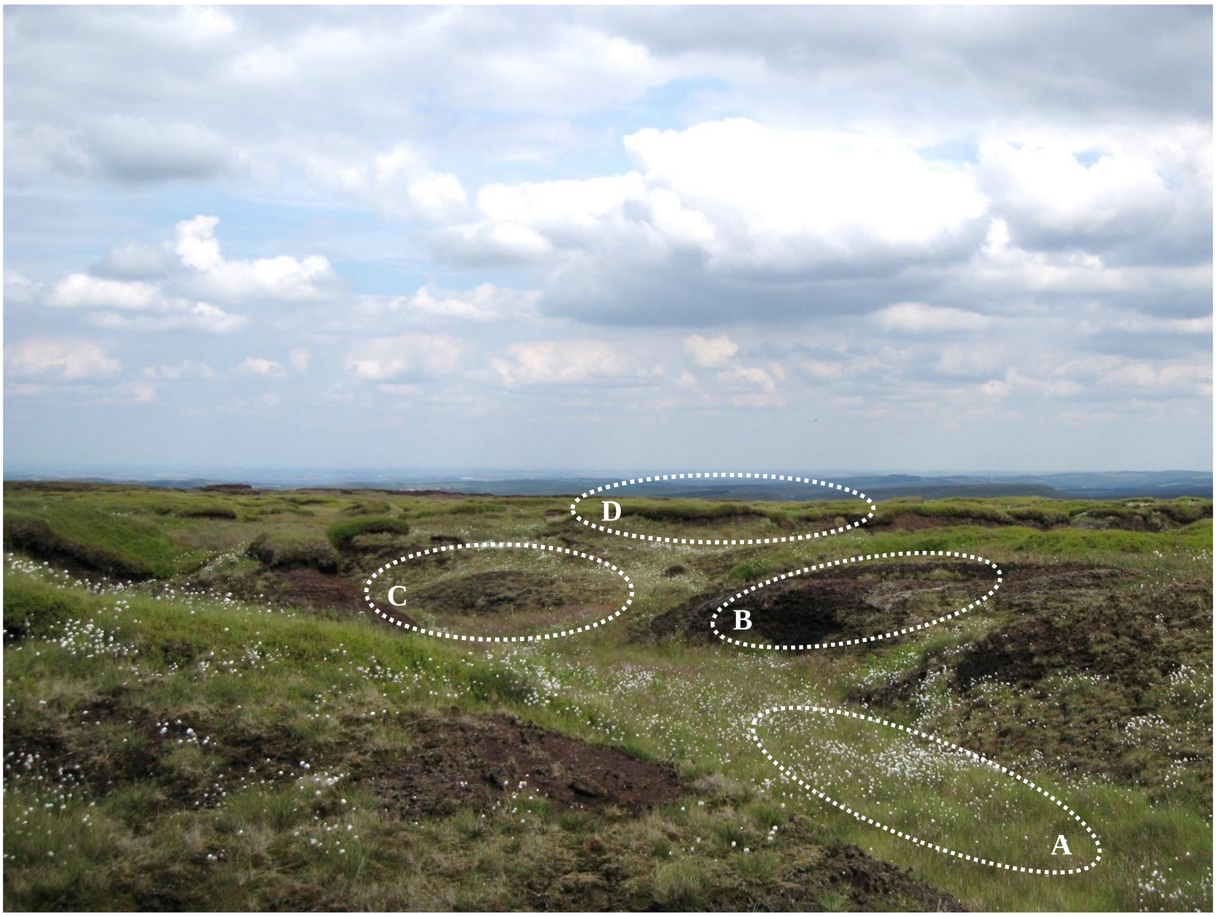


Figure 1 – Typically degraded blanket bog, displaying a number of highlighted features. A: naturally revegetated gully containing grasses and sedges; B: bare peat dune with some heather brash applied; C: early revegetation of bare peat dune, with nurse grasses; and D: vegetated hag dominated by bilberry and crowberry. See Section 1.5 for details on natural and managed revegetation.

Sphagnum was not entirely eradicated from the region, with small patches managing to survive in sheltered pockets and flushes (Conlan, 1991; Conway, 1949; Johnson *et al.*, 1990; Montgomery & Shimwell, 1985), where deposition of atmospheric sulphur and nitrogen was only 60 – 70 % of that on the exposed plateaux (Conlan, 1991). Minerotrophic conditions helped to counter the effects of sulphur deposition (Baxter *et al.*, 1989), and as a result, minerotrophic species were the most common (Tallis, 1964), with occasional ombrotrophic species (Studholme, 1989).

1.4.2 Physical erosion

Blanket bog erosion is considered by some to be a natural process (Tallis, 1985a; b), but one which can be triggered or exacerbated by anthropogenic factors (Lindsay, 2010). Climate, geology and landform have all been identified as significant natural drivers of this erosion through the action of water (Bower, 1960, 1961, 1962). Blanket peat is considered to be inherently unstable (Tallis, 1987) due to the high water content of the peat, typically > 90 % in active ombrotrophic systems (Proctor, 2006).

Whilst climate has a key role in blanket bog formation, it is also a factor in its erosion and degradation. The southern Pennines have been subjected to both wetter and drier periods over the last 2,800 years (Tallis, 1994, 1997a). During wetter periods, rapid *Sphagnum* growth can produce structurally-unstable peat (Tallis, 1985b), whilst drier periods cause shrinking and cracking of the peat which can affect hydrological regimes. Lowered water tables will cause a shift in species composition from *Sphagnum* dominance to *Empetrum nigrum* and *Racomitrium lanuginosum* (Tallis, 1985b, 1987, 1994, 1995b, 1997a).

Any substantial disruption in vegetation cover allows water to flow in what quickly become differentiated drainage channels (Tallis, 1987), leading to more widespread erosion of the system (Lindsay, 2010). Water will always follow the route of least resistance, hence once such channels have opened, they will tend to persist collecting more run-off and develop into gullies. Over time, gullies will incise deeper (~ 5.5 mm yr^{-1} (Anderson *et al.*, 1997; Tallis, 1997b)), lowering the water table of the surrounding peat (Holden, 2006). However, spontaneous revegetation can halt this (e.g. Crowe *et al.*, 2008; Lindsay & Freeman, 2008). Not all routes will form above ground. Pipes can develop within the peat mass as water flows through and off the catchment, and can be found in intact bog systems (Lindsay, 2010). These internal drainage systems can cause the collapse of the overlying peat (Johnson & Dunham, 1963; Pearsall, 1950).

Areas of exposed bare peat will be susceptible to erosion through freeze-thaw action, desiccation and wind. Frost action loosens the upper most layer of peat (6 – 7 cm (Evans, 1989; Francis, 1990)) through repeated freeze-thaw cycles which is then removed by rain and wind (Francis, 1990; Tallis, 1998). During spring and summer, the peat surface is smoothed by desiccation and wind (Radley, 1962; Tallis & Yalden, 1983). In the southern Pennines, wind erosion could occur on more than 47 days per year (Evans, 1989), and may be a major cause of damage to the blanket peat in exposed conditions (Radley, 1962). Storms following periods of drought can cause the most significant loss of peat from eroding peatlands, with up to 20 mm being lost during a single storm (Hulme & Blyth, 1985). The loss of peat in this way can be so great, that the peatland as a whole becomes a net source of carbon (Evans *et al.*, 2006b).

Until recently, 74 % of blanket peat in the southern Pennines was actively eroding (Anderson & Tallis, 1981), with 8 % of peat bare and eroding at rates of up to 30 mm yr^{-1} (Tallis, 1997b). The incidence of erosion increases with altitude (Bower, 1961); > 90 % above 550 m is eroded (Anderson & Tallis, 1981) with the most severe found at the south-east limits of blanket bog extent (Tallis, 1997b; Taylor, 1983; Yeo, 1997). Heavily eroding catchments can remove an estimated 260 t km^{-2} yr^{-1} of suspended sediment (Evans *et al.*, 2006b), compared to < 1 t km^{-2} yr^{-1} in intact Scottish moorland (Hope *et al.*, 1997). This material is transported downstream leading to the infilling of reservoirs, and transporting and releasing pollutants deposited in the uplands (Rothwell *et al.*, 2005b; Shotbolt *et al.*, 2006). As a direct consequence of eroding catchments, reservoirs of the Peak District have seen reductions in water storage capacity of up to 75 % per century (Anderson *et al.*, 1997), with economic implications of reduced quality and quantity of drinking water (Labadz *et al.*, 1991; Pattinson *et al.*, 1994).

1.4.3 Pollution

Overview

The Industrial Revolution marked the onset of emission of atmospheric pollution on an unprecedented scale. The vast increase in both the amount and type of manufacturing released large amounts of a range of pollutants. Coal burning, smelting and other processes emitted large quantities of sulphur and metals into the atmosphere, which were then deposited locally and further afield. During the 19th and early 20th century, the effects of this pollution upon ecosystems would have been widespread (Caporn & Emmett, 2009). The decline of heavy industry in the UK resulted in reduced levels of sulphur and metal deposition, but an increase in levels of nitrogen, ozone and organic compounds associated with agriculture and transport, a problem encountered across most populated regions of the world (Bell & Treshow, 2002). Ecological effects arise due to the increased availability of biologically active compounds, disturbing biogeochemical cycles and balances in which ecosystems have developed over millennia. The blanket bogs of the southern Pennines offer an example; these are nutrient-poor ecosystems where plants tend to be slow growing and efficient at acquiring and retaining nutrients (Chapin, 1980). Deposition of nutrients such as nitrate (NO_3^-) and ammonium (NH_4^+) shifts the competitive balance of these communities, whilst pollutants such as sulphur and heavy metals have a direct toxic effect on species such as *Sphagnum* (Lee, 1998; Lee *et al.*, 1993). Eutrophication and acidification are the widespread current effects of pollution (RoTAP, 2012).

The southern Pennine blanket bogs are especially prone to atmospheric pollution. Sandwiched between numerous conurbations of northern England, these upland areas have been subjected to around 250 years of heavy pollution deposition. To the west lie Manchester and Lancashire, to the east is Yorkshire with its cities of Huddersfield and Sheffield, and to the south lie Stoke-on-Trent and Staffordshire. These towns and cities were sites of intense industrial activity some 200 – 250 years ago. However, where once there were factories and chimneys, there are now dense residential areas. A population of more than 16 million live within 40 miles of the Peak District (Dougill *et al.*, 2006), emitting a cohort of pollutants, including oxidised nitrogen (NO_x) from vehicle exhausts, reduced nitrogen (NH_y) from intensive agricultural, nitrogen and sulphur from electricity generation, and volatile organic compounds (VOCs) from industrial and combustion processes (Caporn & Emmett, 2009; Van der Wal *et al.,* 2011). Ozone (O_3) is generated by the photochemical reaction between NO_x and VOCs and is an important phytotoxic gaseous pollutant. Unlike products of nitrogen and sulphur, O_3 is of increasing concern, especially in the uplands due to the periods of prolonged high concentrations (Ashmore, 2005; NEGTAP, 2001).

Blanket bogs in the southern Pennines form at altitude where there are high levels of precipitation (Lindsay *et al.*, 1988). Pollution is deposited in this rainfall (wet deposition), hence these areas receive greater overall inputs, increased further by orographic cloud cover (Fowler *et al.*, 1988). Isolated areas with relatively clean rainwater therefore still receive a relatively high pollutant input. Many of the pollutants and their reaction products form aerosols, resulting in two harmful deposition mechanisms. These particles can be scavenged by water droplets in rain and clouds, or due to their life span of several days, can be transported over long distances (Fowler, 2002). Water droplets form around these aerosols, hence they contain higher concentrations of pollutants which are then deposited more easily due to their large size (Dore *et al.*, 2001). Upland regions are covered by cloud for a significant amount of time (25 % of the year in the north Pennines (Fowler, 2002)), hence there are implications for pollution deposition. Similarly, snow can act to concentrate atmospheric pollution, releasing large amounts during snowmelt (Woolgrove & Woodin, 1996).

The impact of pollution is very much dependent upon the features of the ecosystem on which it is deposited. Blanket bogs are particularly susceptible due to their vegetation communities, soil type and underlying geology. The main component of intact bog vegetation is *Sphagnum* mosses, however, like most other bryophytes, they lack the protection of a cuticle and so are vulnerable to deposition of phytotoxic metals and compounds (Lee, 1998; Press *et al.*, 1986). Mosses also lack a root system and so are very efficient scavengers of atmospheric and deposited nutrients. These are nutrient-poor ecosystems, with the flora reflecting a limitation of available N. This renders them prone to the effects of N deposition and subsequent eutrophication. Higher plants respond with increased growth often at the expense of other species, whilst N accumulates in bryophytes, causing damage to some species (Mitchell *et al.*, 2004; Pearce *et al.*, 2003). The wet acidic deposition of S and N is particularly detrimental due to the poor buffering capacity of organic soils. They contain little in the way of mineral content and are effectively isolated from the basal substrate by meters of peat. Weathering of this underlying mineral material is extremely slow and insufficient to replace base cations lost through acidification and leaching, and uptake and removal by fire and grazing.

The UK uplands are noted as being particularly sensitive to pollutant inputs (Hall *et al.*, 2004). Whilst individual pollutants can be harmful enough, their combined effects can be greater than the sum of their parts (Fangmeier *et al.*, 2002). Conversely, some beneficial synergistic effects of this mixed pollution have also been observed (e.g. Baxter *et al.*, 1991). The response of blanket bogs to such pollutant inputs includes shifts in plant community composition (RoTAP, 2012), changes in carbon and nutrient cycling (Chapman & Edwards, 1999; Evans *et al.*, 2006a; Fog, 1988; Pilkington *et al.*, 2005) and soil acidification (Holden *et al.*, 2007b).

Sulphur

The disappearance of *Sphagnum* coincided with the appearance of soot (i.e. small carbonaceous particles) in peat cores taken from the southern Pennines (Tallis, 1964, 1987). Increases in coal burning during the Industrial Revolution released huge quantities of sulphur dioxide. Between the 1880s and 1970s, there was a ten-fold increase in anthropogenic SO_2 emissions (Mylona, 1996). The southern Pennines received much greater levels of sulphur deposition than other areas of the country (Table 2), areas where *Sphagnum* did not suffer such extensive decreases. Oxidised and reactive sulphur is phytoxic (Lee, 1998), with bryophytes being particularly susceptible to SO_2, as both a gas and its solution products (Inglis & Hill, 1974; Türk & Wirth, 1975). Mosses lack a cuticle and most have leaves only one cell thick, resulting in almost direct and continual contact between their photosynthetic cells and atmospheric pollutants (Lee, 1998). The growth of ombrotrophic *Sphagnum* species is slowed by high sulphur deposition rates, however, the toxicity of SO_2 in solution is pH-dependent (Ferguson *et al.*, 1978). At low pH values, such as those found on blanket bog, the damage to photosynthetic rates is greater (Hill, 1971; Puckett *et al.*, 1973; Türk & Wirth, 1975). This is thought to be caused by the pH-dependent equilibrium of ionic species of SO_2 in solution, giving rise to bisulphite (HSO_3^-) and sulphate (SO_4^{2-}) which is subsequently deposited on the vegetation (Puckett *et al.*, 1973; Vas & Ingram, 1949).

Bisulphite is a potent phytotoxin, with effects on *Sphagnum* chlorophyll and photosynthesis observed at levels as low as 0.01 mM HSO_3^-, compared with no effect on either at 5 mM SO_4^{2-} (Ferguson *et al.*, 1978). Experimental application of dilute HSO_3^- onto a *Sphagnum*-dominated bog in Snowdonia, north Wales, resulted in the loss of *Sphagnum* cover within 12 months, with *Eriophorum* species surviving the treatment (Ferguson & Lee, 1979). During the late 1970s, analysis of Manchester rainwater found concentrations of up to 0.15 mM HSO_3^-, and up to 1.8 mM SO_4^{2-} (Ferguson *et al.*, 1978). Sulphur dioxide itself has been shown to be 30 times as toxic as SO_4^{2-} (Thomas, 1961), however, SO_4^{2-} does not appear to affect photosynthesis, even at levels of 50 mM, with no effect on *Sphagnum* chlorophyll up to at least 5 mM (Hill, 1974). Fumigation experiments found a reduction of moss species at 191 µg m^{-3} SO_2 (Bell, 1973), and *Sphagnum* growth affected at 131 µg m^{-3} SO_2 (Ferguson *et al.*, 1978). These values are well within range of observed concentration, with mean annual SO_2 levels in Manchester ~ 500 µg m^{-3} as late as the early 1950s (Lee, 1998). *Sphagnum* and associated species (e.g. *Andromeda polifolia* L. and

Drosera spp.) were all but lost from much of the southern Pennines (Lee, 1998), with *S. fallax* the only species found in any significant quantities across the region (Tallis, 1973), in part due to its ability to withstand relatively high levels of sulphur pollutants (Ferguson *et al.*, 1978). Some *Sphagnum* species in minerotrophic flushes were also able to survive due to their uptake of transition elements. These metals, namely iron, catalyse the oxidation of toxic HSO_3^- to less harmful SO_4^{2-} (Baxter *et al.*, 1989).

Table 2 – Total deposition of oxidised sulphur to blanket bogs over the period 1880 – 1991 (Mylona, 1993).

Location	*Deposition oxidised sulphur (kg S ha^{-1})*
Southern Pennines	6400
North Pennines	1580
Central Scottish Highlands	1000
North-western Scotland & Ireland	400

Nitrogen

The deposition of nitrogen arises from the conversion of inert atmospheric N_2 into reactive oxidised and reduced forms (NO_x and NH_y) through industrial process such as fertiliser production, agriculture and fossil fuel burning. An estimated 140 Tg of reactive N per year is released into the environment, with a 10-fold increase in N deposition rates over the last 40 years (Lee, 1998). Deposition over northern Europe ranges from 5 – 60 kg N ha^{-1} yr^{-1} (Wedin & Tilman, 1996), with rates of 40 kg N ha^{-1} yr^{-1} over large areas of the UK (NEGTAP, 2001). An increase of 60 % in anthropogenic N fixation and release by 2020 is projected, due to increasing fossil fuel and fertiliser use (Galloway *et al.*, 1995; Matthews, 1994).

The plant communities of blanket bogs have developed over thousands of years in low nutrient conditions, with nitrogen being limiting in most pristine examples. This renders them susceptible to the effects of N deposition through eutrophication (Bobbink *et al.*, 1992) bringing subsequent shifts in vegetation composition. Nitrogen can also have direct toxic effects, with gaseous ammonia (NH_3) being the most damaging form (RoTAP, 2012). Bryophytes are particularly susceptible to the effects of elevated N (Van der Wal *et al.*, 2011), exhibiting rapid increases in tissue N levels, reduced growth, cover and diversity (Carroll *et al.*, 1999; 2000; Edmondson *et al.*, 2013; Edmondson *et al.*, 2010; Pilkington *et al.*, 2007a).

The main effect of N deposition is eutrophication (Van der Wal *et al.*, 2011), with competitive species, such as graminoids, increasing in vigour and cover at the expense of slower growing, stress-tolerant species (Grime, 2002). This can lead to a shift in vegetation communities, from the nutrient-poor species typical of ombrotrophic bogs to that dominated by nutrient-loving species (Smart *et al.*, 2003), and the eventual loss of diversity (Borer *et al.*, 2014; Field *et al.*, 2014; Southon *et al.*, 2013). The addition of N can cause nutrient imbalances, such as phosphorus and potassium limitation (Goodman & Perkins, 1968a; b; Hayati & Proctor, 1991; Phoenix *et al.*, 2003), and is linked to the incidence of pest outbreaks, disease and late winter injury (Carroll *et al.*, 1999; Nordin *et al.*, 2009; Power *et al.*, 1998).

Nitrogen is rapidly taken up by the vegetation of blanket bogs, reflecting its limitation in pristine systems (Aerts *et al.*, 1992), with atmospheric N deposition correlated with tissue N concentration (Caporn, 1997; Lee, 1998; Pitcairn *et al.*, 1995; Woodin & Farmer, 1993). There is a gradual accumulation in plant tissues as N addition increases (Bobbink *et al.*, 1998; Lamers *et al.*, 2000). At higher levels of N deposition, uptake saturates (2005; Bragazza *et al.*, 2004) and phosphate becomes growth limiting (Clymo & Hayward, 1982). Bryophytes are particularly rapid in showing this shift in limitation at low levels of N deposition (Aerts *et al.*, 1992). Above 18 kg N ha^{-1} yr^{-1}, *Sphagnum* cannot retain any more deposited N and it is lost to deeper layers of the bog (Lamers *et al.*, 2000; Woodin & Lee, 1987b), becoming available to higher plants and allowing competitive species to encroach (Roelofs, 1986). Higher levels of N addition leads to reduced *Sphagnum* growth and increased higher plant cover (Berendse *et al.*, 2001; Gunnarsson & Rydin, 2000), with direct toxic effects shown at > 80 kg N ha^{-1} yr^{-1} (Lamers *et al.*, 2000; Limpens *et al.*, 2003a).

High levels of atmospheric NH_3 deposition have been shown to remove some species of *Sphagnum* entirely, whilst favouring nutrient-tolerant species, such as *S. fallax* (Sheppard *et al.*, 2009; Sheppard *et al.*, 2011; Twenhöven, 1992). In the southern Pennines, *S. fallax* is the most common *Sphagnum* species (Carroll *et al.*, 2009; Tallis, 1973), with a notable and widespread absence of ombrotrophic species. On the Bowland Fells, mainly north-east Lancashire and part of north Yorkshire, N deposition was 45 – 55 % of that in the southern Pennines (Mackay, 1993) and there is a good range and abundance of *Sphagnum* species present (Tallis, 1998). Levels of NO_3^- and NH_4^+ in samples of bog pool water and litter from the southern Pennines were found to be many times higher than that of a more intact region in Wales (Caporn *et al.*, 2014; Caporn *et al.*, 2006; Edmondson *et al.*, 2010).

Acidic deposition

Oxides of nitrogen (NO_x) and sulphur (SO_2) are transformed in the atmosphere to generate nitric (HNO_3) and sulphuric acid (H_2SO_4) which is deposited in precipitation (Caporn & Emmett, 2009). From the onset of the Industrial Revolution until recently, sulphur from fossil fuel combustion was the major contributor to acid rain. As such, some areas of the UK have been subjected to decades, if not centuries, of acid precipitation (Cohen & Rushton, 1925), with the southern Pennines having the largest accumulation of acid deposition of any region in Europe (Skeffington *et al.*, 1997). Acid deposition strips base cations from soils, lowering the pH and mobilising harmful ions, such as aluminium (NEGTAP, 2001). A threshold of pH 3.5 was suggested for negative effects on *Sphagnum* (Andrus, 1986). Blanket bog landscapes are particularly vulnerable to the effects of acid precipitation due to the high rainfall they receive and the peat which covers them. They are base-poor soils and effectively isolated from their underlying mineral material, making them unable to buffer the acidic inputs. Acidification and mobilisation of toxic metals can lead to decreased plant growth or shifts in species composition (Lee *et al.*, 1993), with soil organisms and microbial communities also being affected; e.g. slower decomposition of litter influencing nutrient cycling (Sanger *et al.*, 1994).

Heavy metals

The southern Pennines have been subjected to potentially toxic levels of metal deposition since the early 19th century (Evans & Jenkins, 2000; Shotbolt *et al.*, 2006; Tipping *et al.*, 2006; Tipping & Smith, 2000) emitted from the nearby industrial conurbations of Lancashire and Yorkshire. Localised inputs from mining and smelting have also contributed to the deposition of metals onto the blanket peat (Livett *et al.*, 1979). Blanket bogs bind pollutant metals by adsorption to organic matter (Tipping *et al.*, 2003) and, as such, they are known to persist in peat soils (Brookes, 1995; Rothwell *et al.*, 2005b). Very high concentrations of a range of metals can be found in these peats, particularly in uneroded areas (Caporn & Emmett, 2009; Linton *et al.*, 2007). Where peat is actively eroding, these metals can be released into aquatic systems (Rothwell *et al.*, 2007a; 2007b). Aluminium, cadmium, chromium, copper, lead, mercury, nickel and zinc are the most ecologically significant in terms of potential ecological damage (Tipping *et al.*, 2003).

In recent decades, emissions of heavy metals have changed, in both their quantity and source (EEA, 2012; Travnikov *et al.*, 2012). For example, lead has seen an average of 74 % reduction in modelled deposition from 1990 to 2010, thanks in part to the phasing out of leaded petrol, originally the source of 76 % emissions and now reduced to 11 % (Harmens *et al.*, 2013). Despite the vast reductions in deposition rates, areas of the southern Pennines are still known to exceed threshold values, beyond which potential toxic effects may occur (see Linton *et al.*, 2007).

The toxicity of metals within soil is correlated with the free ion fraction of the total soil metal pool (Lofts *et al.*, 2004; Sauvé *et al.*, 1998). Heavy metals are generally present in the form of stable complexes with organic matter. However, the strength with which metals bind to organic matter is inversely related to pH (Tipping *et al.*, 2003), hence metals can become remobilised by drought-induced acidification.

Periods of drought allow reduced sulphur stored in the peat to oxidise and produce sulphuric acid (e.g. Dillon *et al.*, 1997; Scott *et al.*, 1998). This increases the concentration of bioavailable metals to plants and soil organisms, thus increasing the toxicity of such polluted soils. The vast amounts of sulphur deposited in the southern Pennines (Mylona, 1993), and poor hydrological condition of many of its blanket bogs (Allott *et al.*, 2009) renders these areas susceptible to these episodes of increased toxicity. Periodic drought-induced acidification is also likely to be a feature of unpolluted peatlands in which marine-sourced sulphur is oxidised (Tipping *et al.*, 2003). However, given the intact hydrology and limited additional pollutant inputs, damage will be slight.

The toxic actions of heavy metal ions are caused by the inhibition of enzymes, which can lead to a range of effects in higher plants (e.g. Adema & Henzen, 1989; Das *et al.*, 1997; Mitchell & Fretz, 1977). In the longer term, this can lead to changes in species composition, as more acid- and metal-tolerant species gain an advantage (Grime, 2002; Stevens *et al.*, 2009). Bryophytes are more susceptible to atmospheric exposure, and subsequent accumulation of heavy metals, since they lack a protective cuticle. This makes them useful biomonitors of metal pollution (Clymo & Hayward, 1982; Harmens *et al.*, 2013).

1.4.4 Land management

Burning and wildfire

Controlled burning has been used as a management technique by hill farmers for centuries, as a means of improving grazing value of their land for livestock (Tallis, 1998). The rotational burning of heather (*Calluna vulgaris*) on sporting estates is more recent, dating back to the early and mid-1800s (Usher & Thompson, 1993). Stands of *Calluna* are burned on intervals of 8 – 25 year, depending on recovery (Lovat, 1911), to produce high densities of red grouse. Over the last 50 years, there has been an increase in the number of management burns (Anderson *et al.*, 1997; McMorrow *et al.*, 2009; Yallop *et al.*, 2006), however, there is increasing evidence to support a ban on burning on blanket bogs (Coulson *et al.*, 1992; Shaw *et al.*, 1996; Tucker, 2003; Usher & Thompson, 1993). It has been suggested that *Calluna* growing on blanket bog does not exhibit the same growth pattern as on drier heathland. Stems become buried by accumulated *Sphagnum* leading to continued new shoot growth, however, this will be limited to areas of intact hydrology (Holden *et al.*, 2007b). This process would render burning unnecessary as a means of *Calluna* rejuvenation (Mowforth & Sydes, 1989). Conversely, burning practices were thought to not be incompatible with *Sphagnum*, when combined with grazing exclusion (Rawes & Hobbs, 1979).

Charcoal is a recurrent feature in the peat profile of many sites (Robinson, 1987; Smith & Cloutman, 1988; Tallis & Livett, 1994) indicating that fire, both managed and wild, has been a consistent feature of blanket bogs throughout their history (Anderson, 1997a). More recently, wildfires are often the result of arson or carelessness, causing substantial environmental damage and economic loss in the uplands (Haskins, 2000; Lindley *et al.*, 2009; Maltby *et al.*, 1990; McMorrow *et al.*, 2009). In 2003, a fire on Bleaklow lasted a month and firefighting costs rose to around £1 million (Van der Wal *et al.*, 2011). Wildfires often burn longer and at a hotter temperature, which can lead to peat being damaged or even destroyed. In these instances, the regenerative potential is also affected as the seed bank, spores and basal buds of vascular plants are consumed. The effects of a fire are dependent upon the vegetation type, fire intensity and hydrology. Wet peat is an excellent insulator, protecting it from damage (Watson & Miller, 1976). However, given the eroded and degraded state of many blanket bogs of the southern Pennines, the impact of such wildfires has been severe. Particularly damaging fires affected the region in 1947, 1959, 1976, 1980, 1984 and 1989 – 1990 (Anderson, 1986; Anderson *et al.*, 1997; Tallis, 1981). Some of these areas remained unvegetated until recent restoration works began (Maltby *et al.*, 1990; Radley, 1965; Tallis, 1981).

Burning of blanket bog not only removes the vegetation but also causes a number of other changes in the surface layers of the peat. Nutrients from ash, increased pH and higher peat temperatures cause an increase in microbial activity (Fullen, 1983; Hobbs & Gimingham, 1987; Lindsay *et al.*, 1988; Stoneman & Brooks, 1997), leading to a reduction in the rate of peat accumulation (Kuhry, 1994). Peat nutrient levels are elevated for the first two years following burning, benefitting regeneration (Hansen, 1969). Other nutrients can be lost during and after the burn in smoke as particulate matter and volatilisation (Holden *et al.*, 2007b), and through leaching (Pilkington *et al.*, 2007b) which can affect subsequent vegetation growth for years to come (Kinako & Gimingham, 1980). The high heat of wildfires produces water-repellent compounds in the surface layers of the peat, forming an impermeable skin (Clymo, 1983; Lindsay *et al.*, 1988; Stoneman & Brooks, 1997). This increases the run-off and reduces the water-holding capacity of these areas (Robinson, 1985). Removal of the vegetation renders peat surfaces susceptible to wind and fluvial erosion, and increased freeze-thaw action (Holden *et al.,* 2007b; Imeson, 1971). The initiation of major periods of erosion have been attributed to historic wildfires or anthropogenic fires (Mackay & Tallis, 1996; Tallis, 1987). For example, Holme Moss, in the southern Pennines, suffered a catastrophic fire in the 1700s, leading to a huge bog-slide in 1777 (Tallis, 1987).

Grazing

Grazing is an important upland management practice and is thought to have been a factor in the original development of blanket bogs (Shaw *et al.*, 1996). Since the end of the Second World War, farming in the uplands has been supported by the UK government and European funding through a variety of schemes (Van der Wal *et al.*, 2011), promoting higher stocking levels and drainage of the landscape. The result of this was a four-fold increase in sheep numbers between the 1930s and 1970s, and subsequent damage to dwarf shrubs and bog vegetation structure (Anderson & Yalden, 1981a; Dallimer *et al.*, 2009; Dixon, 1984; Thompson *et al.*, 1995). The effects of grazing and trampling are well known (Hulme *et al.*, 2002; Lake *et al.*, 2001; Stevenson & Thompson, 1993; Welch & Scott, 1995), and are dependent upon stocking rates, species composition, site wetness and time of year. Over-grazing is thought to be a major cause of blanket bog degradation across the UK (Tallis *et al.*, 1997), and even at moderate stocking levels, vegetation community composition will be affected (Tallis, 1998), allowing tolerant species, such as graminoids, to become dominant (Gimingham, 1995). The Hill Grazing Management Model recommends < 0.4 sheep ha^{-1} to avoid damage to blanket bog vegetation (Tallis, 1998). Stocking levels in some areas of the southern Pennines were 2.5 sheep ha^{-1} as recently as the 1980s (Anderson & Radford, 1994), indicating the severity of damage occurring. Grazing-induced erosion is prevalent throughout the world (Evans, 1998), and in some upland areas of the UK, may be the main cause of soil degradation (Evans, 2005).

The vegetation communities of blanket peat are amongst the most susceptible to trampling (Shimwell, 1981), exposing bare peat and causing compaction, with effects lasting up to 7 years (Bayfield, 1979). Wet and *Sphagnum*-covered areas are particularly susceptible (Slater & Agnew, 1977), with severe damage to pool margins and subsequent loss of *Sphagnum*. However, sheep usually avoid the wettest areas affording them some protection (Rodwell, 1991). On the wettest of sites other factors, such as atmospheric pollution, may be more important drivers of degradation.

In the mid-1990s, a reduction in sheep numbers was advocated (Marrs & Welch, 1991; Thompson *et al.*, 1995) and realised through changes in agricultural policy and the introduction of Environmentally Sensitive Areas scheme (Holden *et al.*, 2007b). Improvements in vegetation could be seen following 10 years of grazing exclusion (Anderson *et al.*, 1997), with reduced trampling of benefit to *Sphagnum*.

Drainage

During the 1960s and 1970s, government subsidies encouraged the digging of drainage ditches across 1.5 million ha of blanket peat in upland Britain in an attempt to improve grazing and game production (Lindsay *et al.*, 1988). This process, known as gripping, did little to enhance productivity (Stewart & Lance, 1983) but did cause hydrological and ecological changes in blanket bogs, favouring dwarf shrub communities (Van der Wal *et al.*, 2011). These channels cause a lowering of the water table (Stewart & Lance, 1991) and increased export of carbon from the system in fluvial (Holden *et al.*, 2007b; Worrall *et al.*, 2003) and dissolved organic form (Worrall *et al.*, 2011). The altered hydrology causes a reduction in typical blanket bog vegetation communities, with the reduction of *Sphagnum*. This effect is exacerbated by the roots of dwarf shrubs, which act to further dry the peat through transpiration (Shepherd *et al.*, 2013). The drying of peat can lead to physical changes, such as drying and cracking, with consequences for the hydrology and ecology of affected areas (Holden & Burt, 2002a; b). However, it would appear that these effects are reversible in some instances, with more typical vegetation returning with increased water table height (Komulainen *et al.*, 1998).

1.4.5 Climate change

Due to increased anthropogenic emissions of greenhouse gases, changes in global temperature and climate are taking place and likely to continue (Houghton, 2004; IPCC, 2007). Climate models predict warming and changes in patterns of precipitation (Meehl *et al.*, 2007; Sweeney & Fealy, 2002). In the north and west of Britain, precipitation is expected to increase but with greater distinction between winter and summer (Burt *et al.*, 1998). This is thought to lead to an increase in the frequency and/ or severity of summer droughts, interspersed with intense storm events (Meehl *et al.*, 2007; Worrall *et al.*, 2006). On bare blanket peat, such periods of drought followed by intense rainfall can remove significant quantities of peat (Hulme & Blyth, 1985). In the northern Pennines, at least 80 % of total peat loss occurred in only 3 % of the time period (Crisp & Robson, 1979).

Temperatures in the uplands are expected to increase by 0.8 – 2 ^{o}C by 2050 (Tallis *et al.*, 1997). Higher summer temperatures may cause a range of effects in peatlands: e.g. accelerated mineralisation and cycling of nutrients by microbes; increased plant growth (Emmett *et al.*, 2004); acidification and release of phytotoxic metals (Tipping *et al.*, 2003); additional fire risk from greater fuel loads and increased visitor numbers (Albertson *et al.*, 2009). Increases in temperature and changes in precipitation are thought to alter species composition and distribution in peatlands, affecting their functioning (Bragazza, 2006; Dorrepaal *et al.*, 2003; Mauquoy *et al.*, 2002; Moore, 2002). The impact of such environmental changes may depend upon the species composition of the ecosystem (Robroek *et al.*, 2007b).

The Peak District and southern Pennines represent the south-east limit of modelled climatic envelope of blanket bog in the UK (Clark *et al.*, 2010a), making the region especially susceptible to the effects of climate change. The accumulation and maintenance of peat is controlled by the vegetation community, temperature, hydrology and peat chemistry (Holden *et al.*, 2007b). Given the atypical, species-poor plant communities of the southern Pennines, severely eroded state and legacy of pollution, changes in temperature and precipitation will have grave consequences for the blanket bogs of the region as functional ecosystems. This effect is not limited to the southern Pennines; under the most extreme climate models, peat formation and occurrence in the UK is expected to decline by up to 84 % (Clark *et al.*, 2010a; 2010b; Gallego-Sala *et al.*, 2010), indicating even intact, high quality bogs are at risk of degradation.

Stratigraphic records illustrate both the sensitivity and resilience of bog vegetation to climate change, documenting shifts in vegetation according to prevailing climatic conditions (Tallis, 1997a). *Sphagnum austinii* (previously *S. imbricatum* (Andrus, 1987)) was once abundant across the peatlands of northwest Europe but began to disappear during the late Holocene (Barber, 1981; Barber *et al.*, 2003; Dickson, 1973; Godwin & Conway, 1939; Green, 1968; Langdon & Barber, 2005; Mauquoy & Barber, 1999; Mauquoy *et al.*, 2002; Overbeck, 1975; Smith, 1985; Stoneman *et al.*, 1993; Van Geel & Middeldorp, 1988; Wimble, 1986). This has been linked to increased surface wetness at many sites (Barber, 1981; Mauquoy & Barber, 1999; Mauquoy *et al.*, 2002; Stoneman, 1993), typically occurring between AD 1030 and AD 1730 (Barber *et al.*, 2003; Mauquoy & Barber, 1999; Van Geel & Middeldorp, 1988). Peat profiles record a shift towards *S. magellanicum*, *S. papillosum*, section Cuspidata or section Acutifolia, sometimes occurring abruptly over only a few decades (Mauquoy & Barber, 1999; Van Geel & Middeldorp, 1988). Human disturbance may also have had a role to play (e.g. Pearsall, 1956; Piggot & Piggot, 1963) and may go some way to explain the abrupt changes at some sites. However, *S. affine* and *S. austinii* are known to be able to withstand such effects (e.g. Chapman & Rose, 1991; Lindsay *et al.*, 1988; Slater & Slater, 1978). The loss of these species from peatlands across northwest Europe indicates localised human influence was not the main cause, although may have accelerated their decline at some sites.

1.5 Blanket bog recovery and restoration

1.5.1 Environmental improvements

Pollution

A reduction in industrial activity, clean air legislation, alternative fuel sources and clean fuel technology has led to the reduction in emissions of a range of pollutants. The major controls on national emissions of sulphur and nitrogen have been a number of agreements under the UN Economic Commission for Europe Convention on Long Range Transboundary Air Pollution and the European Union National Emissions Ceiling Directive, that came into force in 1991 (Van der Wal *et al.*, 2011). The 1999 Gothenburg Protocol set emissions limits for 2010 for sulphur, oxidised nitrogen, volatile organic compounds and ammonia, and the 1998 Aarhus Protocol committed the UK to the reduction of heavy metal deposition to below 1990 levels (Holden *et al.*, 2007b).

The onset of the Industrial Revolution saw anthropogenic emission of SO_2 increase ten-fold between the 1880s and 1970s (Mylona, 1996), reducing by 87 % between 1970 and 2004 (Caporn & Emmett, 2009; Lee, 1998). From 1986 to 1997, emissions of sulphur fell by 57 %, matched by a reduction in deposition of 52 %. These figures do hide considerable variation, with more than 70 % reduction in the east

Midlands whilst the west coast showed little evidence of reduction (Beswick *et al.*, 2003). Despite the variability, deposition in most rural areas of the UK is now below critical loads (NEGTAP, 2001). Levels of sulphur in the southern Pennines, both gaseous and deposited, have fallen dramatically over the last 30 years (Figure 2 & Figure 3) to below critical levels established for the protection of vegetation (UKCLAG, 1996). However, elevated levels of sulphur can still be found in *Sphagnum* and bog water samples from polluted areas (Bottrell & Novak, 1997; Thompson & Bottrell, 1998), suggesting a legacy of pollution accumulation. However, the responses of organisms to such low levels of sulphur are difficult to predict or measure (Lee, 1998).

Acidic deposition has fallen by over 50 % in the last two decades, largely due to reductions in sulphur deposition (Van der Wal *et al.*, 2011). Atmospheric nitrogen is now a greater source of deposited acidity in the southern Pennines (Evans & Jenkins, 2000). Increases in pH and base cations are expected in response to the reduction in deposition, however, this is an extremely slow process in deep peat soils, with more mineral soils quicker to recover (Evans *et al.*, 2014; Evans & Jenkins, 2000; Morecroft *et al.*, 2009).

Between 1988 and 2008, emissions of nitrogen in the UK have also fallen, with both oxidised and reduced nitrogen falling by 50 % and 18 %, respectively. Despite this, total nitrogen deposition for the UK has only fallen by 13 % over the same period (RoTAP, 2012). This may be due to the complexity of chemical transformations of atmospheric pollutants, therefore cuts in emissions may not necessarily result in the expected reduction in atmospheric concentrations (Fowler *et al.*, 2005). Emissions of oxidised nitrogen (NO_x), produced by transport and energy generation, have fallen slower than those of sulphur (Figure 2). Improvements in combustion technology were the main cause of this reduction (Beswick *et al.*, 2003). Emissions of reduced nitrogen (NH_y) from agricultural sources are set to follow a modest decline (RoTAP, 2012). However, the southern Pennines lie close to sources of NO_x and NH_y, and rates of nitrogen deposition in the region have fallen little over the last 30 years (Figure 3). In the UK, over 50 % of bogs (of all types) exceeded the critical load for nitrogen deposition in 2006 – 2008, representing a slight increase from 1986 – 1988 (RoTAP, 2012).

Ozone (O_3) is another pollutant of current concern, causing reduced growth and productivity in plants (Ashmore, 2005). Concentrations of O_3 are increasing across nearly all populated regions of the world (Bell & Treshow, 2002; RoTAP, 2012), a trend not necessarily reflected in the southern Pennines (Figure 2). Rising levels of ozone are a particular concern for the uplands (Hayes *et al.*, 2006), however, interactions with other atmospheric gases means ecosystem effects are difficult to predict (e.g. Gedney *et al.*, 2006; Harmens *et al.*, 2007).

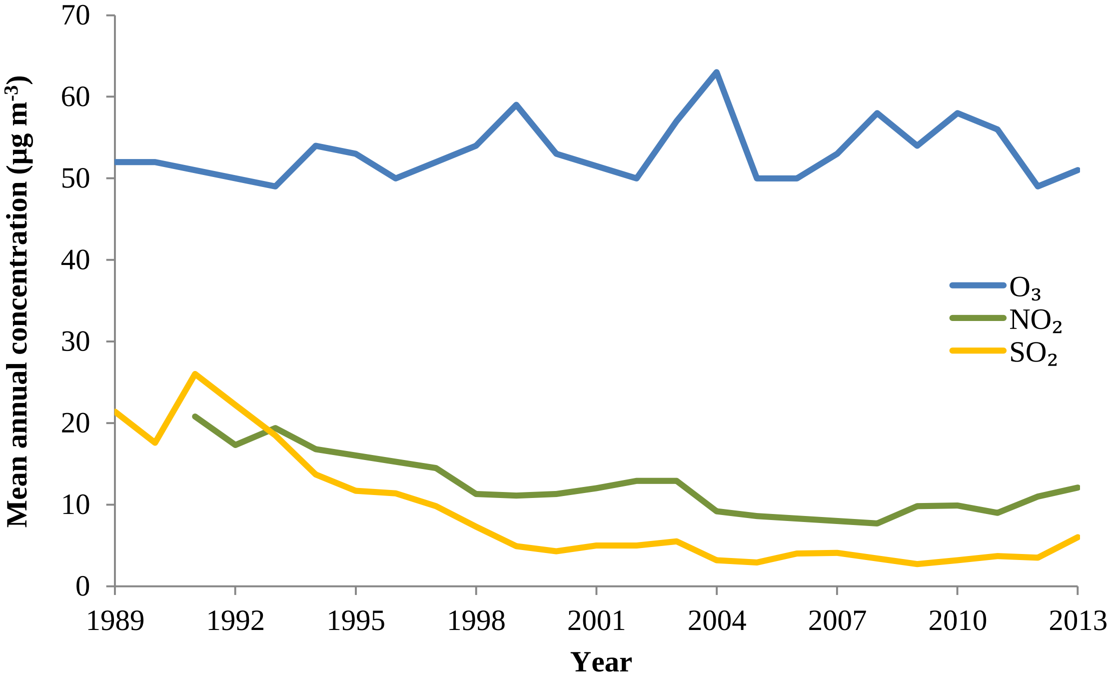


Figure 2 – Mean annual gaseous concentration (µg m^{-3}) of ozone (O_3), nitrogen dioxide (NO_2) and sulphur dioxide (SO_2), recorded at Ladybower monitoring station, Derbyshire (data from uk-air.defra.gov.uk).

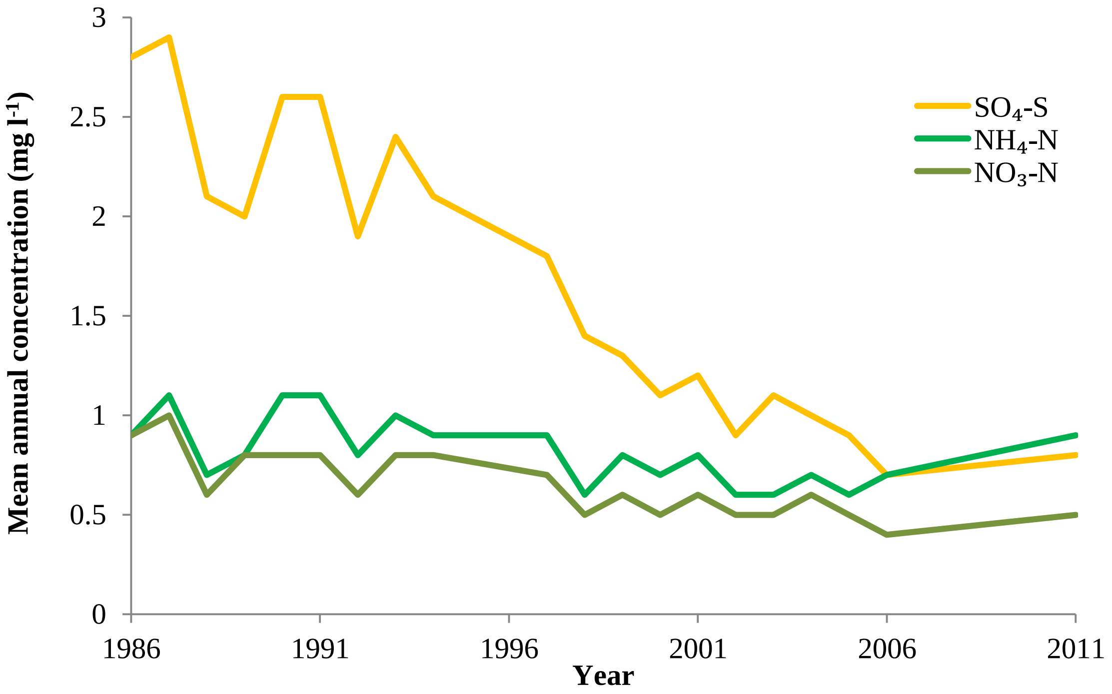


Figure 3 – Mean annual concentration (mg l^{-1}) wet deposition of nitrate (NO_3–N), ammonium (NH_4–N) and sulphate (SO_4–S), recorded at Wardlow monitoring station, Derbyshire (data from uk-air.defra.gov.uk).

Land management

Farming in the uplands operates at the margin of financial viability and is heavily reliant upon agricultural subsidies (Dougill *et al.*, 2006), thus subsidies provide an effective means of managing entire landscapes. A move away from production-based subsidies has resulted in reduced grazing in some upland regions (RSE, 2008) and land managers are rewarded for environmentally beneficial practices (Lowe *et al.*, 2002). Higher Level Stewardship (HLS) and Environmentally Sensitive Areas (ESAs) are examples of such agri-environment schemes. ESAs were introduced in 1986, allowing damaged areas to recover (Anderson *et al.*, 1997; Whitby, 1994). The Water Framework Directive is another legislative driver of environmental improvement in the uplands, prioritising water quality. However, over the short term it is difficult to assess the ecological benefit of such schemes (Whittingham, 2007), and the appropriate management required to maintain *Sphagnum*-rich bog vegetation is still far from clear (Tallis, 1998).

1.5.2 Natural recovery

Amid the devastated and eroding landscape of the southern Pennines, natural revegetation of bare peat surfaces occurs frequently (Clements, 2005; Crowe, 2007). *Eriophorum angustifolium* and *E. vaginatum* are important species in the regeneration of peatlands (Lavoie *et al.*, 2005a; Tuitilla *et al.*, 2000). *E. angustifolium* has a preference for wetter conditions whilst *E. vaginatum* has a greater tolerance for drier areas. *E. vaginatum* can produce favourable conditions for the colonisation of *Sphagnum* (Rochefort, 2000) through the provision of microclimate and nutrients (Chapin *et al.*, 1979), whilst forming peat itself. In the Peak District, revegetation of gullies has been shown to significantly reduce the amount of fluvial peat lost from an eroding catchment (Evans & Warburton, 2005), with vegetation increasing the surface roughness of these channels leading to deposition of material carried in suspension. From stratigraphic evidence, it appears pioneer species rapidly recolonise and stabilise the bare peat gully floor, providing a suitable microhabitat for less resilient species (Crowe, 2007). Successive gradual shifts in community composition of slower establishing species follow (Evans *et al.*, 2005), resulting in either *Sphagnum*-dominated communities (Lindsay & Freeman, 2008) or dry heath assemblages, depending on the prevailing hydrological conditions (Crowe *et al.*, 2008).

Improvements in air quality and land management have been beneficial for *Sphagnum* and other bryophytes, with increased abundance and diversity in the southern Pennines (Caporn *et al.*, 2006; Carroll *et al.*, 2009). Despite these improvements, cover and frequency of *Sphagnum* in the region is still lower than more northerly sites, such as the Forest of Bowland (Carroll *et al.*, 2009). Minerotrophic species are by far the most common (e.g. *S. fallax, S. fimbriatum, S. subnitens*), reflecting the nutrient-enriched conditions (Smith, 2004) and selection pressure exerted by pollution in the past (Crowe *et al.*, 2008). Recolonisation by *Sphagnum* is a slow process, and appears to be limited to cotton grass-dominated areas with high water tables (Caporn *et al.*, 2006) and gullies (Crowe *et al.*, 2008). The legacy of industrial pollution deposition has been suggested as a factor limiting *Sphagnum* recovery (Tallis, 1995b), along with a lack of propagules, disrupted hydrology and severity of degradation.

1.5.3 Managed revegetation of blanket bog

Despite observed incidences of spontaneous revegetation in the southern Pennines, landscape-scale regeneration of these bare peat areas is unlikely to occur naturally due to continued erosion, removing the viable seed bank and uprooting seedlings. Until such areas are stabilised, peat will continue to be lost, with reduced provision of ecosystem services from these upland areas. Restoration of blanket bog in this region has focused on revegetation of bare peat to limit further erosion and provide a baseline for further ecological improvements (Anderson *et al.*, 1997). International legislation such as the Kyoto agreement and EC Habitats Directive, has led to efforts to restore peatlands to active, functioning ecosystems (Gorham & Rochefort, 2003).

Since 2003, the Moors for the Future Partnership have carried out landscape-scale restoration works in the Peak District and southern Pennines, scaling up methods developed in the 1980s (Anderson *et al.*, 1997; Anderson *et al.*, 2011; Tallis & Yalden, 1983). Lime is applied to temporarily raise the pH of these very acidic peats to ~ pH 4, and fertiliser (N:P:K) is added to enhance the establishment of the subsequently applied grass seed. A suite of lowland amenity grass species (e.g. *Agrostis*, *Festuca* and *Lolium* spp.) are sown to act as a nurse crop, helping to bind the peat surface together and improve microclimatic conditions. Heather brash (harvested and chopped *Calluna vulgaris*) is applied, providing a physical covering to exposed peat whilst containing large quantities of heather seed and propagules of many other moorland species. The combined lime, fertiliser, grass seed and brash forms a superficial surface crust where the peat is held together by nurse crop roots and twigs of the heather brash. On steeper, more rapidly eroding slopes, geotextiles are used to physically restrain the peat, allowing seed to germinate, take root and stabilise the area. Grazing is excluded from treated areas since fertilised vegetation is known to be particularly attractive to sheep for some time after application (Lunt *et al.*, 2010). More typical moorland species, such as *Empetrum nigrum*, *Eriophorum angustifolium*, *E. vaginatum*, *Rubus chamaemorus* and *Vaccinium myrtillus*, are able to recolonise these stabilised areas, spreading by seed or vegetatively from remnant patches of intact vegetation. Where this process is slow due to poor surrounding diversity, plug plants are used. These are propagated from locally sourced individuals and produced on a large scale to meet the quantities required. The use of these species in bare peat restoration is well established, and they respond positively to additions of lime and fertiliser (Bridges, 1985; Caporn *et al.*, 2007; Richards *et al.*, 1995; Skeffington *et al.*, 1997; Sliva & Pfadenhauer, 1999). After about 5 years, the grass nurse crop is expected to die out (Anderson *et al.*, 1997) as the effects of lime and fertiliser dissipate and bog species increase their cover. Bog species are deeper rooting than the grass nurse crop and so help to more securely bind and anchor the peat.

The revegetation of bare peat is successful, with an average of 45 % vegetation cover 3 years after treatment, whilst control areas have remained bare (Anderson *et al.,* 2009). The establishment of grasses and *Calluna* reduce the loss of particulate organic carbon (POC) by up to an order of magnitude, however, levels of dissolved organic carbon (DOC) are not reduced by this new growth (Worrall *et al.*, 2010; 2011). Following application of restorative treatments, revegetated areas show increased activity and abundance of soil microbes, which can result in greater CO_2 emissions (Caporn *et al.*, 2007; Worrall *et al.*, 2011). Restoration is, however, an expensive process, due in part to the transportation and application of materials by helicopter. To treat an area of bare peat costs £11,000 ha^{-1} for capital works for a 3 year restoration project, plus additional associated management and monitoring costs (Moors for the Future, 2008). Over larger expanses of degraded bog, encompassing a range of degraded features, costs were £2,900 ha^{-1} (Van der Wal *et al.*, 2011).

Gully blocking was developed in the Peak District in the 1990s as a means of reducing erosion and improving the hydrology of degraded areas. Heather bales, plastic piling, stone and wood are used to construct dams which trap peat sediment which can then be colonised by plants, especially *E. angustifolium* (Anderson *et al.*, 2011; Burtt & Hawke, 2008; Evans *et al.*, 2005). Whilst the impact of gully blocking on sediment export can be clearly demonstrated, the hydrological effect is yet to be quantified (Shepherd *et al.*, 2013).

The recovery of active blanket bog vegetation is anticipated to take 15 – 20 years, conditional upon the re-establishment of bog hydrology, a functional acrotelm layer and the presence of *Sphagnum* (Chambers *et al.*, 2007b; Gunnarson *et al.*, 2008; Proctor, 2003; Van der Wal *et al.*, 2011). The ecological and hydrological restoration of degraded blanket peatlands has the potential to deliver a number of ecosystem services, such as the maintenance of carbon stores (Lindsay, 2010; Worrall *et al.*, 2009), reduced wildfire risks (McMorrow *et al.*, 2009) and enhanced biodiversity. Van Der Wal *et al*. (2011) provides a detailed summary of ecosystem services provided by areas of degraded blanket peat before, during and after restoration. However, it is thought in some cases irreversible changes in peat chemistry and hydrological properties may prevent active blanket bog from being established (Holden, 2005a; b; Holden *et al.*, 2004).

1.6 *Sphagnum* reintroduction

1.6.1 Reintroduction on raised bog

The recovery or reintroduction of *Sphagnum* is essential to return degraded ombrotrophic peatlands to an active, functional state (Rochefort, 2000; Van Breemen, 1995a). The majority of research on *Sphagnum* restoration has been conducted on lowland raised bogs following commercial exploitation for peat extraction, forestry plantation and agriculture. After the cessation of such activities, these areas are not readily recolonised by typical peatland vegetation (Lavoie *et al.*, 2003; 2005b; Money, 1995; Poulin *et al.*, 2005; Rowlands & Feehan, 2000; Salonen, 1992). The surface peat is modified to such an extent that it no longer represents a suitable substrate for *Sphagnum* and other bog species to recolonise (Groeneveld & Rochefort, 2005; Poschlod, 1990; Price, 1996; 1997; Tomassen, 2004; Van Seters & Price, 2001). Active intervention is required to re-establish a functioning peatland, capable of sequestering carbon, cycling nutrients and resisting species invasion within the timescale of decades (Gorham & Rochefort, 2003; Rochefort, 2001; Wheeler & Shaw, 1995).

Propagules of *Sphagnum* and associated vegetation are harvested, applied and covered by a protective mulch to reduce desiccation, whilst ditch blocking and surface reprofiling improve hydrological conditions (Blankenburg & Tonnis, 2004; Bugnon *et al.*, 1997; Price *et al.*, 2000; Rochefort *et al.*, 2003; Tuitilla *et al.*, 2003; Wheeler & Shaw, 1995). Bog vegetation from nearby intact areas is harvested to a depth of 10 cm, shredded and applied to the peat surface using agricultural machinery at a ratio of 1:15 donor to receptor surface area (Rochefort *et al.*, 2003). In Canadian post-vacuum mined peatlands, this was a required step as naturally dispersed propagules are too small or too few to enable regeneration (Rochefort, 2000). Straw mulch is then applied at 3000 kg ha^{-1}, improving the microclimate of the introduced propagules. Soil moisture and surface humidity are increased, whilst temperature extremes and evaporation are reduced (Chirino *et al.*, 2006; Price, 1997; Price *et al.*, 1998; Rochefort, 2000; Rochefort *et al.*, 2003). The final step is rewetting of the site by blocking drainage systems, improving the water level and humidity of the peat, both of which are beneficial to *Sphagnum* (Campeau & Rochefort, 1996; Campeau *et al.*, 2004; Grosvernier *et al.*, 1997a; Karofeld & Toom, 1999; Lindholm & Vasander, 1990; Rochefort *et al.*, 2002; Wheeler & Shaw, 1995). However, water levels must be carefully managed to avoid inundation which can be detrimental to *Sphagnum* establishment (Tuitilla *et al.*, 2003).

Vascular plants and other mosses can provide similarly beneficial microclimatic conditions, in particular *Eriophorum* spp. and *Polytrichum strictum*, whilst also stabilising the peat surface (Boudreau & Rochefort, 1999; Ferland & Rochefort, 1997; Groeneveld & Rochefort, 2005; Grosvernier *et al.*, 1995; Sliva, 1998). Addition of phosphorus improves the establishment and performance of such nurse species, accelerating the recolonisation process (Sliva & Pfadenhauer, 1999; Sottocornola *et al.*, 2007). *Sphagnum* species vary in their suitability for use in restoration. Those of the section Acutifolia are better able to colonise bare peat, with section Sphagnum performing poorly (Campeau & Rochefort, 1996; Chirino *et al.*, 2006; Rochefort & Bastien, 1998). Hummock-forming species are favoured, with a view to rapidly establishing an acrotelm (Sliva & Pfadenhauer, 1999). Once *Sphagnum* plant size and cover surpass a threshold, a positive feedback loop will be established where limitation by water availability and retention, substrate instability and humidity levels is continually reduced (Rochefort, 2000).

1.6.2 Reintroduction on blanket bog

There is a dearth of literature regarding the reintroduction of *Sphagnum* to blanket bog, with no recorded attempts at landscape-scale *Sphagnum* restoration. From within the upland community of land managers, owners and conservation organisations, it is evident that there have been many small-scale attempts at *Sphagnum* reintroduction, however, these are almost entirely on an *ad hoc* basis. As such, there is little in the way of any rigorous protocol or monitoring, and any reported results, however informal, are likely to be skewed in favour of successful trials. Common methods include the use of *Sphagnum* turves and the application of liquidised *Sphagnum*. Anecdotally, success varies considerably, but without accurate records of methods, environmental variables and long term monitoring, there is little chance of establishing which factors are of importance.

In 1979, Ferguson & Lee (1983a) transplanted *Sphagnum* cores from Cumbria to an area of blanket bog at Holme Moss, in the Peak District. The experiment was thought to have failed so was repeated in 1981, but this was believed to have suffered a similar fate. In the short term only *S. fallax* survived, but ~ 25 years later numerous transplanted bog species were found (Caporn *et al.*, 2006), indicating the potential for successful reintroduction of *Sphagnum*. Bayfield (1976) successfully grew moorland bryophytes from liquidised material, albeit not *Sphagnum* nor in the field.

In parts of the Peak District and southern Pennines, *Sphagnum* has been inadvertently reintroduced during the process of revegetating bare peat. Heather brash is harvested from a number of regional sites, some of which contain wet heath vegetation, including *Sphagnum*. Brash can provide a source of *Sphagnum* propagules, although the quantity of material and species contained is entirely dependent upon the donor site. Thus heather brash is an inconsistent source of *Sphagnum* and considered unsuitable for landscape-scale reintroduction.

1.7 Knowledge gaps

Degradation of the southern Pennine blanket bogs has occurred as the combined result of atmospheric pollution, poor land management and wildfire, with natural recovery slow due to the legacy of these. The restoration and/or recovery of *Sphagnum* is essential to return these peatlands to an active, peat-forming state. Given the slow rates of natural recolonisation, it is clear that active intervention is required to restore widespread *Sphagnum* cover within the timespan of several decades. The techniques developed and shown to be successful on lowland raised bogs may be relevant. However, translation to success in these highly degraded landscapes cannot be assumed. Raised bog restoration requires consistent and high water availability and the provision of a humid microclimate, whilst on blanket bog, peat stabilisation is essential. Restoration treatment is a lengthy and expensive process, with considerable timescales required to develop vegetation approaching that of high quality blanket bog communities. The potential for *Sphagnum* reintroduction to these previously bare areas has yet to be established. Additions of lime and fertiliser may prove incompatible with *Sphagnum* growth. Remaining areas of typical bog vegetation may therefore represent a more appropriate substrate for propagule introduction.

Contemporary analysis of peat and bog water shows the southern Pennine region still contains elevated levels of sulphur, nitrogen and heavy metals. Whilst current rates of atmospheric deposition have declined markedly and are now below toxic levels, there remains substantial pools of pollutants within the peat and vegetation. These remain a concern; drought-induced acidification can release acute flushes of toxic metals, whilst the effects of chronic exposure are poorly understood. Elevated levels of nitrogen and acidity, disrupted hydrology and harsh climate persist, make these degraded blanket peats immensely complex with frequent instances of interactions between these factors, both beneficial and detrimental. Whilst comparisons with bogs of better condition reveal these raised levels of pollutants (e.g. Caporn *et al.*, 2006; Carroll *et al.*, 2009), it is not known to what extent they currently affect *Sphagnum* growth and its subsequent recovery.

1.8 Research objectives

The southern Pennines provide the opportunity to pioneer restoration methods in some of the most degraded upland landscapes within the UK. With legislative drivers highlighting the ecosystem services provided by peatlands, it is likely that the methods trialled here will form the basis of restorative works to be carried out in other regions of the UK. Methods and understanding gained from this work may also be more broadly applicable to lowland raised bogs following exploitation. Thus, from the literature and conservation community it is apparent there is a need to fill those knowledge gaps identified in Section 1.7. The aims of this research are therefore:

1. *Evaluate the potential for Sphagnum reintroduction on degraded blanket bog*
2. *Elucidate those biogeochemical factors affecting the natural recovery and performance of Sphagnum*

Restorative works on blanket bog are carried out by a number of land owners and managers, such as utility companies and conservation agencies. Development of best practice guidelines for *Sphagnum* reintroduction will undoubtedly benefit these efforts, helping to improve efficiency and inform decision making, reducing the amount of trial-and-error experimentation. This work provides an examination of experimental *Sphagnum* reintroduction, within the existing framework of wider restoration measures, for the benefit of applied conservation. As such, best practice guidelines should be continually updated and amended in line with feedback from practitioners, making use of invaluable and often unrecorded expertise.

The success of *Sphagnum* is critical for the renewed formation of active blanket bog. It is imperative to understand those factors which influence the growth and performance of these species. This work identifies those biogeochemical variables which continue to exert influence upon *Sphagnum*. This understanding will provide the scientific basis to inform and direct conservation measures both in the southern Pennines and further afield.

Chapter 2 – Reintroduction of *Sphagnum* to degraded blanket bog

2.1 Introduction

Over the last 30 years, land managers and scientists in the Peak District and southern Pennines have been at the forefront of ecological restoration on blanket peat. Methods developed in the 1980s (Anderson *et al.*, 1997) have been modified and scaled up to successfully revegetate large swathes of previously bare and eroding peat (Anderson *et al.*, 2009). However, the revegetation of bare peat is only the first step in restoring active blanket bog vegetation. *Sphagnum* provides the form and function of blanket bogs, with its widespread dominance required to confer a suite of ecosystem services (Lindsay, 2010; Rydin & Jeglum, 2013). Improvements in land management and reduced levels of atmospheric pollution have seen an increase in bryophyte diversity and frequency (Caporn *et al.*, 2006), demonstrating that environmental conditions are no longer preventing the growth of *Sphagnum*. However, legacy effects of this pollution, such as metals, acidity and nitrogen, may still be influencing success (Caporn & Emmett, 2009). Recent surveys (e.g. Carroll *et al.*, 2009) and personal observation revealed there has been no widespread recolonisation of the bog surface, with *Sphagnum* seemingly limited to radial, vegetative expansion of existing patches. This makes the process of recolonisation extremely slow due to the low number and dispersed nature of these foci. The application of *Sphagnum* propagules has the potential to generate new growth, as demonstrated on degraded raised bog (Rochefort *et al.*, 2003; Sliva & Pfadenhauer, 1999). On blanket bog there are fewer published reports of successful *Sphagnum* application (e.g. Hinde, 2009). Transplanting *Sphagnum* into the bog surface of the southern Pennines 35 years ago initially met with only limited success (Ferguson & Lee, 1983a) but better results in the longer term (Caporn *et al.*, 2006)

Following commercial peat extraction, *Sphagnum* cover can be successfully restored to lowland raised bog (Gaudig *et al.*, 2014). However, the methods employed raise a number of questions regarding its applicability to degraded blanket peatlands, particularly in the southern Pennines. The process requires nearby areas of intact bog to act as donor sites from which *Sphagnum* can be harvested but such areas do not exist in the region. Material would need to be gathered from parts of the country which have not suffered the same level of degradation, such as Cumbria and north Wales, increasing operational costs whilst raising concerns of sustainability and biosecurity. Many sites with *Sphagnum*-dominated vegetation are designated Sites of Special Scientific Interest (SSSI) and protected from such activities, leading to potential over exploitation of other suitable donor sites. Transferring vegetation from one site to another may also inadvertently introduce pest species and pathogens; e.g. heather beetle (*Lochmaea suturalis*), bulgy eye (*Cryptosporidium baileyi*) (Baines *et al.*, 2014) and parasitic fungi (*Lyophyllum palustre*) (Limpens *et al.*, 2003b). Further to this, the harvesting, shredding and application of bog vegetation is a mechanised process, utilising heavy machinery, with surfaces prepared by levelling and creation of bunds to retain surface water. On drained, compacted peat surfaces following extraction and exploitation, this is less of a problem. However, blanket peat is generally much more inaccessible and unstable, where even light vehicles can cause significant damage (Shepherd *et al.*, 2013).

To address these challenges, an alternative source of *Sphagnum* was developed by Micropropagation Services (EM) Ltd. *BeadaMoss* (Micropropagation Services, 2015) is a gel pellet containing growing fragments of locally sourced *Sphagnum*. A small quantity is collected, identified and then propagated under sterile conditions to produce sufficient biomass, before being shredded, encapsulated and incubated. Exact details are not discussed for reasons of commercial sensitivity. *BeadaMoss* (subsequently referred to as *Sphagnum* beads) has a number of potentially beneficial features for its use in blanket peat restoration. The small initial sample eliminates any concerns of sustainability, whilst the local provenance may help to retain any adaptive traits. *Sphagnum* beads provide a convenient and quantifiable means of handling material of a known quantity, origin and species; issues likely to be critical in landscape scale reintroduction of *Sphagnum*.

2.2 Experimental aim

The potential for *Sphagnum* reintroduction has been indicated through both deliberate and accidental addition of propagules. However, unlike raised bog restoration, there has been little in the way of research to inform and direct such works on blanket bog. The development of best practice guidelines based on sound experimental design and scientific understanding is essential, hence the overall aim:

Evaluate the potential for Sphagnum reintroduction on degraded blanket bog

Such an aim is expansive and could cover a range of practical management considerations. Therefore, the scope will be limited to provide the fundamental knowledge required for successful *Sphagnum* reintroduction; namely, what source of *Sphagnum* and species to use, when and where to apply propagules, and which revegetation practices are compatible with reintroduction. A series of pilot studies, both in the field and under controlled conditions, were established to provide answers to these questions, broadly split into two categories: *Sphagnum* source trials and *Sphagnum* bead trials.

2.3 *Sphagnum* source trials

2.3.1 Rationale

Three potential sources of *Sphagnum* propagules were identified from literature, preliminary trials and field observations: heather brash, chopped *Sphagnum* (subsequently referred to as *Sphagnum* mulch) and *Sphagnum* beads. Whilst each method is known to be a viable source of *Sphagnum* growth (Hinde, 2009; Moors for the Future, unpublished data; Rochefort *et al.*, 2003), their comparative success and relevance to landscape scale restoration of degraded blanket bog is yet to be assessed.

Sphagnum beads contain multiple fragments of *Sphagnum*, each with the potential to develop into a new plant. The small size of these fragments will mean development into sizeable plants may be lengthy, although excellent results were observed over 18 weeks in glasshouse trials (pers. comm., N. Wright, Micropropagation Services Ltd.). *Sphagnum* mulch may therefore provide a better source of propagules, with larger initial fragment sizes helping to speed establishment of plants. Increased propagule size may also have implications for drought tolerance, with larger pieces better able to retain moisture and therefore resist drought. However, *Sphagnum* mulch is likely to be more difficult to apply, the contents will be determined by the donor site, and issue of sustainability and biosecurity remain. Heather brash has proven to be effectively a free source of *Sphagnum*, where propagules have been inadvertently harvested, applied and established during initial revegetation works. The *Sphagnum* content of this material is variable depending upon the donor site so this too offers little control in the way of species choice and application rates.

There is uncertainty surrounding the reintroduction of *Sphagnum* within the current framework of revegetation measures. The application of lime and fertiliser are thought to be detrimental to the growth of *Sphagnum* propagules (Hinde, 2009), a genus typically of acidic, nutrient-poor environments. Conversely, additions of phosphorus have been shown to improve *Sphagnum* establishment (Rochefort *et al.*, 2003). These chemical additions are required for the successful establishment of nurse vegetation and stabilisation of peat (Anderson *et al.*, 2009; Caporn *et al.*, 2007). Without prior stabilisation, any *Sphagnum* propagules applied are vulnerable to the effects of erosion and burial. The nurse vegetation may also afford other benefits, such as improved microclimate, helping to reduce desiccation of the *Sphagnum* added. However, other vegetation, such as *Calluna*, may lead to drying of the peat and development of drainage features (Holden, 2005c; Shepherd *et al.*, 2013). Establishing beneficial association between vegetation and successful *Sphagnum* growth will help to focus larger reintroduction works.

Research conducted on lowland raised mires provides clues to these issues, however, the harsh conditions of southern Pennine blanket peatlands means direct relevance cannot be assumed. Severe climatic conditions, disturbed hydrology, variable topography, and a legacy of industrial pollution confound individual challenges.

2.3.2 Objectives

Field and indoor trials were established to provide experimental evidence for the following aim:

Evaluate different sources of propagules for use in landscape-scale Sphagnum reintroduction to degraded blanket bog

A series of objectives were identified for the field trials:

- Compare *Sphagnum* establishment between *Sphagnum* beads, *Sphagnum* mulch, and heather brash
- Compare establishment of *Sphagnum* propagules on bare and revegetated substrates
- Establish associations between successful *Sphagnum* establishment/ growth and the surrounding vegetation

A concurrent indoor trial was also established to provide results over a much shorter timescale. *Sphagnum* growth is known to be very slow in the southern Pennines due to harsh climatic conditions, exacerbated by poor hydrological and biogeochemical environment (e.g. Carroll *et al.*, 2009). This trial was designed to complement the field trial, with the objectives of:

- Identify species present in *Sphagnum* mulch and heather brash
- Determine the impact of polluted substrate upon the growth of *Sphagnum*

2.3.3 Methods

Field trials

Trials were established in May 2010 on Holme Moss, a high level plateau (524 m above sea level) in the northern Peak District (SE 095040). The site has been extensively studied since the 1970s (e.g. Anderson *et al.*, 1997; Ferguson & Lee, 1983a; Tallis, 1997a), and is noted for the severity, variety and extent of degradation features present (Tallis, 1987). Bare peat, gullies and species-poor vegetation are widespread whilst *Sphagnum* is largely absent, thought to be the combined result of wildfire, over-grazing and atmospheric pollution. Holme Moss has a history of pioneering ecological restoration. Construction of a replacement radio transmitter in 1982 – 83 devastated 8 – 10 ha of blanket bog, providing the opportunity to develop methods of revegetation (Anderson, 1997b). It is these methods which have been modified, scaled up and employed since 2003, when Holme Moss was one of the first sites to be subjected to landscape-scale restoration measures. Much of the once bare peat has now been revegetated with a nurse crop of lowland amenity grasses and significant cover of *Calluna vulgaris*, *Eriophorum angustifolium* and *E. vaginatum*. Areas of continuous vegetation cover broadly fall into one of three types: dwarf shrub, cotton grass, and *Deschampsia*/ *Nardus* dominated, broadly approximating NVC communities M19 and M20a (Rodwell, 1991).

Trials consisted of three replicate blocks each on bare peat and treated surfaces (previously bare, now revegetated following treatment). Replicate blocks were located near one another to ensure the substrate was similar in each of the three, and were searched for *Sphagnum* before proceeding to ensure its absence. Blocks consisted of four treatment strips, dimensions 12.5 m × 2 m separated by 0.5 m gap between each strip (total block dimensions 12.5 m × 9.5 m). The four treatments were control, heather brash only (brash only), *Sphagnum* beads and heather brash (beads and brash), and *Sphagnum* mulch and heather brash (mulch and brash). *Sphagnum* beads were applied at a rate of 400 m^{-2}, with equal proportions of *S. fallax* and *S. palustre*, before being covered with brash. *Sphagnum* mulch was applied until the surface was covered (< 1 cm depth), before being covered with heather brash. Brash was spread in all cases to a depth of 1 cm until the surface was covered, and no additions were made to the control strip. Brash was added to each treatment to ensure the *Sphagnum* material applied was not removed by wind or rain, and to enhance microclimatic conditions for *Sphagnum* establishment (Price *et al.*, 1998).

The *Sphagnum* mulch was harvested from an unknown donor site in Cumbria and double chopped to produce the mulch (provided by Barker and Bland Ltd.), which appeared to contain *S. capillifolium* and *S. papillosum*. *Sphagnum* beads contained equal proportions of *S. fallax* and *S. palustre* and were provided by Micropropagation Services (EM) Ltd. Heather brash was provided by the Moors for the Future Partnership; standard material used in peat stabilisation works.

The experimental blocks were visited annually and established *Sphagnum* marked using small canes. Final plot monitoring and recording of *Sphagnum* took place in August 2013, 39 months after establishment. Treatment strips were searched intensively for all visible *Sphagnum* plants, and when found, a record of the species, size and associated vegetation was made. *Sphagnum* size was measured as the diameter of individual plants, or dimensions of simple polygons for clumps, allowing the area to be calculated. This method was used as it was very difficult to count individual plants or capitula, which may have originated from a single bead. A record of the vegetation associated with the *Sphagnum* was also made, using a 25 cm × 25 cm quadrat. Any additional features of the treatment strip or experimental block as a whole were also recorded. Trampling of the plots was minimised by surveying from the treatment strip edges.

Indoor trial

Twelve half-trays were filled with peat to a depth of 3 cm, six with commercial peat (horticultural *Sphagnum* peat: *Growmoor Irish moss peat*), and the other six with peat from an unvegetated area of Holme Moss. Triplicates of *Sphagnum* mulch and heather brash (same material used in field trials) were added separately to each of the two peat types, to a depth of 1 cm. The trays were randomly arranged in a 3 × 4 configuration and covered with clear plastic sheeting to maintain high levels of humidity. Trays were left to grow in an artificially lit room (150 µmol m^{-2} s^{-1}, 16 hour day length), mean temperature ~ 20 ^{o}C, and watered weekly with deionised water using a spray bottle. After 12 months, all species were identified and their percentage cover estimated.

Statistical analyses

Univariate statistical analyses were carried out in Minitab v.16 (Minitab Inc., 2010). Multivariate analyses were implemented in the R software environment (R Core Team, 2013), using RStudio (RStudio Team, 2013), lattice (Sarkar, 2008), MASS (Venables & Ripley, 2002), permute (Simpson, 2013) and vegan (Oksanen *et al*., 2013) packages.

2.3.4 Results and analysis

Field trials

No *Sphagnum* growth was recorded on the bare peat substrate for any of the treatments across all three replicate blocks. Consequently, it is excluded from further analysis. Similarly, no *Sphagnum* was found on control treatments (i.e. no brash, beads or mulch) on the vegetated substrate and so they have been omitted from the following results.

On the revegetated surface, the greatest total numbers of *Sphagnum* plants/ clumps were found where mulch and brash had been applied, with *S. capillifolium* being most common. *Sphagnum* beads and brash produced the next highest number of plants, predominantly *S. capillifolium* and *S. papillosum*. Brash only treatments produced a low number of *Sphagnum* plants, except for in a single replicate (rep. 3), where numbers were much higher. Table 3 provides full details of plant counts and species identification.

Table 3 – Identity and number of *Sphagnum* plants/ clumps across replicates of the three field treatments

Treatment	*Replicate*	*S. capillifolium*	*S. fallax*	*S. palustre*	*S. papillosum*	*Total*
Brash only	1	1				1
	2	3			1	4
	3	30	17		20	67
Beads and brash	1	15			6	21
	2	12	1	1	9	23
	3	12			11	23
Mulch and brash	1	285			165	450
	2	177	2		74	253
	3	283			86	369

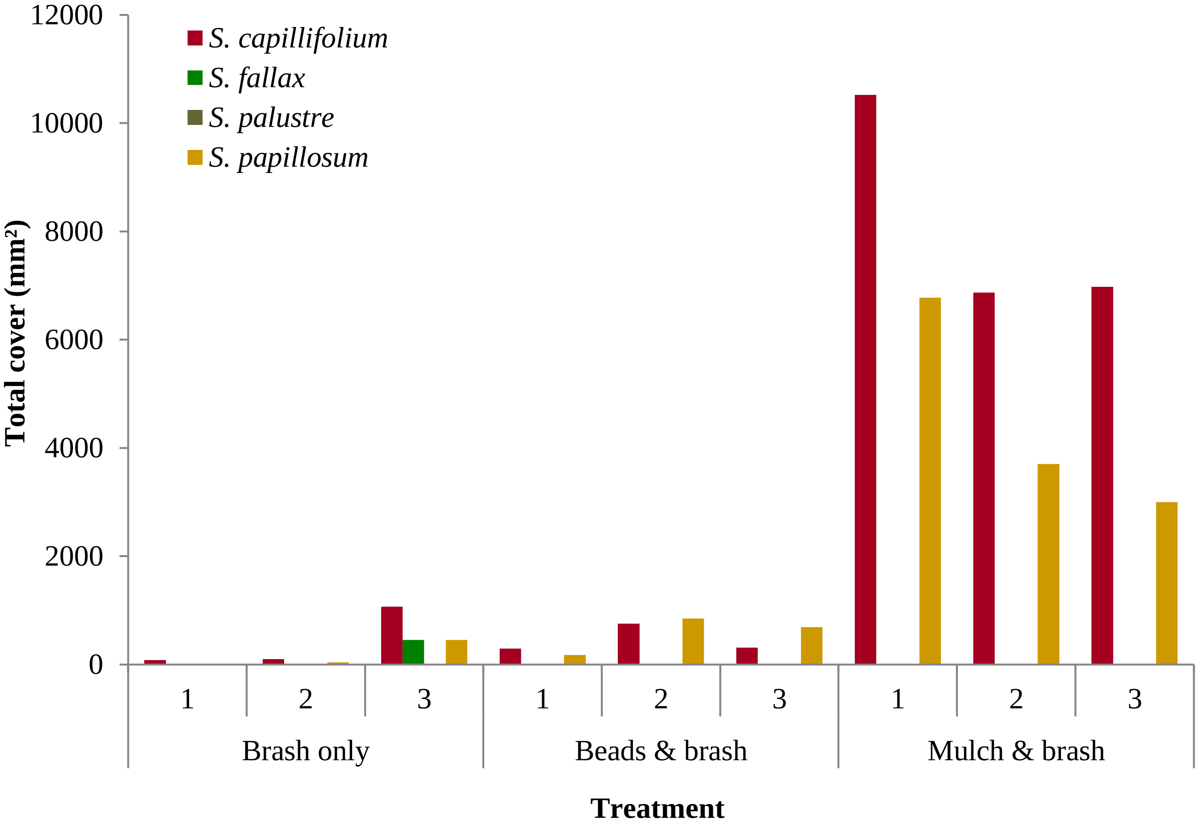


Figure 4 – Total *Sphagnum* cover (mm^2) of four species across three replicates of the treatments.

Figure 4 clearly shows *Sphagnum* cover was much greater on treatments of mulch and brash, with *S. capillifolium* consistently higher in cover than *S. papillosum*. Both *S. capillifolium* and *S. papillosum* were found in variable quantities across replicates of the beads and brash treatments. There was negligible cover of *S. fallax* and *S. palustre*. Brash only treatments generated little *Sphagnum* cover, except for in the case of replicate 3; *S. capillifolium*, *S. fallax* and *S. papillosum* were found in considerable quantity here.

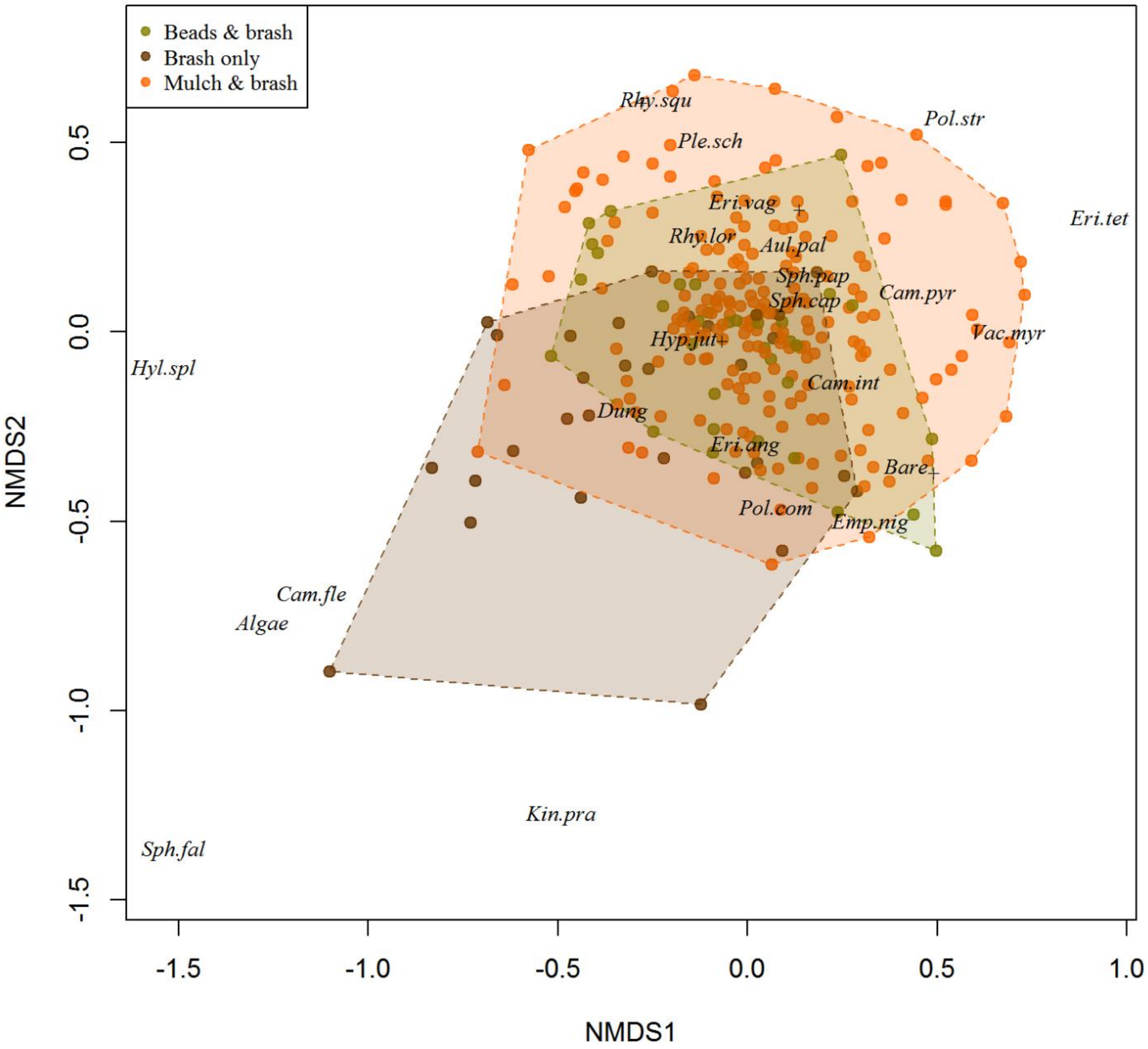


Figure 5 – Non-metric multidimensional scaling (NMDS) ordination of vegetation composition from 25 cm × 25 cm quadrats containing *Sphagnum*, separated by the three treatments. Species abbreviations can be found in Appendix 1. The most abundant species are added first and where species labels overlap, they have been omitted and the locations marked (+); all species labels are displayed in Appendix 2.

Non-metric multidimensional scaling (NMDS) was used to characterise the vegetation composition, and to detect positive associations between *Sphagnum* establishment and small-scale species composition. NMDS maps observed community dissimilarity nonlinearly onto ordination space, using Bray-Curtis index in this case. Rare species (single occurrences) were removed from the vegetation cover data, before being $\log_{10}(x+1)$ transformed (Alday *et al.*, 2011).

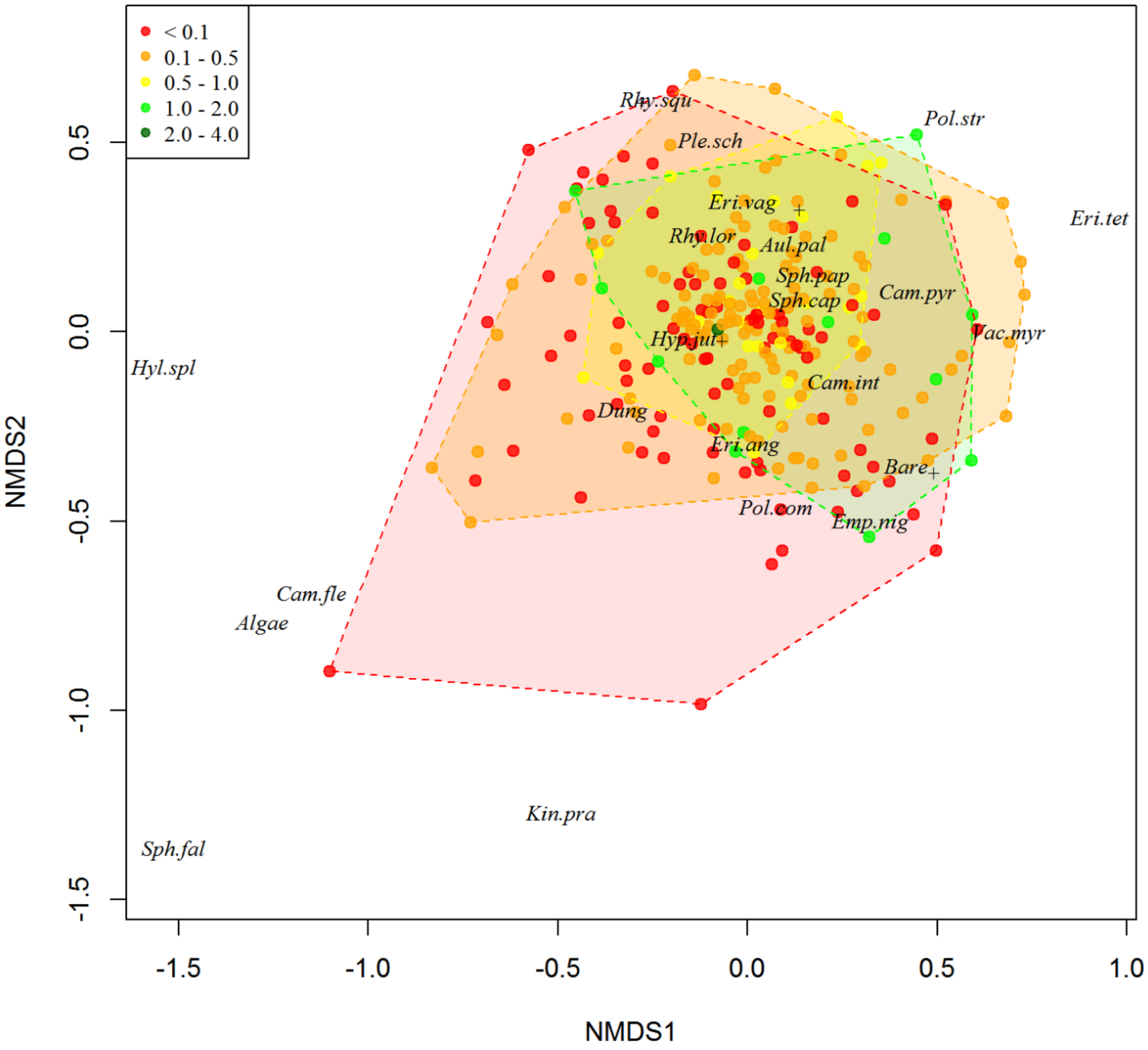


Figure 6 – Non-metric multidimensional scaling (NMDS) ordination of vegetation composition from 25 cm × 25 cm quadrats containing *Sphagnum*, separated by % cover of *Sphagnum*. Species abbreviations can be found in Appendix 1. The most abundant species are added first and where species labels overlap, they have been omitted and the locations marked (+); all species labels are displayed in Appendix 2.

Figure 5 and Figure 6 shows NMDS ordinations of vegetation recorded from 25 cm × 25 cm quadrats containing *Sphagnum*. Figure 5 distinguishes between *Sphagnum* source treatments, whilst Figure 6 separates by differences in *Sphagnum* cover within quadrats. Vegetation was found to be different between *Sphagnum* source treatments (Figure 5), using permutational analysis of variance (PERMANOVA, P = 0.001). Brash only quadrats appear to be associated with *Campylopus flexuosus* and occupy a different region of the ordination, compared to the mulch and brash quadrats. The region occupied by beads and brash quadrats is almost entirely contained within that of mulch and brash, with common associations of *Campylopus introflexus*, *Aulacomnium palustre* and *Eriophorum vaginatum*. Vegetation composition was found to be significantly different between varying levels of *Sphagnum* cover (PERMANOVA, P = 0.006, Figure 6).

Indoor trial

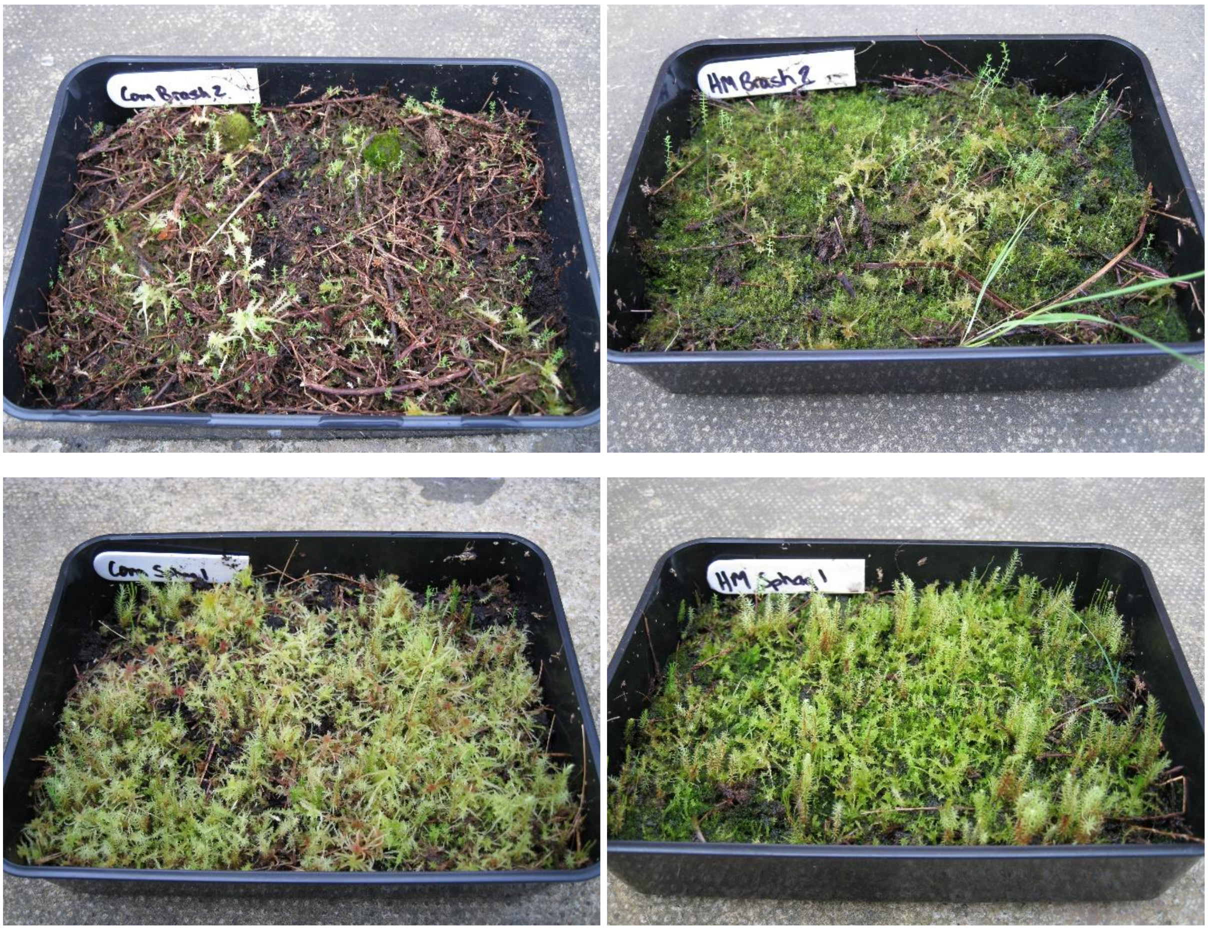


Figure 7 – Heather brash (top) and *Sphagnum* mulch (bottom) growth on commercial (left) and Holme Moss peat (right) after ~ 3 months.

After 12 months, species identity and cover were recorded. Heather brash grown on commercial peat produced substantial cover of *Sphagnum papillosum* (> 40 %) and *Trichodon cylindricus,* with lesser amounts of *Calluna vulgaris* and *Vaccinium oxycoccos*. When grown on Holme Moss peat, the brash trays were dominated by *C. vulgaris,* with *S. papillosum* and *T. cylindricus* forming a much smaller component. *S. capillifolium* was present in two of the trays, along with *Polytrichum commune*. *Sphagnum* mulch grown on commercial peat produced a high cover of *S. capillifolium* (~ 30 %) and *S. papillosum* (70 %), with minor contributions from *C. vulgaris*, *Odontoschisma sphagni*, *S. cuspidatum, T. cylindricus* and *V. oxycoccos*. When grown on peat from Holme Moss, the *Sphagnum* mulch produced an even higher cover of *S. papillosum* (~ 90 %) at the expense of *S. capillifolium* (~ 10 %). *P. commune* and *T. cylindricus* were also present in notable quantity (see Figure 7). Table 4 gives full details of the vegetation for each of the 12 trays.

Table 4 – Vegetation composition of the indoor trial, with additions of heather brash (Brash) and *Sphagnum* mulch (Mulch) grown on commercial and Holme Moss peat.

Substrate	*Addition*	*Replicate*	Algae	*Calluna vulgaris*	*Campylopus flexuosus*	*Festuca pratensis*	*Odontoschisma sphagni*	*Polytrichum commune*	*Sphagnum capillifolium*	*Sphagnum cuspidatum*	*Sphagnum papillosum*	*Trichodon cylindricus*	*Vaccinium oxycoccos*
Commercial	Brash	1	-	5	-	1	1	-	-	-	40	60	1
Commercial	Brash	2	-	10	-	-	1	-	-	-	40	60	5
Commercial	Brash	3	-	10	-	-	2	-	-	-	70	15	5
Commercial	Mulch	1	-	3	-	-	1	-	25	5	70	0.5	1
Commercial	Mulch	2	-	5	-	-	1	-	30	0.5	70	1	1
Commercial	Mulch	3	-	2	-	-	1	-	30	-	70	5	1
Holme Moss	Brash	1	-	90	-	-	-	10	0.5	-	5	10	-
Holme Moss	Brash	2	-	30	15	-	-	15	5	-	25	20	-
Holme Moss	Brash	3	15	90	-	-	-	-		-	5	10	-
Holme Moss	Mulch	1	-	1	-	10	-	10	10	-	80	10	5
Holme Moss	Mulch	2	-	-	-	-	-	1	5	-	95	1	-
Holme Moss	Mulch	3	-	-	2	-	-	2	15	-	85	2	-

2.3.5 Discussion

Field trials

Following application of materials to bare peat, there was no *Sphagnum* growth found on any of these plots, thought to be the result of heavy erosion they suffered. Initially, *Sphagnum* fragments could be found on the mulch treated strips, appearing hydrated and in contact with the peat surface, indicating their potential for establishment and growth. However, with successive field visits, the amount of material remaining on the peat surface decreased until only the heaviest heather stems remained (Figure 8). During periods of drought *Sphagnum* fragments became visibly desiccated, whilst propagules were thought to be washed off and/or buried in fluvial peat during subsequent rainfall events. The greatest losses in surface material occurred over winter, presumably due to increased precipitation, wind and the effects of snow cover, despite the inclusion of heather brash in each of the treatments intended to reduce this (Caporn *et al.*, 2007). No *Sphagnum* beads were found during any visits to the plots. However, the beads are known to shrivel and all but disappear before establishing into plants (Hinde, 2009). The application of heather brash to the plots did appear to reduce erosion, with the surface of treatment strips standing slightly proud of the control treatments and surrounding bare peat, which displayed a uniform surface pattern of erosion. The plots were located on a sloping area of bare peat, estimated to be a gradient of ~ 6.5° from GPS recorded data, although this does not include smaller scale variations in topography. This is considerably less than the 18° suggested to be sensitive to disturbance (JNCC, 2009), but this is likely to relate to vegetated slopes. However, slopes > 4° were found to produce continued erosion in drainage channels (Holden *et al.*, 2007a), demonstrating the slight gradient required for erosion to continue.

Despite the complete failure of these experimental plots, it serves to support the current revegetation and surface stabilisation works currently employed. Without this, the application of *Sphagnum* propagules directly to sloping and erosion prone bare peat is likely to fail. Flatter areas not susceptible to such rapid rates of erosion may prove more suitable substrates for propagule application directly to bare peat.

Sphagnum reintroduction treatments were more successful on the revegetated substrate, with no *Sphagnum* found on any of the control strips, giving a clear indication that all plants found were a result of the treatments applied. Plots were intentionally established in areas with no *Sphagnum* present. The *Sphagnum* mulch and heather brash treatment generated the greatest number of plants and cover, with *S. capillifolium* accounting for > 60 % of plants in each replicate. The unknown and likely variable proportions of *S. capillifolium* and *S. papillosum* contained in the *Sphagnum* mulch makes it difficult to offer any meaningful assessment of their relative performance. From the indoor trial, it appears *S. papillosum* was the most frequent species present, yet in the field trials *S. capillifolium* was dominant. This may be due to the variability in the harvested material, or perhaps be the result of selective pressures, such as desiccation and pollution tolerance, including the additions of lime and fertiliser used in revegetation works. Donor material is inherently variable, with inter-site differences likely to be largest, but with significant intra-site variation as the harvester passes over various microtopographical niches.

Figure 8 – Establishing the *Sphagnum* propagule trial, May 2010 (left). Note the density of material applied to the peat surface. Monitoring of the same experimental block, July 2012 (right). Erosion has removed nearly all the material applied.

From the brash only results, it is likely that the contribution to *Sphagnum* plant numbers is low; replicates one and two produced only 1 and 4 plants, respectively. Replicate three appears to have been inadvertently inoculated with *Sphagnum* mulch from the adjacent treatment strip; this is probably the result of wind during application of the material. However, heather brash should not be ignored as an important, if inconsistent, potential source of *Sphagnum*. Some areas subjected to restorative works in the Peak District have seen increases in *Sphagnum* cover (Moors for the Future, unpublished data). These can be explicitly linked to applications of heather brash from particular donor sites. Whilst undoubtedly a viable source of propagules, issues of sustainability would arise if *Sphagnum*-rich areas were repeatedly targeted for cutting. As with the *Sphagnum* mulch, inter- and intra- donor site variation could be considerable within heather brash material.

The results from *Sphagnum* bead and brash treatments are more difficult to interpret. The species sown, *S. fallax* and *S. palustre*, show almost no establishment across the replicates, in contrast to *S. capillifolium* and *S. papillosum* which show a low but consistent presence. This is problematic since in the brash only treatments, *Sphagnum* occurrence was very low, indicating only a small amount of propagules were present in the brash. However, on the beads and brash treatments, a greater number of plants were found. This could be attributed to:

a) The dispersed and variable quantities of *Sphagnum* propagules within the heather brash, reflecting the heterogeneous vegetation of the donor site. From the indoor trial, it is known that the heather brash contained a quantity of *S. capillifolium* and *S. papillosum*, but more importantly is the variable amount of each (Table 4).
b) The misidentification of *Sphagnum*. Identification of individuals can be problematic, exacerbated in this scenario by their small size, the non-destructive method used, and the atypical growth and colouration displayed. *S. palustre* and *S. papillosum* are notoriously difficult to distinguish, with microscopy often required for a diagnostic assessment. Small, green *S. capillifolium* could easily be confused with *S. fallax* too. Identification in the field usually relies upon the observation of stem leaves under a hand lens, along with noting the prevailing environmental conditions; e.g. habitat type, hydrological conditions. However, the very nature of these trials seeks to reintroduce *Sphagnum* to an atypical habitat over the course of several years. Thus, plants could not be removed to assist identification, nor would the environment provide any cues. Plants grown from beads look very alike in their early growth stages, with none of the features used to differentiate between species yet evident. Further to this, *Sphagnum* mulch grown indoors was observed to take on a brown, sickly appearance with uncharacteristic growth form.
c) The variable success in *Sphagnum* establishment between the strips. This seems unlikely given the fairly constant level of *S. capillifolium* and *S. papillosum* found across the beads and brash replicates, and that experimental blocks were chosen for their surface homogeneity.

The apparent poor establishment of the *Sphagnum* beads may be due to the considerable period of lag between application and establishment as a sizeable plant (Hinde, 2009), due to the small initial propagule size and challenging environmental conditions. Indeed, the lag can be such that plots are written off as failures only to be revisited several years later, with significant *Sphagnum* cover present (Figure 9). Hence, a lack of presence should not be considered a failure until many (> 5) years later. This apparent failure, or perhaps dormancy, has also been observed in transplanted *Sphagnum* material (Caporn *et al.*, 2006; Ferguson & Lee, 1983a). Time, it appears, may be one of the greatest factors influencing the success of *Sphagnum* reintroduction.

The vegetation associated with successful *Sphagnum* establishment was found to be different between treatments. Mulch and brash, and beads and brash treatments shared similar vegetation compositions, as shown by their over-lying regions on the NMDS ordination, whilst brash only displayed some separation (Figure 5). This difference is more than likely due to the material applied to the treatment strips; *Hylocomium splendens*, *Kindbergia praelonga* and *Pleurozium schreberi* are locally uncommon, supporting this conclusion. Propagules of additional heathland and bog species will always be present in any material harvested, however, it is difficult to apportion origin in this trial, nor does the indoor growth trial offer any insight either. It would be expected that beads and brash, and brash only treatments would be the most similar in species composition, since they have received the same source of material. This was not the case, and may once again be an indication of the variable nature of harvested material.

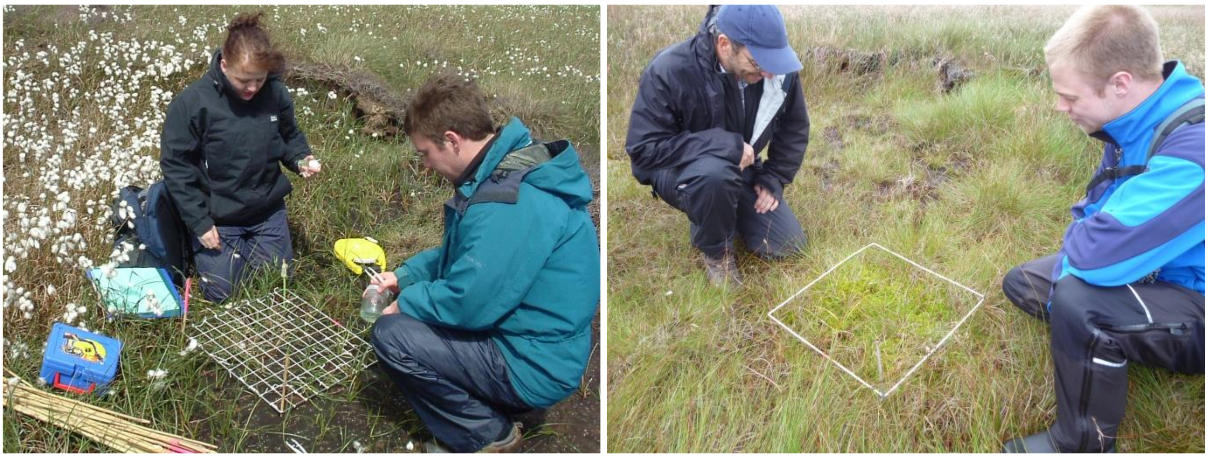


Figure 9 – Preliminary *Sphagnum* bead trial being established in June 2008 (left). Resulting *Sphagnum* cover in August 2012 (right), following presumed failure in the intervening years.

There appeared to be no such distinction in vegetation between levels of *Sphagnum* cover. From the NMDS ordination, there does appear to be a narrowing focus towards the centre of the plot but not to any statistically significant degree (Figure 6).

The successful experimental plots were established on a revegetated area, treated some 4/5 years earlier with lime, fertiliser, grass seed and heather brash. At the time of the *Sphagnum* trial set up, the plot vegetation was well established with numerous small breaks in the surface cover, exposing the underlying peat. These gaps were observed to be preferentially colonised by *Sphagnum*, indicating that contact with the underlying substrate was beneficial (Figure 10).

Figure 10 – Set up of the *Sphagnum* propagule trial on the revegetated surface, May 2010 (left). Note the gaps in vegetation through to the peat below. New *Sphagnum* plants found and marked with canes, August 2012 (right). Note the unvegetated area covered by the quadrat where *Sphagnum* was found.

It was not possible to quantify this relationship from the data collected, however, there were indicators from the vegetation associated with successful *Sphagnum* establishment. Both *S. capillifolium* and *S. papillosum* share close association with *Campylopus introflexus*, *C. pyriformis* and *Hypnum jutlandicum* (Figure 5, *Sph.cap* label obscures *Sph.pap*); these three mosses being well-known pioneer species able to rapidly colonise bare ground (Atherton *et al.*, 2010; Smith, 2004). This was thought to be due to the underlying peat remaining moist for a greater proportion of time, compared to the vegetated surface, hence the greater establishment in these locations. The revegetation of bare peat is necessary to limit further erosion (Worrall *et al.*, 2011), however, the resulting surface crust of heather brash and nurse crop appears to be somewhat hostile, rapidly drying out after exposure to heat and wind. Any *Sphagnum* propagules caught in this layer are likely to succumb to desiccation. With increasing vegetation cover microclimatic conditions improve as more moisture is trapped, movement of air is reduced and shading increases (Groeneveld *et al.*, 2007; Rochefort *et al.*, 2003). Furthermore, vegetation increases surface roughness and intercepts occult precipitation increasing the amount of water made available to plants (Herckes *et al.*, 2002). Thus, it would appear there is a need to balance surface stabilisation with the provision of suitable niches for *Sphagnum* to establish.

From the results collected, it would seem clear that *Sphagnum* mulch and heather brash was the most successful treatment at establishing *Sphagnum* plants. However, comparing establishment of the different *Sphagnum* sources is not simple; both measures presented here (counts and cover) are not directly comparable between treatments. The amount of *Sphagnum* found should increase proportionally with the number of propagules applied. However, depth of *Sphagnum* mulch, number of beads, and depth of heather brash are not comparable measures. The number of propagules applied is not known in all cases, hence a direct comparison cannot be drawn. Assessment of *Sphagnum* cover suffers from a similar drawback, since cover will be related to the number of plants present. Furthermore, cover based measures will be skewed in favour of larger initial fragment size. *Sphagnum* mulch and heather brash contained entire capitula and stems up to 20 mm, whereas the beads contain fragments no bigger than a few mm.

The fundamental requirements for successful *Sphagnum* reintroduction appear to be a stable substrate and the provision of sufficient moisture (Quinty & Rochefort, 2003; Rochefort *et al.*, 2003). On mobile surfaces, *Sphagnum* propagules are exposed to environmental extremes. Desiccation, erosion and burial, effectively destroy any recolonisation potential. On revegetated substrates, the surface is sufficiently stabilised to avoid burial and the nurse vegetation acts to improve microclimatic conditions. However, the surface of this vegetation is still a hostile environment where propagules can become trapped and succumb to desiccation. *Sphagnum* only successfully established where propagules were able to make contact with the peat surface. Whilst the upper layers of vegetation readily dry out, the underlying peat remains moist for greater proportion of the time. Intact bog systems provide this moisture through a high and stable water table, helping to mitigate periods of drought. On Holme Moss, and indeed many other areas of the Peak District and southern Pennines, the hydrology is severely disturbed with very low water tables (Allott *et al.*, 2009). This exacerbates the effects of drought periods, with severe consequences for *Sphagnum* propagules. Smaller propagules will be most severely affected, with larger fragments better able to regulate their moisture content and therefore resist desiccation (Gaudig *et al.*, 2014; Rochefort *et al.*, 2003). This may be a critical factor in the performance difference between *Sphagnum* mulch and *Sphagnum* beads.

Indoor trial

After only a short period of growth, there were obvious differences in the growth of both *Sphagnum* mulch and heather brash on the two substrates. *Sphagnum* establishment occurred more rapidly on commercial peat than Holme Moss peat, for both treatments. This growth also appeared to be healthier, with *Sphagnum* plants appearing chlorotic or discoloured when grown on Holme Moss peat. Given the shared growing conditions, the chemical properties of the substrate are potentially exerting an influence (see Chapter 3 for assessment of Holme Moss peat).

Early growth of *Sphagnum* mulch on Holme Moss substrate was typified by the dominance of algae and smaller mosses, such as *Trichodon cylindricus* and *Polytrichum commune*, thought to be caused by elevated levels of nutrients (Atherton *et al.*, 2010; Corradini & Clément, 1999). However, with passing time, the balance of vegetation shifted in favour of *Sphagnum*. By the end of the 12 month growing period, mulch applied to both commercial and Holme Moss peat had resulted in almost complete

Sphagnum cover. Whilst levels of cover were similar between the substrate types, the species composition was not. *S. papillosum* was dominant on both peat types. However, *S. capillifolium* made up at least 25 % of cover on commercial peat, with this value being closer to 10 % on Holme Moss peat. This difference in vegetation included other species (e.g. *Vaccinium oxycoccos* and *Odontoschisma sphagni*), and may be the result of selection pressure caused by the biogeochemistry of the southern Pennine peat (see Chapter 3). The apparent lag in growth of *Sphagnum* could be caused by a shift in competitive ability, as the more rapidly growing species make use of the available nutrients and they become depleted (Bates, 1992; 2000). The early growth of *Sphagnum* may also have served to improve the chemical conditions of the peat by accumulating pollutant ions (Clymo, 1963), hence giving rise to the poor initial growth but facilitate subsequent development. Once these were bound or otherwise depleted, *Sphagnum* growth became healthy. Analysis of peats from the southern Pennines and Peak District has shown levels of nutrients and heavy metals to be elevated, when compared with references sites in the UK (e.g. Caporn *et al.*, 2006; Carroll *et al.*, 2009; Rothwell *et al.*, 2005a).

The growth of heather brash was markedly different on the two substrates. Initially, *Calluna vulgaris* and *Sphagnum* grew well on commercial peat. *S. papillosum* remained a significant component (at least 40 %) of the vegetation, however, *C. vulgaris* formed only a minor part (maximum 10 %). On Holme Moss peat, initial growth was dominated by *T. cylindricus* with little in the way of *C. vulgaris*. However, by 12 months, *C. vulgaris* was dominant in all cases and had very high cover (90 %) in two of the replicates. Again, this was attributed to the presence of increased nutrients. The occurrence of *S. papillosum* from brash appears to be variable, in both the indoor and field trials, suggesting the brash material itself is highly variable in *Sphagnum* content.

Indoor experiments, under controlled conditions, are a useful means of rapidly answering very specific questions. Some of the challenging environmental conditions of the field are removed, with increased water availability, humidity and temperature allowing establishment and growth at an increased rate. Similarly, the effects of polluted substrate can be seen more rapidly because of this. However, care must be taken when interpreting the results; they cannot simply be extrapolated into the field scenario. Indoor trials are extremely simple and lack the complexity of their *in situ* equivalents. Conversely, the immense complexity of field trials in such polluted and environmentally challenging conditions may render field results extremely difficult to interpret. Thus, the use of indoor experiments provides a rapid means with which to aid the understanding of their concurrent field trial.

2.3.6 Conclusion

These preliminary trials serve to illustrate the potential for successful *Sphagnum* reintroduction to degraded blanket bog, and highlight critical factors. In the field, surface stability and contact with the peat surface were implicated as being significant for *Sphagnum* to establish. To prevent propagules being buried or washed off, unstable bare peat areas must first be revegetated. Contact with the underlying bare peat in these revegetated conditions was thought to be beneficial because of increased moisture availability. *Sphagnum* mulch was found to produce a high number of established plants on revegetated substrate. The real measure of success will only be known in years to come, with continued monitoring of these plots required to assess increases in *Sphagnum* cover. Heather brash was confirmed as an inconsistent source of *Sphagnum* propagules, whilst the establishment of *Sphagnum* beads proved disappointing. The polluted peat substrate of Holme Moss, and perhaps much of the southern Pennine region, was found to influence the growth of *Sphagnum*, but not prevent it. Water availability was thought to be the critical in the establishment of *Sphagnum* from small propagules, as found by others (Price, 1997; Sagot & Rochefort, 1996). Sustainability and biosecurity issues were raised regarding the use of *Sphagnum* mulch, in addition to transport and handling difficulties. Given the vast tracts of degraded blanket peatland targeted for reintroduction, such operational issues become extremely important. The micropropagation of *Sphagnum* may be the only viable means of obtaining the quantities required, whilst providing the greatest number of options; e.g. species selection, method of delivery. To this end, these preliminary trials serve to validate alternative methods of *Sphagnum* reintroduction, providing practitioners with a toolbox of tested techniques for use in different degradation scenarios. For example, small peat pans on level ground are not prone to erosion, as on larger, sloping expanses. These areas could be more intensively targeted with *Sphagnum* mulch and heather brash applications directly, potentially bypassing the many years required for typical revegetation measures (lime, fertiliser, seed and brash).

2.4 *Sphagnum* bead trials

2.4.1 Rationale

The development of *Sphagnum* beads provides a convenient means with which to experimentally introduce propagules of known species identity at quantifiable rates. The southern Pennines provide the ideal setting for such trials, with a range of degradation types and features, combined with on-going restoration works of various ages. This provides a unique opportunity to investigate *Sphagnum* reintroduction as part of pioneering ecological restoration works.

Sphagnum species occupy distinct niches, separated by hydrological and biogeochemical tolerances. However, these niches are typically governed by their competitive ability rather than preference (Robroek *et al.*, 2007a). Thus, species selection for use in restoration works should not be limited by typical niche characteristics. Given the polluted nature of these peatlands, and additions of nutrients and lime as part of revegetation works, tolerance of these is likely to be a defining feature of *Sphagnum* species used in landscape scale reintroduction. Similarly, the often disturbed hydrology of degraded blanket peatlands means there is a balance to be addressed in species choice. *Sphagnum* species typical of hollows and lawns are highly productive under optimal conditions but are susceptible to periods of drought, whilst hummock-forming species are less productive but have a greater capacity for withstanding drought (Robroek *et al.*, 2007b; Wagner & Titus, 1984).

The revegetation of bare peat is a lengthy and expensive process requiring many years to restore typical bog vegetation where there is little, if any, *Sphagnum* present. If *Sphagnum* could be successfully introduced during or early in the revegetation process, it may be possible to shorten the pathway to restoring active bog vegetation. It may also be possible to identify priority areas for reintroduction based on the vegetation types associated with successful *Sphagnum* reintroduction.

Research on lowland raised bogs shows a high and stable water table is required for successful *Sphagnum* restoration (Quinty & Rochefort, 2003; Wheeler & Shaw, 1995). However, it has also been noted that with sufficient precipitation or cloud cover (e.g. upland areas), conditions could easily be wet enough to support *Sphagnum* (Grosvernier *et al.*, 1995). Given the lower temperatures and reduced rates of evaporation, higher levels of precipitation and regular occult inputs, *Sphagnum* growth on degraded blanket bog may be less influenced by the prevailing hydrological conditions.

In areas of compromised hydrology, *Sphagnum* beads will be vulnerable to the prevailing climatic conditions. Propagules are likely to be susceptible to drought (Glime, 2007; Rochefort *et al.*, 2003), thus making the annual timing of application relevant. Autumn and winter months represent greater water availability but a reduced capacity for growth and possible exposure to frost, whilst spring and summer months present a greater opportunity for growth but a greater risk of drought and desiccation.

Establishing the what, where and when of *Sphagnum* reintroduction will provide the fundamental knowledge and understanding required to make landscape scale blanket bog restoration successful. This will provide the foundation for best practice guidelines and further refinement through additional manipulations and stakeholder feedback.

2.4.2 Objectives

Field and indoor trials were established to provide experimental evidence for the following aim:

Evaluate the potential for landscape-scale Sphagnum reintroduction to degraded blanket bog

This Section aims to provide the fundamental knowledge required for successful *Sphagnum* reintroduction; namely, which species to use, what substrate to apply propagules to, and when to apply propagules in terms of both the season and stage of the revegetation process.

A series of objectives were identified for the field trials:

- Compare performance of *Sphagnum* species used in reintroduction
- Compare establishment of *Sphagnum* beads on bare and revegetated substrates, and existing vegetation substrates
- Establish associations between successful *Sphagnum* establishment/ growth and surrounding vegetation
- Identify the characteristics of areas with successful *Sphagnum* establishment
- Establish compatibility of *Sphagnum* reintroduction with current revegetation methods

A concurrent indoor trial was also established to provide results over a much shorter timescale. This trial was designed to complement the field trial, with the objectives of:

- Compare growth of *Sphagnum* beads between species
- Determine the impact of polluted substrate upon the growth of *Sphagnum*

2.4.3 Methods

Field trials

Numerous pilot field trials were established between November 2009 and August 2012 on Holme Moss and Black Hill (Figure 12). Black Hill (SE 070040, 582 m a.s.l.) is adjacent to Holme Moss (SE 078046), on the same high level, peat covered plateau. Heyden Clough separates the two sites, with Black Hill to the west, and Holme Moss to the east. Black Hill has suffered a similar fate to Holme Moss, with extensive erosion and degradation and has subsequently received the same revegetation treatments. The site is typified by bare peat, large areas of nurse crop vegetation, peat hags topped with *Empetrum nigrum* and *Vaccinium myrtillus*, and extensive gullies both bare and naturally revegetated, comprising grass and sedge mixtures.

Figure 11 – Typical plot configuration, showing 4 m × 1 m treatment strips separated by 0.5 m gap.

Trials consisted of replicate blocks on a number of substrate types, broadly categorised as bare (no vegetation), treated (revegetated following applications of lime, fertiliser, grass seed and heather brash), or vegetated (natural, original, continuous vegetation). Replicate blocks were chosen for their similar substrates and nearby locations. The experimental blocks consisted of a number of 4 m × 1 m treatments strips, separated by at least 0.5 m gap between each strip (Figure 11). Treatments were sown with a range of individual *Sphagnum* bead species at a rate of 400 m^{-2}, provided as required by Micropropagation Services (EM) Ltd. Across various trials *S. capillifolium*, *S. cuspidatum*, *S. fallax*, *S. fimbriatum*, *S. palustre* and *S. papillosum* were used; species naturally present in the region (Carroll *et al.*, 2009). Appendix 3 gives full details of dates, substrate and species of each trial.

The experimental blocks were visited annually and established *Sphagnum* was marked using small canes. Monitoring and recording of *Sphagnum* was completed in August 2013. Treatment strips were searched intensively for all visible *Sphagnum* plants, and when found, a record of the species, size and associated vegetation was made. *Sphagnum* size was measured (to the nearest mm) as the diameter of individual plants, or dimensions of simple polygons for clumps, allowing the area to be calculated. A record of the vegetation associated with the *Sphagnum* was also made, using a 25 cm × 25 cm quadrat. Any additional features of the treatment strip or experimental block as a whole were also recorded. Monitoring made use of the spacer strips to avoid trampling of treatment areas, whilst allowing for thorough searching.

Indoor trial

Ten half-trays were filled with peat to a depth of 3 cm, five with commercial peat (horticultural *Growmoor Irish moss peat*), and the other five with peat from an unvegetated area of Holme Moss. To each of the trays five rows of six *Sphagnum* beads were added, with each row containing a different *Sphagnum* species. The species used were *S. cuspidatum*, *S. fallax*, *S. fimbriatum*, *S. palustre* and *S. papillosum* (*S. capillifolium* beads were still under development at this stage); rows were randomly assigned. Trays were randomly arranged in a 2 × 5 configuration and covered with clear plastic sheeting to maintain high levels of humidity. Trays were left to grow in an artificially lit room (150 µmol m^{-2} s^{-1} 16 hour day length), mean temperature ~ 20 ºC, and watered weekly with deionised water using a spray bottle. After six months, all plants were harvested, cleaned of all peat and dried at 40 °C for 48 hours. Dry mass of plants originating from individual beads was recorded using a four-point balance. Great care was taken to ensure all peat was removed, and there was no loss of plant tissue during the process.

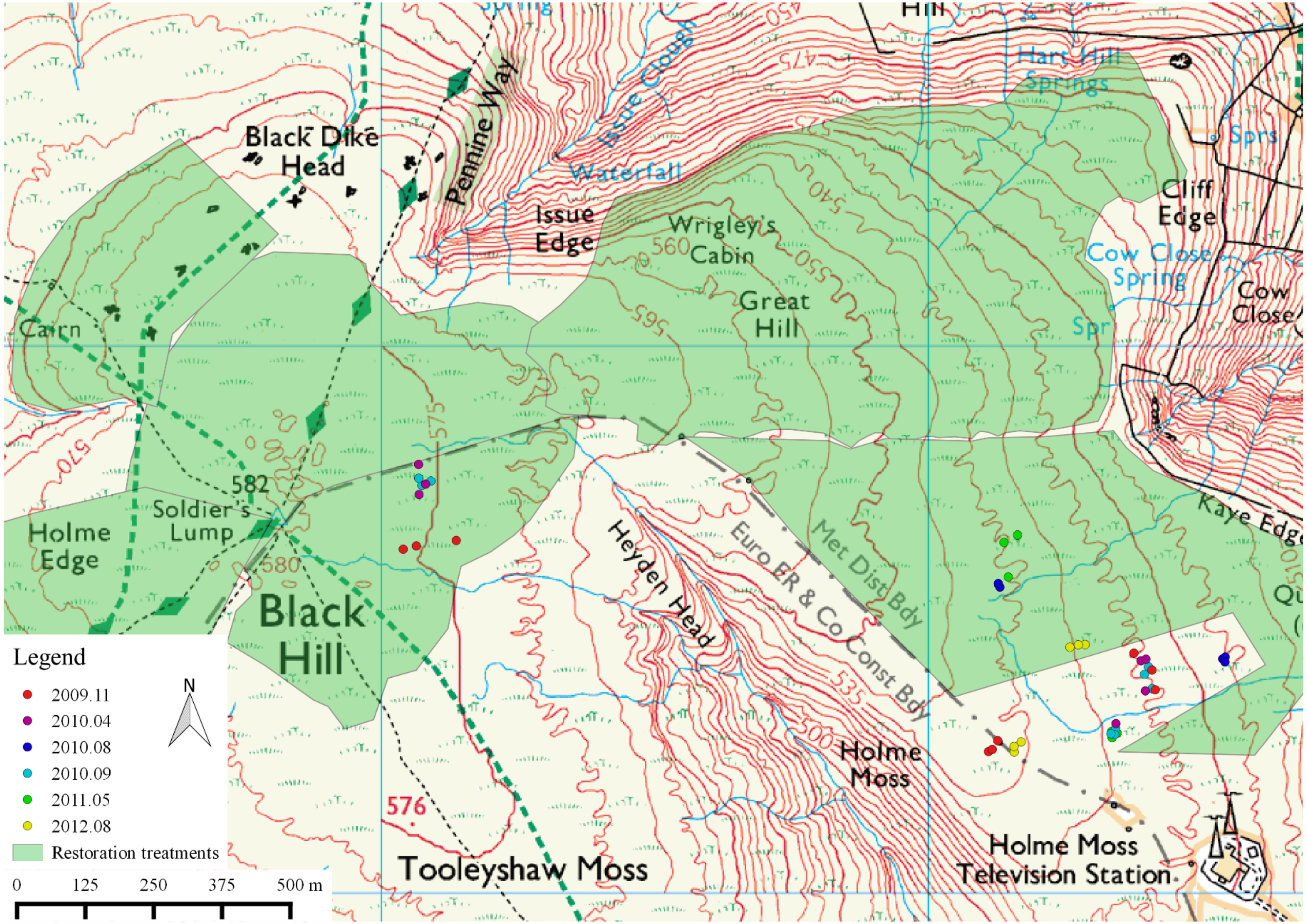


Figure 12 – Location and date of experimental trials established on Holme Moss and Black Hill.

2.4.4 Results and analysis

Field trials

No *Sphagnum* growth was recorded on any of the control treatments strips (i.e. no *Sphagnum* applied) and so they are omitted from further analysis. Trials established in August 2010 were the most successful (Figure 13), with 3.05 % of all *Sphagnum* beads sown establishing successfully. November 2009 was the next most successful month (0.33 %), followed by April 2010 (0.03 %), May 2011 (0.02 %), September 2010 (< 0.01 %) and finally August 2012 (0 %). Growth of *Sphagnum* beads on bare peat was very poor, with a successful establishment rate of 0.004 % across all trials plots. Vegetated and treated (revegetated) substrates proved more successful, with rates of 0.299 % and 0.507 %, respectively.

Statistical analyses are not reported due to the nested and irregular experimental design.

Table 5 – Summary of % (and number) of successfully established *Sphagnum* beads across the field trials. Percentages are calculated from the initial number of *Sphagnum* beads applied. No data (-) indicates that species was not used as part of the trial. Substrate types are broad categories and not comparable between establishment dates. Species abbreviations can be found in Appendix 1.

Date	*Substrate*	*Sph.cap*	*Sph.cus*	*Sph.fal*	*Sph.fim*	*Sph.pal*	*Sph.pap*
2009/11	bare	-	0	0.02 (1)	0	0	0
	vegetated	-	3.75 (60)	1.79 (86)	-	-	-
	treated	-	0	0.02 (1)	0.08 (4)	0.29 (14)	0.25 (12)
2010/04	bare	-	0	0	0.04 (2)	0	0
	vegetated	-	0	0	0.06 (1)	0.44 (7)	0
	treated	-	0.04 (2)	0	0	0.06 (3)	0.06 (3)
2010/08	bare	-	-	0	-	0	-
	treated	-	-	12.19 (585)	-	0	-
2010/09	bare	-	0	0	0	0	0
	vegetated	-	-	0.06 (3)	-	0.02 (1)	-
	treated	-	0	0	0	0	0
2011/05	vegetated	-	-	0	-	0	-
	treated	0	0	0.19 (9)	0	0	0
2012/08	vegetated	0	-	0	0	0	-
	treated	0	-	0	0	-	-

Across all trials, *S. fallax* was the most successful species, with an overall establishment rate of 0.996 %, followed by *S. cuspidatum* (0.168 %), *S. papillosum* (0.043 %), *S. palustre* (0.042 %), *S. fimbriatum* (0.016 %), and *S. capillifolium* which failed to grow. Combined *Sphagnum* bead establishment was 0.306 %. Table 5 provides a summary of establishment rates across the trial plots; full details can be found in Appendix 3.

S. fimbriatum had the largest mean plant/ clump size (92.43 mm^2), followed by *S. papillosum* and *S. palustre* which were similar (75.27 mm^2 and 70.03 mm^2, respectively), with *S. cuspidatum* (52.48 mm^2) and *S. fallax* the smallest (38.83 mm^2).

Non-metric multidimensional scaling was used to examine relationships between *Sphagnum* growth and surrounding vegetation. Figure 14 shows NMDS ordination of vegetation (using Bray-Curtis dissimilarity index) recorded from 25 cm × 25 cm quadrats taken on experimental plots sown with *Sphagnum* beads. Cover data were improved by removing rare species (single occurrences), before being $\log_{10}(x+1)$ transformed (Alday *et al.*, 2011). Quadrats were grouped by number of new *Sphagnum* plants/ clumps found; vegetation composition was found to be different between these groups (PERMANOVA, $P < 0.001$). Those quadrats containing the highest numbers of *Sphagnum* plants/ clumps were associated with atypical bog vegetation: algae, *Agrostis stolonifera* and *Juncus squarrosus*. There is a dense clustering of records associated with more typical bog vegetation (*Eriophorum* spp., *Empetrum nigrum* and *Vaccinium myrtillus*).

Figure 13 – *Sphagnum fallax* beads from 2010/08 trial on treated substrate. Canes indicate successfully established *Sphagnum* plants.

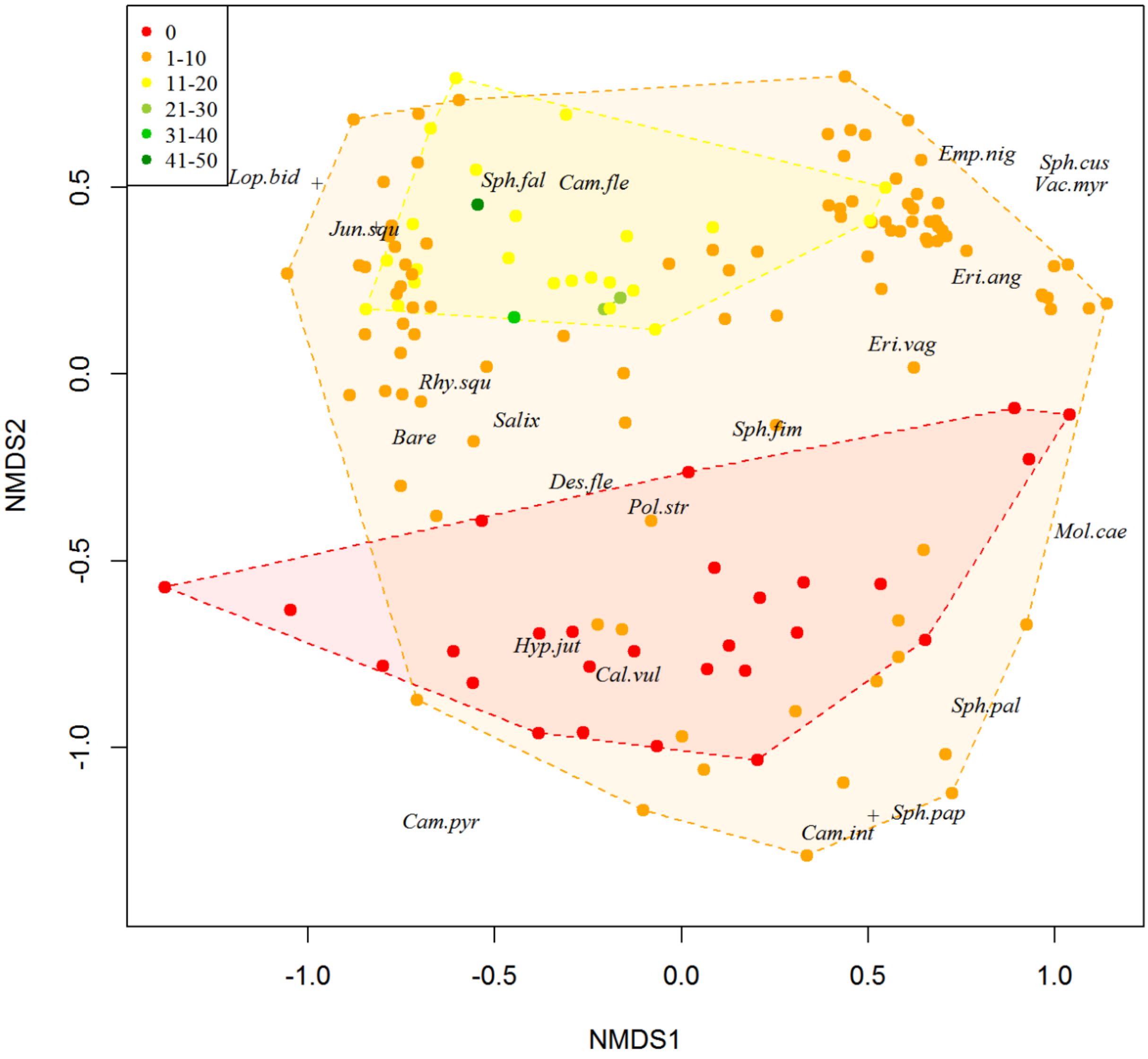


Figure 14 – Non-metric multidimensional scaling (NMDS) ordination of vegetation composition recorded from experimental plots sown with *Sphagnum* beads. Records are coloured according to the number of individual plants/ clumps per 25 cm × 25 cm quadrat (top left). Where no *Sphagnum* was found, the overall plot vegetation was recorded. Species abbreviations can be found in Appendix 1. The most abundant species are added first and where species labels overlap, they have been omitted and the locations marked (+); all species labels are displayed in Appendix 4.

To examine the relationship between *Sphagnum* success and climatic conditions, weather data from June 2009 – December 2012 was gathered from Pole Moor weather station (Weather Underground, 2013), ~ 10 km north of Black Hill. This site was chosen for its location and complete set of records. Monthly total rainfall and mean temperature were calculated from daily measurements (Figure 15). Success of *Sphagnum* bead applications were assessed for associations with the climatic data relating to: a) the sowing month; b) three-month mean rainfall and temperature, using sowing month and the pre- and proceeding months; and c) cumulative total of these three-months. Spearman's rank correlation coefficients were calculated between *Sphagnum* establishment success and these climatic measures (Table 6). No significant correlations were found between *Sphagnum* success and any of these measures.

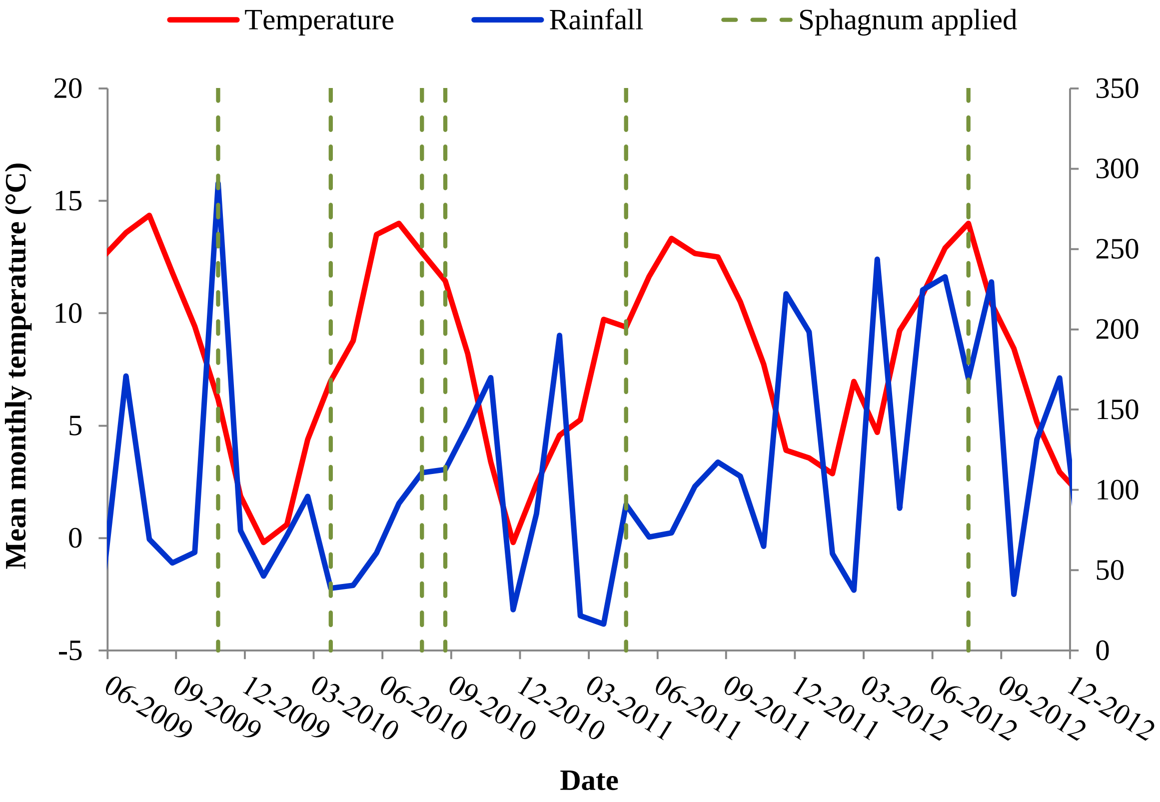


Figure 15 – Mean monthly temperature (°C) and total monthly rainfall (mm) from June 2009 – December 2012 (Weather Underground, 2013). Dates of *Sphagnum* bead applications have been marked.

Table 6 – Spearman's rank correlation coefficient (r_s) of *Sphagnum* bead rate of establishment and climatic variables.

Measure	*Climatic variable*	r_s	*P*
Sowing month	Temperature	-0.429	0.397
	Rainfall	-0.143	0.787
Three-month average	Temperature	-0.143	0.787
	Rainfall	-0.371	0.468
Three-month total	Temperature	-0.143	0.787
	Rainfall	-0.371	0.468

Indoor trial

Growth of all *Sphagnum* species was found to be greater on commercial peat than on Holme Moss peat (Figure 16). *S. cuspidatum* had the greatest mass on both substrates and *S. fallax* the least, although not significantly so on Holme Moss peat. Rank ANOVA was used to assess the significance of peat used and *Sphagnum* species; both peat and species were highly significant (P < 0.001) however, the interaction term was not.

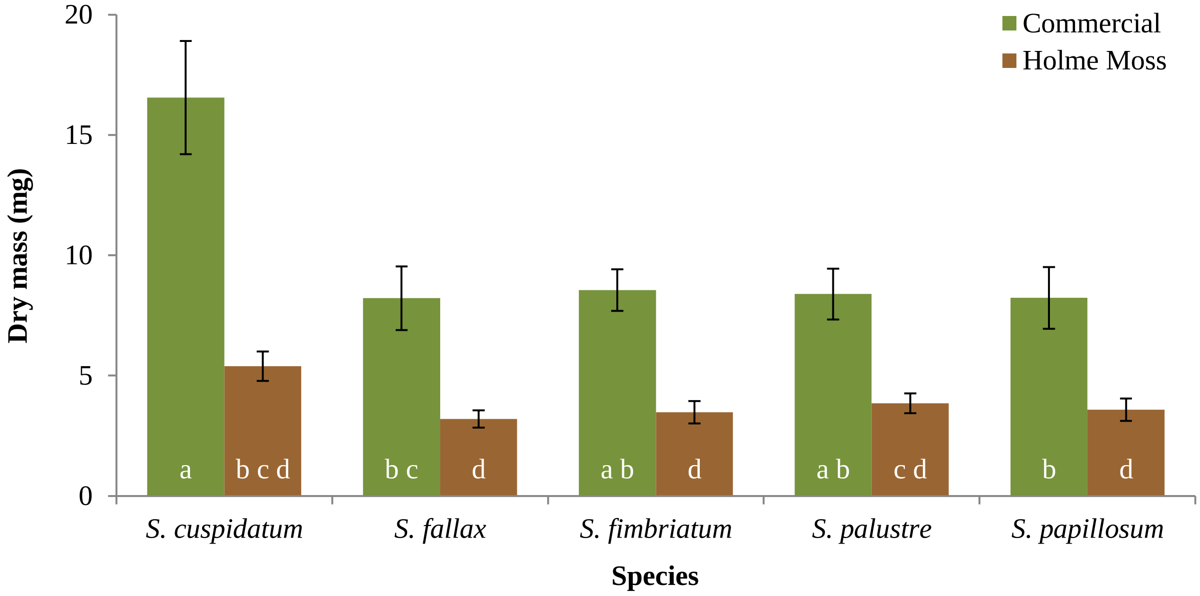


Figure 16 – Mean (± 1 SE) dry mass (mg) of *Sphagnum* plants of the five species, grown on commercial and Holme Moss peat for 6 months. Columns which do not share a letter are significantly different (Rank ANOVA, Bonferroni-corrected pairwise comparisons).

2.4.5 Discussion

Field trials

No *Sphagnum* was found on any of the control strips across all plots, giving a clear indication that plants found on treatment strips were the result of the *Sphagnum* beads applied. *Sphagnum* beads applied to bare peat substrate performed very poorly, with very low rates of establishment; 0.004 % across all trials. This was thought to be due to the mobile peat surface which would allow the propagules to be easily moved and/ or buried. The bare peat surface would also be totally exposed, offering no shelter to the drying effects of the sun and wind. *Sphagnum* beads would then be susceptible to desiccation and death.

The results of these preliminary trials suggest *S. fallax* applied to treated surfaces in August will result in the greatest success rates. However, the irregular structure of the experimental trials makes direct comparison between the various sowing months, substrate types and *Sphagnum* species impossible. Plots were established on an *ad hoc* basis, using *Sphagnum* beads and space available at that time. Trials on bare substrate were omitted in later trials as it became apparent they were a fruitless endeavour. This resulted in an unbalanced experimental design with nested results, which could lead to incorrect conclusions being drawn. For example, August 2010 was the most successful sowing month, however, this is more than likely due to the influence of a few highly successful plots (2010/08, Treated, *S. fallax*; Table 5). Climatic parameters were found to not be related to *Sphagnum* success (Table 6), thus making any assessment based on sowing month invalid. Assessment based on substrate type was also problematic; substrate categories were arbitrary terms which often encompassed considerable variation. For example, vegetated surfaces included distinct areas dominated by *Eriophorum* spp. and others by *Deschampsia flexuosa*.

Analysis of *Sphagnum* success is more meaningful when considered alongside the surrounding vegetation community. From the NMDS ordination (Figure 14), the highest levels of success were associated with algae, *Agrostis stolonifera* and *Juncus squarrosus*. This is undoubtedly due to the influence of highly successful *S. fallax* plots sown in August 2010. This suite of species is atypical of blanket bog and provides useful cues which may help to explain the high success rate in these plots. *A. stolonifera* is indicative of elevated nutrient and pH conditions (Hill *et al.*, 1999), with *J. squarrosus* and algal growth supporting this assessment. These plots were established on what appeared to be a flush or drainage channel between revegetated peat dunes. The soil here was very thin (> 5 cm) with much greater mineral content than the surrounding peat. This was due to the extent of erosion, exposing underlying gritstone in some places, and the deposition of fine gritstone sediment carried from further upstream. This channel was thought to collect and concentrate levels of moisture, nutrients and other solutes, such as lime and fertiliser from surrounding revegetation works. Whilst it is not possible to determine which, if any, of these inputs contributed to the success of *S. fallax* beads in this location, it is worth noting the much poorer performance of *S. fallax* on treated substrates in other experimental plots. These surfaces will also have been subjected to inputs of lime and fertiliser, and yet did not see comparable rates of establishment. Thus, moisture availability is suggested as a key factor. It should be noted that *S. palustre* sown in these August 2010 plots failed to establish, potentially a result of differential desiccation tolerance between the species (see Section 2.6), or simply a poor batch of *S. palustre* beads.

On the ordination, a cluster of points were associated with *Eriophorum angustifolium*, *E. vaginatum*, *Empetrum nigrum* and *Vaccinium myrtillus*. These species are typical components of blanket bog vegetation and their relative abundances are indicative of the prevailing hydrological conditions. Dwarf shrub cover is generally associated with drier areas, whilst *E. angustifolium* is indicative of wetter environments (Hill *et al.*, 1999). These wetter conditions appear to be the greatest influence in the establishment of *Sphagnum* beads. The successful plots of November 2009 were established on an area of blanket bog exhibiting little in the way of erosion features. The vegetation was dominated by *E. angustifolium* and the water table appeared high and stable; small, infrequent patches of *Sphagnum* were also present. Both *S. cuspidatum* and *S. fallax* established well, although without replicate plots for both species, it is difficult to compare their performance. *Sphagnum* species of lawns and hollows, such as *S. cuspidatum* and *S. fallax*, are productive under favourable conditions (Clymo & Reddaway, 1971, 1974), with water availability considered a major limiting factor in restoring active peatland vegetation (Robroek *et al.*, 2007b; Rochefort *et al.*, 2003).

Following larger scale application of *Sphagnum* beads, monitoring was required to assess their effectiveness. The Moors for the Future Partnership proposed criteria based on suggested rates of *Sphagnum* bead application (Table 7). When expressed as a percentage, these values appear very low; aiming for establishment of 0.5 – 0.8 %. However, when considering the quantities involved, the potential impact becomes clear; to date, 1.5 billion propagules have been applied (Moors for the Future, 2015). If the criteria were met, this equates to 7,500,000 – 12,000,000 new *Sphagnum* plants.

From the summary of results (Table 5), these criteria were only met on three occasions: *S. cuspidatum* and *S. fallax* sown on vegetated substrate in November 2009, and *S. fallax* sown on treated substrate in August 2010. These summary values do hide some variation in the performance of individual plots. From a potential 162 treatment strips (excluding controls), 10 were found to meet or exceed the criteria, the majority of these being sown with *S. fallax*. Full details of individual plots and treatments, and their performance relative to these criteria can be found in Appendix 3.

These criteria were exceeded by ten treatment strips across all experimental trials. Of these, seven were located in areas of high water availability; four on original blanket bog vegetation with a stable water table, and three were located in a shallow channel which appeared to be gathering water from the immediate surrounding area.

Table 7 – Proposed Moors for the Future Partnership *Sphagnum* application rates and success criteria.

Success criteria:	1 new *Sphagnum* plant in 80 % of 4 m^2 quadrats
Sphagnum bead sowing density:	25 – 40 m^{-2}
Sphagnum beads per 4 m^2:	100 – 160
Establishment required to satisfy criteria:	0.625 – 1 %
Corrected for 80 % incidence:	0.5 – 0.8 %
Lower success threshold:	0.5 %
Upper success threshold:	0.8 %

Plots where no *Sphagnum* could be found were also plotted on the NMDS ordination (Figure 14), and showed an association with vegetation species typical of drier habitats, such as *Campylopus* spp. and *Hypnum jutlandicum*. Whilst it is not impossible for *Sphagnum* beads to establish on such substrates, it is a much less frequent occurrence than in the wetter communities, as is clearly visible on the ordination. This is thought to be directly related to the availability of water; preliminary trials using *Sphagnum* beads showed success was greatest in the wettest sites (Hinde, 2009). Areas typified by these mosses are usually revegetated peat dunes, where the water table is thought to be extremely low (Allott *et al.*, 2009).

Of the species trialled, *S. fallax* appeared the best suited for reintroduction, with the greatest overall establishment rate (0.996 %). However, *S. fallax* also had the smallest plant/ clump size (38.83 mm^2). Conversely, *S. fimbriatum* and *S. papillosum* had the largest mean plant/ clump sizes (92.43 mm^2 and 75.27 mm^2, respectively) but much lower rates of establishment (0.016 % and 0.043 %, respectively). *S. fimbriatum* and *S. papillosum* may only be able to grow in the most equable of conditions. Thus, when beads do establish, they perform well, producing larger plants and clumps. Alternatively, those plots where *S. fimbriatum* and *S. papillosum* managed to grow were established in November 2009 and April 2010, and so have had the greatest period of time to grow. Since *S. fimbriatum* and *S. papillosum* did not establish on any later plots, the mean plant/ clump size was not reduced by smaller, younger plants. The inverse of these arguments may also help to explain the smaller plant/ fragment size of *S. fallax*: perhaps this species is better able to establish under poorer conditions (Buttler *et al.*, 1998), albeit growing less vigorously in these locations, and with *S. fallax* beads establishing on plots from November 2009, August 2010 and May 2011, younger plants/ clumps are likely to reduce the mean size.

Ten treatment strips across all experimental plots exceeded the success criteria, of which seven of these were sown with *S. fallax*. Due to the complex experimental structure, as discussed earlier, it is difficult to attribute these successes solely to species choice. The remaining three successful treatment strips are also the oldest, indicating time since application may be a significant factor. Some of the most consistent performing, successful trials were established in November 2009 on an area of bog with good hydrology.

Further plots were established nearby in August 2012, however, with only a year since bead application before monitoring took place, no plants were found. The difficulty in monitoring the success of *Sphagnum* bead applications is the significant time lag between application and visible growth (18 – 24 months was not uncommon during this work), and the presumed failure in the interim period (e.g. Figure 9). *Sphagnum* beads shrivel, bleach and all but disappear, however, the viability of these propagules has been shown through removal from the field and subsequent growth in the glasshouse (N. Wright, pers. comm.).

The climatic variables assessed showed no relation to the success of *Sphagnum* bead growth, indicating that the season of application was much less important than where they were applied. The climatic data does serve to illustrate extended periods of snow cover in the winter of 2009/10 and 2010/11, and drought in spring 2010 and 2011 (Figure 15), and more importantly, the ability of *Sphagnum* beads to withstand such conditions and continue growing.

Indoor trial

The growth of *Sphagnum* beads was significantly better on commercial peat than on Holme Moss peat. This difference in performance was attributed to the adverse biogeochemical characteristics of the peat from the southern Pennines (Carroll *et al.*, 2009; Linton *et al.*, 2007); potentially damaging levels of nutrients, sulphur and heavy metals remain as a legacy of industrial pollution and continued rates of deposition (see Chapter 3). On commercial peat, *S. cuspidatum* produced significantly greater biomass than any other species. Under ideal field conditions, this species is known to be highly productive (Clymo & Reddaway, 1971, 1974). All species produced significantly less biomass on Holme Moss peat than their commercial peat counterpart, with all species producing similar amounts of biomass.

Whilst these results show differential rates of productivity, the conditions must be considered. These results cannot be extrapolated into a field scenario, since these equable conditions are rarely found or sustained in degraded peatlands. Where water availability is high, *S. cuspidatum* has demonstrated its high levels of productivity, however, these trials are extremely simple and convey none of the complex interactions of *in situ* trials. For example, climatic conditions were eliminated along with the continued deposition and input of pollutants (e.g. N). Artificial lighting within the growth room was noted to be particularly weak, with readings of 150 µmol m^{-2} s^{-1} in contrast to > 800 µmol m^{-2} s^{-1} in the glasshouse on an overcast day. Humidity was maintained by covering trays with transparent plastic sheeting. During a visit to the production facility of Micropropagation Services Ltd., *Sphagnum* was observed growing vigorously in naturally lit glasshouses, with misting units maintaining humidity levels.

2.4.6 Conclusion

Sphagnum beads have been shown to be a viable method of reintroducing *Sphagnum* to areas of degraded blanket bog. They provide a convenient means of applying propagules of a known identity and provenance at quantifiable and controllable rates. The beads can generate significant new *Sphagnum* cover, however, a number of influential factors have been implicated in this work; namely, water availability, substrate stability, time, and the legacy of effects of industrial pollution. The wider implications of these preliminary trials was, however, limited due to a lack of replication.

Sphagnum beads require sufficient moisture to prevent desiccation. These conditions were met in obvious locations such as areas of bog with high and stable water tables, but also in less apparent channels and simply by remaining in contact with the underlying peat surface. Surrounding vegetation serves to improve microclimatic conditions and prevent erosion of the peat surface, which would otherwise bury and remove such propagules. However, revegetation measures can result in the development of extensive *Hypnum* mats which prevent the *Sphagnum* beads from reaching the peat surface. Thus, sowing location will be critical.

Concerns regarding the additions of lime and fertiliser appear to be unfounded, with *Sphagnum* establishing in treated areas and in channels draining these areas. The continuing negative impacts of historic industrial pollution in southern Pennine peats was clearly demonstrated and may help to explain the very slow rates of *Sphagnum* growth. Time is and will clearly be a major factor in the establishment of significant *Sphagnum* cover.

2.5 *Molinia* grassland trials

2.5.1 Rationale

The southern Pennines, and indeed the UK as a whole, exhibits a range of blanket bog degradation types. The most obvious of these are the bare peat surfaces and extensive gullies of eroded areas, currently the subject of intensive restoration efforts. However, there are more subtle forms of degradation, such as shifts in vegetation away from typical bog communities. *Molinia caerulea* is perennial grass, and natural component of numerous NVC mire communities (Rodwell, 1991), thought to contribute towards peat formation (Chambers *et al.*, 2007b). Excessive grazing, burning and N deposition can lead to areas becoming dominated by *Molinia*, resulting in reduced biodiversity (Shepherd *et al.*, 2013; Stoneman & Brooks, 1997; Ward *et al.*, 1972). The ability of *Molinia* to withstand these pressures and exploit increased nutrient availability, allows it to expand at the expense of other species; potentially including *Sphagnum* (Shepherd *et al.*, 2013; Taylor *et al.*, 2001). Some success has been achieved in diversifying such swards although this has been limited to heathland species (Marrs *et al.*, 2004). Many of these *Molinia* dominated areas are on deep peat and therefore a return to more typical bog communities would be more appropriate. Hence, the return of *Sphagnum* and a diversity of bog vegetation is required.

These areas represent a new set of challenges to overcome, and may require completely different methods to do so. Bare and eroding peat surfaces present the problems of mobile substrate and severely disrupted hydrological regimes. Peatlands currently dominated by *Molinia* are less likely to have suffered severe erosion because of their continued vegetation cover. Instead, it is likely the vigorous growth and competitive ability of *Molinia* which need to be addressed, alongside long term management of such sites to ensure the continued growth and expansion of *Sphagnum*.

2.5.2 Objectives

Field trials were established to:

Evaluate the potential for Sphagnum reintroduction to Molinia grassland

A series of objectives were identified for the field trials:

- Compare establishment of *Sphagnum* beads between different species on *Molinia* dominated grassland
- Establish associations between successful *Sphagnum* establishment/ growth and the surrounding vegetation
- Compare *Sphagnum* establishment between *Molinia* flailing regimes

2.5.3 Methods

Butterly Hill (SE 0409) forms part of the Marsden Moor estate, a large expanse (~ 2,500 ha) of moorland at the most northerly extent of the Peak District National Park. Three trials were established at Butterly (Figure 17) in October 2010, with final monitoring completed in September 2013. *Sphagnum* beads were applied at the standard experimental rate of 400 m^{-2}, and monitoring followed the methods outlined in Section 2.4. At the time of establishment, *Molinia* litter covered the site as flailing was being conducted.

Trial 1 – Sphagnum species on flailed Molinia

Three replicate blocks (8.5 m × 4 m) were established on flailed *Molinia* at the foot of Butterly hill, each consisting of five 4 m × 1 m treatment strips separated by a 0.5 m gap, sown with an individual species of *Sphagnum* beads, plus an additional control strip which received no treatment. *S. cuspidatum*, *S. fallax*, *S. fimbriatum*, *S. palustre* and *S. papillosum* were the species used.

Trial 2 – Sphagnum on flailed and unflailed Molinia

Beads of *S. fallax* were sown into two 3 m × 3 m plots of dense *Molinia*, adjacent to the plots of trial 1. One of these was immediately flailed whilst the other remained unflailed.

Trial 3 – Sphagnum in dense tussocks of Molinia

To the north of trials 1 and 2, *Molinia* growth had resulted in a far greater number of tussocks, resulting in a network of channels and islands. Three experimental plots were established in this unflailed *Molinia*, consisting of 3 m × 1 m strips sown with *S. fallax*.

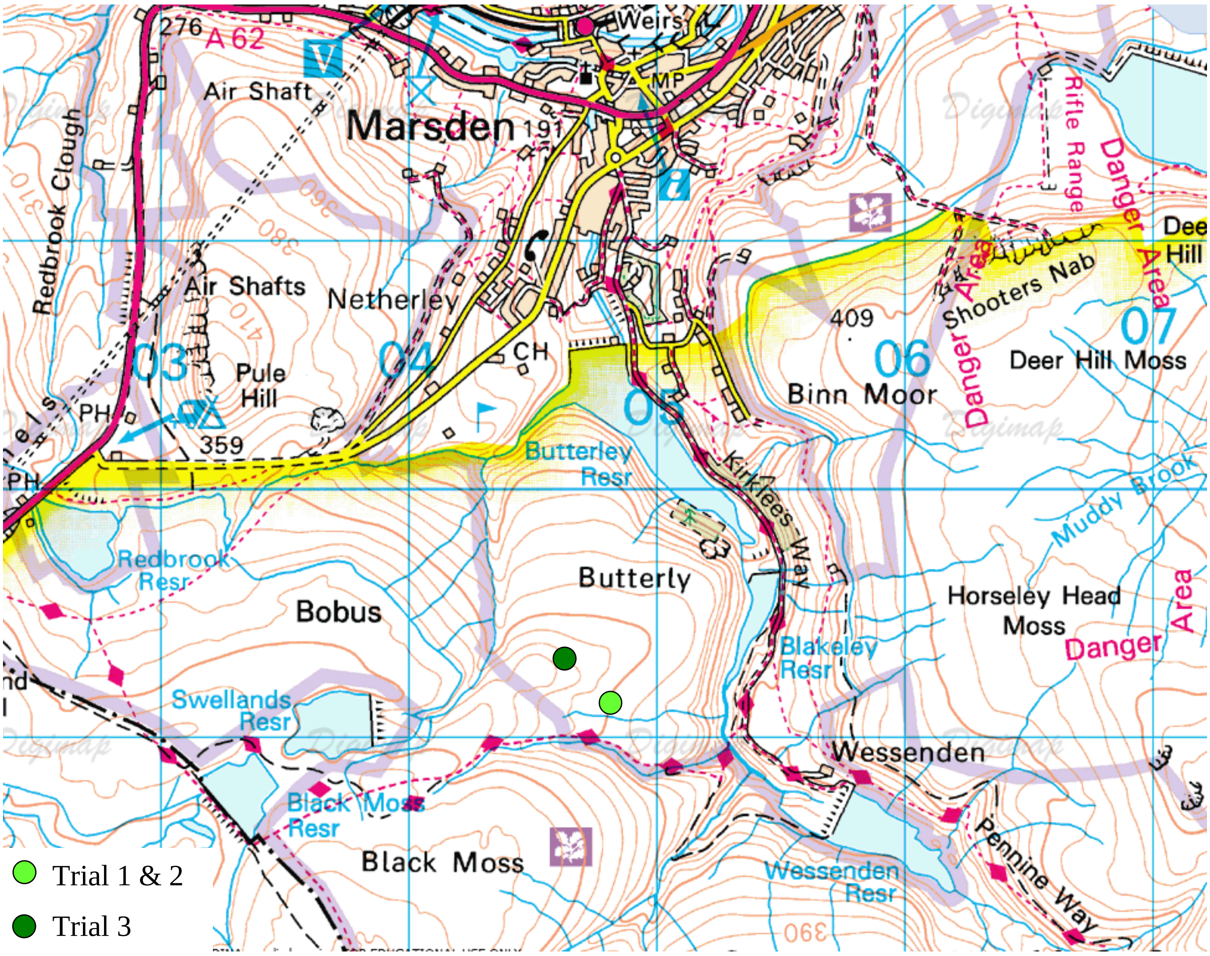


Figure 17 – Butterly and surrounding areas, with the locations of experimental plots marked.

2.5.4 Results and analysis

Trial 1 – Sphagnum species on flailed Molinia

No *Sphagnum* growth was recorded on any of the control treatment strips and so were omitted from further analysis. *S. fallax* was found close to the experimental plots meaning plants of this species could not be reliably identified as originating from the *Sphagnum* beads. Therefore, *S. fallax* was excluded from any further analysis. Statistical analysis was not included due to inconsistency in subsequent flailing between the plots.

The performance of *Sphagnum* beads was found to vary widely between the experimental plots, in terms of both the rate of successful establishment (Table 8) and cover (Figure 18). *S. cuspidatum* performed very strongly in plot 1, but only moderately and then poorly in plots 2 and 3, respectively. Conversely, *S. fimbriatum* performed poorly on plot 1, but at an improved and consistent level on plots 2 and 3. *S. palustre* was the worst performing species, failing to establish on one plot, and having low establishment and cover on the remaining two. *S. papillosum* performed the most consistently across all three plots, with moderate cover recorded in each replicate. Despite the apparent low number of *S. papillosum* beads established in plot 3, their cumulative cover surpasses that of the 20 plants/ clumps found in plot 2.

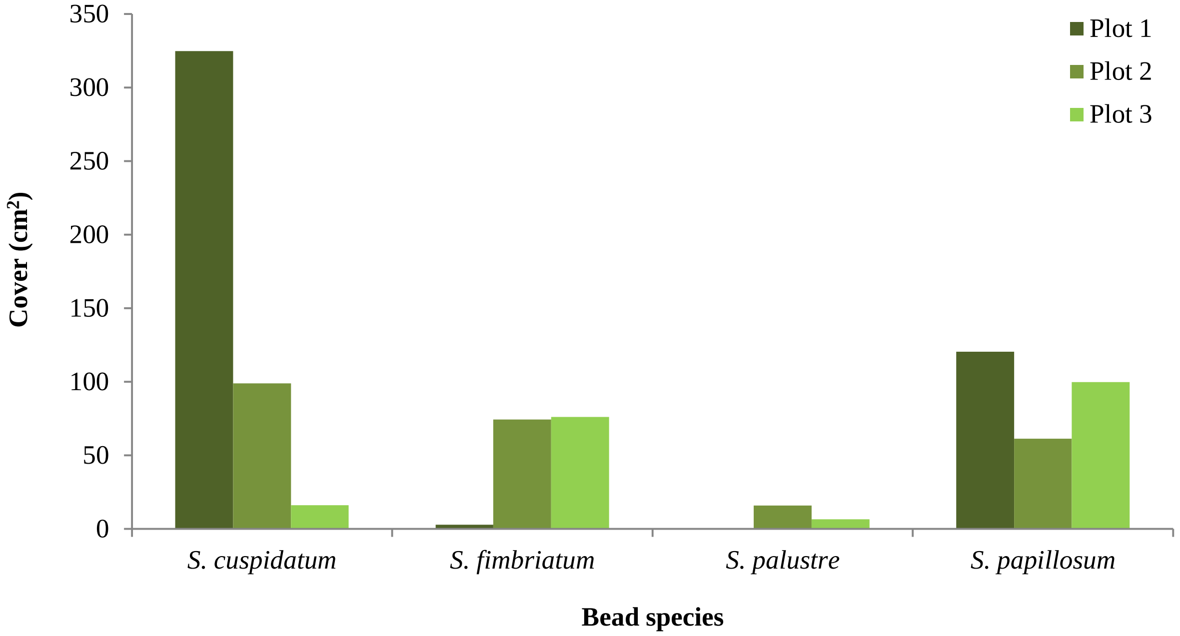


Figure 18 – Total cover (cm^2) of *Sphagnum* species across treatment plots.

Table 8 – Percentage (and number) of successfully established *Sphagnum* beads in flailed *Molinia* plots.

Plot	*S. cuspidatum*	*S. fimbriatum*	*S. palustre*	*S. papillosum*
1	6.13 (98)	0.44 (7)	0	3.88 (62)
2	1.56 (25)	2.13 (34)	1.00 (16)	1.25 (20)
3	0.25 (4)	1.31 (21)	0.25 (4)	0.88 (4)

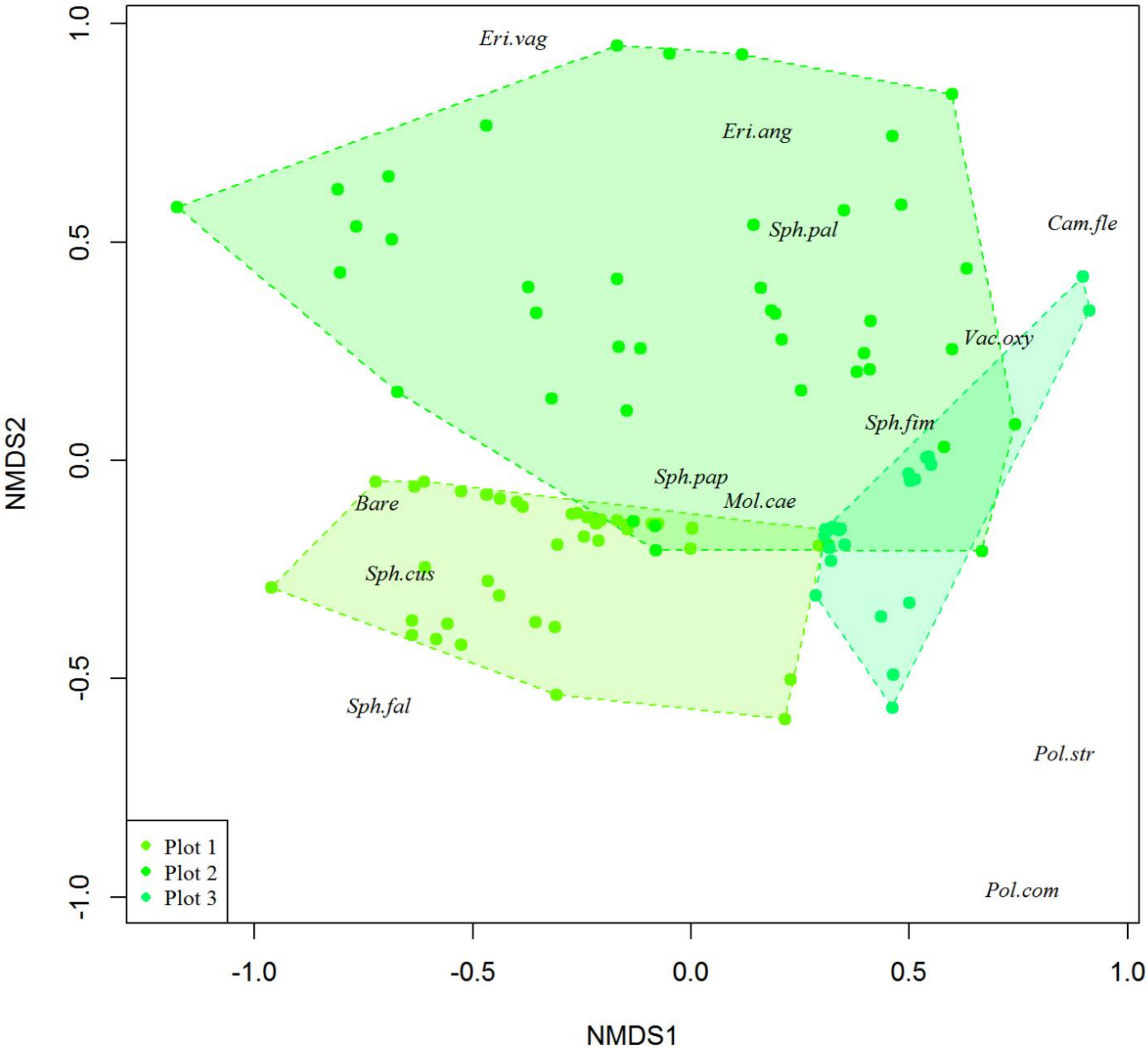


Figure 19 – Non-metric multidimensional scaling (NMDS) ordination of vegetation composition from 25 cm × 25 cm quadrats on flailed *Molinia* containing *Sphagnum*, separated by experimental plot. Species abbreviations can be found in Appendix 1. The most abundant species are added first and where species labels overlap, they have been omitted and the locations marked (+).

Non-metric multidimensional scaling (NMDS) was used to examine relationships between *Sphagnum* growth and associated vegetation. Figure 19 shows NMDS ordination of vegetation (using Bray-Curtis dissimilarity index) recorded from 25 cm × 25 cm quadrats taken on experimental plots sown with *Sphagnum* beads. Cover data were improved by removing rare species (single occurrences), before being

$\log_{10}(x+1)$ transformed (Alday *et al.*, 2011). Quadrats have been grouped according to the plot in which they were found; vegetation composition was found to be different between these groups (PERMANOVA, $P < 0.001$). Plot 1 appears to have a distinct association with *S. cuspidatum, S. fallax* and bare ground. Plot 2 has the greatest variation in vegetation composition, occupying the largest area on the ordination, including species typical of blanket bog, such as *Eriophorum angustifolium* and *Vaccinium oxycoccos*. Plot 3 appears to share associations with bryophyte species, including *Campylopus introflexus*, *Polytrichum commune* and *P. strictum*. *Molinia caerulea* can be found on the ordination where all three plots overlap, demonstrating its occurrence across the trial plots.

Trial 2 – Sphagnum on flailed and unflailed Molinia

Sphagnum was only found in the flailed plot, with 28 plants/ clumps found generating a cumulative cover of 24.41 cm^2 (mean plant/ clump size 2.03 cm^2).

Trial 3 – Sphagnum in dense tussocks of Molinia

When monitored, extensive *Sphagnum* cover was noted in this area. Thus, *Sphagnum* found on these experimental plots could not be reliably attributed to having originated from beads.

2.5.5 Discussion

Trial 1 – Sphagnum species on flailed Molinia

Searching experimental plots for *Sphagnum* was difficult in most cases due to the density of *Molinia*. No *Sphagnum* was found on any of the control strips across all plots, giving a clear indication that plants found on treatment strips were the result of the *Sphagnum* beads applied. However, *S. fallax* and *S. subnitens* were present in considerable quantity and close proximity to the plots, hence *S. fallax* treatments were excluded from analysis. The natural presence of these species at Butterly suggests conditions were suitable for the reintroduction of *Sphagnum*.

There was significant variation in vegetation composition of the trial plots, thought to be due to varying levels of water availability and as a result of the flailing regime in particular areas. Consequently, the response of *Sphagnum* was highly variable between the experimental plots. *S. cuspidatum* was most successful in plot 1, with reducing amounts of cover and plants in plots 2 and 3. This was thought to reflect the decreasing levels of water availability from plot 1 through to 3. However, under conditions of greatest water availability, and in the absence of competition, all *Sphagnum* species would be expected to perform well. *S. papillosum* demonstrates this, growing best in plot 1, but *S. fimbriatum* displays the opposite trend (Figure 18).

The flailing management of *Molinia* at Butterly was thought to offer further explanation of the results observed. These possible distinctions in both water availability and *Molinia* flailing can be seen between the plots on the NMDS ordination (Figure 19). Plot 1 was the wettest, with the greatest levels of *S. cuspidatum* and *S. fallax*, however, this plot only received the initial flailing and therefore has relatively limited floristic diversity, as demonstrated by the small region it occupies on the ordination. This was due to the rapid regrowth and continued dominance of *Molinia*. Similarly, plot 3 had limited species diversity and was only flailed at the start of the trial. This plot was driest, however, this only appeared to impact upon the success of *S. cuspidatum*. Plot 2 was reflailed during the course of the trial, with apparently beneficial effects on the floristic diversity. The shortened sward height and breaks in canopy allowed other species to establish (Figure 20); *Vaccinium oxycoccos*, *Eriophorum angustifolium* and *E. vaginatum* were found almost exclusively on this plot. *S. cuspidatum*, *S. fimbriatum* and *S. papillosum* were all able to grow moderately under these conditions. *S. palustre* performed poorly across all plots. From Figure 20 it is also possible to identify a possible flush across the site, which corresponds with the location of Plot 1. At the time the plots were established, the heavy *Molinia* litter and growth effecetively hid these features, hence they were not originally accounted for.

Figure 20 – Plot 2 showing *Molinia* reflailed since plot setup (left); and *Molinia* regrowth on plot 1, two years after original flailing (right).

Trial 2 – Sphagnum on flailed and unflailed Molinia

Flailing appeared to be influential in the successful reintroduction of *Sphagnum*. In a separate study, cutting *Molinia* in summer was found to restore *Sphagnum* growth (Hogg *et al.*, 1995). The density of *Molinia* and depth of litter severely restricted searching in the unflailed plot. It is possible *Sphagnum* was present in this treatment but it was not possible to find it. Equally, the density of *Molinia* may have proven too dense for the beads to find their way down to the peat surface and moisture below, causing them to succumb to desiccation (Figure 21). The results of trials 1 and 2 suggests the order of bead application and *Molinia* flailing is less important; beads were applied both before and after flailing with no great effect on success. Flailing before sowing was thought to be beneficial since *Sphagnum* beads would be better able to find their way through the dense vegetation canopy and standing litter layer. However, flailing may generate more litter, preventing the beads from making contact with the moist substrate leading to a risk of desiccation. Alternatively, flailing after sowing may prove beneficial by removing the problem of additional material generated during cutting, and may actually serve as a protective mulch, covering the beads and reducing desiccation. Concerns were raised about the potentially damaging effect of flailing upon beads. Indeed, shredded beads were easily found following application and flailing. However, this did not appear to have any detrimental effects on rates of successful establishment. In areas of compromised hydrology, where moisture availability is more variable, the order of flailing and sowing may become more important and the protective properties of *Molinia* mulch more apparent. These results and conclusions will require further verification in larger, replicated trials, due to the single treatment plots used. However, this pilot study demonstrates a potentially important management consideration.

Figure 21 – Flags indicating *Sphagnum* establishment in the flailed plot (left); and *Molinia* density and litter depth in the unflailed plot.

Trial 3 – Sphagnum in dense tussocks of Molinia

Extensive *Sphagnum* was present in the trials located at the base of the hill; this formed part of a much larger body of *Sphagnum* occupying the spaces between tussocks and in flushes. *Sphagnum* found in the plots here could not be verified as originating from the beads. However, it did provide an opportunity, albeit anecdotal, to look at potentially beneficial effects of grazing and flailing alongside natural *Sphagnum* recovery. Flailing undoubtedly breaks up the cover of *Molinia*, providing gaps in the canopy for *Sphagnum* to reach the peat substrate and establish. The flailing of *Molinia*-*Sphagnum* mixed vegetation may be beneficial by providing these gaps whilst simultaneously introducing new fragments of *Sphagnum*. The height and severity of such flailing would be critical; too high and no *Sphagnum* is spread and vegetation canopy breaks not achieved, too low and *Sphagnum* clumps could be severely damaged. This management requires sites to be accessible to agricultural machinery; on very wet or steep sites this may not be possible. Grazing appears to have a similar potential benefit. Sheep had reduced the sward length in some areas, also opening up the canopy. However, it appears to be the light trampling disturbance they create which is beneficial (Smith *et al.*, 2003). Their hooves create small, wet, and often bare depressions and sheep will often transfer strands and fragments of *Sphagnum* from areas of establishment to previously uncolonised areas. Finding this favourable balance could prove crucial, not only to *Molinia*-dominated areas, but also on blanket bog for the benefit of *Sphagnum*.

2.5.6 Conclusion

These initial trials revealed *Sphagnum* grew successfully when *Molinia* was flailed prior to, or during, application of the beads. The presence of *S. fallax* on site made assessment of this species difficult as its origin could not be reliably attributed to the beads. *S. papillosum* performed consistently across replicate plots, whilst *S. cuspidatum* performed best in a single replicate.

Flailing was thought to allow the beads to reach the peat surface and moisture required to grow, although these result require verification through further trials. Both flailing and grazing of areas already containing *Sphagnum* could prove beneficial, opening up the vegetation canopy and allowing fragments of *Sphagnum* to establish. Finding the correct balance between disturbance and benefit will be crucial. Following such management, vegetation changes should be monitored to track the progress not only of *Sphagnum*, but a wider range of bog species, and warn of reversion to *Molinia* dominance.

2.6 Drought trial

2.6.1 Rationale

Despite the lack of a protective cuticle and epidermal layer, desiccation tolerance is a common feature amongst bryophytes (Glime, 2007), although it has been demonstrated that mosses recover more slowly with increasing duration of desiccation up to a point, beyond which they are unable to recover (Dilks & Proctor, 1976). Desiccation tolerance of *Sphagnum* is thought to vary between taxonomic sections, reflecting the typical niches of those species (Wagner & Titus, 1984), however, there is some disagreement. Hummock-forming species are considered desiccation-avoiders, by holding and transporting water more effectively within their tissues, allowing them to maintain photosynthetic activity (Glime, 2007; Hájek & Vicherová, 2014). Species of lawns and pools are likely to be subjected to more frequent and more severe periods of desiccation, due to reduced precipitation and lowered water tables. Thus, species of wet hollows are physiologically more desiccation-tolerant than their hummock-dwelling counterparts (Wagner & Titus, 1984). However, this has only been demonstrated in a single study (Sagot & Rochefort, 1996), with others indicating the contrary (Hájek & Beckett, 2008; Schipperges & Rydin, 1998). Therefore, it could be concluded there are no general differences in desiccation tolerance (survival and recovery) between hummock and hollow species (Rydin *et al.*, 2006).

Desiccation has been repeatedly suggested as a major limiting factor in the successful establishment of *Sphagnum* propagules (see Sections 2.3, 2.4 & 2.5). The resilience of *Sphagnum* beads was brought to the forefront following extended periods of severe weather. Snowfall in the winter of 2009/10 and 2010/11 remained until late spring, followed by prolonged drought during early summer. *Sphagnum* beads are known to become shrivelled and dry before becoming established (Hinde, 2009), however, their tolerance to desiccation has yet to be quantified. The impact of desiccation upon *Sphagnum* propagules is of great concern in the restoration of degraded, hydrologically-compromised peatlands. Desiccation tolerance in some bryophytes, including *Sphagnum*, can be induced through a number of hardening treatments (e.g. Beckett, 1999; Hájek & Vicherová, 2014; Hellewege *et al.*, 1994; Proctor & Pence, 2002). Such manipulations have the potential to improve survival and establishment of moss propagules, with beneficial implications for peatland restoration.

2.6.2 Objectives

A range of physical and chemical treatments were developed by Micropropagation Services Ltd., in an attempt to improve *Sphagnum* bead desiccation tolerance. An indoor trial was established to provide experimental evidence for the following aim:

Evaluate Sphagnum bead treatments to improve drought resistance.

A series of objectives were identified:

- Compare *Sphagnum* growth between bead treatments, drought periods and *Sphagnum* species

2.6.3 Methods

A range of treatments (Table 9) and were applied to *Sphagnum* beads of *S. fallax* and *S. palustre*. Concentrations of chemical treatments were not revealed due to commercial sensitivity. Half trays were half filled with peat from a bare area of Holme Moss, and the treated beads applied. Five beads of each treatment were added in an X configuration, with the treatments arranged randomly on each tray (Figure 22). Trays were then subjected to drought for 0, 7, 14 and 28 days of drought in replicates of three. This process was followed for both bead species, producing a total of 24 trays (2 species × 4 drought lengths × 3 replicates). Trays were placed in a growth cabinet (20 °C day temperature, 800 µmol m^{-2} s^{-1} light, 16 hour day length) during both drought and growing phases. Following drought, trays were watered with deionised water from a spray bottle and covered with plastic to improve moisture conditions. After 3 months growth, *Sphagnum* plants were individually harvested, dried at 40 °C for 48 hours, and their dry mass recorded. Peat was cleaned from the *Sphagnum* using a mounted needle and forceps, whilst submerged in water. Great care was taken to ensure no *Sphagnum* tissue was lost during the process and all peat was removed.

Table 9 – *Sphagnum* bead treatments used in the drought trial.

Treatment	*Description*
Standard	Standard beads, incubated following production
PEG 100	Standard beads treated with polyethylene glycol 100
PEG 100 + Wax	Standard beads treated with PEG 100, coated with wax
PEG 50	Standard beads treated with PEG 50
PEG 25	Standard beads treated with PEG 25
ABA	Standard beads treated with abscisic acid
ABA + Dry to 50 % + Wax	Standard beads treated with ABA, dried to 50 % of mass, and coated with wax
Dry to 50 % × 3	Standard beads dried to 50 % mass three times, rehydrated between
Dry to 50 %	Standard beads dried to 50 % mass
Dry to 50 % + Wax	Standard beads dried to 50 % mass, coated with wax
Dry to 50 % + Wiltpruf	Standard beads dried to 50 % mass, treated with anti-transpirant (aqueous terpene emulsion)
Fresh	Standard beads, no incubation period

Figure 22 – Arrangement of *Sphagnum* bead treatments on experiment trays. Treatments form an X configuration in a 4 × 3 matrix.

2.6.4 Results and analysis

Sphagnum beads were severely affected by 7 days of drought, leading to reduced growth and, ultimately, the death of propagules. After 14 days drought, all beads had succumbed to desiccation, hence they are excluded from further analysis.

Rank ANOVA was used to assess the effects of species, drought length and bead treatment, and all interaction terms. All were found to be highly significant (Table 10). *S. fallax* produced greater dry mass than *S. palustre* across almost all bead treatments and both drought durations. Drought reduced the dry mass across all treatments in both species. The significant interaction effect terms indicate the varying differences in *Sphagnum* growth between the *Sphagnum* species, bead treatments and drought durations. Bonferroni-corrected pairwise comparisons were used to identify the worst performing of all the bead treatments. The mean dry *Sphagnum* mass of these treatments was calculated to be 1.4 mg and assumed to represent the quantity of *Sphagnum* contained within each bead. This value has been added to Figure 23 to enable visual comparison between bead treatments; a *Sphagnum* bead treatment with mean dry mass above this threshold was presumed to indicate growth of the propagule.

With no drought, *S. fallax* produced greater biomass than *S. palustre* across all bead treatments. Indeed, there are numerous treatments where *S. palustre* dry mass was only marginally greater than the 1.4 mg threshold. These were treatments including wax which may explain their slightly greater mass over non-waxed beads. *Fresh S. palustre* beads were the only treatment which grew with any success. *S. fallax* also grew largest from *Fresh* beads, but unlike *S. palustre,* growth occurred from nearly all other bead treatments. *Standard* beads were the only exception to this, performing poorly in both species. *S. fallax* bead growth was negatively affected by the treatments, with drying treatments producing the least biomass, except for *ABA + Dry to 50 % + Wax* treatments.

Table 10 – Effect of species, drought length and bead treatment upon *Sphagnum* dry mass. Significance of effects analysed using Rank ANOVA (F).

Terms	*F*	*P*
Species	296.88	< 0.001
Drought length	351.99	< 0.001
Bead treatment	36.00	< 0.001
Species * Drought length	125.30	< 0.001
Species * Bead treatment	6.91	< 0.001
Drought length * Bead treatment	12.32	< 0.001
Species * Drought length * Bead treatment	6.17	< 0.001

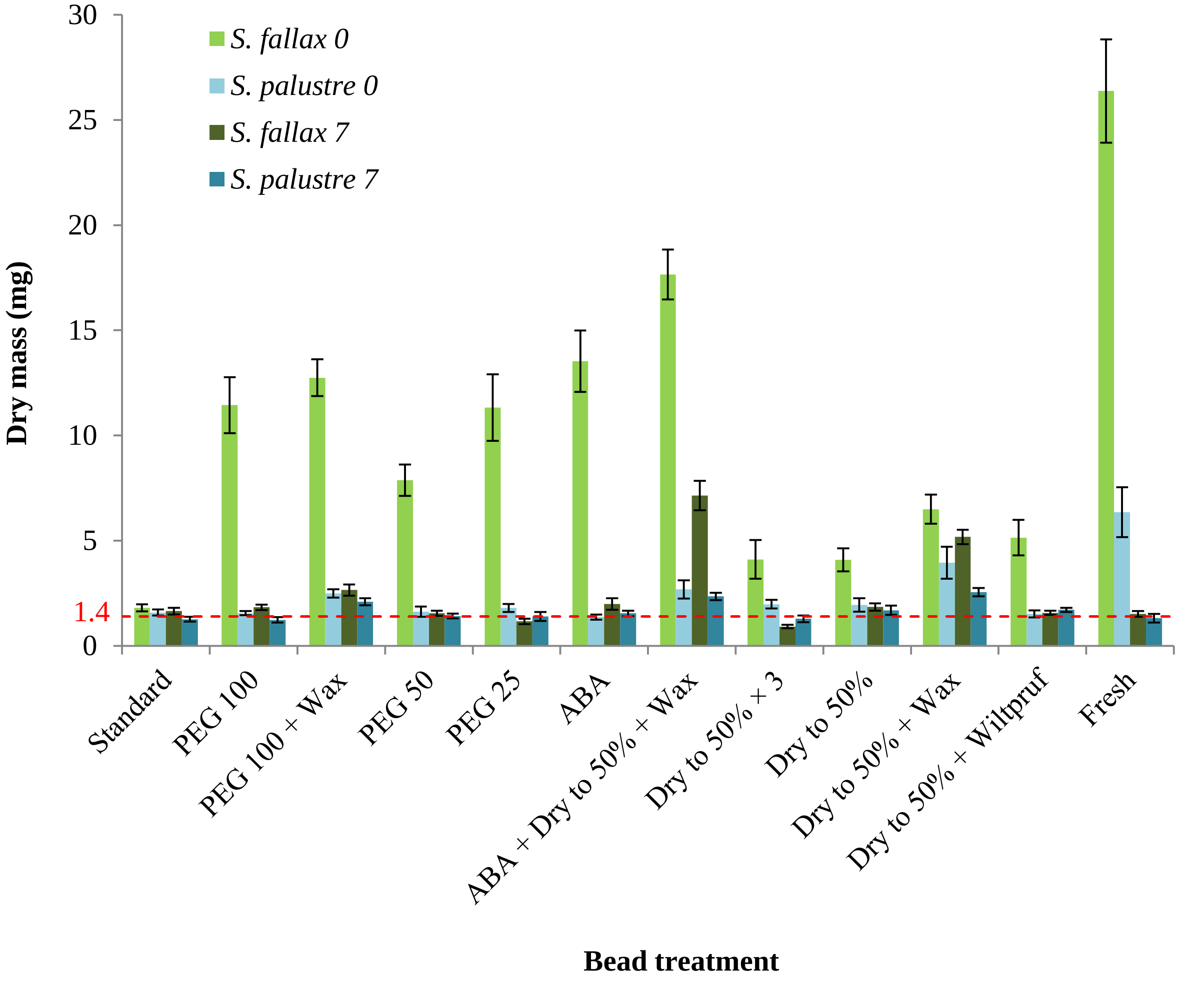


Figure 23 – Mean (± 1 SE) dry mass (mg) of plants grown from a range of treated *Sphagnum* beads. *S. fallax* and *S. palustre* were subjected to drought for 0 and 7 days. The threshold value of 1.4 mg has been added.

Following 7 days of drought, *Sphagnum* growth was severely affected in both species and across all treatments. Very little *S. palustre* growth was recorded following drought; *Dry to 50 % + Wax* was the only treatment which realistically represented any growth. Those *S. palustre* treatments with mass above the 1.4 mg threshold contain wax, as described above. *S. fallax* growth was also strongly influenced by drought, with numerous treatments succumbing to desiccation. Many treatments which performed well when not subject to drought were unable to grow, with *Fresh* beads displaying the most striking contrast. Only those treatments which included wax provided any protection against desiccation. Indeed, these were the only beads to show convincing signs of growth following drought.

2.6.5 Discussion

Sphagnum beads were strongly affected by drought, with reductions in growth across all treatments. Drought conditions indoors were thought to be more severe than in the field, with both increased temperature and reduced humidity levels. These two measures dictate the speed at which water is depleted from the surface of the plant tissue, and therefore the severity of the desiccation experienced (Oliver *et al.*, 2005). However, evidence of *Sphagnum* recovery following drought is unclear. Desiccation at high humidity has proven fatal (Abel, 1956; Clymo, 1973), whilst recovery from drying at much lower levels of humidity has also been reported (e.g. Sagot & Rochefort, 1996). Further to this, beads contain shredded fragments of tissue with a proportionally high surface area, and so are vulnerable to desiccation. In the field, the substrate is unlikely to become totally dehydrated due to their larger size and water contained within the peat body. Hydraulic conductivity within the peat and transpiration stream of vegetation prevents all but the upper most layers from drying out.

The *Sphagnum* tissue contained in the beads is grown under equable conditions to stimulate growth and therefore the greatest amount of biomass. However, under these optimal conditions, any desiccation tolerance present in the initial sample taken from the field is lost (Hájek & Vicherová, 2014). This may explain the severe effect of 7 day drought on *Fresh* beads of both species.

The effect of desiccation in bryophytes is thought to be related to the frequency of hydration/ dehydration, the duration of hydration/ dehydration, and the degree and rate of water loss (Glime, 2007; Norris, 1990). *Sphagnum* is considered to be one of the least desiccation tolerant mosses (Abel, 1956), however, tolerance can be induced. Species typical of lawns and hollows are thought to be more physiologically desiccation tolerant (Wagner & Titus, 1984) than hummock species, which avoid desiccation by having higher water retention and conductivity (Robroek *et al.*, 2009). Thus, it is likely that *S. fallax* has greater potential for desiccation tolerance being induced than *S. palustre*, and hence grew better following drought and responded to some bead treatments. The physiological adaptations of *S. palustre*, and other hummock-forming species, would be irrelevant in their shredded state within the beads.

The difference in performance between the two species may also be simply a result of a poor batch of beads; a known occurrence in previous trials. Due to the small scale and manual nature of bead production, there is considerable opportunity for variation in quality, and may also explain the lack of growth of either species from *Standard* beads without exposure to drought.

The growth of *Sphagnum* was negatively affected by the treatments applied to the beads when compared to fresh beads, presumably as a direct consequence of the physiological stress exerted upon them. Polyethylene glycol (PEG) induces osmotic stress (Marschall & Borbély, 2011), abscisic acid induces cellular protection mechanisms (Proctor *et al.*, 2007), whilst drying removes water from the plants, and application of wax and anti-transpirant affect water movement in to and out of plants.

Following 7 days drought, the greatest growth of *S. fallax* came from *ABA + Dry to 50 % + Wax* and *Dry to 50 % + Wax* bead treatments. Drying by itself did not produce any beneficial effects and so we can conclude the application of wax was the beneficial treatment. However, *PEG 100 + Wax* did not grow as successfully as the aforementioned treatments, indicating a potential interaction effect. No information from the manufacturer was available on the treatment of the beads; i.e. time taken to dry to 50 %, strength of ABA applied, order of treatments in multi-treated beads. Drying is known to induce desiccation tolerance in bryophytes, but its efficacy is dependent upon several factors, including drying rate. Thus, if beads were dried to 50 % slowly, this may have proved beneficial. If wax treatments were applied before drying then this would help to limit the amount of water lost, also increasing the drying period. ABA has been demonstrated to increase desiccation tolerance in bryophytes, including *Sphagnum* (Marschall & Borbély, 2011; Oliver *et al.*, 2005), however, this effect was not observed. Again, the interactive effects of ABA, drying and wax were greater than their individual effects.

2.6.6 Conclusion

Drought was found to be a critical factor in the successful establishment of *Sphagnum* from beads. A drought period of 7 days in indoor growth cabinets was sufficient to greatly reduce, or in many cases prevent, *Sphagnum* growth. Tolerance to drought was increased by treating propagules with wax, thought to be due to reduced water loss. These treatments illustrate the potential for increasing resistance of beads, with numerous other possibilities to try; e.g. increased bead size, or increased tissue fragment size. Whilst this indoor trial cannot replicate the complexities of *in situ* experiments, it clearly demonstrates the acute effect of drought upon *Sphagnum* beads and their requirement for moisture.

2.7 General discussion

2.7.1 Success

The success of *Sphagnum* reintroductions appeared to be strongly influenced by moisture availability, surface stability, and species used. Moisture availability was strongly implicated despite not being measured in any of the experimental work, and was thought to be highly influential as the propagules of *Sphagnum* are prone to desiccation due to their small size. In some field plots, the availability of water was evident in the form of a high and stable water table, at or just below the peat surface. Examples included plots at Holme Moss on original bog vegetation, and plots at Butterly around the foot of the hill. In these locations, *Sphagnum* established and grew well compared to drier areas of the experimental sites. The vegetation of these areas also indicated hydrological conditions were likely to be suitable; e.g. dominated by *Eriophorum angustifolium* (Hill *et al.*, 1999). However, moisture availability was not always so obvious. The most successful plots were located on very shallow peat (~ 2 cm), unlikely to sustain a water table, vegetated by atypical bog species. The success of *Sphagnum* here was thought to be due to a gentle channel in which these plots were situated. The topography evidently gathered water from the surrounding area, hence the lack of remaining peat due to erosional losses. Nutrients were also thought to be concentrated here, giving rise to the minerotrophic species found here.

Sphagnum reintroduction was found to be almost impossible on areas of eroding, bare peat. Without vegetation, the peat surface is prone to rapid erosion (Worrall *et al.*, 2011), and subsequent removal and/ or burial of *Sphagnum* propagules, whilst the sun and wind causes the surface to dry rapidly. Many of these eroded areas have severely disrupted hydrological regimes, amplifying the risk of desiccation. Vegetation helps to mitigate these effects by stabilising the peat substrate and improving microclimatic conditions, with taller vegetation, such as grasses and dwarf shrubs, reducing air movement, increasing shading and interception of occult precipitation. Hence, on revegetated substrates *Sphagnum* was able to establish and grow, although this seemed to only occurred where propagules could make contact with the underlying peat substrate, which retained moisture longer than the vegetated surface. Whilst *Sphagnum* is able to establish and grow in these hydrologically-compromised conditions, propagules are undoubtedly more successful where moisture levels and water availability are higher (e.g. Hinde, 2009).

Following restorative treatments (lime, fertiliser, heather brash and grass seed), previously bare areas can become completely covered with a carpet of *Hypnum* moss, preventing the *Sphagnum* from making this contact. Propagules held on the surface of vegetation will be vulnerable to desiccation, as on bare peat surfaces. This was observed across many trial plots, dominated by *Hypnum*, *Deschampsia* and *Molinia*. Trials on *Molinia* provided the most striking illustration of the detrimental impact that dense vegetation can have on the success of *Sphagnum* reintroduction. Flailing improved establishment, thought to be a result of breaks in cover of both plants and litter, allowing access to the moist, underlying substrate. Repeated cutting to a very short sward also improved the species diversity of plots without affecting the stability of the substrate. Such management may prove beneficial to *Sphagnum* establishment in other areas, such as those dominated by dense *Eriophorum angustifolium*.

The disrupted hydrology of many areas of degraded blanket bog means that much of the *Sphagnum* reintroduced is likely to experience some degree of drought and/ or desiccation, both as propagules and established plants. Simulated drought in an indoor experiment was found to severely affect the success of *Sphagnum*, although this effect was reduced through hardening treatments. *Sphagnum* species responded differently to both drought and hardening treatments, with *S. fallax* outperforming *S. palustre*.

The legacy of industrial pollution contained within the peat appears to continue to influence the performance of *Sphagnum*. Peat taken from Holme Moss had a significantly negative impact on the growth of *Sphagnum* propagules. Initial growth from *Sphagnum* mulch was slow, discoloured and sickly. However, over time much healthier plants developed, including typical ombrotrophic species, such as *S. capillifolium* and *S. papillosum*. The early *Sphagnum* tissue appeared to isolate the newer growth from the polluted substrate, potentially also binding and immobilising harmful ions to its tissues. The presence of any *Sphagnum* species will undoubtedly improve conditions through increased moisture availability (Van Breemen, 1995a). In the field, mulch propagules established well on revegetated substrates, although concerns of sustainability, application and possibly biosecurity rendered them second choice to *Sphagnum* beads. Mulch may provide a more rapid means of generating *Sphagnum* cover on small areas, where erosion and desiccation risks are considered lower. Smaller amounts would therefore be needed, increasing the chances of local sources meeting the quantity requirements. The combination of challenging environmental conditions proved to have differential effects on the *Sphagnum* species under test. *S. fallax* performed better than *S. capillifolium*, *S. fimbriatum*, *S. palustre* and *S. papillosum*, with *S. cuspidatum* only gaining an advantage in the wettest of conditions. The combination of desiccation and pollution tolerance exhibited by *S. fallax* resulted in the best performance of the species under test, and therefore would be suggested for future reintroduction works. Conversely, *S. palustre* performed consistently poorly.

The success of any *Sphagnum* reintroduction will only accurately be determined over the years to come. However, there are several uncertainties regarding the persistence and expansion of reintroduced *Sphagnum*. Whilst *Sphagnum* was able to establish on some of the revegetated, yet hydrologically-compromised areas, the longer term potential of these propagules to generate significant cover is unclear. Occult precipitation and irregular rainfall may or may not be sufficient to sustain increased *Sphagnum* cover and growth. The increased presence of *Sphagnum* may further improve conditions and promote growth, forming a positive feedback loop (Clymo & Hayward, 1982; Van Breemen, 1995a). The application of *Sphagnum* propagules is likely to occur alongside on-going revegetation works, with continued applications of lime and fertiliser required to maintain the stabilised peat surfaces. These additions are known to adversely affect *Sphagnum* growth (Clymo, 1963; Hinde, 2009), raising questions of longer term compatibility. The impact of these treatments upon reintroduced *Sphagnum* is currently under investigation, using some of the field plots established for this research.

2.7.2 Monitoring

The work presented here is intended to illustrate the potential for *Sphagnum* reintroduction to degraded peatlands, hence the amplified rates of propagule application and intensive monitoring regime employed. As part of landscape scale *Sphagnum* reintroduction, application rate of propagules will be an order of magnitude lower due to cost, whilst treatment areas will be vast compared to the trials surveyed; > 1000 ha have been targeted for application, compared with 648 m^2 total area of the trials of Section 2.4). Monitoring of areas treated with *Sphagnum* propagules is essential to assess the success of these reintroductions. However, monitoring effort, in terms of time and energy expended, must be balanced against the diminishing number of new *Sphagnum* plants found. The small experimental plots established were searched intensively, with the aim of finding all *Sphagnum* plants successfully established from the propagules applied. From monitoring experimental plots with dense vegetation, it is clear that a 100 % discovery rate is not possible without spending a grossly disproportionate amount of effort on the task. *Sphagnum* growth can vary from miniscule young plants (< 2 mm in diameter), to much larger (> 60 cm^2) patches of multiple plants, with obvious implications when assessing the successful establishment of *Sphagnum* within an effective monitoring framework. Thus, the need to develop an efficient but accurate monitoring strategy is crucial, allowing the success of *Sphagnum* propagule applications to be assessed.

Two monitoring methods were considered, along with their impact on perceived success, using data from Section 2.4 and criteria prescribed by the Moors for the Future Partnership (Table 7, Section 2.4.5). The two scenarios considered here were used to demonstrate the effect of reduced monitoring effort on assessment accuracy (Table 11). *Sphagnum* plant size was used as a proxy for monitoring effort in these examples, with larger plants being easier to find therefore representing reduced effort.

Reduced monitoring effort will inevitably lead to fewer *Sphagnum* plants being found, however, the scale of this reduction is striking (Figure 24). Data collected from experimental plots in Section 2.4 was used to demonstrate this. Plots were searched intensively, recording plants as small as 2 mm in diameter, producing a total of 795 individual records. From this, the size and number of records were plotted, demonstrating the rapid decrease in records with increasing *Sphagnum* size. Thus, the impact of reduced monitoring effort could be severe. In this scenario, increasing the minimum noticeable *Sphagnum* size to 10 mm has the effect of reducing the number of records by 77 %, and at 30 mm more than 95 % will be ignored (Table 11).

Table 11 – Comparison of three monitoring scales on *Sphagnum* discovery, using data from Section 2.4.

Monitoring scale	*Size of Sphagnum to notice (mm)*	*Area covered (mm^2)*	*Records exceeding noticeable size*	*Percentage of total records (%)*
Intensive	2	3.14	795	100
Hands and knees	10	78.54	182	22.9
2 pence piece	30	706.86	36	4.5

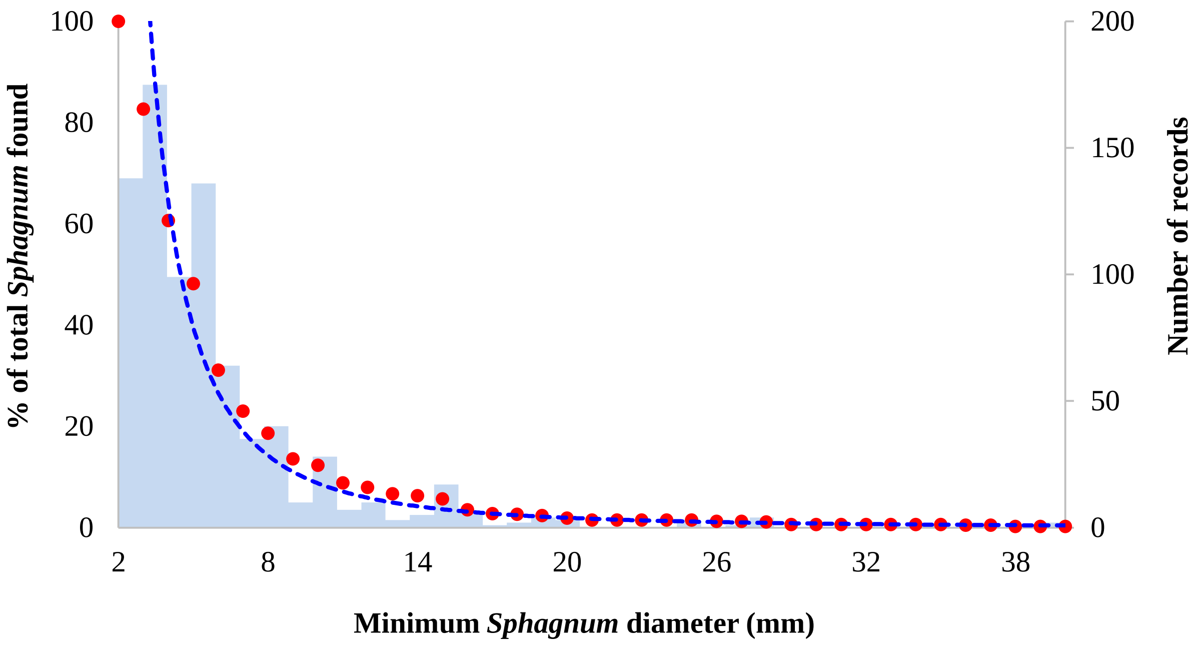


Figure 24 – Number of *Sphagnum* records with increasing noticeable size, used as a proxy for reduced monitoring effort. Points represent % of *Sphagnum* found at a given minimum diameter, and histogram of number of plants at each size. Data from field trials results of Section 2.4.

Using success criteria established by the Moors for the Future Partnership (Table 7), 10 experimental application strips (out of 162) were categorised as successful when including *Sphagnum* records of all sizes. By including only *Sphagnum* of 10 mm or greater, the number of successful treatment strips falls to 3, and at 30 mm or greater there would be none.

Vegetation type and time elapsed since application were found to strongly influence the amount of effort required to find *Sphagnum*, and therefore have the greatest potential to affect accuracy of monitoring. An open canopy made *Sphagnum* easier to find, as did a contrasting colour of the substrate or surrounding vegetation. *Sphagnum* was often found within stands of dense vegetation, such as *Eriophorum angustifolium*, which may have further consequences for monitoring. Increased time since application allowed *Sphagnum* plants to become well established, larger, and therefore easier to find. However, given the need to qualify and quantify the success of such restoration treatments, time frames are likely to restrictive. The need for long term monitoring was clearly illustrated when resurveying plots established by Hinde (2009). Established in 2008 on Holme Moss, *Sphagnum* covered ~ 80 % with little indication of this success in the intermediate years (Figure 9, Section 2.3.5). The survey methods employed will vary according to the features of a given restoration site, taking into account the factors discussed. Early surveys (< 1 year since sowing) are likely to yield few results, but may prove an ideal opportunity to identify areas likely to support significant *Sphagnum* growth. Other areas should not be excluded from future surveys since atypical areas may prove to be extremely successful, as was the case in this work. To avoid expending unnecessary time and resources, subsequent surveys should be made no more frequent than annually as growth rates are likely to be slow, even in the most equable of field conditions.

2.8 Conclusion

Sphagnum can be successfully reintroduced to areas of degraded blanket bog, producing significant cover in some instances, within the space of three years. The primary constraints on successful establishment and growth of propagules were thought to be moisture availability and surface stability. The small pieces of *Sphagnum* tissue which comprised the beads and mulch were vulnerable to desiccation and required high levels of moisture availability. Successful propagules were all found in contact with the underlying peat substrate, thought to be a crucial source of moisture in areas of compromised hydrology. *Sphagnum* application was a complete failure on areas of bare peat, where rapid rates of erosion and harsh microclimatic conditions removed, buried or otherwise killed propagules applied. *Sphagnum* beads were considered well suited propagule for landscape scale reintroduction, offering a sustainable source of material whilst giving control over application rates and choice of which species to use. *S. fallax* was the best performing species, appearing tolerant to the legacy effects of industrial pollution and desiccation (Grosvernier *et al.*, 1997a). Crucially, *Sphagnum* reintroduction is compatible with revegetation measures currently employed. The application of lime and fertiliser did not appear to severely affect the performance of reintroduced *Sphagnum*, with successful establishment and growth recorded on previously bare peat. Succession and diversification of *Sphagnum* could follow on a longer time scale, moving towards more typical ombrotrophic species (Buttler *et al.*, 1998; Wheeler & Shaw, 1995). Increased experimental scales and replication, accompanied by long term monitoring will provide a more accurate assessment of success, as *Sphagnum* propagules are known to appear dormant before beginning to grow. As in their formation, time will prove critical in the restoration of blanket bogs.

Chapter 3 – Biogeochemical influences on *Sphagnum*: a comparison of some UK bogs

3.1 Introduction

The southern Pennines are the most degraded blanket bogs in the UK, due, in part, to the deposition of industrial pollution over the last *c.* 250 years. As a habitat, blanket bog is particularly susceptible to the effects of air pollution (see Chapter 1), with the southern Pennines especially so given its proximity to major conurbations of northern England. The effects of individual pollutants upon bog vegetation, and *Sphagnum* in particular, have been well demonstrated through experimental applications, with trials conducted *in situ* (e.g. Sheppard *et al.*, 2014) and under controlled conditions (e.g. microcosm experiments (Ferguson *et al.*, 1978)). Over the last 50 years or so, there have been vast improvements in air quality, and subsequent reductions in deposition of most pollutants to these areas. Concentrations of these contaminants are now below levels known to be toxic to blanket bog vegetation communities (Press *et al.*, 1986), including the most vulnerable species, such as *Sphagnum* and other bryophytes (Ferguson *et al.*, 1978).

Sphagnum mosses were all but eradicated from much of the southern Pennines, with their demise generally attributed to increases in air pollution. However, in sheltered pockets across the region, fragments of *Sphagnum* managed to persist, with minerotrophic species being the most common (Tallis, 1964), and occasional ombrotrophic species found (Studholme, 1989). Improvements in air quality and concurrent land management reforms have resulted in increased *Sphagnum* cover (Caporn *et al.*, 2006; Carroll *et al.*, 2009), although some may be due to introduced material in heather brash used in restoration works (see Chapter 2). However, this appears to be occurring very slowly and only in some instances. Increases in cover seem limited to expansion of remnant patches by asexual, vegetative reproduction, or through physical disturbance and subsequent dispersal of plant fragments (e.g. foraging birds/ mammals, overland water flows), both known methods of propagation (Andrus, 1986; Cronberg, 1993). *Sphagnum* produces vast numbers of spores (Sundberg, 2005) which can be dispersed over long distances, demonstrating the potential for widespread recolonisation following disturbance (Clymo & Duckett, 1986; Jones, 1986; Sjörs, 1949; Soro *et al.*, 1999), as recorded in areas affected by summer drought and fire (Andrus, 1986; Popov, 2000). Vegetative propagation is thought to be the most important means of both maintaining and increasing presence at a site (Andrus, 1986; Cronberg, 1993).

The continued lack of *Sphagnum* prevalence and cover in the southern Pennines indicates limiting factors are still influencing the establishment, growth and reproduction of these species. Whilst there are large swathes of blanket bog in poor condition, actively eroding with severely disrupted hydrological regimes, there are also areas where the higher plant vegetation and hydrology approaches that of good quality bogs. If hydrology were the only constrain on *Sphagnum* success, these areas should prove suitable. However, with only infrequent and small patches of *Sphagnum* to be found, it seems these areas are extremely slow to be colonised. The presence of appropriate conditions yet widespread absence of *Sphagnum* suggests biogeochemical conditions may be influential. The widespread absence of

Sphagnum may therefore represent a legacy effect of the intense air pollution, and subsequent deposition, these areas suffered.

Air pollution is widely accepted as a major driver of degradation in numerous ecosystems, particularly bogs (e.g. Bobbink *et al.*, 1998; Lee, 1998). Acute effects of pollution upon bog vegetation species have been well documented, but rarely in real world scenarios. Pollutants are generally applied as high concentration, individual treatments to vegetation over short durations (e.g. Brown & Wells, 1990; Ferguson *et al.*, 1978), with far fewer long-term experimental manipulations (e.g. Evans *et al.*, 2006a; Sheppard *et al.*, 2014). Whilst useful in understanding the effect of a given pollutant, their wider relevance is questionable. A raft of additional, compounding factors found in the field may reduce the broader applicability of any conclusions. Bogs are unlikely to receive input of a single pollutant in isolation, but rather a cohort of pollutants from a particular source, or several transported long distances from multiple sources. The effect of a given pollutant will depend upon a range of biotic and abiotic factors. Whilst an experiment in controlled conditions may serve to remove some of this abiotic variation, in doing so, it is likely to reduce the relevance of such a trial to natural scenarios. Similarly, *in situ* experiments may fail to unpick the myriad of abiotic and biotic factors at play, leading to inaccurate conclusions being drawn.

Chemical elements of interest in such studies include essential plant nutrients, balances of which can be affected by perturbations to natural nutrient cycling by anthropogenic activities, such as industrial processes and release of reactive chemical species into the environment. Emissions of substances hazardous to human and environmental health, such as numerous heavy metals are also studied extensively (e.g. Harmens *et al.*, 2013; RoTAP, 2012). Table 12 provides a summary of elements of potential ecological significance in ombrotrophic peatland vegetation, their roles and effects as nutrients or pollutants. Broadly speaking, elements can be separated into essential macro- and micro-nutrients, and contaminants/ pollutants. Macronutrients are required in large quantities, whilst only small amounts of micronutrients are needed. In excess, both macro- and micro-nutrients are capable of becoming toxic, whilst pollutants, such as heavy metals are frequently potent toxins.

Table 12 – Summary of elements of potential ecological significance in ombrotrophic peatlands.

Element	*Nutrient role*	*Details*	*Source*
Aluminium	No	Can stimulate plant growth, although it has no beneficial action in plant metabolism; causes suppressed nutrient uptake and translocation.	(Blamey *et al.*, 2015; Foy, 1988; Raynal *et al.*, 1990)
Arsenic	No	Inhibits essential metabolic enzymes and is moderately toxic to plants; toxicity depends upon speciation, with inorganic forms more toxic than organic.	(Harmens *et al.*, 2008)
Barium	No	Phytotoxic, causing reduced growth and photosynthetic activity. Ba, Ca and Sr have similar biogeochemical behaviour in some ecosystem processes. Concentrations in ombrotrophic peat mirror the concentrations of other lithogenic elements and can be used as a surrogate for the abundance of mineral matter.	(Baes & Bloom, 1988; Krachler & Shotyk, 2004; Suwa *et al.*, 2008)
Cadmium	No	Has a medium, direct toxicity, but is a cumulative poison. Can replace other essential metals in biological systems, where it binds more strongly	(Harmens *et al.*, 2008)
Calcium	Macro	Functions in cell signalling, membranes and walls, activation of some enzymes. Displaced by increased soil acidity, causing accumulating on surface and eventually killing *Sphagnum.*	(Kilham, 1982; White, 2015)
Cobalt	No	Toxic to plants at high concentrations, affecting growth and metabolism.	(Nagpal, 2004; Palit *et al.*, 1994)
Copper	Micro	Involved in many enzyme systems and proteins. Causes oxidative stress at higher concentrations and is toxic to vascular plants, and very toxic to algae; highly phytotoxic above micro-molar concentrations	(Harmens *et al.*, 2008; Marschner, 2012; Yruela, 2005, 2008, 2015)

Element	*Nutrient role*	*Details*	*Source*
Iron	Macro	Role in enzymatic reactions. Fe toxicity has been recorded, but as an element is less potent than Mn or Al.	(Allen, 1989; Barker & Stratton, 2015)
Lead	No	Replaces other biologically important metals, such as Ca, Fe and Zn in enzymatic reactions, impairing their function. Pb in soluble ionic form is toxic to most organisms.	(Harmens *et al.*, 2008)
Magnesium	Macro	Used in metabolic processes and growth. Displacement through increased acidity can lead to accumulation on *Sphagnum* surface and subsequent death.	(Grzebisz, 2015; Kilham, 1982)
Manganese	Micro	Involved in proteins, enzyme function and plant growth, including some of the reactions required for photosynthesis and nitrogen metabolism.	(Allen, 1989; Eaton, 2015)
Molybdenum	Micro	Catalyses certain enzymatic reactions, particularly nitrate reductase.	(Allen, 1989; Kopsell *et al.*, 2015)
Nickel	Micro	Used in enzymes and proteins. At higher concentrations, Ni is toxic to most plants and fungi.	(Harmens *et al.*, 2008; Wood, 2015)
Nitrogen	Macro	Used for proteins and nucleic acids. Compounds of N at high concentrations have detrimental effect on *Sphagnum*; e.g. NH_3 is toxic, and NH_4^+ reduces growth.	(Pilbeam, 2015a; Rudolph *et al.*, 1987; Sheppard *et al.*, 2013)
Phosphorus	Macro	Key role in cell metabolism, particularly in ATP-ADP cycling. Has significant interactions with micronutrient metals in soil.	(Bieleski & Ferguson, 1983; Hopkins, 2015)
Potassium	Macro	Used in enzyme activation, protein synthesis and osmotic function.	(Fageria, 2015)

Element	*Nutrient role*	*Details*	*Source*
Sodium	No	Role in plants by replacing K in some instances, but smaller ionic diameter prevents it from being used in critical systems; e.g. charge balance, enzyme activation and osmotic effects.	(Schubert, 2015)
Strontium	No	Uptake by plants may compete with Ca, Mg, K and Na, due to similar ionic radius.	(Dawson, 1985; Kabata-Pendias, 2010)
Sulphur	Macro	Used for growth and physiological functioning of plants, and is contained in a range of lipids proteins and other compounds. Products of sulphur (HSO_3^- especially) are toxic to *Sphagnum*.	(Allen, 1989; Ferguson & Lee, 1980; Grant & Hawkesford, 2015)
Tin	No	Phytotoxic in solution culture to higher plants.	(Cohen, 1940)
Titanium	No	Induces chlorosis, necrosis and stunting in higher plants..	(Wallace *et al.*, 1977)
Vanadium	No	High rates of supply are harmful to plants, and can induce Fe deficiency. Products of V (vanadate) can inhibit ATPases.	(Arnon & Wessel, 1953; Pilbeam, 2015b)
Zinc	Micro	Role in metabolic function and enzyme structure; required for maintaining biomembranes. At high concentrations it is moderately toxic to plants, and excessive uptake can induce deficiencies in other metals, such as Cu, Fe and Mg.	(Barker & Eaton, 2015; Harmens *et al.*, 2008)

3.2 Aim and objectives

3.2.1 Aim

The southern Pennines represent an extremely complex combination of biotic and abiotic factors, thanks to extensive anthropogenic impact. These degraded blanket bogs are identified as polluted when compared to reference sites. These reference sites typically contain significant areas of high quality vegetation (as defined by Common Standards Monitoring (JNCC, 2009)) including a large proportion of *Sphagnum* cover (e.g. Carroll *et al.*, 2009). Biogeochemical analysis revealed the southern Pennine region to be higher in a number of pollutant elements and chemical species. However, the relationship between these measures and present vegetation is unclear. The presence of a pollutant in the environment cannot automatically be categorised as detrimental; there are instances of synergistic effects where benefits are conferred (e.g. Baxter *et al.*, 1989, 1991). Similarly, the biogeochemistry of high-quality sites is likely to be varied and may contain elevated levels of any number of pollutant elements, without apparent ill effects on the ecosystem. Some upland areas of the UK with good quality blanket bog receive high levels of nitrogen and acidic deposition exceeding critical loads for blanket bog (RoTAP, 2012). The chemistry of these degraded Pennine peatlands has changed but the effect on *Sphagnum* is unknown, therefore the influential biogeochemical drivers of bog vegetation must be identified in order to understand their role in limiting *Sphagnum* performance. Thus, this Chapter aims to:

Elucidate those biogeochemical factors affecting the natural recovery and performance of Sphagnum

3.2.2 Objectives

Vegetation, biogeochemistry and environmental gradients

By comparing reference sites from across the UK to degraded sites of the southern Pennines, vegetation and biogeochemical differences can be illustrated, providing context at the national scale. Significant biogeochemical drivers of vegetation composition can be identified and *Sphagnum* species responses modelled along those gradients.

Observing variation in vegetation and biogeochemistry between reference and Pennine sites can help to illustrate those differences between obviously good and poor condition habitats. However, there is likely to be considerable difference in the plant communities of geographically distinct sites, along with their biogeochemistry, perhaps due to geological and climatic differences or anthropogenic influences of their own. There is likely to be variation between degraded sites, in their biogeochemical characteristics and plant communities. Of perhaps greater interest is the contrast between areas with natural *Sphagnum* growth, whether remnant patches or more recent expansion, and those areas without *Sphagnum*. How, or indeed if, the biogeochemistry of these patches differ from nearby *Sphagnum*-less vegetation may help to unpick the reason for their continued existence and lack of widespread recolonisation.

Thus, the objectives are:

- Assess differences in vegetation: a) at the national scale between reference sites and degraded Pennine sites, and b) within the Pennine sites only, separated by site and presence/ absence of *Sphagnum*
- Assess differences in the biogeochemistry of the sites, using the subsets a) and b), as outlined above
- Identify biogeochemical drivers of the vegetation for a) and b)
- Model the response of *Sphagnum* species along these gradients

Vegetation, peat total, and comparative chemistry

The southern Pennines were exposed to high levels of air pollution for over two centuries, resulting in acidic deposition and subsequent leaching of base cations, enrichment by atmospheric N inputs, and the accumulation of heavy metals (Holden *et al.*, 2007b). Whilst current atmospheric concentrations and rates of deposition are much lower, these peat-covered landscapes represent substantial stores of pollutants. Erosion and biogeochemical processes can mobilise these contaminants, with implications for the vegetation communities of these ecosystems. The presence of toxic chemical elements and ions, and disturbances in nutrient availability, can lead to adverse effects in *Sphagnum* performance (e.g. Li & Glime, 1990). Differences in the nutritional status of *Sphagnum* from the southern Pennines and reference sites may help to explain their relatively poorer performance, and may also illustrate which are influential limitations.

Individual assessment of peat extractable, total and vegetation chemistry is useful in describing the prevailing chemical conditions of individual sites and differences between them. By combining these data, the behaviour of chemical elements and ions at the survey sites can be better understood, further helping to identify potential limitations to *Sphagnum* performance.

Thus, the objectives are:

- Assess differences in elemental concentrations and ratios of *Sphagnum* species from the sample sites
- Identify possible causes of reduced *Sphagnum* performance
- Assess differences in peat total biogeochemical concentrations and elemental ratios of the sample sites
- Identify potential future biogeochemical issues of these stored pollutants
- Compare peat extractable, total and *Sphagnum* chemistry between the survey sites
- Compare the behaviour of chemical elements and ions between the survey sites, across peat extractable, total and vegetation chemistry data

3.3 Materials and methods

3.3.1 Site descriptions

All sites sampled, are categorised as, or form part of, Special Areas of Conservation (SAC) or Sites of Special Scientific Interest (SSSI). Relevant site and vegetation descriptions have mainly been gathered from the Joint Nature Conservation Committee (JNCC), the statutory body which designates such areas. Sites were selected to incorporate a range of severity of anthropogenic impacts, whilst taking into consideration practical issues, such as access and permissions to conduct this research.

Reference sites

“Reference site” in this context is used to describe sites containing a significant quantity of high quality, active ombrotrophic bog; i.e. the presence of substantial amounts of *Sphagnum* and actively peat-forming. Whilst these sites are in comparatively better condition than those of the degraded southern Pennines, it would be incorrect to refer to them as pristine due to past and current anthropogenic influences, as mentioned in each site descriptions below. The reference sites include several raised bogs and whilst these habitats differ from blanket bog in a number of ways, they are ecologically analogous habitats (Shepherd *et al.*, 2013). Indeed, raised bogs can, in some cases, coalesce to become blanket bogs.

Borth Bog (also known as Cors Fochno (JNCC, 2014a)) is a *c.* 650 ha SAC, located in Ceredigion, Wales and forms part of the Dyfi Biosphere reserve. Although a substantial part of the former peatland complex has been taken for agriculture, the surviving core area supports the largest expanse of primary near-natural raised bog in an estuarine context within the UK. Extensive areas of patterned mire include occasional hummocks of *Sphagnum fuscum* and, more rarely, *S. austinii*, with hollows and lawns supporting extensive *S. pulchrum*, greater sundew (*Drosera anglica*), white beak sedge (*Rhynchospora alba*) and bog rosemary (*Andromeda polifolia*). Areas of domestic peat cutting peripheral to the dome are now actively regenerating and support a significant area of active bog vegetation. There are also a range of vegetation types in which peat formation has ceased as a consequence of intensive drainage followed in places by peat removal and/ or agricultural management.

Glasson Moss, along with Wedholme Flow, Bowness Common and Drumburgh Moss, make up the South Solway Mosses SAC (JNCC, 2014f); an estuarine complex of nearly 2000 ha in Cumbria, England. Although affected by past drainage and peat cutting, much of these sites support typical bog vegetation, including bog rosemary, cranberry (*Vaccinium oxycoccos*) and greater sundew. The central part of Glasson Moss displays some of the most diverse raised bog vegetation in the UK today, with *Sphagnum* species, including abundant *S. pulchrum* as well as *S. fuscum*.

Whim Bog is a SSSI of around 90 ha, located in Peeblesshire, Scotland. It is an example of a transitional bog between lowland raised bog and blanket bog (Sheppard *et al.*, 2013). The vegetation is classified as NVC M19 *Calluna vulgaris-Eriophorum vaginatum* blanket mire community, dominated by varying ages of *C. vulgaris* occurring as mosaics with hummocks of *Sphagnum capillifolium* and *S. subnitens*, and hollows containing *S. fallax*, *S. magellanicum* and *S. papillosum* with occasional *E. angustifolium*. Other common species include *Erica tetralix*, *Empetrum nigrum*, *Hypnum jutlandicum*, *Pleurozium schreberi*, *Polytrichum* spp. (Central Environmental Surveys, 2006; Sheppard *et al.*, 2013).

Whixall Moss forms part of Fenn's, Whixall, Bettisfield, Wem and Cadney Mosses SAC (JNCC, 2014b), a large (950 ha) lowland raised bog that straddles the England-Wales border in Shropshire and Wrexham. It is amongst the largest and most southerly raised bogs in the UK. Although much of the site has been subject to peat extraction, areas of partially cut and uncut mire still remain, in areas formerly subject to commercial peat-cutting, recent conservation management has led to the regeneration of bog-forming vegetation. Mire vegetation includes *Sphagnum papillosum*, *S. magellanicum*, *S. pulchrum*, all three species of sundew (*Drosera* spp.), cranberry, bog asphodel (*Narthecium ossifragum*), royal fern (*Osmunda regalis*), white beak sedge and bog rosemary, together with the nationally scarce moss *Dicranum affine*.

Migneint is an area of upland blanket bog, forming part of the Migneint-Arenig-Dduallt SAC (JNCC, 2014c) which covers nearly 20,000 ha in Conwy and Gwynedd, Wales. Two vegetation types define the SAC: blanket bog and European dry heath. Migneint and Dduallt mark the limits of a large upland block located along the eastern fringe of Snowdonia National Park. The site supports the largest area of blanket bog in north Wales after Berwyn and is particularly significant for the extent and quality of comparatively *Sphagnum*-rich M19 *Calluna vulgaris-Eriophorum vaginatum* blanket mire. M18 *Erica* *tetralix-Sphagnum papillosum* blanket mire is also widespread, with localised representation of *S. magellanicum* and, rarely, *S. affine*. The significant representation of more degraded vegetation types, including M20 *Eriophorum vaginatum* blanket mire, attests to a long history of anthropogenic modification including burning, grazing and drainage – significant parts of the site were formerly managed as grouse moor. Large areas of dry and wet heath are also present, while soligenous mire communities feature as widespread and extensive components of the blanket mire. Upland European dry heath at Migneint-Arenig-Dduallt is predominantly of NVC type H12 *Calluna vulgaris-Vaccinium myrtillus* heath. Other forms of heath present include H18 *Vaccinium myrtillus-Deschampsia flexuosa* heath, H21 *Calluna vulgaris-Vaccinium myrtillus-Sphagnum capillifolium* heath in damp north to north-east facing cliffs, and H8 *Calluna vulgaris-Ulex gallii* heath at lower altitudes.

Moidach More (JNCC, 2014d) is an SAC located in Moray and Highland regions of Scotland, covering just over 900 ha. Although it lies at 300 m, it is a low-altitude example of blanket bog in the eastern Highlands. Of major interest on this site is the surface patterning, which consists of soft, low hummocks and shallows or water-filled pools, and is not known to occur elsewhere in Grampian. While the hummocks contain *Sphagnum fuscum* and *S. austinii*, the hollows are dominated by *S. cuspidatum*. Other species include small cranberry (*Vaccinium microcarpum*) and the rare moss *Dicranum undulatum*. Areas of wet and dry heath are also found, particularly on the adjacent hill slopes.

These sites are subsequently referred to as Borth, Glasson, Whim, Whixall, Migneint and Moidach, respectively.

Pennine sites

Alport Moor, Black Hill, Bleaklow and Holme Moss are all part of the vast (~ 65,000 ha) South Pennine Moors SAC (JNCC, 2014e), reaching from Staffordshire in the south to Lancashire and Yorkshire in the north, and from Cheshire in the west to Derbyshire in the east. The SAC represents blanket bog in the south Pennines; the most south-easterly occurrence of the habitat in Europe. The bog vegetation communities are botanically poor: hare’s-tail cottongrass (*Eriophorum vaginatum*) is often overwhelmingly dominant and *Sphagnum* mosses are scarce. Where the blanket peats are slightly drier, heather, crowberry (*Empetrum nigrum*) and bilberry (*Vaccinium myrtillus*) become more prominent. The uncommon cloudberry (*Rubus chamaemorus*) is locally abundant in bog vegetation. Bog pools provide diversity and are often characterised by common cottongrass (*E. angustifolium*). Substantial areas of the bog surface are eroding, and there are extensive areas of bare peat. In some areas, erosion may be a natural process reflecting the great age (9,000 years) of the south Pennine peats. Upland dry heaths are found at the southern end of the Pennine range; the habitat’s most south-easterly upland location in the UK. Dry heath covers extensive areas, occupying the lower slopes of the moors on mineral soils or where peat is thin, and occurs in transitions to acid grassland, wet heath and blanket bog. The upland heath of the south Pennines is strongly dominated by *C. vulgaris*. Its main NVC types are H9 *Calluna vulgaris-Deschampsia flexuosa* heath and H12 *Calluna vulgaris-Vaccinium myrtillus* heath. More rarely H8 *Calluna vulgaris-Ulex gallii* heath and H10 *Calluna vulgaris-Erica cinerea* heath are found. On the higher, more exposed ground H18 *Vaccinium myrtillus-Deschampsia flexuosa* heath becomes more prominent.

3.3.2 Vegetation surveying and sample collection

At each of the survey sites, ten 0.5 m × 0.5 m quadrats containing *Sphagnum* were selected. Effort was made to gather data on replicates of *Sphagnum* species; e.g. several quadrats containing *S. capillifolium*. Species identity and percentage cover were recorded for all vegetation, including lichens and liverworts, where possible. Location (12-figure British National Grid format) and elevation of the sample quadrats were recorded using a GPS unit (Garmin GPSmap 62). Table 13 provides a summary of the survey sites and their characteristics.

From within the quadrat, a sample core was taken (65 mm diameter × 95 mm depth), passing through the vegetation and into the peat. Porewater (~ 30 ml) was collected using Rhizon samplers (a narrow cylindrical probe made of a porous hydrophilic polymer with 0.15 µm pore size, supplied by Van Walt, UK) and syringes to generate a vacuum, before transferring to a universal tube. All material gathered was stored at < 5 ^{o}C upon returning to the laboratory.

Sampling at the Pennine sites followed the same protocol, with the addition of a further ten quadrats and samples collected. These were non-*Sphagnum* samples, immediately adjacent (< 3 m away) to those samples with *Sphagnum*, giving a total of twenty samples per Pennine site (reference sites n = 10, Pennine sites n = 20).

Figure 25 – Location of bog survey sites, with inset showing the southern Pennine sites (© 2013 Google Earth).

Table 13 – Survey site characteristics. Numeric values are means of quadrats sampled at each site.

Site	*Date sampled*	*Easting*	*Northing*	*Elevation (m)*	*Bog type*
Alport Moor	08/05/2012	411151	393479	539	blanket
Black Hill	06/10/2011	408302	404599	577	blanket
Bleaklow	19/06/2012	409588	395154	587	blanket
Borth	23/05/2011	263578	291271	12	raised
Glasson	25/05/2011	323557	560607	23	raised
Holme Moss	02/08/2011	409344	404376	530	blanket
Migneint	24/05/2011	278029	345555	457	blanket
Moidach	27/05/2011	302420	841471	281	blanket
Whim	26/05/2011	320260	653259	294	transitional
Whixall	08/06/2011	348249	335561	94	raised

3.3.3 Laboratory analysis

Porewater samples were filtered to 0.2 µm before any subsequent analysis. Nutrient analysis was conducted using ion chromatography (IC, Dionex ICS-2000) for anions and cations, and metals were analysed using inductively coupled plasma optical emission spectrometry (ICP-OES, Thermo Scientific iCAP 6000 series). pH was determined using an electronic pH meter (Sartorius PB-20 with KCl-filled electrode) after the other analyses to avoid contamination.

Vegetation was removed from the core samples and the fresh peat was homogenised prior to analysis. Moisture content of the peat samples was determined by drying at 40 ºC to a constant mass. All values reported for peat chemistry were adjusted for moisture content and expressed on a dry weight basis. pH of the peat was measured using a peat and deionised water slurry (1:2.5 ratio (Allen, 1989)), stirring with a glass rod for 30 seconds before measuring using the pH meter as before.

Extractable nutrients and metals were measured by adding a 5 g sample of fresh peat to 20 ml of 1 % KCl and 0.1 M EDTA, respectively. The samples were mixed on an orbital shaker for 30 min before being centrifuged at 4000 rpm for 5 min. The supernatant was then filtered to 0.2 µm before analysis using IC and ICP-OES.

Total metals, phosphorus and sulphur were measured by acid digestion of dried, ground peat samples. 10 ml conc. HNO_3 (> 70 %) was added to 0.5 g peat in a PTFE digestion vessel. Samples were sealed and left to cold-digest overnight, before being heated to 165 ºC for 30 min using a microwave digester (CEM Mars 5; adapted from EPA 3051A (Moore, 1993)). Once cool, the samples were vacuum filtered through Whatman #3 cellulose papers and diluted to 50 ml with deionised water, before being analysed using ICP-OES. Total carbon and nitrogen were measured on a Leco Truspec elemental analyser, using 0.2 g samples of dried, ground peat.

Vegetation was dried at 40 ^{o}C to a constant weight before being ground. Total metals, P, S, C and N were measured using the methods outlined above using 0.5 g and 0.1 g of plant material for acid digest and Leco, respectively.

Table 14 provides a summary of the biogeochemical analyses outlined above.

3.3.4 Statistical analyses

Univariate statistical analyses were carried out in Minitab v.16 (Minitab Inc., 2010). Multivariate analyses and hierarchical logistic regression were implemented in the R software environment (R Core Team, 2013), using RStudio (RStudio Team, 2013), and packages eHOF (Jansen & Oksanen, 2013), lattice (Sarkar, 2008), MASS (Venables & Ripley, 2002), mgcv (Wood, 2004, 2006, 2011), nlme (Pinheiro *et al.*, 2013), permute (Simpson, 2013) and vegan (Oksanen *et al.*, 2013).

Vegetation

Vegetation cover data of quadrats were improved by removing grouped taxa (e.g. liverwort and lichen) and rare species occurring in single samples, to avoid undue influence on subsequent analysis. Values were then $\log_{10}(x+1)$ transformed (Alday *et al.*, 2011). Multivariate exploratory analysis was carried out to visualise the plant community composition using non-metric multidimensional scaling (NMDS) and Bray-Curtis dissimilarity matrices. Differences in vegetation were then analysed using permutational multivariate analysis of variance (PERMANOVA).

Unconstrained environmental calibration

Environmental variables can be considered alongside the ordination of sites and species by calculating correlation values between the ordination and environmental variables. These can then be displayed on the ordination plots as vectors; their length being proportional to the strength of the correlation, and direction governed by a weighted average of the values. Some caution must be used in interpreting the results since not all responses will be linear.

Table 14 – Summary of laboratory biogeochemical analyses.

Variable	*Symbol*	*Analysis by*	*Porewater*	*Peat extractable*	*Peat total*	*Vegetation total*
Moisture content	MC	Balance			✓	
Acidity	pH	pH meter	✓	✓		
Ammonium	NH_4^+	IC	✓	✓		
Calcium	Ca^{2+}		✓	✓		
Magnesium	Mg^{2+}		✓	✓		
Nitrate	NO_3^-		✓	✓		
Phosphate	PO_4^{3-}		✓	✓		
Potassium	K^+		✓			
Sodium	Na^+		✓	✓		
Sulphate	SO_4^{2-}		✓	✓		
Aluminium	Al	ICP-OES	✓	✓	✓	✓
Arsenic	As			✓	✓	✓
Barium	Ba		✓	✓	✓	✓
Cadmium	Cd		✓	✓	✓	✓
Calcium	Ca		✓	✓	✓	✓
Cobalt	Co		✓	✓	✓	✓
Copper	Cu		✓	✓	✓	✓
Iron	Fe		✓	✓	✓	✓
Lead	Pb		✓	✓	✓	✓
Magnesium	Mg		✓	✓	✓	✓
Manganese	Mn		✓	✓	✓	✓
Molybdenum	Mo		✓	✓	✓	✓
Nickel	Ni		✓	✓	✓	✓
Phosphorus	P		✓	✓	✓	✓
Potassium	K		✓	✓	✓	✓
Sodium	Na		✓		✓	✓
Strontium	Sr		✓	✓	✓	✓
Sulphur	S			✓	✓	✓
Tin	Sn			✓	✓	✓
Titanium	Ti		✓	✓	✓	✓
Vanadium	V		✓	✓	✓	✓
Zinc	Zn		✓	✓	✓	✓
Carbon	C	Leco			✓	✓
Nitrogen	N				✓	✓

Surface fitting

Generalised additive models (GAMs) can be used to surface fit contour lines onto the ordination, in order to test if the response of a vector is linear. This may provide an additional opportunity to explain the distribution of points on the ordination, which would otherwise be missed using the linear representation of vectors. Figure 26 gives an example of a vector describing a linear trend, and Figure 27 shows a non-linear gradient and its associated vector; its direction and magnitude calculated by a weighted average value.

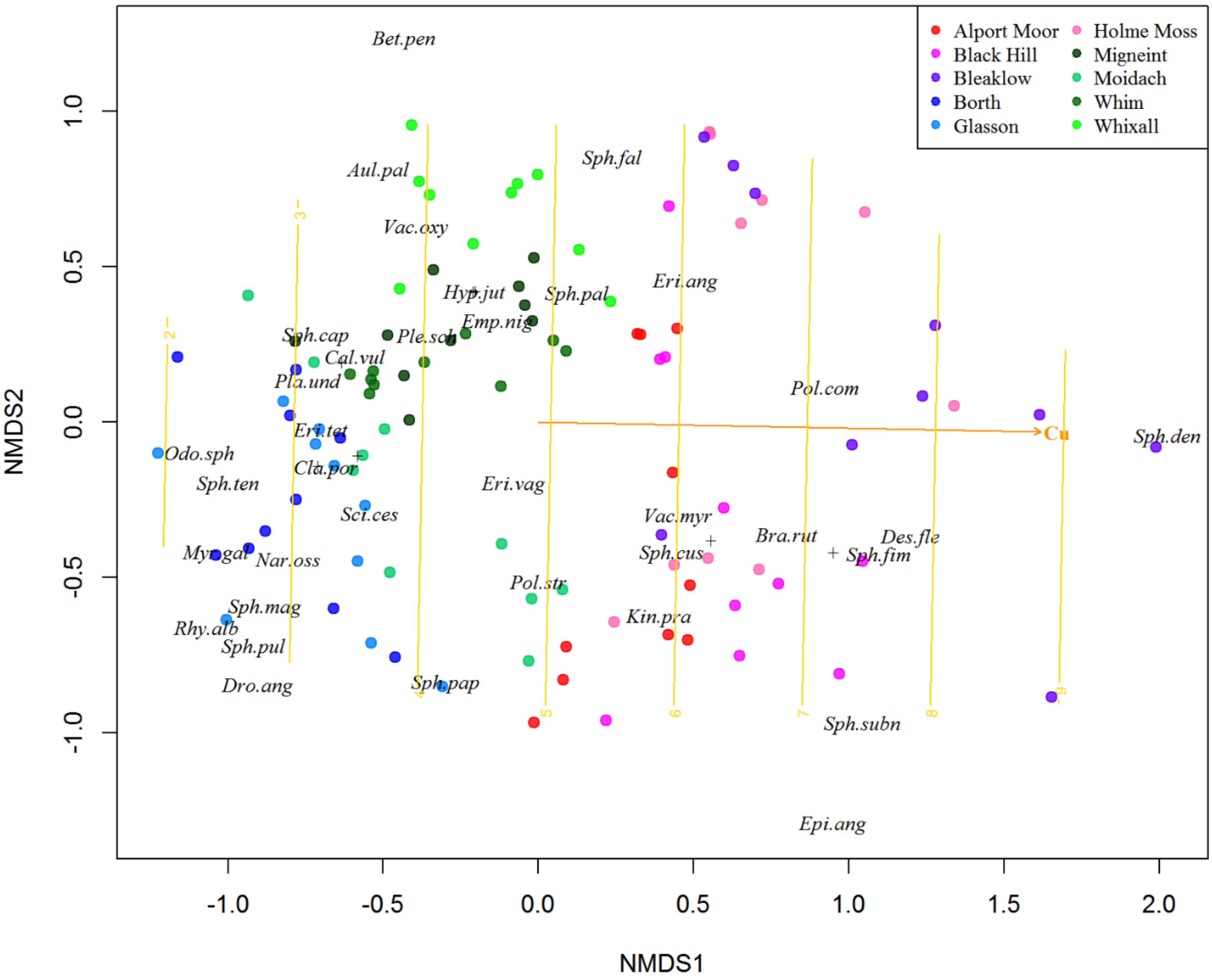


Figure 26 – Non-metric multidimensional scaling (NMDS) ordination of the vegetation composition data of the sample sites, with fitted copper (Cu) vector and contour lines showing a linear relationship.

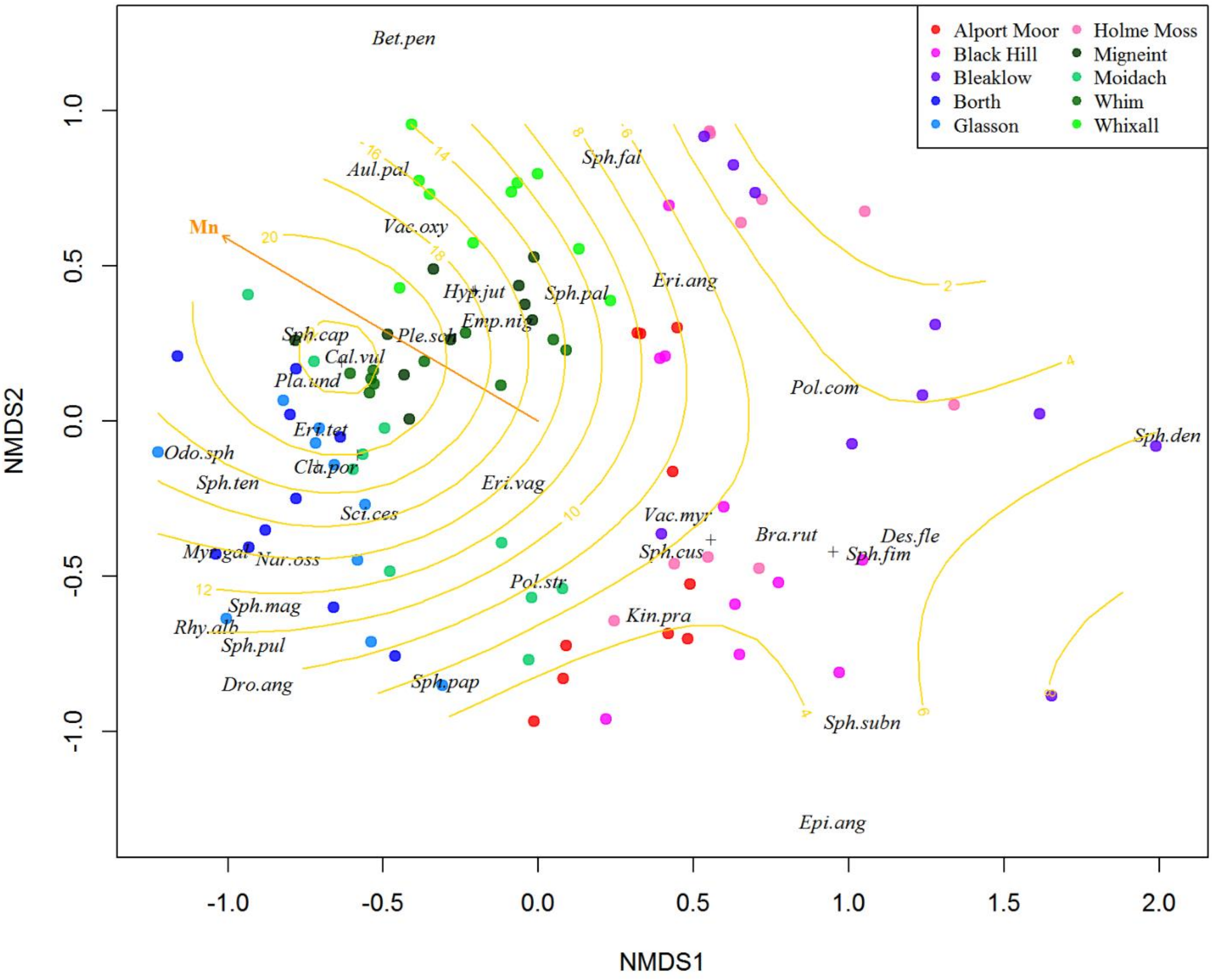


Figure 27 – Non-metric multidimensional scaling (NMDS) ordination of the vegetation composition data of the sample sites, with fitted manganese (Mn) vector and contour lines showing a non-linear relationship.

The reason for this apparent lack of linearity is due to the unconstrained nature and multi-axis approach of non-metric multidimensional scaling. NMDS generates values across numerous axes, which are impossible to visualise simultaneously, and even three dimensions can prove unclear and confusing. Hence, from NMDS ordination plots, there is more certainty in concluding that two distant points are dissimilar, rather than two points close together are similar (they may be close in terms of the first two axes, but be quite different along subsequent axes).

Constrained ordination

In unconstrained ordination, the major compositional variation is found and then related to observed environmental variation. In constrained ordination, only the variation explained by those environmental variables of interest, or the constraints, is shown. Constrained ordination is akin to multivariate linear models; with no *a priori* judgments made on the environmental variables, model building is used to reduce the number of constraints and identify the most important environmental factors. Automatic stepwise model building was performed for constrained ordination, using forwards and backwards stepwise model selection based on permutation tests.

Species-gradient modelling

The response curves of individual species can be used for a range of ecological applications, such as predicting site conditions or species co-occurrence (Jansen & Oksanen, 2013); their purpose being to model the realised niche of species for any gradient type (Huisman *et al.*, 1993). Even if the physiological niche of a species is simple to describe (e.g. unimodal or with a specific threshold), it cannot be expected that its realised niche will be equally as simple to describe (Jansen, 2013). Given the usually large number of hidden, unmeasured gradients in field data, it is unwise to use unrestricted modelling techniques, but limit results to a set of conservative and interpretable model types. In this way, hierarchical logistic regression models (also known as Huisman-Olff-Fresco (HOF) models) have been shown to perform better than other methods, such as general linear models (GLM) or beta functions (Lawesson *et al.*, 2003; Oksanen & Minchin, 2002). More flexible modelling shapes provided by general additive models (GAM) have also been used (Heikkinen & Mäkipää, 2010) but suffer from problems of over and under-fitting; resulting in lack of ecological interpretability with limited transferability (McCune *et al.*, 2002), or reduced flexibility than other methods, respectively (Jansen & Oksanen, 2013). HOF models are particularly suited to data with an upper bound (M), such as % cover. The arcsin ($\sqrt{[x/100]}$) transformation is used to improve the homoscedasticity of the data (Miller, 1986; Sokal & Rohlf, 1981); with $M = 90$.

In HOF modelling, the best model is chosen from a set of predetermined models using statistical information criteria, i.e. a balance between model fit to the data and the simplicity of the model, with bootstrapping used to safeguard model stability (Jansen & Oksanen, 2013). Originally, five HOF models were described (Huisman *et al.*, 1993), with an additional two bimodal responses added later (Jansen & Oksanen, 2013) (Figure 28); the seven models are of increasing complexity. Model I is a flat response, indicating there is no significant trend along the gradient for that species. It represents the null hypothesis and ensures that only species with a clear response will be modelled with one of the further model types. Model II is monotone sigmoid with a maximum at one end of the gradient; model III is monotone sigmoid with a plateau below the maximal upper abundance value. Model IV is the canonical form of species response, a unimodal symmetric model; V is a unimodal skewed model and models VI and VII have two optima, with maxima being equal in VI but not in VII (Jansen, 2013).

In short, HOF models can be used to model species responses along particular environmental gradients. By restricting the shape of these models to a series of predefined models, based on ecological niche concepts, the resulting output should be applicable to a wider range of scenarios.

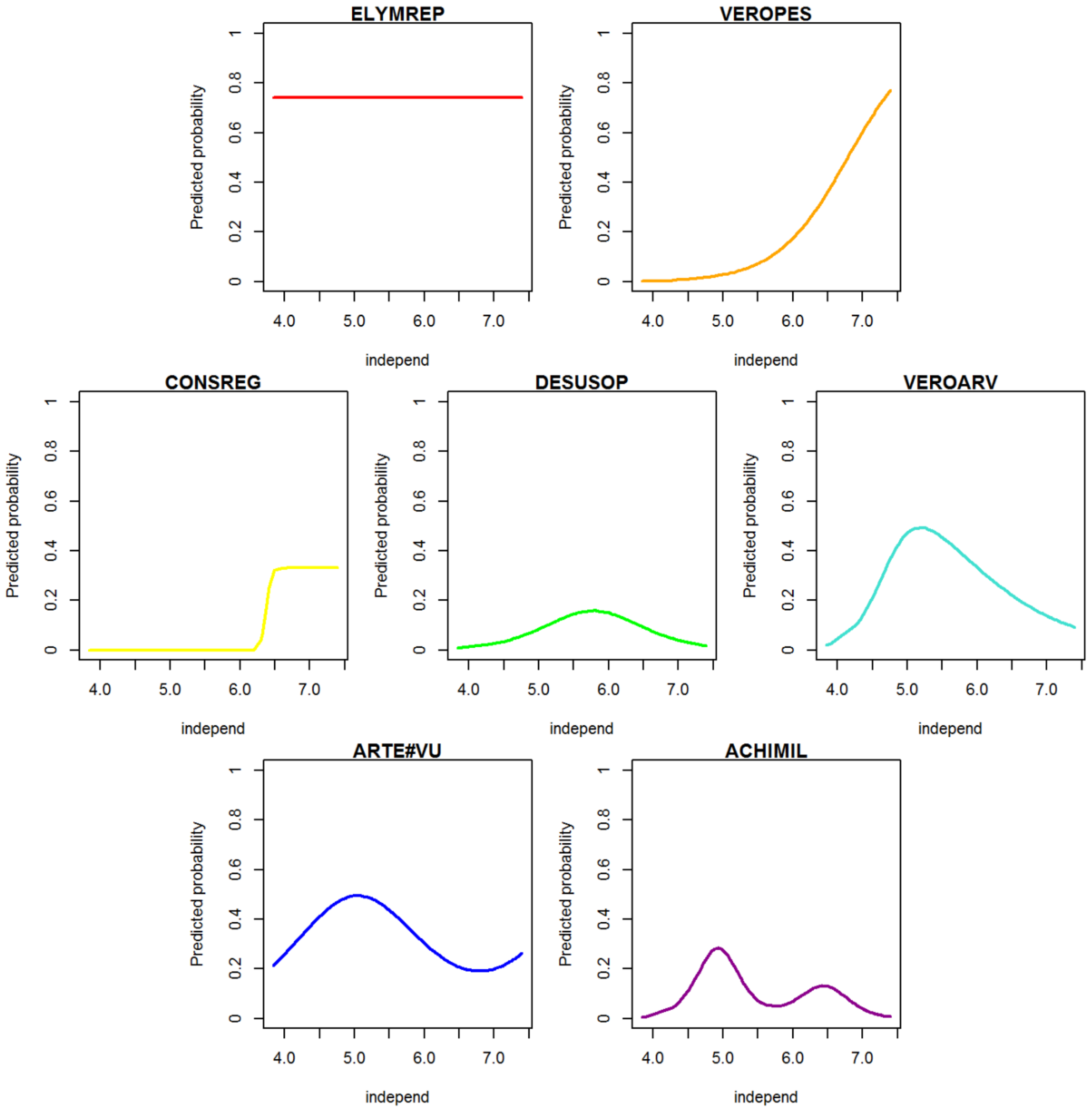


Figure 28 – Examples of the seven HOF models types: Model I (red), Model II (orange), Model III (yellow), Model IV (green), Model V (aqua), Model VI (blue), Model VII (purple) (after Jansen, 2013).

3.3.5 Method development

Rationale

Nutrient analysis of peat varies between authors, employing individual modification of methods developed for vegetation or mineral soil analysis. Since peat forms a continuum from easily distinguishable plant material to amorphous soil-like mass, its analysis as either vegetation or soil could be considered as valid. Nutrient status of vegetation is typically measured through acid digestion of dried material or by combustion, returning a total value for a given element. Whilst useful in some applications, a total measure of nutrients is less useful than that of an extractable value; i.e. that which is available to plants. To this end, peat must be treated as a soil to determine plant-available nutrients. However, protocols developed for the assessment of soils are mainly based on agricultural systems (e.g. Rowell, 1994) and substrates containing significantly more mineral and less organic matter than peat. Thus, the nutrient analysis of peat has been somewhat open to interpretation, influenced by the analytical equipment available and main nutrient(s) of interest.

An efficient, single extraction method was required to allow the determination of peat nutrients using ion chromatography (IC). From the literature, three extraction reagents were identified as potentially suited: deionised water (H_2O (e.g. Van der Paauw, 1971)), barium chloride ($BaCl_2$ (e.g. Hendershot & Duquette, 1986)) and potassium chloride (KCl (e.g. Allen, 1989)). H_2O might be considered the ideal reagent since it contains no additional anions or cations, allowing a full range to be measured from a sample. Additionally, there is no large influx of reagent ions into the IC column which can mask the detection of other ions. However, H_2O may not give an accurate measure of potential available nutrients. The use of a chemical reagent to measure exchangeable nutrient aims to achieve a more accurate representation of plant-available nutrients. The concentration of an extractant is critical in IC analysis; a higher concentration will recover a greater proportion of nutrients within a given sample, but can saturate the detection mechanism and produce poor results. Such samples would require diluting before analysing, a potentially time-consuming and unnecessary step.

Methods

A comparison of extractant reagent and concentration was conducted using H_2O, and $BaCl_2$ and KCl at 1 % and 6 % concentrations. The nutrient extraction and analysis procedure outlined in Section 3.3.3 was followed, using peat samples from an earlier glasshouse growth trial (Section 2.4). Each extraction method was replicated 5 times.

Results and Analysis

Table 15 provides a summary of the results; mean values and standard error were calculated and the data then tested for normality (Anderson-Darling test). Significance of the extractants was assessed using rank ANOVA, with Bonferroni-corrected pairwise comparisons used to establish differences between extractants.

Table 15 – Mean (and SE) of nutrient anions and cations in peat using a range of extractants. Rank ANOVA results (F) and Bonferroni-corrected pairwise comparisons are reported. Means which do not share a letter are significantly different. (* P ≤ 0.05, ** P ≤ 0.01, *** P ≤ 0.001)

Nutrient	*H_2O*	*$BaCl_2$ 1 %*	*$BaCl_2$ 6 %*	*KCl 1 %*	*KCl 6 %*	*F*
Ca^{2+}	15.65 ^{c}	117.22 ^{b}	135.63 ^{b}	521.15 ^{a}	122.82 ^{b}	50.77 ***
	(0.44)	(9.17)	(9.60)	(19.22)	(9.19)	
K^{+}	35.38 ^{a}	0.00 ^{b}	36.39 ^{a}			103.47 ***
	(1.67)	(0.00)	(1.58)			
Mg^{2+}	5.24 $^{b\ c}$	0.00 ^{c}	39.44 ^{b}	216.85 ^{a}	56.80 ^{b}	17.61 ***
	(0.09)	(0.00)	(1.25)	(7.58)	(0.67)	
Na^{+}	22.12 ^{b}	17.01 ^{c}	19.51 ^{b}	166.36 ^{a}	13.82 ^{c}	271.32 ***
	(0.94)	(0.68)	(0.56)	(2.15)	(1.18)	
NH_4^{+}	23.72 ^{b}	18.56 ^{b}	25.32 ^{b}	101.31 ^{a}	18.85 ^{b}	135.31 ***
	(1.75)	(1.67)	(0.37)	(6.41)	(0.41)	
NO_3^{-}	36.06 ^{a}	0.28 ^{d}	1.93 ^{c}	48.01 ^{a}	5.02 ^{b}	84.38 ***
	(2.86)	(0.13)	(0.55)	(1.69)	(0.53)	
PO_4^{3-}	0.00 ^{b}	0.00 ^{b}	0.07 ^{a}	0.34 $^{a\ b}$	0.44 ^{a}	12.63 **
	(0.00)	(0.00)	(0.05)	(0.21)	(0.10)	
SO_4^{2-}	195.51 ^{a}	42.78 ^{c}	49.26 ^{b}	224.73 ^{a}	49.25 $^{b\ c}$	30.63 ***
	(3.92)	(0.72)	(1.64)	(4.11)	(2.69)	

Discussion and conclusion

KCl 1 % yielded the greatest value for each nutrient ion with the exception of PO_4^{3-}; H_2O produced the greatest value, however, it was not significantly greater than that returned by extraction in KCl 1 %. It was not possible to measure K^+ using this extractant as the detection mechanism would be saturated by the influx of reagent ions. This is of little concern since K can be measured by ICP-OES following extraction in Na_2EDTA. All other reagents performed poorly as extractants. H_2O was found to be of use in determining NO_3^-, SO_4^{2-}, and K^+ for the reason given above. $BaCl_2$ 1 % was out-performed in all cases, whilst at 6 % concentration it proved suitable for K^+ and PO_3^{4-}. KCl 6 % would appear to be of less use than its weaker 1 % counterpart, being less effective across all ions except PO_4^{3-}. This may be due to problems encountered during IC analysis, where the influx of reagent ions in higher concentration extractants caused such complete saturation of the IC column that detection of other nutrient ions became difficult, or indeed, impossible. Bearing this in mind, in terms of performance and suitability, KCl 1 % would appear to be the extractant of choice for analysis of nutrients by ion chromatography.

3.3.6 Quality control

The methods outlined in Section 3.3.3 were tested for accuracy and reproducibility. A sample of peat (~ 500 g) collected from Holme Moss was homogenised and analysed for moisture content, pH, extractable nutrients, total carbon and nitrogen, and extractable and total metals. Ten replicates of each measure were obtained, and a mean value and relative standard deviation (RSD) calculated (Appendix 5). In general, extractable measures had higher RSD values than total measures. Across 25 variables, RSD values for the extractable measures ranged from 4.21 – 62.77 %, with 19 variables having an RSD > 10 %. For the total measurements, of a potential 24, 19 variables had an RSD < 10 %, and an overall RSD range of 0.36 – 29.01 %. Thus, it would appear that total values of soil nutrients and metals are more reliable than extractable values. This may be due to incomplete suspension of the peat during extraction; a problem unlikely to be faced in microwave digestion using ground material. Degradation of samples during storage may represent another factor; e.g. the formation of precipitate; another occurrence unlikely to affect acid digest samples. Despite these differences within the measurements of nutrients and metals, the methods outlined are more than sufficient to capture the scale of differences expected between regional sites and those of the southern Pennines. The combination of porewater, extractable and total measurements will enable a critical assessment of these values and erroneous data will be quickly and easily identified.

3.4 Results and analyses

<u>3.4.1 Vegetation</u>

National comparison

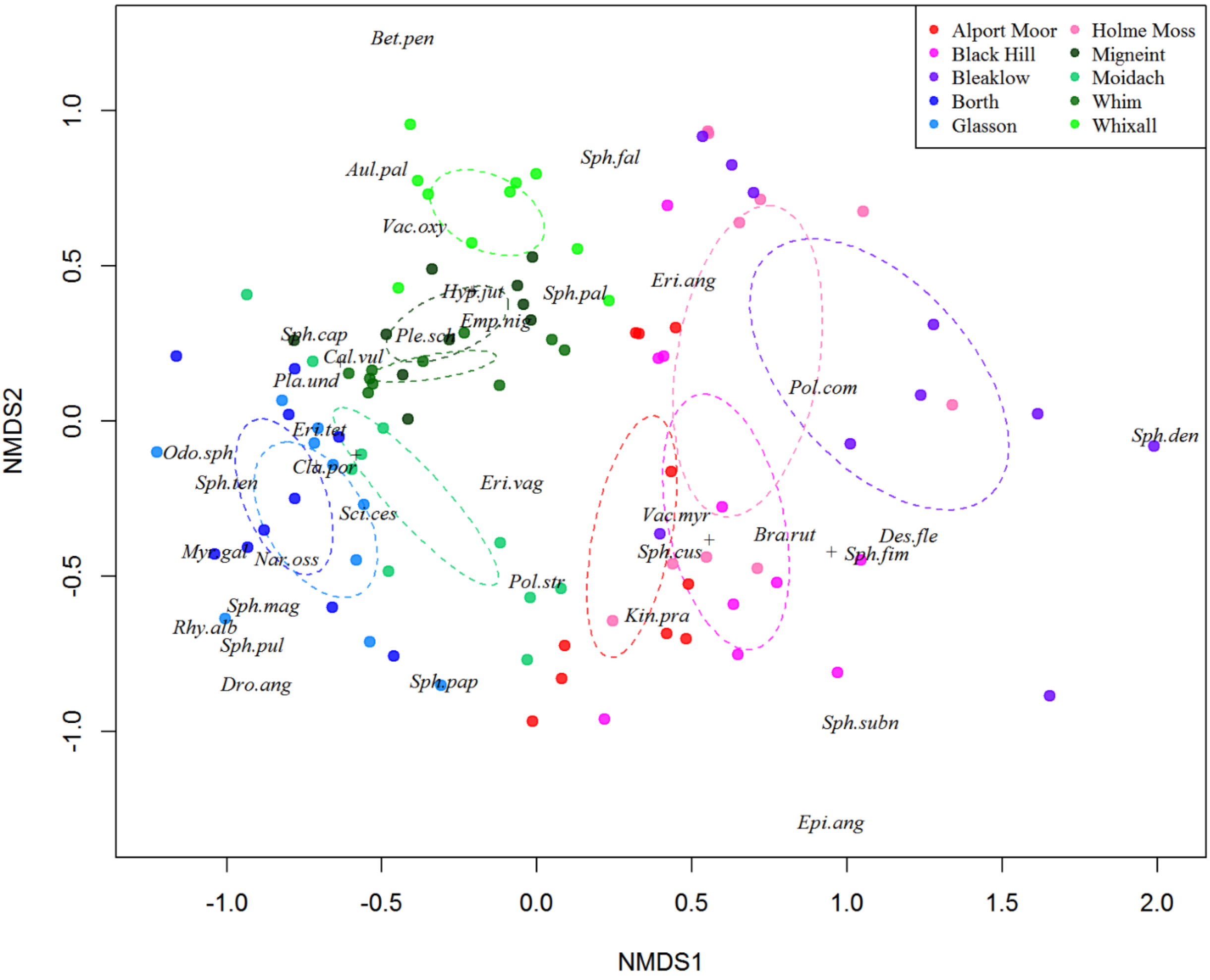


Figure 29 – Non-metric multidimensional scaling (NMDS) ordination of vegetation composition from the sample sites (n = 100), overlain with their bivariate SE ellipses. Species abbreviations can be found in Appendix 1. The most abundant species are added first and where species labels overlap, they have been omitted and the locations marked (+); all species labels are displayed in Appendix 6.

Vegetation cover data of quadrats containing *Sphagnum* from the ten sample sites (n = 100) was assessed using NMDS (Figure 29). The different sites were fitted onto the NMDS ordination, with their class centroids and bivariate standard error ellipses drawn. Species composition was found to be significantly different between the sites (PERMANOVA, P < 0.001). From the ordination and SE ellipses, it is apparent there is a marked distinction between the reference and Pennine sites. Samples from Borth and Glasson showed similar species composition, with Moidach also closely related. Migneint and Whim shared similarities, whilst samples from Whixall appeared more distinct. Samples from the Pennine sites had greater levels of variability, as shown by their larger standard error ellipses. Species composition of samples from Alport Moor and Black Hill were similar, with Bleaklow appearing distinct and Holme Moss intermediary between them.

Pennine sites

Vegetation cover data of quadrats from the four Pennine sites, both with and without *Sphagnum* (n = 80), were assessed using NMDS, as for the national comparison. Vegetation composition was found to be significantly different between quadrats containing *Sphagnum* (with) and those which did not (without) (PERMANOVA, P < 0.001), as was clearly visible from the ordination (Figure 30). Despite considerable overlap in ordination space, both quadrats with and without *Sphagnum* occupied some regions exclusively. Quadrats containing *Sphagnum* appeared to have the largest variation in vegetation composition, occupying the largest region of the ordination space.

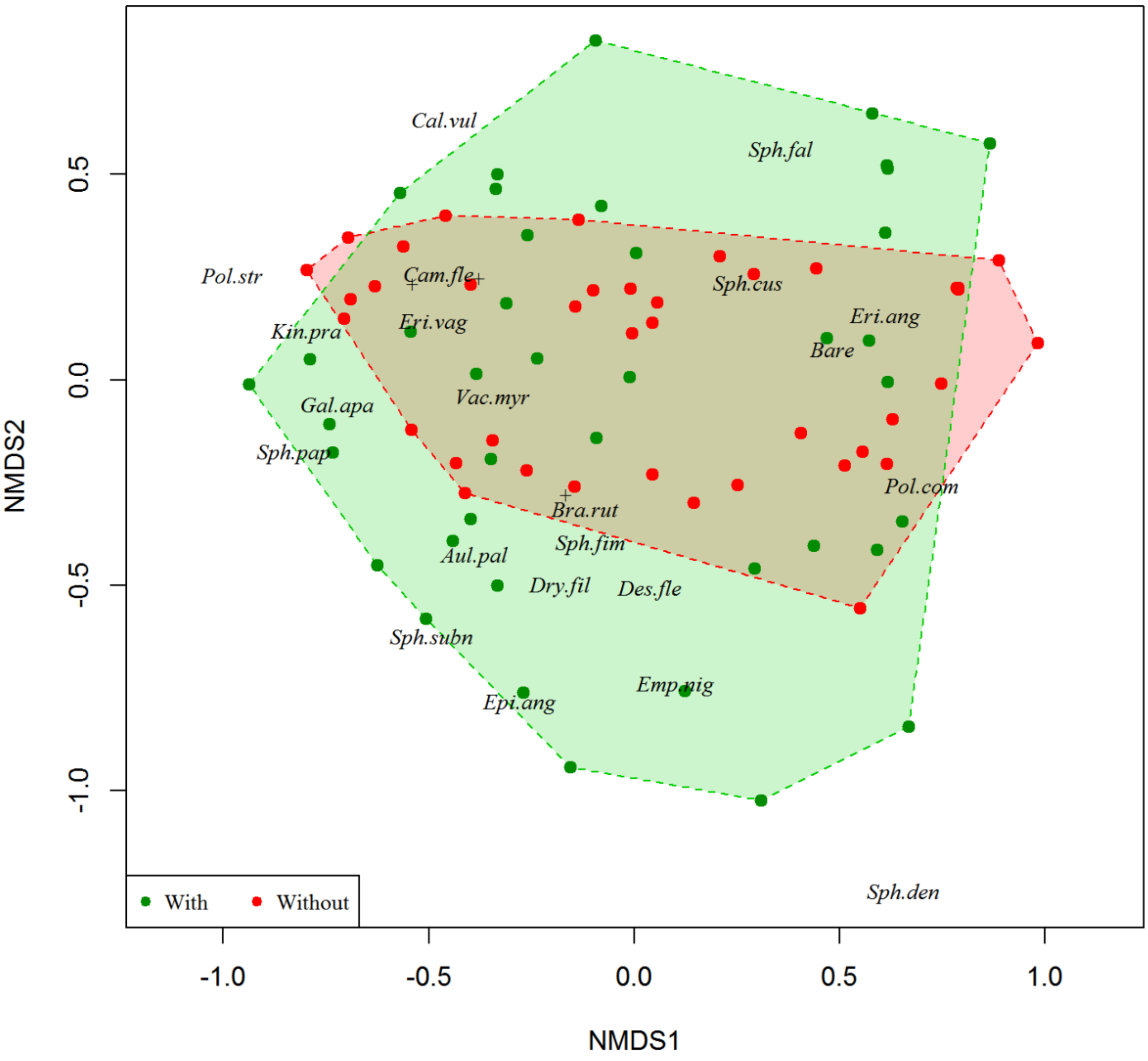


Figure 30 – Non-metric multidimensional scaling (NMDS) ordination of the vegetation composition data, separated by samples with and without *Sphagnum* present. The most abundant species are added first and where species labels overlap, they have been omitted and the locations marked (+); all species labels are displayed in Appendix 7.

3.4.2 Biogeochemistry

Selection of biogeochemical variables

Biogeochemical data were collected from the 10 survey sites; porewater, extractable and total peat values were recorded, generating a substantial number of environmental variables. Spearman's rank correlation coefficients were calculated for each chemical variable measured, comparing porewater, extractable and total values (Table 16). The highlighted results indicate a significant positive correlation. For comparison with total values, ions were correlated with their total elemental measurement.

There were 10 significant positive correlations between porewater and extractable chemistry, and 9 with total peat chemistry, out of a potential 26 and 28, respectively (Table 16). These values were based on all of the data collected. This compares poorly with the 23 (out of 26) significant positive results between extractable and total peat chemistry (Table 17).

It was thought that this may be due to the influence of the Pennine sites upon the complete dataset. The Pennine sites are severely eroded with extremely disturbed hydrological regimes, characterised by flashy responses to precipitation events (e.g. Holden *et al.*, 2008); i.e. rainfall passes quickly through these systems and is not held for any significant period of time due to the free-draining nature of these sites. This would give the water insufficient time to take on the chemical characteristics of the peat, and thus be reflected in porewater chemistry.

To test this, correlations were recalculated for subsets of the data: reference sites and Pennine sites, separately (Table 16). An increase in positively correlated variables was expected from the reference sites, with fewer in the Pennine sites, given the reasons outlined. Whilst significant positive correlations were indeed greater in the reference sites (9 with extractable values, 9 with totals) compared to the Pennine sites (6 with extractable values, 4 with totals), these results are still way short of the maximum possible (26 with extractable and 28 with total) and much fewer than the significant correlations between extractable and total values, as outlined earlier (23 of 26, Table 17).

The difference between reference and Pennine sites was thought to be exacerbated through the one-off sampling scheme. This would make all porewater measurements from Pennine sites highly influenced by the amount of precipitation immediately preceding sampling. It is interesting to note that the reference sites show correlations with base cations (Ca^{2+}, Mg^{2+} and Na^{+}), whilst the Pennine sites do not. This may be a reflection on the acidification and subsequent leaching of these ions from southern Pennine sites. Aluminium (Al), manganese (Mn), titanium (Ti) and vanadium (V) are also well represented in the porewater from reference sites. Pennine sites appear to have strong relationships with phosphorus (P) and phosphate (PO_4^{3-}), perhaps due the additions of fertilisers as part of the restoration process.

Despite a few observable trends, it would appear evident that porewater chemistry is of little use as a biogeochemical measure in this case. It inadequately describes differences observed in the peat chemistry and is influenced by the hydrological condition of the site. For the purposes of further analysis, porewater chemistry was not used. There was no such notable difference in the extractable/ total chemistry correlations in the Pennine and reference sites (23 of 26 and 21 of 26, respectively; see Table 17).

With porewater data effectively eliminated from the analysis, environmental variables were reduced to extractable and total peat chemistry. Further analysis made use of extractable peat chemistry as this was deemed to be plant-available (Rowell, 1994), and therefore influence the vegetation. Total values include quantities of elements locked up in plant tissue or peat, bound in complexes, and so not available to affect the vegetation. Extractable magnesium (Mg/ Mg^{2+}) values collected were either incomplete or considered to be unreliable due to problems in IC and ICP-OES analysis so were not used. However, due to the importance of magnesium as a plant nutrient it was not excluded entirely.

Total Mg was used as a proxy due to its very high correlation with extractable Mg; Mg^{2+} values (IC) were considered reliable but incomplete for all samples, whilst Mg values (ICP-OES) were thought to be erroneous and showed no relation to other Mg measures.

Table 18 provides a summary of the biogeochemical measures assessed here and the analytical methods used.

Table 16 – Spearman's rank correlation coefficients of porewater chemistry with extractable and total values. Subsets have been used for comparisons; all the data (All, n = 140), data from the reference sites only (Reference, n= 60), and data from the Pennine sites only (Pennine, n = 80). Significant positive correlations have been highlighted. (* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$)

Variable	*Extractable*			*Total*		
	All	*Reference*	*Pennine*	*All*	*Reference*	*Degraded*
pH	0.125	0.229	0.096			
Al	0.300 ***	0.342 **	0.181	0.333 ***	0.381 **	0.209
Ba	-0.264 **	0.252	-0.199	0.354 ***	-0.161	0.307 **
Ca^{2+}	0.089	0.340 **	-0.098	0.022	0.234	-0.034
Ca	0.189 *	0.148	0.241 *	0.133	0.051	0.179
Cd	0.024	0.192	-0.252 *	0.063	0.209	-0.086
Co	-0.094	-0.163	-0.101	0.088	0.082	-0.018
Cu	0.139	0.014	-0.006	0.162	0.134	-0.002
Fe	0.140	-0.082	0.262 *	0.150	0.095	0.225
K^{+}				0.135	0.321 *	0.172
K	0.105	-0.093	0.336 **	0.127	0.115	0.193
Mg^{2+}	0.494 ***	0.277 *	0.238	0.431 ***	0.274 *	0.100
Mg	-0.404 ***	0.504 ***	-0.148	0.488 ***	0.071	0.200
Mn	0.300 ***	0.374 **	0.219	0.268 **	0.282 *	0.260 *
Mo	0.034	-0.113	0.055	-0.065	-0.173	-0.080
Na^{+}	-0.263 **	0.420 ***	-0.287 **	0.192 *	0.325 *	-0.099
Na				0.011	0.546 ***	-0.194
NH$_4^{+}$	0.150	-0.067	0.120	0.073	-0.085	0.127
Ni	-0.238 **	-0.175	-0.121	-0.149	0.196	-0.018
NO$_2^{-}$				0.055	-0.022	0.155
NO$_3^{-}$	0.449 ***	0.248	0.253 *	0.105	0.173	-0.020
P	0.301 ***	-0.100	0.442 ***	0.174	-0.063	0.277 *
Pb	0.241 **	0.276 *	-0.062	0.316 ***	0.324 *	0.081
PO$_4^{3-}$	0.323 ***	-0.170	0.547 ***	0.173 *	-0.071	0.339 **
SO$_4^{2-}$	-0.007	-0.074	-0.090	0.132	-0.188	-0.116
Sr	-0.249 **	-0.074	0.195	-0.034	-0.103	0.184
Ti	0.247 **	0.419 **	0.219	0.258 **	0.457 ***	0.193
V	0.049	0.284 *	0.122	0.140	0.293 *	0.213
Zn	0.301 ***	0.239	0.211	0.041	0.226	0.098
Total	10	9	6	9	9	4

Table 17 – Spearman's rank correlation coefficients of extractable and total chemistry values. Subsets have been used for comparisons; all the data (All, n = 140), data from the reference sites only (Reference, n= 60), and data from the Pennine sites only (Pennine, n = 80). Significant positive correlations have been highlighted. (* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$)

Variable	*All*	*Reference*	*Pennine*
Al	0.828 ***	0.751 ***	0.757 ***
Ba	0.124	0.148	0.345 **
Ca^{2+}	0.847 ***	0.781 ***	0.902 ***
Ca	0.754 ***	0.662 ***	0.835 ***
Cd	0.842 ***	0.896 ***	0.735 ***
Co	0.620 ***	0.578 ***	0.457 ***
Cu	0.780 ***	0.675 ***	0.614 ***
Fe	0.647 ***	0.801 ***	0.717 ***
K	0.688 ***	0.644 ***	0.728 ***
Mg^{2+}	0.762 ***	0.806 ***	0.570 ***
Mg	-0.215 *	0.250	0.477 ***
Mn	0.824 ***	0.846 ***	0.821 ***
Mo	0.732 ***	0.383 **	0.557 ***
Na^{+}	0.862 ***	0.509 ***	0.769 ***
NH_4^{+}	0.361 ***	0.489 ***	0.356 ***
Ni	0.301 ***	-0.108	0.263 *
NO_3^{-}	0.147	0.111	0.105
P	0.708 ***	0.723 ***	0.585 ***
Pb	0.898 ***	0.886 ***	0.808 ***
PO_4^{3-}	0.565 ***	0.416 ***	0.509 ***
S	0.255 **	0.321 *	-0.083
SO_4^{2-}	0.660 ***	-0.027	-0.003
Sr	0.695 ***	0.590 ***	0.756 ***
Ti	0.729 ***	0.669 ***	0.556 ***
V	0.788 ***	0.603 ***	0.645 ***
Zn	0.666 ***	0.782 ***	0.626 ***
Total	23	21	23

Table 18 – Summary of biogeochemical variables and methods of analysis.

Variable	*Symbol*	*Measure*	*Reagent*	*Analysis by*
Moisture content	MC	-	-	Balance
Acidity	pH	-	H_2O	pH meter
Ammonium	NH_4^+	Extractable	KCl (1 %)	IC
Nitrate	NO_3^-			
Phosphate	PO_4^{3-}			
Sodium	Na^+			
Sulphate	SO_4^{2-}			
Aluminium	Al	Extractable	Na_2 EDTA (0.1 M)	ICP-OES
Arsenic	As			
Barium	Ba			
Cadmium	Cd			
Calcium	Ca			
Cobalt	Co			
Copper	Cu			
Iron	Fe			
Lead	Pb			
Manganese	Mn			
Molybdenum	Mo			
Nickel	Ni			
Phosphorus	P			
Potassium	K			
Strontium	Sr			
Sulphur	S			
Tin	Sn			
Titanium	Ti			
Vanadium	V			
Zinc	Zn			
Magnesium	Mg	Total	HNO_3 (> 70 %)	ICP-OES

National comparison

Bar charts of mean biogeochemical values (± 1 SE error bars) across the ten sample sites can be found (in alphabetical order) in Figure 31 and Figure 32. A table of mean values (with standard errors), rank ANOVA and Bonferroni-corrected pairwise comparisons can be found in Appendix 8.

Black Hill and Holme Moss peats were significantly higher across a range of nutrient elements and ions than the other sites. Black Hill and Holme Moss had significantly higher levels of nitrate (NO_3^-) and phosphate (PO_4^{3-}) than almost all of the other sites, with Holme Moss also having higher levels of ammonium (NH_4^+), and Black Hill elevated levels of phosphorus (P).

Base cations trends were less distinct. Calcium (Ca) levels at Black Hill were significantly higher than those of five other sites. Potassium (K) was found to be lower at Whixall than six of the other survey sites. Magnesium (Mg) was lower at the Pennine sites and Whixall, with Alport Moor and Holme Moss having the lowest levels. Sodium (Na^+) was significantly lower at Alport Moor and Bleaklow than all of the reference sites, except for Whim. Strontium (Sr) was found to be higher at four of the reference sites than in the Pennines. Barium concentrations were found to be different, but pairwise comparisons between sites were unable to determine where this lay.

Sulphate (SO_4^{2-}) was significantly higher at Holme Moss than six other sites, whilst three of the Pennine sites were higher in sulphur (S) than four of the reference sites.

A number of pollutant elements were found at significantly higher levels in the Pennines compared to the reference sites. Aluminium (Al), arsenic (As), cobalt (Co), copper (Cu), molybdenum (Mo), nickel (Ni), lead (Pb), tin (Sn), vanadium (V) and zinc (Zn) are all found at elevated levels across the Pennine sites, compared to levels found at the reference sites.

Heavy metal pollution was not limited to the Pennine sites. Cadmium (Cd) levels at Migneint and Whim were higher than three of the other reference sites, but not significantly higher than most of those found in the Pennines. Whim and Migneint had greater levels of iron (Fe) than most other sites, and Migneint along with Borth had significantly raised levels of manganese (Mn). Higher titanium (Ti) levels were found at Whim and most of the Pennine sites, compared with four of the other sites.

Moisture content (MC) and pH were not found to be significantly different between the sites.

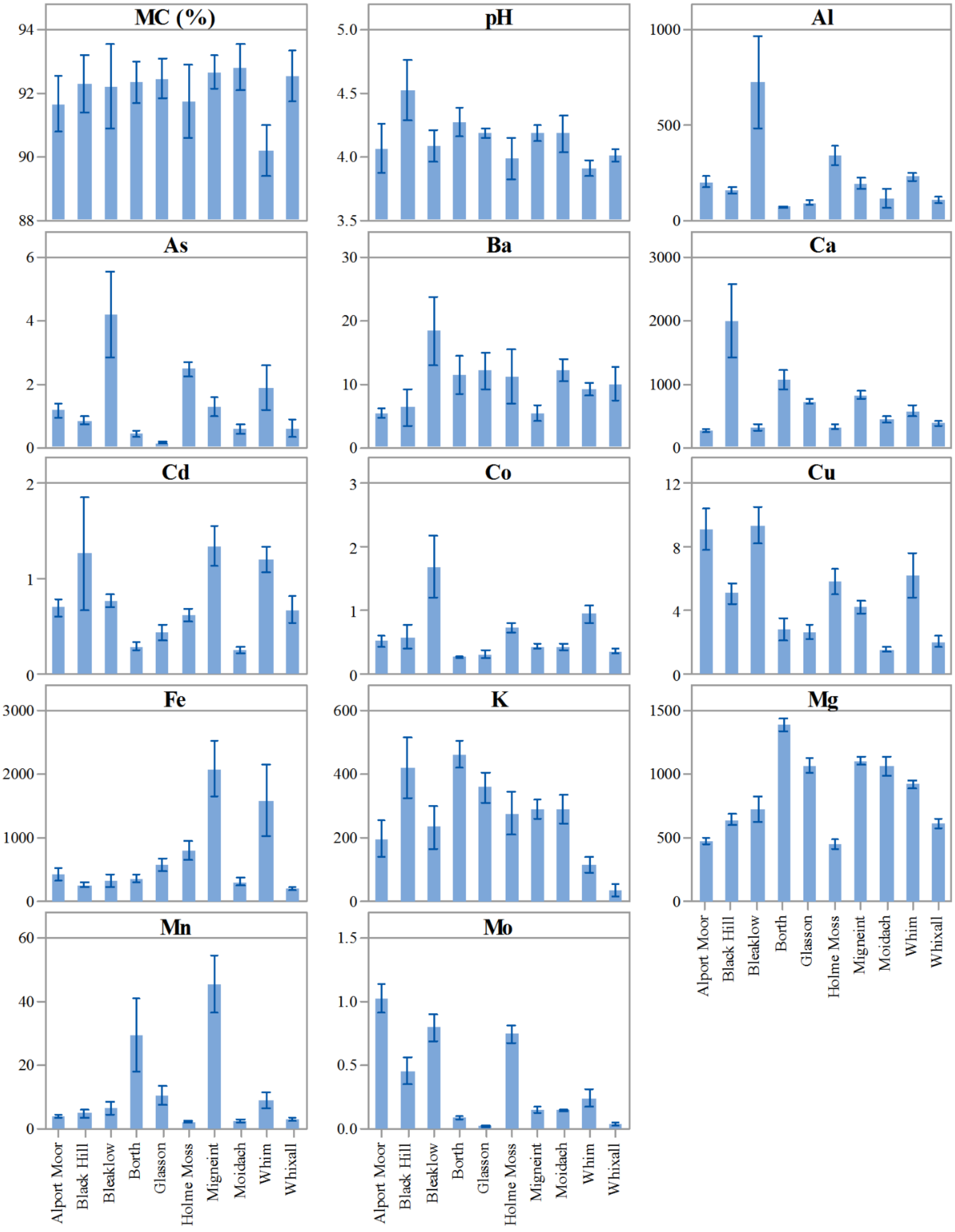


Figure 31 – Mean (± 1 SE) biogeochemical variables of quadrats containing *Sphagnum* from the survey sites (see Table 18 for more details). Values in µg g^{-1} dry weight unless indicated otherwise.

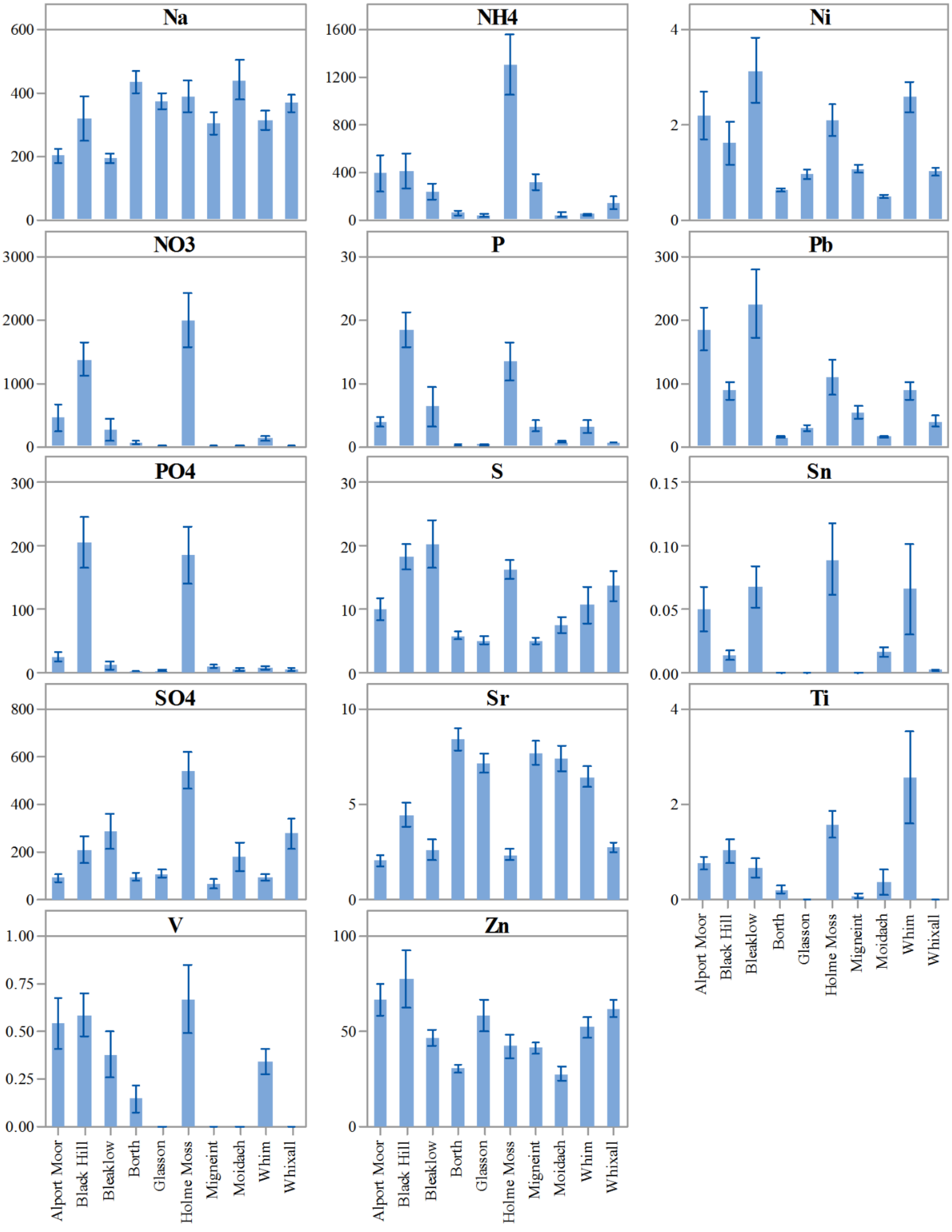


Figure 32 – Mean (± 1 SE) biogeochemical variables of quadrats containing *Sphagnum* from the survey sites (see Table 18 for more details). Values in µg g^{-1} dry weight unless indicated otherwise.

Pennine sites

Holme Moss was found to have higher levels of NH_4^+, Na^+ and Fe, and lower levels of Mn than the other Pennine sites. Black Hill had the highest levels of Ca and Sr, but the lowest levels of Mo and Sn. Al, As and SO_4^{2-} were greater at Holme Moss than Alport Moor and Black Hill, whilst Zn was significantly lower. Ti and V were higher at Holme Moss than Bleaklow, and Ba greater than at Black Hill. Black Hill and Holme Moss had greater levels of NO_3^- and PO_4^{3-} than Alport Moor and Bleaklow. Alport Moor had significantly more Cu than Black Hill, and levels of Pb were higher than Black Hill and Holme Moss. Black Hill and Bleaklow had higher levels of S than Alport Moor, and Mg levels were greater at these sites than Alport Moor and Holme Moss. Black Hill had greater levels of P than Alport Moor and Bleaklow, and K levels were lower at Bleaklow than Black Hill. Levels of MC, As, K, Mn, Mo, Na^+, NO_3^+, P, PO_4^{3-}, S and SO_4^{2-} were significantly greater in samples containing *Sphagnum* than without, whilst V was found to be significantly lower. Interaction effects were recorded for Al, Ba and Co, showing the response was not consistent between sites or the presence of *Sphagnum*. Table 19 provides details of mean values and statistical analysis.

Table 19 – Mean (and standard error) and rank ANOVA test of biogeochemical variables from the Pennine sample sites (* P ≤ 0.05, ** P ≤ 0.01, *** P ≤ 0.001). Values in µg g^{-1} dry weight, unless indicated otherwise.

	Alport Moor		*Black Hill*		*Bleaklow*		*Holme Moss*		*Rank ANOVA F*		
Variable	*With*	*Without*	*With*	*Without*	*With*	*Without*	*With*	*Without*	*Site*	*Sphagnum*	*Site*Sphagnum*
MC (%)	91.66	87.92	92.29	86.43	92.20	80.86	91.73	87.58	0.21	46.72 ***	0.69
	(0.87)	(1.13)	(0.91)	(1.04)	(1.34)	(5.57)	(1.13)	(1.01)			
pH	4.06	4.34	4.52	3.99	4.08	3.91	3.98	4.26	0.56	0.11	2.80 *
	(0.19)	(0.09)	(0.24)	(0.12)	(0.12)	(0.08)	(0.16)	(0.16)			
Al	195.48	202.02	148.40	180.92	720.21	196.90	336.68	381.32	8.88 ***	0.40	3.24 *
	(27.15)	(29.58)	(17.28)	(19.46)	(242.29)	(32.87)	(50.63)	(56.53)			
As	1.14	1.45	0.82	0.78	4.17	1.07	2.44	2.21	12.79 ***	4.50 *	1.87
	(0.21)	(0.56)	(0.12)	(0.11)	(1.37)	(0.28)	(0.24)	(0.31)			
Ba	5.27	4.48	6.21	4.52	18.33	3.44	11.11	7.60	2.93 *	3.67	3.03 *
	(0.82)	(0.57)	(2.84)	(0.81)	(5.42)	(0.63)	(4.28)	(1.48)			
Ca	242.25	203.77	1988.88	726.67	292.31	253.75	313.53	258.79	12.85 ***	1.84	0.18
	(25.95)	(17.26)	(568.44)	(134.95)	(51.36)	(37.88)	(34.01)	(22.86)			
Cd	0.70	0.66	1.27	0.72	0.77	0.64	0.62	0.59	0.66	1.28	0.15
	(0.10)	(0.08)	(0.60)	(0.14)	(0.07)	(0.09)	(0.06)	(0.06)			
Co	0.52	0.66	0.59	0.46	1.70	0.50	0.73	0.57	2.90 *	2.36	2.76 *
	(0.08)	(0.10)	(0.20)	(0.08)	(0.49)	(0.08)	(0.08)	(0.02)			
Cu	9.16	8.19	5.10	4.69	9.39	7.00	5.87	6.22	3.82 *	2.52	0.40
	(1.32)	(1.86)	(0.68)	(0.70)	(1.18)	(1.32)	(0.82)	(1.44)			
Fe	434.86	422.22	259.44	214.16	329.79	231.26	797.35	515.52	12.12 ***	2.26	0.03
	(101.98)	(147.67)	(38.32)	(31.99)	(97.89)	(52.81)	(148.63)	(53.77)			
K	198.49	188.20	425.07	205.28	235.38	72.56	278.93	105.78	3.91 *	10.26 **	1.42
	(56.80)	(35.32)	(96.03)	(39.60)	(68.26)	(42.83)	(69.26)	(25.34)			
Mg	478.15	464.02	643.88	718.30	731.71	620.36	456.03	413.29	12.65 ***	0.39	0.09
	(24.51)	(39.95)	(42.90)	(92.90)	(103.97)	(46.72)	(36.44)	(53.48)			
Mn	3.91	2.78	4.81	4.59	6.76	2.88	2.15	1.48	6.28 ***	6.97 **	0.16
	(0.52)	(0.32)	(1.15)	(1.45)	(1.99)	(0.62)	(0.26)	(0.37)			

	Alport Moor		*Black Hill*		*Bleaklow*		*Holme Moss*		*Rank ANOVA F*		
Variable	*With*	*Without*	*With*	*Without*	*With*	*Without*	*With*	*Without*	*Site*	*Sphagnum*	*Site*Sphagnum*
Mo	1.03	1.10	0.46	0.22	0.80	1.01	0.75	0.58	12.68 ***	8.25 **	0.32
	(0.11)	(0.26)	(0.11)	(0.03)	(0.11)	(0.55)	(0.07)	(0.08)			
Na^+	199.91	127.55	317.52	163.42	190.26	146.83	385.47	192.35	8.39 ***	26.08 ***	0.57
	(23.09)	(7.28)	(71.94)	(20.73)	(15.24)	(18.74)	(50.24)	(10.01)			
NH_4^+	384.13	341.25	403.03	262.66	226.35	122.80	1301.08	594.27	9.50 ***	0.68	0.50
	(153.88)	(85.54)	(143.37)	(77.91)	(69.07)	(37.79)	(260.36)	(81.79)			
Ni	2.19	2.61	1.61	2.27	3.13	2.21	2.09	2.16	0.60	0.25	0.84
	(0.50)	(0.59)	(0.45)	(0.54)	(0.69)	(0.41)	(0.33)	(0.19)			
NO_3^-	446.02	20.82	1368.45	519.65	250.56	111.90	1996.13	169.91	10.32 ***	18.44 ***	1.98
	(213.89)	(12.18)	(257.85)	(181.79)	(165.19)	(74.17)	(430.46)	(102.09)			
P	3.77	3.27	18.37	7.89	6.20	4.26	13.37	3.78	14.78 ***	9.04 **	1.04
	(0.73)	(0.68)	(2.81)	(1.11)	(3.15)	(2.94)	(3.03)	(0.79)			
Pb	184.69	161.06	88.08	79.20	224.50	100.50	108.20	97.14	3.62 *	2.34	1.24
	(33.89)	(36.42)	(13.84)	(11.50)	(54.25)	(26.49)	(28.11)	(21.70)			
PO_4^{3-}	25.37	25.89	207.22	106.27	11.41	7.98	186.34	92.21	40.81 ***	7.37 **	1.08
	(6.51)	(16.89)	(40.75)	(21.61)	(6.27)	(3.78)	(46.19)	(55.03)			
S	9.99	6.58	18.36	7.68	20.30	9.14	16.39	7.64	3.90 *	43.07 ***	1.35
	(1.72)	(1.04)	(2.11)	(0.76)	(3.80)	(1.75)	(1.49)	(1.18)			
Sn	0.05	0.06	0.01	0.01	0.07	0.03	0.09	0.05	9.84 ***	2.71	1.05
	(0.02)	(0.03)	(0.00)	(0.00)	(0.02)	(0.01)	(0.03)	(0.01)			
SO_4^{2-}	90.92	47.20	209.02	75.58	285.85	134.87	545.32	173.79	12.28 ***	21.92 ***	0.74
	(19.62)	(12.49)	(57.32)	(16.35)	(74.07)	(29.83)	(78.51)	(42.87)			
Sr	2.07	1.70	4.49	3.47	2.63	2.19	2.37	2.30	10.87 ***	0.72	0.30
	(0.28)	(0.23)	(0.61)	(0.36)	(0.56)	(0.33)	(0.29)	(0.20)			
Ti	0.77	1.83	1.03	0.85	0.67	0.41	1.59	1.69	6.30 ***	0.60	0.43
	(0.14)	(0.86)	(0.25)	(0.20)	(0.21)	(0.13)	(0.30)	(0.43)			
V	0.55	0.99	0.59	0.81	0.38	0.43	0.67	1.37	3.86 *	4.01 *	0.48
	(0.13)	(0.30)	(0.11)	(0.13)	(0.12)	(0.15)	(0.18)	(0.33)			
Zn	67.24	59.47	78.21	67.79	46.81	53.34	42.39	32.86	9.60 ***	0.02	0.91
	(8.46)	(5.00)	(14.85)	(7.19)	(4.09)	(6.70)	(6.21)	(4.88)			

3.4.3 Biogeochemical drivers of vegetation

Unconstrained environmental calibration

Nineteen (of 28 measured) environmental variables were found to be significantly correlated with the vegetation composition data ordination (Table 20). The most significantly correlated vectors ($P \leq 0.001$) were plotted onto the ordination (Figure 33), since adding all significant vectors ($P \leq 0.05$) would produce an extremely congested figure. Even at this highest significance level there were still 15 drawn. The reference sites appeared to be associated with magnesium and strontium, whilst the Pennine sites were associated with nutrients and a number of metal pollutants.

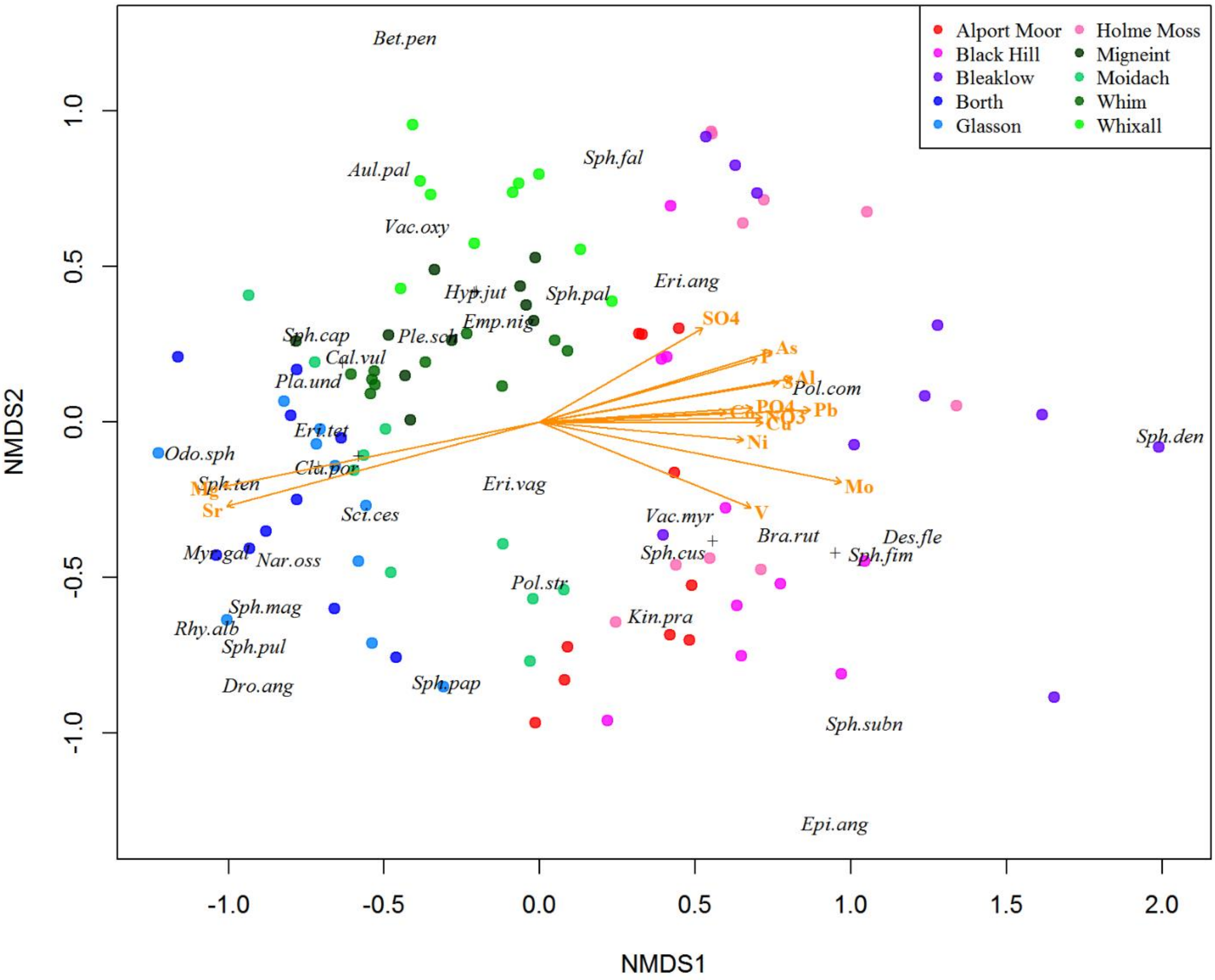


Figure 33 – Non-metric multidimensional scaling (NMDS) ordination of vegetation composition from the sample sites, overlain with the most significantly correlated ($P \leq 0.001$) environmental variables.

Table 20 – Correlations of environmental variables with the vegetation and site ordination (Figure 33). (* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$)

Vector	*NMDS1*	*NMDS2*	*r^2*	
MC	0.8532	0.5216	0.0010	
pH	-0.5017	-0.8651	0.0133	
Al	0.9855	0.1695	0.2841	***
As	0.9564	0.2919	0.2553	***
Ba	0.0998	-0.9950	0.0351	
Ca	-0.5852	-0.8109	0.0067	
Cd	0.8331	0.5532	0.0237	
Co	0.9986	0.0536	0.1509	***
Cu	1.0000	-0.0031	0.2159	***
Fe	-0.5294	0.8484	0.0536	
K	-0.3127	-0.9498	0.0490	
Mg	-0.9797	-0.2005	0.4528	***
Mn	-0.8740	0.4859	0.0868	*
Mo	0.9808	-0.1950	0.4098	***
Na^+	-0.9805	-0.1966	0.0952	**
NH_4^+	0.9075	0.4201	0.1421	**
Ni	0.9961	-0.0888	0.1815	***
NO_3^-	0.9998	0.0215	0.2142	***
P	0.9601	0.2797	0.2225	***
Pb	0.9990	0.0452	0.3185	***
PO_4^{3-}	0.9978	0.0665	0.1975	***
S	0.9865	0.1636	0.2551	***
Sn	0.9731	0.2305	0.0988	**
SO_4^{2-}	0.8666	0.4989	0.1534	***
Sr	-0.9658	-0.2591	0.4552	***
Ti	0.9501	0.3118	0.0121	
V	0.9265	-0.3762	0.2258	***
Zn	0.9698	-0.2440	0.0181	

National comparison

Using the procedure outlined above using data from all the sites, the model selected was:

$\text{Log}_{10}\ (\text{veg}+1) \sim \text{Mg} + \text{Al} + \text{Ba} + \text{Cd} + \text{NO}_3^- + \text{MC} + \text{SO}_4^{2-} + \text{V} + \text{Fe} + \text{Mo} + \text{Zn}$

Significance of the terms in the model were assessed using permutations ($P \leq 0.031$ for all terms), and only terms which reduced the Akaike information criterion (AIC) value were included (model AIC = 347.56, Appendix 9). The constrained model was plotted (Figure 34), and the constraining variables checked for linearity using GAMs (see *Surface fitting*). Most of the plotted vectors were found to be linear, with the exception of SO_4^{2-} and V. This was thought to be due to the strong influence of a small number of samples, as clearly visible on the ordination, causing elongation of the CCA axes and distortion of these vectors.

There was a general separation between the Pennine and reference sites at CCA1 ≈ -0.5. Magnesium displayed a strong gradient, along which both the reference and Pennine sites were aligned, with Borth and Glasson showing positive associations. Barium and moisture content were most closely associated with samples from Moidach and *S. cuspidatum*. Whixall, Whim and Migneint demonstrated a relationship with iron, albeit one of the weaker influences, as denoted by the shorter arrow drawn on the ordination (Figure 34). The Pennine sites were characterised by a number of pollutant metals and ions: aluminium, sulphate, molybdenum, vanadium, nitrate, cadmium and zinc. A number of samples from Bleaklow appeared to have a strong influence on the ordination, showing a strong relationship with aluminium. Mo, V, NO_3^-, Cd and Zn demonstrated close associations with the majority of samples from the Pennine sites, forming a narrow “wedge” in ordination space. SO_4^{2-} appeared to form a more general gradient, helping to separate the reference and Pennine sites.

Variance inflation factor (VIF) values were calculated for the terms of the model to assess levels of covariance with the other constraints (Table 21). As a general rule, VIF > 10 indicates that a variable is strongly dependent upon another and does not contribute any independent information (Montgomery & Peck, 1992; Oksanen, 2013). The VIF values, all < 2.4, indicate the significance of each constraint, even when compared to a more stringent threshold of 3 (Zuur *et al.*, 2010).

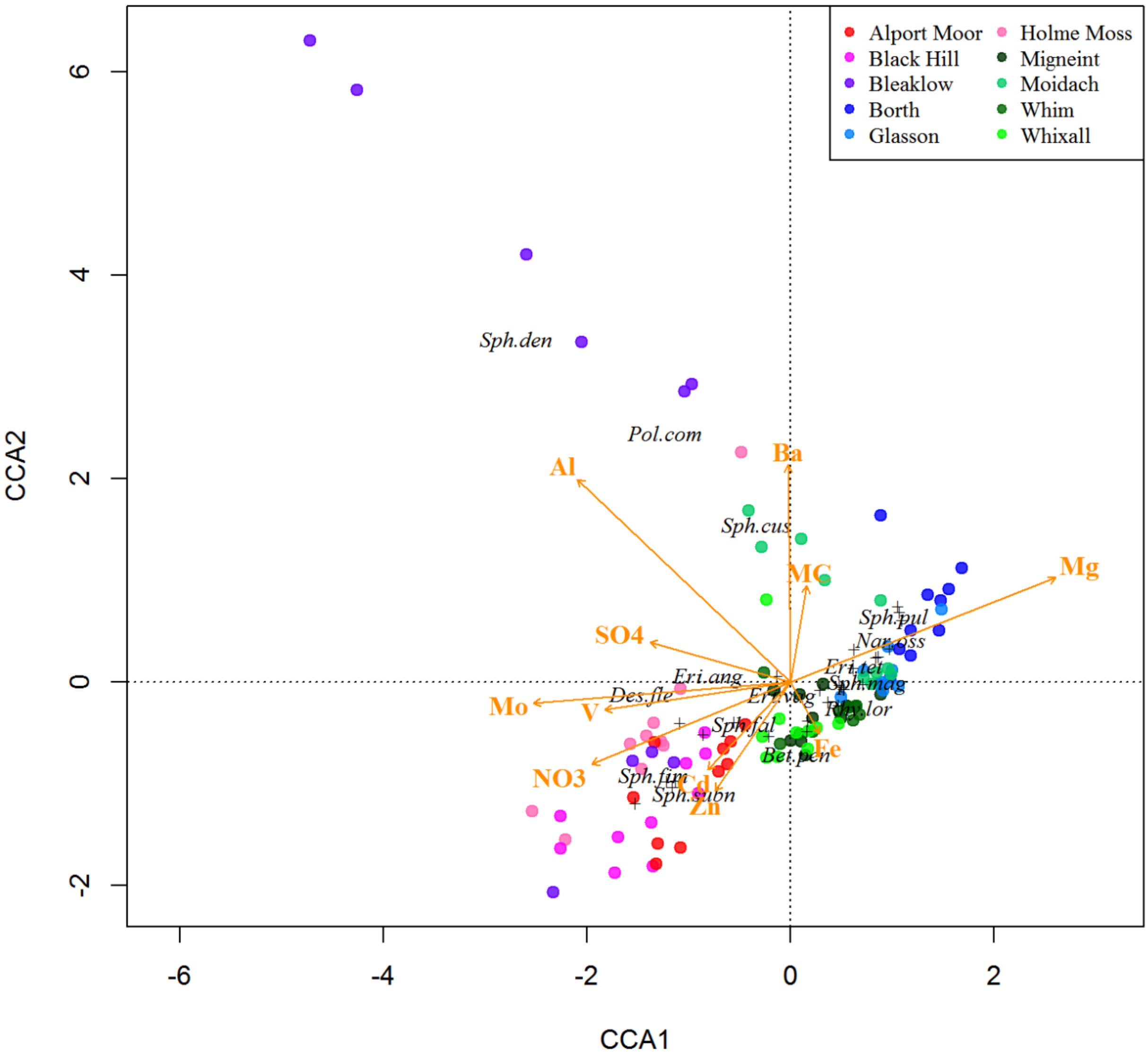


Figure 34 – Canonical correspondence analysis (CCA) ordination of the vegetation composition data and species distribution of the sample sites, constrained by those environmental variables selected in the model building process (Mg + Al + Ba + Cd + NO_3^- + MC + SO_4^{2-} + V + Fe + Mo + Zn). The most abundant species are added first and where species labels overlap, they have been omitted and the locations marked (+); all species labels are displayed in Appendix 10.

Table 21 – Variance inflation factor (VIF) values of the model terms for the national comparison.

Mg	2.069	Al	1.756	Ba	1.966	Cd	1.625
NO_3^-	1.607	MC	1.371	SO_4^{2-}	1.675	V	2.070
Fe	1.183	Mo	2.343	Zn	1.968		

Pennine sites

The process was repeated for the Pennine sites, generating the model:

$\text{Log}_{10}\ (\text{veg}+1) \sim \text{Ba} + \text{Al} + \text{P} + \text{Mg} + \text{Mo} + \text{Pb} + \text{Fe} + \text{S}$

Significance of the terms in the model were assessed using permutations ($P \leq 0.04$ for all terms) and only terms which reduced the AIC value were included (model AIC = 247.78, Appendix 11). The model was plotted (Figure 35), and the constraining variables checked for linearity using GAMs. The plotted vectors were found to be linear, with the exception of Mo and S. As in the national comparison, a small number of samples appeared to be highly influential, which may explain these non-linear gradients.

The majority of samples were distributed along CCA2, between 0 and -1 on CCA1. A small number of samples formed a separate group, located between 2.5 and 4 on CCA1. All but one of these samples were collected from Bleaklow, and most were those which contained *Sphagnum*. There were numerous strong gradients associated with these isolated samples. Pb, Al, Ba and Mg displayed strong gradients, separating the two groups of samples on the ordination (Figure 35). The main group of samples showed strong association with P and Fe, determining their position along CCA2. There was considerable overlap in the regions occupied by samples with and without *Sphagnum* on the ordination. Most samples containing *Sphagnum* were found at higher values on CCA2 than samples without *Sphagnum*.

Variance inflation factor (VIF) values were calculated for the terms of the model to assess levels of covariance with the other constraints (Table 22). All values were < 2.4 indicating that each constraint added independent information to the model (Zuur *et al.*, 2010).

Table 22 – Variance inflation factors (VIF) values for the model terms for the Pennine sites.

Ba	2.336	Al	2.338	P	1.389	Mg	1.363
Mo	1.631	Pb	2.394	Fe	1.395	S	1.922

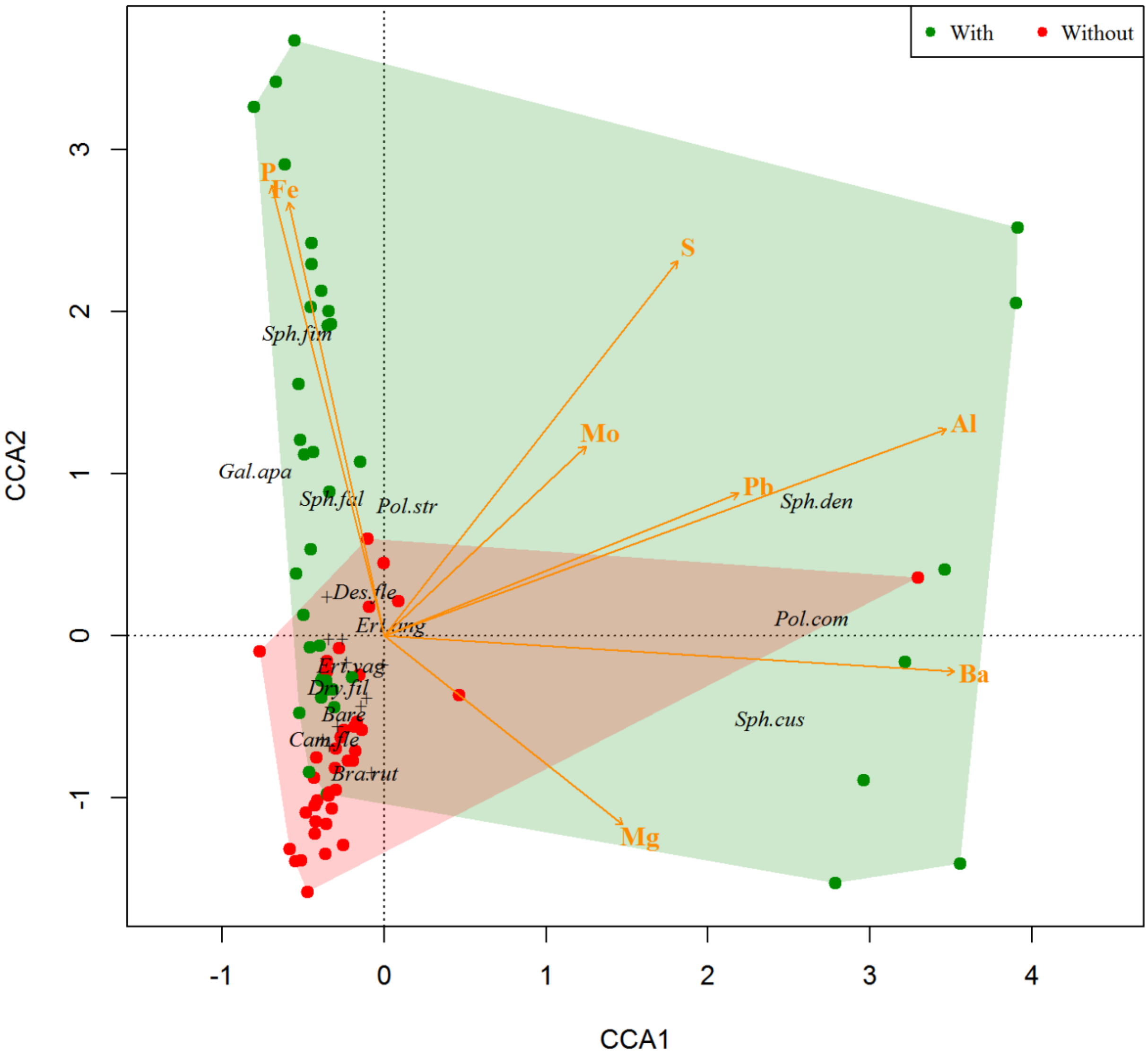


Figure 35 – Canonical correspondence analysis (CCA) ordination of the vegetation composition data and species distribution of the Pennine sites, constrained by those environmental variables selected in the model building process (Ba + Al + P + Mg + Mo + Pb + Fe + S). The most abundant species are added first and where species labels overlap, they have been omitted and the locations marked (+); all species labels are displayed in Appendix 12.

3.4.4 Species-gradient modelling

National comparison

Performance of the most abundant *Sphagnum* species (occurring in at least 5 quadrats) were examined over those environmental gradients shown to be significant in the CCA (Mg + Al + Ba + Cd + NO_3^- + MC + SO_4^{2-} + V + Fe + Mo + Zn). Species responses were assessed using HOF models; cover data were transformed (arcsin[√(x/100)]) and a Gaussian error structure was used (Huisman *et al.*, 1993). The results can be found in Appendix 13. Table 23 provides a summary of the HOF models describing the response of *Sphagnum* along those significant environmental gradients.

Table 23 – Summary of HOF model selected (bold) and gradient concentration (µg g^{-1} unless otherwise indicated) at which modelled *Sphagnum* species maxima occur, for the national comparison. Species abbreviations can be found in Appendix 1.

Gradient (Range)	*Sph.cap*	*Sph.cus*	*Sph.fal*	*Sph.mag*	*Sph.pal*	*Sph.pap*	*Sph.pul*	*Sph.subn*	*Sph.ten*
Mg	**7**	**7**	**7**	**4**	**4**	**7**	**5**	**7**	**7**
(250 – 1750)	1600	750	500	1100	350	300	1250	500	1750
Al	**2**	**7**	**7**	**3**	**4**	**5**	**3**	**7**	**4**
(0 – 2500)	0	1200	400	0	750	200	0	200	0
Ba	**7**	**5**	**7**	**7**	**4**	**7**	**7**	**3**	**4**
(0 – 60)	15	55	15	35	5	0	25	0	10
Cd	**7**	**7**	**7**	**2**	**4**	**7**	**4**	**7**	**2**
(0 – 7)	2	0	2.5	0	0	0	0.25	7	0
NO_3^-	**7**	**2**	**7**	**2**	**2**	**7**	**7**	**5**	**2**
(0 – 3500)	0	0	2400	0	3400	1750	250	1250	0
MC (%)	**7**	**5**	**5**	**4**	**4**	**7**	**5**	**7**	**5**
(84 – 97)	90.5	95.5	95.5	92	92	91	94	84	91
SO_4^{2-}	**7**	**7**	**7**	**3**	**4**	**7**	**7**	**4**	**4**
(0 – 900)	50	700	900	100	400	450	0	0	150
V	**7**	**7**	**7**	**2**	**4**	**7**	**7**	**5**	**2**
(0 – 2)	0	0.5	2	0	0.4	1.5	0.6	0.9	0
Fe	**7**	**7**	**7**	**4**	**4**	**7**	**5**	**2**	**7**
(0 – 5000)	5000	250	3500	800	800	900	500	0	600
Mo	**7**	**7**	**7**	**2**	**4**	**7**	**7**	**5**	**7**
(0 – 2)	0.1	0.4	1.2	0	0.5	2	0.1	0.9	0
Zn	**7**	**7**	**7**	**4**	**4**	**7**	**5**	**7**	**3**
(0 – 200)	80	0	60	140	25	40	25	200	0

When the HOF models were inspected (Appendix 13), it was noted that they appeared to suffer from over-fitting of the data, and were unduly influenced by extreme values. Whilst some models appeared realistic (e.g. *S. capillifolium* response to aluminium), many more models seemed erratic and unrealistic (e.g. *S. palustre* response to aluminium, *S. fallax* response to molybdenum). Therefore, HOF models were thought to be unsuitable for modelling responses of *Sphagnum* to influential environmental gradients in this instance.

3.4.5 Vegetation, peat total, and comparative chemistry

Vegetation chemistry

Differences in vegetation chemistry between survey sites were assessed using rank ANOVA and Bonferroni-corrected pairwise comparisons (see Table 24 for full details). Vegetation from Borth contained higher levels of Sn than any other site, whilst C, Mg and Sr were greater than a number of reference and Pennine sites. Glasson and Borth had significantly higher N:P than most other sites. Migneint had greater levels of Mn than Alport Moor, Holme Moss and Moidach. Ni was significantly greater at Moidach and Black Hill than Holme Moss, whilst C:N ratio was higher at three of the reference sites than most of the Pennine sites. Vegetation from Alport Moor contained higher levels of Cu than any reference sites, with Alport Moor and Bleaklow having significantly greater amounts of Mo and Pb. Bleaklow was higher in Co than the reference sites, whist N was higher at Holme Moss, and P was greater at Holme Moss and Black Hill. Levels of As, S, Ti, V and Zn were greatest at Alport Moor, significantly higher than many of the reference sites. Black Hill had the greatest Ca levels, whilst Bleaklow had the highest levels of Al, Ba, Cd and Fe. Holme Moss and Bleaklow contained the highest levels of K, greater than four reference sites, and Na was higher at Holme Moss than Moidach and Alport Moor.

Table 24 – Mean (and standard error) of vegetation chemistry variables from samples containing *Sphagnum*. Values in µg g^{-1} dry weight, unless indicated otherwise. Rank ANOVA (F) and Bonferroni-corrected pairwise comparisons are reported; sites which do not share a letter are significantly different. (* P ≤ 0.05, ** P ≤ 0.01, *** P ≤ 0.001)

Variable	*Alport Moor*	*Black Hill*	*Bleaklow*	*Borth*	*Glasson*	*Holme Moss*	*Migneint*	*Moidach*	*Whim*	*Whixall*	*F*
Al	464.97 $^{a\,b\,c}$	268.49 $^{c\,d}$	1492.75 ^{a}	173.06 $^{d\,e}$	186.74 $^{d\,e}$	440.96 $^{b\,c\,d}$	194.90 $^{d\,e}$	74.30 ^{f}	502.45 $^{a\,b}$	111.05 $^{e\,f}$	23.95 ***
	(60.21)	(39.86)	(365.99)	(12.52)	(16.04)	(113.88)	(35.80)	(9.77)	(41.54)	(11.42)	
As	1.75 ^{a}	0.47 $^{b\,c\,d\,e}$	1.39 $^{a\,b}$	1.83 $^{a\,b\,c}$	0.05 $^{d\,e}$	1.13 $^{a\,b}$	0.78 $^{b\,c\,d}$	0.04 ^{e}	0.14 $^{c\,d\,e}$	0.20 $^{b\,c\,d\,e}$	11.48 ***
	(0.28)	(0.18)	(0.38)	(0.90)	(0.02)	(0.24)	(0.37)	(0.01)	(0.08)	(0.04)	
Ba	19.83 $^{a\,b}$	13.05 $^{b\,c\,d}$	139.84 ^{a}	5.89 ^{d}	9.08 $^{c\,d}$	12.02 $^{b\,c\,d}$	8.31 $^{c\,d}$	18.23 $^{a\,b\,c}$	13.82 $^{a\,b\,c}$	16.61 $^{a\,b\,c}$	7.59 ***
	(2.09)	(1.93)	(36.97)	(0.42)	(1.18)	(1.45)	(1.02)	(3.82)	(1.42)	(3.88)	
C (%)	48.61 $^{a\,b\,c}$	47.37 ^{d}	46.09 ^{d}	50.95 ^{a}	50.36 $^{a\,b}$	50.86 $^{a\,b\,c}$	48.09 $^{c\,d}$	48.49 $^{b\,c\,d}$	50.35 $^{a\,b}$	48.11 $^{b\,c\,d}$	8.72 ***
	(1.82)	(0.21)	(1.08)	(0.43)	(0.46)	(1.42)	(0.41)	(0.35)	(0.36)	(0.56)	
Ca	2337.14 $^{a\,b}$	14832.17 ^{a}	1698.50 ^{b}	2318.52 $^{a\,b}$	2126.59 $^{a\,b}$	1584.83 ^{b}	1540.28 ^{b}	1633.11 ^{b}	2464.24 $^{a\,b}$	3297.96 $^{a\,b}$	3.33 **
	(621.43)	(3778.41)	(217.93)	(534.41)	(337.03)	(278.56)	(193.79)	(272.67)	(548.76)	(814.32)	
Cd	0.48 $^{a\,b}$	0.33 $^{b\,c\,d}$	0.65 ^{a}	0.16 $^{d\,e}$	0.32 $^{b\,c\,d\,e}$	0.44 $^{a\,b\,c\,d}$	0.60 $^{a\,b\,c}$	0.07 ^{e}	0.17 $^{c\,d\,e}$	0.25 $^{b\,c\,d\,e}$	9.16 ***
	(0.06)	(0.08)	(0.05)	(0.03)	(0.10)	(0.08)	(0.18)	(0.01)	(0.03)	(0.04)	
Co	0.45 $^{a\,b}$	0.37 $^{b\,c\,d}$	2.16 ^{a}	0.11 ^{e}	0.17 $^{d\,e}$	0.21 $^{c\,d\,e}$	0.15 $^{d\,e}$	0.08 ^{e}	0.36 $^{b\,c}$	0.16 $^{d\,e}$	18.91 ***
	(0.05)	(0.12)	(0.44)	(0.01)	(0.04)	(0.03)	(0.03)	(0.01)	(0.04)	(0.06)	
Cu	9.79 ^{a}	6.28 $^{a\,b\,c}$	8.64 $^{a\,b}$	5.92 $^{b\,c}$	4.19 $^{c\,d}$	5.78 $^{b\,c}$	4.58 $^{c\,d}$	2.72 ^{d}	4.58 $^{c\,d}$	2.96 ^{d}	14.16 ***
	(0.95)	(0.60)	(1.30)	(0.65)	(0.31)	(0.66)	(0.36)	(0.28)	(0.33)	(0.53)	
Fe	911.28 ^{a}	537.38 $^{a\,b\,c}$	1376.52 ^{a}	304.15 $^{b\,c}$	350.03 $^{b\,c}$	819.70 ^{a}	879.96 $^{a\,b\,c}$	264.47 ^{c}	668.74 $^{a\,b}$	281.90 ^{c}	7.83 ***
	(131.41)	(138.53)	(356.80)	(36.42)	(67.44)	(103.32)	(341.75)	(69.39)	(59.46)	(57.50)	
K	2300.21 $^{b\,c}$	2965.34 $^{a\,b}$	4192.93 ^{a}	2361.01 $^{b\,c}$	2017.87 $^{b\,c}$	5416.80 ^{a}	1782.43 ^{c}	2020.83 $^{b\,c}$	2528.10 $^{a\,b\,c}$	2822.02 $^{a\,b\,c}$	6.60 ***
	(401.66)	(253.00)	(590.00)	(358.69)	(193.16)	(968.14)	(117.42)	(149.95)	(242.82)	(333.87)	

Variable	*Alport Moor*	*Black Hill*	*Bleaklow*	*Borth*	*Glasson*	*Holme Moss*	*Migneint*	*Moidach*	*Whim*	*Whixall*	*F*
Mg	758.26 $^{c d}$	981.13 $^{a b c d}$	1092.68 $^{a b c}$	1344.14 ^{a}	912.12 $^{b c d}$	834.25 $^{c d}$	1187.99 $^{a b}$	1250.07 $^{a b}$	1055.01 $^{a b c}$	689.70 ^{d}	9.25 ***
	(67.84)	(73.25)	(126.08)	(63.88)	(65.42)	(57.86)	(41.56)	(91.87)	(68.82)	(44.26)	
Mn	44.15 $^{b c}$	80.72 $^{a b c}$	64.74 $^{a b c}$	118.23 $^{a b c}$	95.91 $^{a b c}$	43.51 $^{b c}$	163.46 ^{a}	46.02 ^{c}	130.99 $^{a b}$	124.83 $^{a b c}$	3.60 ***
	(5.87)	(18.92)	(12.83)	(53.03)	(24.73)	(9.02)	(26.17)	(17.67)	(28.60)	(34.96)	
Mo	4.15 ^{a}	1.23 $^{a b}$	3.05 ^{a}	0.08 $^{c d}$	0.05 $^{c d}$	0.09 ^{d}	0.06 ^{d}	0.18 $^{b c}$	0.18 $^{c d}$	0.23 $^{c d}$	28.99 ***
	(0.59)	(0.31)	(0.63)	(0.02)	(0.02)	(0.09)	(0.04)	(0.03)	(0.09)	(0.17)	
N (%)	1.38 $^{a b}$	1.08 $^{b c}$	1.45 $^{a b}$	1.03 $^{b c}$	1.07 $^{b c}$	1.77 ^{a}	1.04 $^{b c}$	0.92 ^{c}	1.11 $^{b c}$	0.77 ^{c}	10.03 ***
	(0.12)	(0.11)	(0.15)	(0.05)	(0.07)	(0.13)	(0.08)	(0.09)	(0.05)	(0.04)	
Na	517.49 ^{b}	761.18 $^{a b}$	745.89 $^{a b}$	847.35 $^{a b}$	790.96 $^{a b}$	1191.71 ^{a}	747.62 $^{a b}$	617.01 ^{b}	778.17 $^{a b}$	739.79 $^{a b}$	2.72 **
	(86.33)	(110.23)	(120.12)	(71.59)	(92.41)	(130.72)	(112.17)	(66.26)	(91.17)	(117.96)	
Ni	0.67 $^{a b}$	4.70 ^{a}	4.76 $^{a b}$	3.97 $^{a b}$	2.54 $^{a b}$	0.67 ^{b}	2.71 $^{a b}$	5.70 ^{a}	4.03 $^{a b}$	2.49 $^{a b}$	3.18 **
	(0.29)	(1.25)	(1.84)	(1.21)	(1.06)	(0.67)	(0.70)	(1.06)	(1.23)	(1.12)	
P	388.76 $^{b c d}$	988.62 ^{a}	711.59 $^{a b}$	248.82 ^{d}	226.19 ^{d}	1128.50 ^{a}	430.21 $^{b c}$	384.97 $^{b c d}$	450.00 $^{b c}$	316.43 $^{c d}$	18.33 ***
	(49.20)	(105.55)	(182.35)	(37.08)	(18.88)	(222.71)	(45.08)	(51.80)	(44.13)	(27.34)	
Pb	82.51 ^{a}	22.54 $^{b c}$	159.77 ^{a}	8.41 ^{c}	9.57 ^{c}	58.98 $^{a b}$	18.51 $^{b c}$	5.41 ^{c}	9.20 ^{c}	8.80 ^{c}	15.40 ***
	(17.12)	(8.69)	(41.76)	(1.65)	(3.05)	(19.72)	(7.02)	(1.61)	(2.91)	(2.28)	
S	1357.06 ^{a}	1222.80 $^{a b}$	1365.17 $^{a b}$	968.94 $^{a b c}$	933.34 $^{a b c}$	1193.21 $^{a b}$	854.95 ^{c}	785.32 ^{c}	912.13 $^{b c}$	798.62 ^{c}	6.81 ***
	(101.21)	(95.28)	(170.82)	(59.29)	(72.77)	(70.67)	(69.49)	(69.44)	(53.48)	(32.87)	
Sn	0.00 ^{b}	0.00 ^{b}	0.07 ^{b}	0.26 ^{a}	0.00 ^{b}	0.00 ^{b}	0.00 ^{b}	0.00 ^{b}	0.00 ^{b}	0.18 ^{b}	4.93 ***
	(0.00)	(0.00)	(0.07)	(0.15)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.18)	

Variable	*Alport Moor*	*Black Hill*	*Bleaklow*	*Borth*	*Glasson*	*Holme Moss*	*Migneint*	*Moidach*	*Whim*	*Whixall*	*F*
Sr	12.34 $^{a b c}$	16.92 $^{a b c}$	18.78 $^{a b}$	13.42 ^{a}	10.47 $^{a b c}$	7.27 $^{b c}$	12.16 $^{a b c}$	14.92 $^{a b}$	10.43 $^{a b c}$	6.81 ^{c}	3.83 ***
	(1.20)	(3.75)	(3.62)	(0.84)	(1.16)	(0.87)	(1.17)	(1.98)	(1.28)	(1.05)	
Ti	14.74 ^{a}	8.08 $^{a b c}$	12.62 ^{a}	1.45 ^{e}	3.19 $^{d e}$	5.21 $^{c d}$	2.09 ^{e}	5.18 $^{b c d}$	9.57 $^{a b}$	2.97 $^{d e}$	24.43 ***
	(1.92)	(1.34)	(2.96)	(0.29)	(0.42)	(0.86)	(0.46)	(0.53)	(0.78)	(0.44)	
V	3.66 ^{a}	1.55 $^{a b}$	3.25 ^{a}	0.47 $^{b c}$	0.56 $^{b c}$	1.93 ^{a}	0.56 $^{b c}$	0.20 ^{c}	1.28 $^{a b}$	0.21 ^{c}	11.73 ***
	(0.68)	(0.46)	(0.80)	(0.11)	(0.16)	(0.41)	(0.24)	(0.08)	(0.28)	(0.11)	
Zn	64.94 ^{a}	54.61 $^{a b}$	56.02 $^{a b}$	35.48 $^{b c}$	58.17 $^{a b}$	64.51 ^{a}	53.55 $^{a b}$	21.61 ^{c}	35.80 $^{b c}$	62.87 ^{a}	7.95 ***
	(3.94)	(8.73)	(4.35)	(2.31)	(8.81)	(5.73)	(10.06)	(2.89)	(3.74)	(5.20)	
C:N	36.68 $^{b c d}$	47.49 $^{a b c}$	34.42 $^{c d}$	50.58 ^{a}	49.85 $^{a b}$	30.00 ^{d}	48.30 $^{a b}$	56.07 ^{a}	46.13 $^{a b}$	64.47 ^{a}	11.98 ***
	(1.92)	(4.25)	(3.15)	(2.16)	(5.18)	(2.24)	(3.21)	(4.39)	(1.83)	(3.56)	
N:P	37.68 $^{a b}$	11.34 ^{d}	25.29 $^{b c}$	45.25 ^{a}	48.73 ^{a}	20.66 $^{c d}$	25.19 $^{b c}$	25.56 $^{b c}$	26.11 $^{b c}$	25.42 $^{b c}$	15.73 ***
	(3.23)	(0.88)	(3.37)	(3.65)	(2.90)	(3.13)	(1.45)	(1.69)	(1.93)	(2.14)	

Peat total chemistry

Differences in peat total chemistry between survey sites were assessed using rank ANOVA and Bonferroni-corrected pairwise comparisons. Table 25 provides full details.

Peat from Borth had the highest levels of C, greater than Black Hill, Moidach and Bleaklow, whilst levels of Mg were higher than all sites except Migneint and Glasson. Similarly, Na was highest at Borth and was significantly greater than all sites but Glasson. N:P ratio was highest at Borth and Glasson. The values at these sites were higher than all other sites. Migneint has greater level of Cd than Holme Moss, Black Hill, Glasson, Borth and Moidach, whilst Mn was also greater than at Whixall, Holme Moss and Moidach. Migneint was found to have the greatest levels of N, more so than Bleaklow, Moidach and Whixall. Sr levels were higher at Migneint, Moidach, Borth, Whim and Black Hill than Alport Moor, Whixall and Holme Moss. Moidach and Glasson were significantly greater in K than Whixall, whilst Whim and Alport Moor had greater levels of Ti than four of the reference sites. Whixall had higher levels of Zn than five of the sites, including three Pennine, whilst C:N ratios were higher than Alport Moor, Whim, Holme Moss and Migneint.

Peat from Alport Moor had significantly greater levels of total Mo than all of the reference sites and Black Hill, and was higher in Sn than four of the reference sites and Bleaklow. Cu was greater at Alport Moor, Bleaklow and Holme Moss than five of the reference sites, whilst V was greater at Alport Moor and Holme Moss than all but one of the reference sites. Alport Moor, Migneint, Bleaklow and Holme Moss had higher levels of As than Glasson and Moidach. Black Hill was characterised by Ca levels greater than Holme Moss and Alport Moor, and Ni was higher than at Glasson and Migneint. Al was significantly higher at Bleaklow than all sites but Holme Moss, Alport Moor and Whim, whilst Ba was greater at Bleaklow than four of the reference sites. Bleaklow and Alport Moor had greater levels of Pb than all sites except for Holme Moss and Whim, whilst Co was greater at Bleaklow and Whim than all sites but Alport Moor and Holme Moss. P levels were highest at Holme Moss, more so than all sites except Migneint, Black Hill and Whim. Fe was found at the greatest levels at Holme Moss, Migneint and Whim, and was significantly greater than the remaining four of the reference sites.

Table 25 – Mean (and standard error) of total peat chemistry variables from samples containing *Sphagnum*. Values in µg g^{-1} dry weight, unless indicated otherwise. Rank ANOVA (F) and Bonferroni-corrected pairwise comparisons are reported; sites which do not share a letter are significantly different. (* P ≤ 0.05, ** P ≤ 0.01, *** P ≤ 0.001)

Variable	*Alport Moor*	*Black Hill*	*Bleaklow*	*Borth*	*Glasson*	*Holme Moss*	*Migneint*	*Moidach*	*Whim*	*Whixall*	*F*
Al	1051.84 ^{abcd}	933.33 ^{bcde}	2892.48 ^{a}	746.23 ^{cde}	531.74 ^{e}	1754.36 ^{ab}	853.18 ^{cde}	530.70 ^{e}	1149.33 ^{abc}	629.30 ^{de}	11.40 ***
	(74.84)	(123.45)	(630.52)	(83.16)	(54.82)	(206.69)	(86.80)	(161.06)	(91.51)	(104.43)	
As	5.13 ^{a}	2.47 ^{abc}	5.31 ^{abc}	5.75 ^{ab}	1.26 ^{bc}	5.35 ^{a}	5.19 ^{a}	0.62 ^{c}	3.30 ^{ab}	5.75 ^{ab}	8.31 ***
	(0.48)	(0.50)	(0.71)	(2.02)	(0.23)	(0.98)	(0.66)	(0.16)	(0.92)	(2.16)	
Ba	24.15 ^{ab}	19.46 ^{abc}	135.02 ^{a}	7.24 ^{d}	16.25 ^{bc}	13.46 ^{bcd}	14.86 ^{cd}	25.08 ^{ab}	21.70 ^{abc}	17.13 ^{bcd}	8.33 ***
	(2.52)	(2.87)	(42.09)	(1.31)	(1.55)	(1.34)	(3.34)	(3.35)	(1.93)	(3.45)	
C (%)	51.75 ^{abc}	50.07 ^{bc}	48.32 ^{c}	53.39 ^{a}	50.49 ^{abc}	52.16 ^{abc}	53.09 ^{ab}	50.34 ^{bc}	53.13 ^{ab}	50.79 ^{abc}	4.48 ***
	(0.65)	(0.79)	(1.32)	(0.41)	(0.39)	(1.67)	(0.33)	(0.62)	(0.44)	(0.74)	
Ca	1186.79 ^{c}	9328.25 ^{a}	1590.10 ^{abc}	1984.35 ^{ab}	1575.02 ^{abc}	1270.70 ^{bc}	1845.04 ^{ab}	1379.74 ^{abc}	1501.34 ^{abc}	1396.80 ^{abc}	3.96 ***
	(63.33)	(2639.77)	(249.27)	(194.25)	(97.30)	(152.98)	(83.54)	(158.07)	(176.12)	(119.51)	
Cd	0.98 ^{abc}	0.85 ^{bcd}	1.21 ^{abc}	0.54 ^{de}	0.76 ^{cde}	0.93 ^{bcd}	2.00 ^{a}	0.30 ^{e}	1.66 ^{ab}	1.28 ^{abc}	12.63 ***
	(0.10)	(0.09)	(0.15)	(0.07)	(0.14)	(0.08)	(0.33)	(0.04)	(0.22)	(0.20)	
Co	1.01 ^{ab}	0.86 ^{bc}	2.63 ^{a}	0.40 ^{e}	0.61 ^{cde}	1.07 ^{ab}	0.52 ^{de}	0.52 ^{de}	1.71 ^{a}	0.80 ^{bcd}	19.39 ***
	(0.07)	(0.09)	(0.58)	(0.05)	(0.07)	(0.12)	(0.03)	(0.06)	(0.18)	(0.09)	
Cu	23.59 ^{a}	14.48 ^{ab}	26.55 ^{a}	12.46 ^{bc}	4.29 ^{c}	25.39 ^{a}	6.60 ^{bc}	3.91 ^{c}	13.05 ^{ab}	10.53 ^{bc}	12.38 ***
	(2.60)	(1.83)	(6.52)	(4.63)	(0.58)	(5.60)	(0.96)	(0.61)	(2.17)	(3.59)	
Fe	2942.18 ^{ab}	2322.61 ^{abc}	3137.00 ^{ab}	1294.89 ^{c}	1709.53 ^{bc}	4567.09 ^{a}	3936.36 ^{a}	1632.66 ^{bc}	4266.09 ^{a}	1195.15 ^{c}	10.00 ***
	(410.81)	(358.07)	(600.24)	(235.88)	(244.88)	(743.66)	(502.47)	(243.97)	(799.11)	(269.42)	
K	500.38 ^{ab}	610.22 ^{ab}	798.63 ^{ab}	745.20 ^{ab}	801.71 ^{a}	752.36 ^{ab}	475.19 ^{ab}	799.43 ^{a}	466.24 ^{ab}	412.69 ^{b}	4.11 ***
	(63.62)	(83.25)	(164.20)	(102.84)	(76.13)	(87.69)	(55.28)	(62.76)	(44.61)	(69.54)	

Variable	*Alport Moor*	*Black Hill*	*Bleaklow*	*Borth*	*Glasson*	*Holme Moss*	*Migneint*	*Moidach*	*Whim*	*Whixall*	*F*
Mg	478.15 ^{e}	643.88 $^{d e}$	731.71 $^{c d}$	1391.57 ^{a}	1075.62 $^{a b}$	456.03 ^{e}	1112.52 $^{a b}$	1070.87 ^{b}	927.18 $^{b c}$	618.54 $^{d e}$	31.63 ***
	(24.51)	(42.90)	(103.97)	(50.81)	(51.61)	(36.44)	(29.99)	(80.23)	(35.21)	(34.27)	
Mn	24.82 $^{a b c}$	31.90 $^{a b c}$	35.53 $^{a b c}$	76.44 $^{a b c}$	39.79 $^{a b c}$	18.13 $^{b c}$	83.98 ^{a}	16.83 ^{c}	41.70 $^{a b}$	25.64 $^{b c}$	4.21 ***
	(3.13)	(6.80)	(7.74)	(36.04)	(7.85)	(1.09)	(12.81)	(3.36)	(6.12)	(3.17)	
Mo	24.01 ^{a}	6.18 $^{b c}$	13.01 $^{a b}$	1.71 $^{d e}$	0.69 $^{d e}$	16.24 $^{a b}$	6.93 $^{b c}$	0.72 ^{e}	8.59 $^{b c d}$	3.00 $^{c d e}$	16.73 ***
	(1.92)	(2.06)	(1.92)	(1.29)	(0.34)	(2.33)	(2.47)	(0.41)	(3.56)	(1.44)	
N (%)	1.66 $^{a b}$	1.44 $^{a b c}$	1.36 $^{b c}$	1.54 $^{a b}$	1.44 $^{a b c}$	1.73 $^{a b}$	1.84 ^{a}	1.37 $^{b c}$	1.72 $^{a b}$	1.05 ^{c}	6.20 ***
	(0.09)	(0.09)	(0.08)	(0.09)	(0.06)	(0.11)	(0.09)	(0.08)	(0.09)	(0.10)	
Na	163.53 ^{d}	247.99 $^{c d}$	174.91 ^{d}	449.56 ^{a}	324.39 $^{a b}$	266.85	271.83 $^{b c}$	257.25 $^{b c}$	240.53 $^{b c d}$	221.29 $^{c d}$	13.15 ***
	(15.20)	(48.56)	(7.76)	(13.43)	(18.63)	(27.90)	(19.45)	(11.08)	(19.90)	(11.40)	
Ni	3.55 $^{a b}$	7.34 ^{a}	6.57 $^{a b}$	5.42 $^{a b}$	1.80 ^{b}	4.86 $^{a b}$	1.12 ^{b}	2.22 $^{a b}$	3.01 $^{a b}$	2.96 $^{a b}$	3.59 ***
	(1.21)	(1.16)	(1.58)	(0.80)	(0.76)	(1.14)	(0.61)	(0.97)	(1.34)	(0.83)	
P	588.90 ^{b}	702.80 $^{a b}$	559.84 $^{b c}$	320.35 ^{d}	337.86 ^{d}	1085.98 ^{a}	741.57 $^{a b}$	584.72 ^{b}	694.70 $^{a b}$	373.34 $^{c d}$	20.61 ***
	(40.44)	(52.61)	(65.10)	(27.85)	(25.70)	(76.80)	(62.98)	(34.98)	(39.97)	(46.44)	
Pb	238.57 ^{a}	100.30 $^{b c}$	324.33 ^{a}	31.67 $^{d e}$	45.95 $^{c d e}$	167.12 $^{a b}$	93.94 $^{b c}$	21.84 ^{e}	140.35 $^{a b}$	70.36 $^{c d}$	20.00 ***
	(37.14)	(19.58)	(75.82)	(6.08)	(6.88)	(29.27)	(13.14)	(2.78)	(17.73)	(15.08)	
S	2466.94	2234.00	2985.56	2326.34	2073.19	3091.88	2232.42	1817.02	2518.15	3835.64	1.68
	(159.02)	(204.75)	(436.83)	(274.62)	(215.54)	(362.02)	(286.04)	(227.96)	(353.81)	(998.95)	
Sn	1.56 ^{a}	0.86 $^{a b}$	1.82 $^{b c d}$	0.06 ^{d}	0.02 ^{d}	0.90 $^{a b c d}$	0.16 ^{d}	0.05 $^{c d}$	0.61 $^{a b c}$	0.86 $^{a b}$	9.09 ***
	(0.19)	(0.21)	(1.55)	(0.05)	(0.02)	(0.39)	(0.15)	(0.04)	(0.21)	(0.32)	

Variable	*Alport Moor*	*Black Hill*	*Bleaklow*	*Borth*	*Glasson*	*Holme Moss*	*Migneint*	*Moidach*	*Whim*	*Whixall*	*F*
Sr	12.13 $^{b c d}$	20.67 ^{a}	19.55 ^{a}	21.51 ^{a}	16.64 $^{a b c}$	9.35 ^{d}	21.64 ^{a}	21.47 ^{a}	19.51 ^{a}	10.53 $^{c d}$	11.33 ***
	(1.01)	(2.50)	(3.38)	(1.98)	(1.06)	(0.54)	(0.74)	(1.63)	(1.16)	(1.25)	
Ti	41.26 ^{a}	34.08 $^{a b c}$	40.86 $^{a b}$	20.71 $^{a b c}$	15.69 ^{c}	41.50 $^{a b c}$	16.43 ^{c}	22.28 $^{b c}$	51.79 ^{a}	18.68 $^{b c}$	6.18 ***
	(3.66)	(5.97)	(9.15)	(3.32)	(2.30)	(10.01)	(2.87)	(7.20)	(8.67)	(4.53)	
V	12.23 ^{a}	8.63 $^{a b c}$	10.71 $^{a b}$	4.10 ^{d}	4.69 $^{b c d}$	13.49 ^{a}	4.31 $^{c d}$	1.87 ^{d}	8.48 $^{a b}$	4.16 ^{d}	14.93 ***
	(1.44)	(1.30)	(2.72)	(0.82)	(0.59)	(2.60)	(0.39)	(0.35)	(0.97)	(1.06)	
Zn	77.75 $^{a b c}$	57.89 $^{c d e}$	56.27 $^{c d e}$	47.41 $^{d e}$	92.49 $^{a b}$	95.27 $^{b c d}$	71.61 $^{a b c d}$	32.75 ^{e}	87.58 $^{a b c}$	123.07 ^{a}	11.14 ***
	(6.14)	(4.98)	(5.34)	(4.29)	(9.45)	(37.29)	(10.65)	(5.06)	(8.22)	(17.64)	
C:N	31.97 ^{b}	35.79 $^{a b}$	36.56 $^{a b}$	35.67 $^{a b}$	35.66 $^{a b}$	31.56 ^{b}	29.49 ^{b}	37.65 $^{a b}$	31.46 ^{b}	50.91 ^{a}	5.06 ***
	(1.45)	(1.88)	(1.99)	(2.01)	(1.43)	(2.72)	(1.30)	(2.05)	(1.33)	(3.22)	
N:P	28.69 ^{b}	21.19 $^{c d}$	26.92 $^{b c}$	49.86 ^{a}	43.74 ^{a}	16.60 ^{d}	25.78 $^{b c}$	23.73 $^{b c d}$	25.01 $^{b c}$	29.41 ^{b}	18.48 ***
	(1.60)	(1.58)	(3.39)	(3.12)	(1.92)	(1.48)	(1.72)	(0.99)	(0.84)	(1.91)	

Comparative peat extractable, total and vegetation chemistry

Relationships between peat extractable, total and vegetation chemistry were assessed using Spearman's rank correlation coefficient (Table 26). Peat extractable and total values were found to be highly significantly correlated ($P \leq 0.001$) in all but four of the measured elements and ions. Extractable and total levels of Ba and Ni were less significantly correlated ($P \leq 0.05$), whilst NO_3^- (N) and SO_4^{2-} (S) values showed no correlation. Relationships between peat extractable and vegetation chemistry were more variable; 15 variables were highly significantly correlated ($P \leq 0.001$), Fe and S were less so ($P \leq 0.01$), and Na^+ (Na), NO_3^- (N) and Sr less so again ($P \leq 0.05$). Ba, K, Sn and SO_4^{2-} (S) were not significantly correlated, and Ni was significantly negatively correlated. Vegetation chemistry and total peat values were significantly correlated in 23 of the chemistry variables; 20 of these were highly significant ($P \leq 0.001$), whilst C:N ($P \leq 0.01$), and N and S were less so ($P \leq 0.05$). K, Ni and Sn were not significantly correlated.

Peat extractable, total and vegetation chemistry values were compared, both within and between the sites (Figure 36 and Figure 37). Cd, Co and Pb behaved similarly, with peat total values greater than extractable, and vegetation values the lowest. This pattern was consistent across most of the site and appeared proportional; i.e. there was a direct relationship between the three chemical measures. Sn and Zn were also followed the general pattern of values: peat total > extractable > vegetation, however, this was not consistent across all the sites nor were changes proportionally represented across the three measures. Al, Ba, Cu, Mo, S, Sr, Ti and V exhibited generally consistent and proportional of the order peat total values > vegetation > extractable. P displayed inconsistent results, with seven of the survey sites following the same pattern, but with the remaining three showing higher vegetation values. Both C and N levels were generally higher in peat total than vegetation; no extractable values were collected. C:N ratio was higher in vegetation than peat total, whilst N:P ratio was broadly similar in vegetation and peat total at each site. Ni behaved in neither a consistent nor proportional fashion between measures or sites. As and Fe were similarly variable, albeit with total peat values highest across all sites. Ca, K and Mn were in general consistently and proportionally represented across the three measures in the following order: vegetation > peat total > extractable. Mg followed this pattern but with the absence of extractable values. Na displayed a different order; vegetation > total peat, but was also consistently and proportionally represented between sites and measures.

Table 26 – Spearman's rank correlation coefficient of peat extractable, vegetation and peat total values of biogeochemical variables. Ions are correlated against their elemental counter parts, as shown in brackets. (* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$)

Variable	*extractable/ total*	*extractable/ vegetation*	*vegetation/ total*
Al	0.840 ***	0.604 ***	0.658 ***
As	0.601 ***	0.525 ***	0.716 ***
Ba	0.202 *	0.167	0.512 ***
C			0.291 ***
Ca	0.743 ***	0.325 ***	0.351 ***
Cd	0.851 ***	0.442 ***	0.480 ***
Co	0.678 ***	0.468 ***	0.618 ***
Cu	0.805 ***	0.528 ***	0.568 ***
Fe	0.673 ***	0.269 **	0.553 ***
K	0.648 ***	-0.040	0.028
Mg			0.649 ***
Mn	0.831 ***	0.586 ***	0.733 ***
Mo	0.728 ***	0.516 ***	0.362 ***
N			0.244 *
Na^+ (Na)	0.767 ***	0.240 *	0.311 ***
NH_4^+ (N)	0.377 ***	0.351 ***	
Ni	0.226 *	-0.216 *	-0.077
NO_3^- (N)	0.146	0.242 *	
P	0.774 ***	0.751 ***	0.684 ***
Pb	0.907 ***	0.648 ***	0.662 ***
PO_4^{3-} (P)	0.563 ***	0.619 ***	
S	0.325 ***	0.269 **	0.253 *
Sn	0.330 ***	-0.194	0.009
SO_4^{2-} (S)	0.132	0.077	
Sr	0.687 ***	0.238 *	0.501 ***
Ti	0.734 ***	0.523 ***	0.511 ***
V	0.745 ***	0.583 ***	0.508 ***
Zn	0.683 ***	0.437 ***	0.493 ***
C:N			0.288 **
N:P			0.662 ***

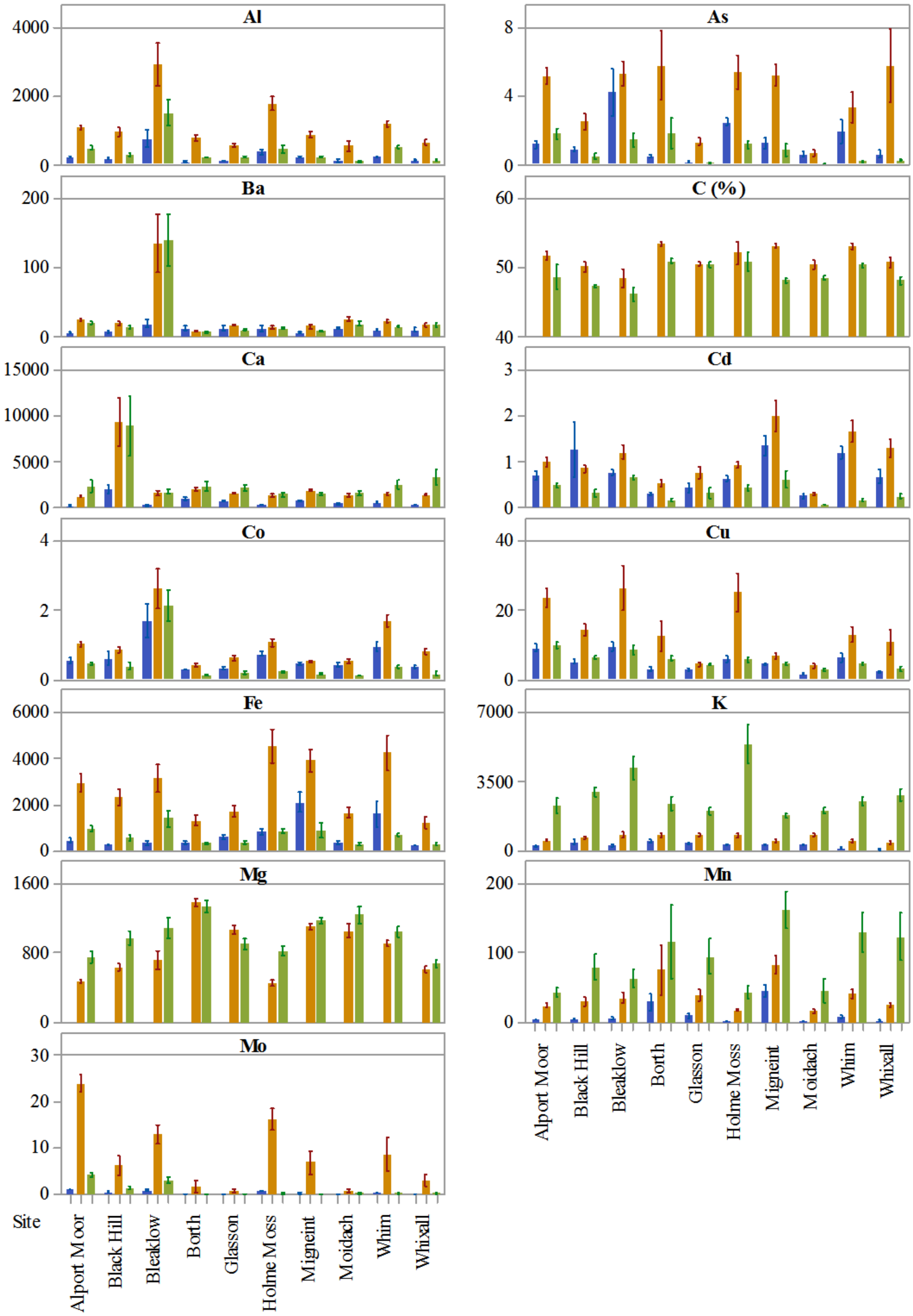


Figure 36 – Mean (± 1 SE) peat extractable (blue), peat total (orange) and vegetation (green) measures of biogeochemical variables. Values in µg g^{-1} unless indicated otherwise.

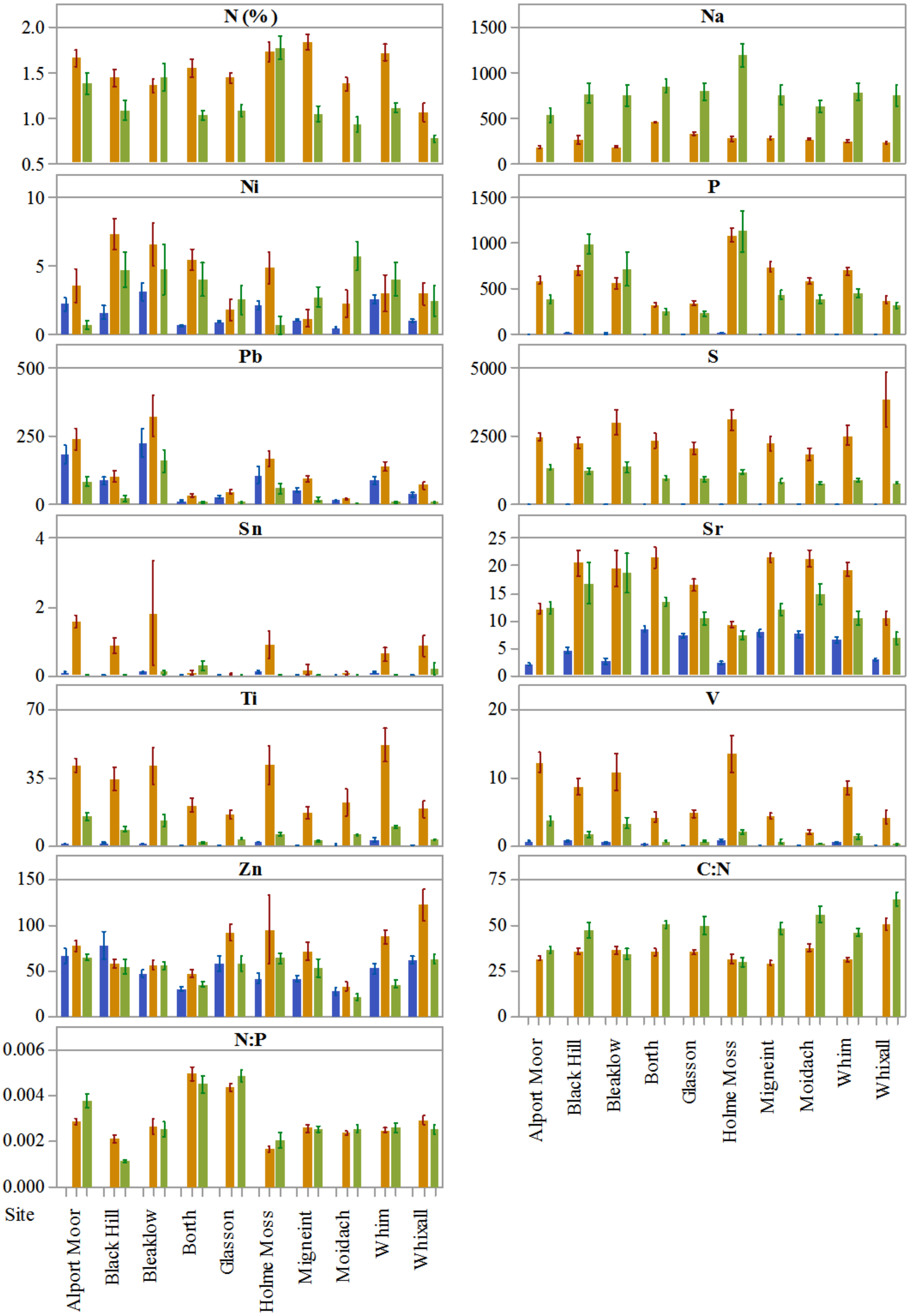


Figure 37 – Mean (± 1 SE) peat extractable (blue), peat total (orange) and vegetation (green) measures of biogeochemical variables. Values in µg g^{-1} unless indicated otherwise.

3.5 Discussion

3.5.1 Vegetation

National comparison

Non-metric multidimensional scaling revealed a clear distinction in the vegetation composition of the reference and Pennine sites (Figure 29). The reference sites were characterised by species typical of high quality ombrotrophic bog, such as *Andromeda polifolia*, *Drosera* spp., *Myrica gale*, *Narthecium ossifragum*, *Rhynchospora alba*, *Scirpus cespitosus* (syn. *Trichophorum cespitosum*) and *Vaccinium oxycoccos*. *Sphagnum* was consistent a major component of the recorded vegetation, the species of which varied between sites. The presence of *Sphagnum*, amongst other species of vascular plants and bryophytes, defines these sites as high quality examples of active blanket and raised bog habitats; i.e. peat-forming (JNCC, 2004, 2009). Species such as *S. capillifolium* and *S. papillosum* were prevalent, along with smaller amounts of *S. tenellum*, and locally abundant *S. magellanicum* and *S. pulchrum*.

In contrast, the Pennine sites contained few of these indicator species; their absence in the southern Pennine and Peak District regions has been conspicuous in the past (Lee, 1998). Vegetation was species-poor, with quadrats usually dominated by one or two of only a few vascular plants; e.g. *D. flexuosa*, *E. angustifolium*, *E. vaginatum* and *V. myrtillus*. The bryophyte flora was more diverse, including some *Sphagnum.* However, these species are more typical of minerotrophic conditions, such as *S. fallax* and *S. fimbriatum* (Hill *et al.*, 2007). There were also a number of atypical species present, indicative of disturbance, elevated nutrient conditions and raised soil pH, such as *Epilobium angustifolium* (syn. *Chamerion angustifolium*) and *Galium aparine* (Hill *et al.*, 1999). Such species are likely to occur due to applications of lime and fertiliser as part of the revegetation process. Indeed, many of these non-bog species are found in channels and gulley floors which act to gather and concentrate run-off from treated areas. Propagules may arrive as seed carried by the wind, or be inadvertently introduced when applying materials such as lime, fertiliser, heather brash or geotextiles. More typical moorland species, such as *Deschampsia flexuosa* and *Hypnum jutlandicum*, indicate conditions are somewhat drier than reference blanket bog would be (Atherton *et al.*, 2010; Hill *et al.*, 1999; 2007).

Pennine sites

Non-metric multidimensional scaling illustrated the significant difference in vegetation composition between samples with and without *Sphagnum* from the Pennine sites (Figure 30). This is perhaps unsurprising given that samples were distinguished by the presence or absence of *Sphagnum*. Indeed, with the exception of *S. cuspidatum*, all *Sphagnum* species were found outside the “without” region of the ordination. The region occupied by samples with *Sphagnum* was larger than that of samples without, indicating a greater diversity of species associated with *Sphagnum* presences. However, the cause of this diversity may be due to the atypical bog species found in the southern Pennines, arising from the application of lime and fertiliser in revegetation works, as discussed.

S. cuspidatum and *S. fallax* were closely associated on the ordination, and close to *E. angustifolium*, indicative of wet conditions. *S. fimbriatum* was most closely linked with *Campylopus pyriformis* and *Brachythecium rutabulum*, suggesting its locations had suffered disturbance and were drier. *S. subnitens* was most closely associated with *Aulacomnium palustre* and *Epilobium angustifolium*, reflecting the nutrient enriched conditions. *S. papillosum* was found close to *Galium aparine* on the ordination; a surprising relationship given their contrasting nutrient requirements (Atherton *et al.*, 2010; Hill *et al.*, 1999; 2007). *S. denticulatum* was isolated on the ordination, demonstrating the dominance of this species in samples where it occurred.

3.5.2 Biogeochemistry

National comparison

Nutrient ions and elements (NH_4^+, NO_3^-, P, PO_4^{3-}) were elevated at some or all of the degraded sites. These sites have been subjected to, and continue to be influenced by, increased rates of deposition due to both their altitude and proximity to sources of emissions from major conurbations of northern England; NO_3^- from fossil fuel combustion and NH_y intensive agriculture (Manninen *et al.*, 2011). In addition to this, the application of NPK fertiliser used in revegetation works is also a likely contributor to these higher levels. This is supported by the high levels of NO_3^-, P and PO_4^{3-} recorded at Holme Moss and Black Hill, where samples came from areas continuing to receive fertiliser applications. Whilst parts of Alport Moor and Bleaklow were also under-going restoration works, samples collected at these sites were not taken from areas under such management. NH_4^+ was greatest at the Pennine sites, however, levels from Migneint were similar, thought to be due to nearby agriculture and high levels of wet deposition (RoTAP, 2012). Concentrations of these elements were significantly higher than those found in comparable studies (Elliott *et al.*, 2015; Nwaishi, 2010; Rosenburgh *et al.*, 2013), with the exception of P which was similar to other UK values, and considerably lower than industrial areas (e.g. Salemaa *et al.*, 2001).

Ca levels appear to further reflect restoration activity; evidence of recent lime application was found at Black Hill, but not the three other Pennine sites. Ca was noted to be very variable, both in this study and others (e.g. Basiliko & Yavitt, 2001; Stevens *et al.*, 2009). Mg and Na^+ were found to be lower at the Pennine sites than the reference sites, thought to be due to acidification and subsequent leaching of cations from the peat (Curtis *et al.*, 2005; Daniels *et al.*, 2008, 2012; Evans *et al.*, 2000). K followed a similar pattern, although concentrations were raised at Black Hill, thought to be a further effect of fertiliser application. Whixall was shown to be lower than the other reference sites in a number of these cations; Ca, K and Mg were at similar concentrations to the Pennine sites. Sr conforms to the same pattern as other group 2 elements, with lower levels found across the Pennine sites and at Whixall. Ca, Sr and Ba are known to have similar biogeochemical behaviours in some ecosystem processes (Watmough, 2014). However, Ba did not exhibit the same site differences and similarities as observed in Ca and Sr. Atmospheric Ba levels, and therefore peat Ba levels, are not affected by anthropogenic activities, but rather can be used as a surrogate measure of mineral matter and soil-derived mineral dust (Krachler & Shotyk, 2004; Shotyk *et al.*, 2014). Ba is the 21st most abundant element in the lithosophere, with quantities varying considerably between rock types (Dawson, 1985).

The legacy of severe atmospheric pollution was evident in the biogeochemistry of the Pennine sites. When compared to the least polluted survey sites, all the Pennine sites showed elevated levels of As, Cd, Cu, Mo, Ni, Pb, Sn, Ti and V, whilst most had raised levels of Al, Co, Fe and Zn. Intensive industrial activity in the surrounding conurbations generated emissions on an unprecedented scale, depositing vast quantities of pollutants on the Peak District and southern Pennines. Consequently, the blanket bogs of the region contain high levels of heavy metals (Hutchinson, 1995; Jones & Hao, 1993; Lee & Tallis, 1973; Livett *et al.*, 1979; Markert & Thornton, 1990). Despite large reductions in atmospheric heavy metal and sulphur concentrations over the last 40 years (Cawse *et al.*, 1994; UKRGAR, 1997), and subsequent rates of deposition (e.g. Pb reduced by 74 % from 1990 to 2010 (Harmens *et al.*, 2013)), the peat still contains a substantial pool of these pollutants (Tipping *et al.*, 2003).

All of the reference sites surveyed showed elevated levels of a number of heavy metals and/ or sulphur. Moidach appeared the least polluted site, perhaps unsurprising, as it was the most northerly site surveyed. S and SO_4^{2-} levels were found to be comparable with the Pennine sites, however, this was the case for most of the reference sites, indicating concentrations of extractable S and SO_4^{2-} were not always due to legacy effects of pollution; most likely to be of marine origin. In contrast, Whim was found to be the most polluted of the reference sites, with concentrations of all heavy metals analysed greater than or equal to the Pennine sites, with the exception of Mo. Whim is situated close to Edinburgh (~ 20 km) and Glasgow (~ 60 km), major industrial centres for the last ~ 200 years. The similarities in terms of pollutant metals present and their concentrations found at Whim and in the southern Pennines suggests they are also the result of industrial pollution. This is further supported by the prevalence and intensity of coal burning and metallurgy, and its associated emissions, in the two regions.

Borth, Glasson, Whixall and Migneint were each found to contain elevated levels of at least some of this suite of industrial pollutants found in the southern Pennines. Migneint had concentrations of Al, As, Cd, Co, Cu, Fe, Mn, Ni and Zn similar to those of the Pennine sites. This was thought, in part, to be due to the altitude of this site, resulting in high levels of precipitation along with orographic enhancement, increasing the overall input of pollutants. Whilst Migneint suffered increased rates of pollution deposition, the elevated levels of some of these pollutants (e.g. Cd and Zn) at low lying sites, such as Glasson and Whixall, indicates additional, localised inputs. Supporting this hypothesis, Mn was found at the highest concentrations at the reference sites, with levels at Migneint and Borth an order of magnitude greater than in the southern Pennines. Although these enrichments are evident in this study, concentrations of such metals are considerably lower than sites affected by activities, such as smelting (Salemaa et al., 2001).

Historically, the Peak District and southern Pennines were an important metal producing region; Cu, Fe, Mn, Pb and Zn having all been mined (Ford, 2002). The Peak District represented a key source of Pb for the Romans, whilst extensive mining and smelting occurred in the medieval period, peaking in the 17th and 18th centuries (Barnatt, 1999; Barnatt & Penny, 2004). Such activities would have generated localised pollution from small-scale extraction and processing. Similarly, historic metal extraction and processing has been recorded at Borth (e.g. Mighall *et al.*, 2009; Poucher, 2009) and Migneint (e.g. Mighall *et al.*, 2002; Rhind & Jones, 2003), which may explain the presence of heavy metals in areas of low atmospheric deposition. For example, Mn was conspicuously high at Borth and Migneint; levels were an order of magnitude higher than the Pennine sites despite receiving high loads of industrial pollution. Thus, it is likely the presence of Mn, and presumably other pollutants, is the localised effects of historic metal works. Metallurgy, manufacturing, power generation and vehicle use are important contemporary sources of heavy metal emissions (Harmens *et al.*, 2013). Localised effects can also be observed from these sources. Elevated levels of Mo observed at Alport Moor, Bleaklow and Holme Moss were thought to be due to a Mo smelter in the nearby town of Glossop (BNG SK 029942), a known source of pollution (2000; Miller, 1993). The comparable levels of other heavy metals at Whim, but significantly lower Mo concentrations supports this conclusion.

Moisture content and pH were similar between the samples sites, with values falling well within the ranges found in regional studies (Lindsay, 2010; Tipping et al., 2003). Indeed, values from the Pennine sites for both variables were akin to those from reference sites, rather than those affected by industry and associated degradation.

Table 27 compares peat extractable values from this study with available literature. Where possible, means or medians have been reported. Care must be taken in comparing values when different analytical processes and reagents have been used.

Table 27 – Summary values of peat extractable variables (mean ± SD, ppm) for reference (R) and Pennine (P) sites, and those from literature for comparison.

Variable		*Study sites*	*Literature values*	*Details*
MC (%)	R:	92.16 ± 2.29	80 – 98	General range, including UK blanket peats (Lindsay, 2010; Tipping *et al.*, 2003)
	P:	91.97 ± 3.30	44 – 98	Holme Moss (Elliott *et al.*, 2015; Nwaishi, 2010)
pH	R:	4.12 ± 0.29	4.1 – 4.8	UK blanket peats (Tipping *et al.*, 2003)
	P:	4.16 ± 0.60	2.87 – 3.86	North Pennines, affected by mining (Chenery *et al.*, 2012)
			3.00 – 4.42	Peak District and southern Pennines (Elliott *et al.*, 2015; Linton *et al.*, 2007; Nwaishi, 2010; Rosenburgh *et al.*, 2013)
			3.31 – 4.48	Canadian smelting region (Barrett & Watmough, 2015)
Al	R:	127.6 ± 98.7	380	Blanket peat in Scotland, using 0.1 M HCl (Cuttle, 1983)
	P:	350.2 ± 442.2		
As	R:	0.79 ± 1.18	0.9	Range of soils from Chile, using H_2O (Flynn *et al.*, 2002)
	P:	2.14 ± 2.53	0.86 – 2.11	Former tin mining catchment, Malaysia, using $MgCl_2$ (Ashraf *et al.*, 2012)
Ba	R:	9.97 ± 7.21	3 – 157	UK national study on acid grasslands, using 1 M KCl (Stevens *et al.*, 2009)
	P:	10.23 ± 12.56		
Ca	R:	656.6 ± 346.9	970 – 6,180	North American peats, using EDTA (Basiliko & Yavitt, 2001)
	P:	709 ± 1,147	28 – 3,547	UK national study on acid grasslands, using 1 M KCl (Stevens *et al.*, 2009)
Cd	R:	0.70 ± 0.57	1.09 – 4.74	Forest in Finland near to smelter, using EDTA (Salemaa *et al.*, 2001)
	P:	0.84 ± 0.97		
Co	R:	0.46 ± 0.31	0.18 – 50.10	North American peats, using EDTA (Basiliko & Yavitt, 2001)
	P:	0.89 ± 0.95		
Cu	R:	3.25 ± 2.68	0 – 3	UK national study on acid grasslands, using 1 M KCl (Stevens *et al.*, 2009)
	P:	7.38 ± 3.69	19.2	Southern Pennines, using EDTA (Livett *et al.*, 1979)

Variable		*Study sites*	*Literature values*	*Details*
Fe	R:	859 ± 1,159	420	Blanket peat in Scotland, using 0.1 M HCl (Cuttle, 1983)
	P:	455.4 ± 380.1	250 – 2,440	North American peats, using EDTA (Basiliko & Yavitt, 2001)
K	R:	259.8 ± 184.9	320	North Pennines, using ammonium acetate (Allen, 1989)
	P:	284.5 ± 241.1	110 – 790	North American peats, using EDTA (Basiliko & Yavitt, 2001)
Mg (total)	R:	1,033 ± 278	447 – 697	Italian Alps (Bragazza & Gerdol, 2002)
	P:	577.4 ± 217.2	346 – 1,015	Southern Pennines (Rothwell *et al.*, 2009)
Mn	R:	16.78 ± 24.68	2 – 195	UK national study on acid grasslands, using 1 M KCl (Stevens *et al.*, 2009)
	P:	4.41 ± 3.98	12.5 – 148.7	Forest in Finland near to smelter, using EDTA (Salemaa *et al.*, 2001)
Mo	R:	0.12 ± 0.12	0.12	Rice paddy, southern China (Jiang *et al.*, 2015)
	P:	0.76 ± 0.37	0.31	Irish pastures, using ammonium oxalate (Brogan *et al.*, 1973)
Na^+	R:	371.6 ± 128.2	46 – 610	UK national study on acid grasslands, using 1 M KCl (Stevens *et al.*, 2009)
	P:	273.3 ± 162.5	10 – 400	North American peats, using EDTA (Basiliko & Yavitt, 2001)
NH_4^+	R:	579.0 ± 673.0	15.9	Canadian raised bog, using 2 M KCl (Andersen *et al.*, 2013)
	P:	97.5 ± 150.0	3.3 – 25.5	Peak District and southern Pennines (Elliott *et al.*, 2015; Nwaishi, 2010; Rosenburgh *et al.*, 2013)
Ni	R:	1.11 ± 0.83	0 – 18	UK national study on acid grasslands, using 1 M KCl (Stevens *et al.*, 2009)
	P:	2.25 ± 1.64	0.1 – 43.4	North American peats, using EDTA (Basiliko & Yavitt, 2001)
NO_3^-	R:	1,015 ± 1,123	6.8	Canadian raised bog, using 2 M KCl (Andersen *et al.*, 2013)
	P:	29.74 ± 77.25	7.38	Holme Moss (Elliott *et al.*, 2015; Nwaishi, 2010)
P	R:	1.21 ± 2.11	10	North Pennines, using ammonium acetate (Allen, 1989)
	P:	10.43 ± 9.89	196 – 845	Forest in Finland near to smelter, using EDTA (Salemaa *et al.*, 2001)
Pb	R:	39.21 ± 34.98	737	North Pennines, affected by mining (Chenery *et al.*, 2012)
	P:	151.4 ± 121.9	232	Southern Pennines, using EDTA (Livett *et al.*, 1979)

Variable		*Study sites*	*Literature values*	*Details*
PO_4^{3-}	R:	107.6 ± 131.1	0.2 – 0.8	South German peatlands (Waughman, 1980)
	P:	5.53 ± 7.63		
S	R:	8.00 ± 5.93	170 – 402	Forest in Finland near to smelter, using EDTA (Salemaa *et al.*, 2001)
	P:	16.26 ± 8.42		
Sn	R:	0.01 ± 0.05	11.87 – 15.88	Former tin mining catchment, Malaysia, using $MgCl_2$ (Ashraf *et al.*, 2012)
	P:	0.06 ± 0.06		
SO_4^{2-}	R:	282.8 ± 252.7	25.6 – 26.1	Organic soil, New Zealand (Sinclair, 1973)
	P:	138.5 ± 134.5		
Sr	R:	6.69 ± 2.49	101 – 146	Inorganic soil, Greece, using ammonium acetate (Veresoglou *et al.*, 1995)
	P:	2.89 ± 1.70		
Ti	R:	0.54 ± 1.57	1.3 – 18	Scotland, using EDTA (Berrow *et al.*, 1978)
	P:	1.02 ± 0.79		
V	R:	0.08 ± 0.18	2.14	German soils, using EDTA (Gäbler *et al.*, 2009)
	P:	0.55 ± 0.44	0.41 – 0.89	Scotland, using EDTA (Berrow *et al.*, 1978)
Zn	R:	45.73 ± 20.08	82 – 308	Forest in Finland near to smelter, using EDTA (Salemaa *et al.*, 2001)
	P:	58.66 ± 31.97	66.4	Southern Pennines, using EDTA (Livett *et al.*, 1979)

Pennine sites

Differences between Pennine sites were generally unchanged from the national comparison, with small changes in significance between sites resulting from reduced ranges of biogeochemical values. Perhaps of greater interest are the differences between samples containing *Sphagnum* and those which did not. MC, As, K, Mn, Mo, Na^+, NO_3^-, P, PO_4^{3-}, S and SO_4^{2-} were all significantly higher in plots containing *Sphagnum*, whilst V was higher in plots without. The eroded state of the southern Pennines effectively limited *Sphagnum* occurrence to remnant patches of blanket bog with stable, near-surface water table, and water collecting depressions and channels, such as gullies. The greater moisture content (MC) levels associated with *Sphagnum* presence was unsurprising for a hydrophilic genus, although its role as a cause or consequence of *Sphagnum* occurrence is unclear. There is likely to be considerable positive feedback between the two. Channels and gullies gather water and solutes from the surrounding peat surface. For example, the application of fertiliser for revegetation works, and run off generated, is concentrated in channels, often producing plant communities typical of more minerotrophic conditions. Thus, *Sphagnum* sampled in these locations will be similarly enriched; the elevated levels of K, NO_3^-, P and PO_4^{3-} may reflect these inputs. Similarly, Na^+ concentrations were greater where *Sphagnum* was present, which could be attributed to a concentrating effect of precipitation, of which Na^+ is the dominant cation (Beswick *et al.*, 2003). Some pollutant elements (As, Mn and Mo) were also greater in samples with *Sphagnum*. These concentrations may be elevated due to the store of pollutants in the peat beneath *Sphagnum* patches. Areas without *Sphagnum* cover may have suffered increased rates of erosion, thereby reducing the store of pollutants in the peat. This eroded material is transported along channels and gullies, where it may be intercepted and deposited, leading to an accumulation of contaminated peat. Unlike the other elements and ions, V was found to have greater concentrations where *Sphagnum* was not present, suggesting a potential limiting effect.

pH, Al, Ba and Co were found to have significant interaction effects when considering sample site and presence of *Sphagnum*. These results were difficult to interpret but served to illustrate the myriad of confounding factors influencing biogeochemical variables in relation to *Sphagnum* presence; e.g. hydrology, erosional process and history.

3.5.3 Biogeochemical drivers of vegetation

National comparison

Automatic model building revealed magnesium, aluminium, barium, cadmium, nitrate, moisture content, sulphate, vanadium, iron, molybdenum and zinc to be significant drivers of the vegetation composition, using data from all the survey sites. These 11 biogeochemical variables represent a reduction from the 19 which were significantly correlated with the unconstrained species ordination (Table 20). Constrained ordination and model building serves to focus on the important dimensions within a data set, helping to avoid (mis)interpreting noise within the data (Gauch, 1982). Spatial variables, including altitude, were not included as they are likely to represent deposition gradients, and therefore be covariables of the biogeochemical measurements (e.g. Caporn & Emmett, 2009; Lovett & Kinsman, 1990; RoTAP, 2012; Zechmeister, 1995). The terms of the model were ordered according to which variables significantly improved the fit of the model; i.e. the largest, significant reductions in AIC (Appendix 9).

Variance inflation factor (VIF) values were calculated for the terms of the model (Table 21), indicating that each variable contributed independent information, improving the explanatory power of the model. However, when ecological signals are weak, even VIF values of 2 may not be sufficient to safeguard against collinearity of variables (Zuur *et al.*, 2010). The constrained ordination model explained 28.98 % of the total variance of the data, giving a clear indication that additional, unquantified factors influence the species composition of these peatlands. However, it has been noted that the result of such calculations may not be meaningful as much of the variance may simply be random noise (Oksanen, 2013).

From the constrained ordination, there was a clear distinction between the reference and Pennine sites (Figure 34). Many of the reference sites displayed strong associations with magnesium, the most influential of the constraints. As coastal sites, Mg at Borth and Glasson would be expected to be elevated compared with other sites, but alongside this was the negative association with the Pennine sites, where cations are depleted due to acidification and leaching. Species indicative of high quality bog showed positive associations with this gradient; e.g. *Cladonia portentosa*, *Drosera rotundifolia*, *Sphagnum magellanicum* and *S. tenellum*. The correlation between *Sphagnum* cover and Mg concentration has been noted previously, and thought to reflect its role as an essential plant nutrient (Carroll *et al.*, 2009; Rydin & Jeglum, 2013). Mg can limit *Sphagnum* growth when there is insufficient deposited in precipitation, or recycled from senescing tissue (Gerdol *et al.*, 2006; Pakarinen, 1978). Whilst a reduction in Mg can have consequences for photosynthetic activity, there are often a number of concurrent processes also at work. Roberts *et al.* (1989) proposed a mechanism for type I decline in Norway spruce, with a striking number of similarities to conditions in the southern Pennines and Peak District (Figure 38). Thus, whilst Mg concentrations have their own physiological effect upon the growth of *Sphagnum*, they also serve as a proxy measure for cation leaching, soil acidification, and potentially phytotoxic heavy metal availability, each of which exert their own selection pressures.

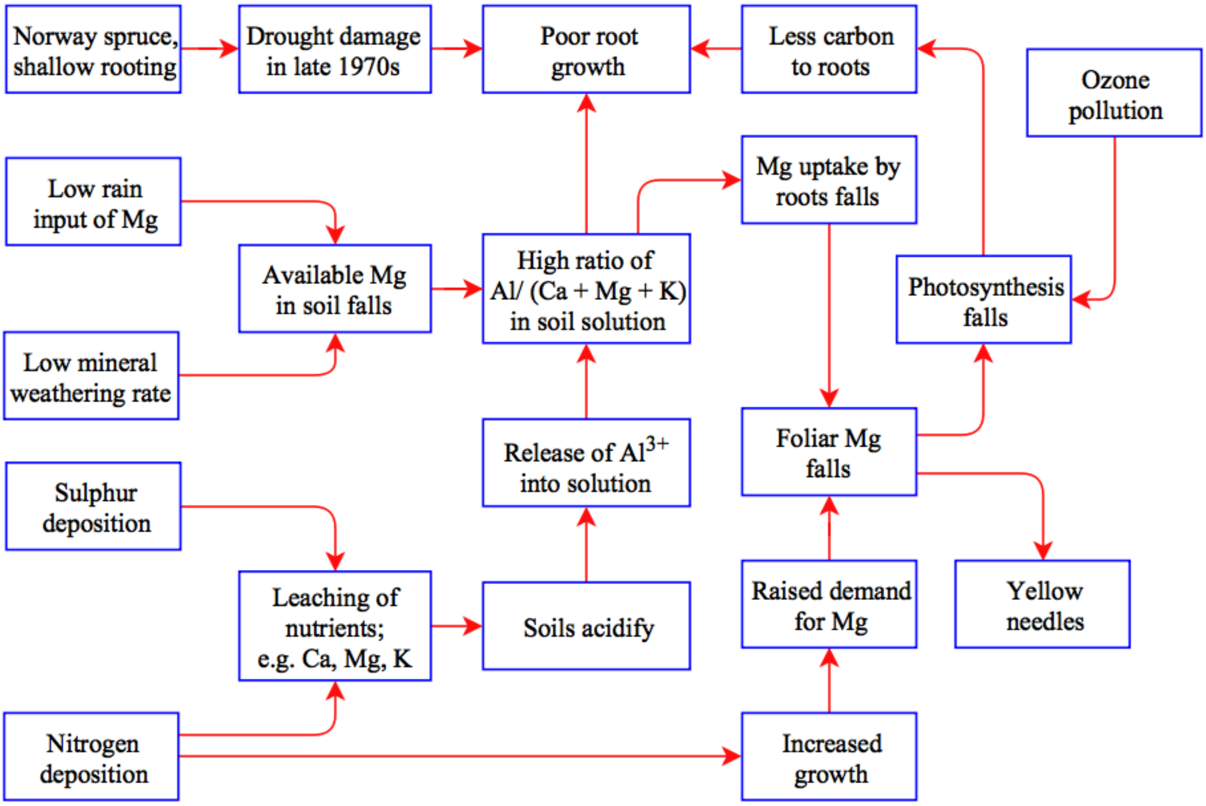


Figure 38 – Proposed mechanism for type I forest decline in Norway spruce trees, as seen in parts of central Europe in the 1980s (after Caporn, 2013; Roberts *et al.*, 1989).

The relationship exhibited by barium was more difficult to interpret, demonstrating positive associations with samples from both Moidach and Bleaklow. From biogeochemical analysis, Ca displays the opposite relationship to Ba; levels are highest at Black Hill due to ongoing revegetation works, and significantly lower at Moidach. Ba can be displaced by Ca (Dawson, 1985), which may explain the response observed. *Sphagnum denticulatum* and *Polytrichum commune* showed a strong connection with Ba. These samples were taken from within an erosion gully, containing large amounts of fluvial mineral material, of which Ba can be used as a surrogate measure (Krachler & Shotyk, 2004; Shotyk *et al.*, 2014). As a non-essential nutrient in plants, a direct role in *Sphagnum* success was less apparent. Ba can have biogeochemical behaviour similar to other cations, such as calcium and strontium (Baes & Bloom, 1988). Thus, it might be expected for the lowest Ba concentrations to be associated with *Sphagnum* species found in regions affected by acidic deposition and subsequent cation leaching. Indeed, *S. subnitens*, *S. palustre* and *S. fallax*, species typical of the southern Pennine sites, were at their most abundant at lower Ba concentrations. However, the results were confounded by *S. cuspidatum* and *S. papillosum* displaying their greatest cover at higher Ba concentrations; species found at numerous sites including within the Pennines. Additionally, Ba can be locally enriched in peat deposits (Dawson, 1985), suggesting a spatial element within and between sites may help to unpick the relationship between Ba concentration and *Sphagnum* success. There are unlikely to be any direct effects caused by excessive Ba at the concentrations recorded (< 57 ppm); green algae (*Scendesmus obliquus*, *Ankistrodesmus falcatus* and *Chlorella kessleri*) treated with 100 ppm showed no toxic effects (Havlík *et al.*, 1980).

Moisture content displayed a weaker association with the ordination, as denoted by the shorter arrow. The MC vector drawn corresponded to the different topographical niches of *Sphagnum* species; e.g. *S. subnitens* and *S. fimbriatum* from the drier hummocks, and *S. cuspidatum* and *S. pulchrum* from wet pools and lawns. *Sphagnum* are highly dependent upon water availability, due to their limited ability to control water loss (Titus & Wagner, 1984), affecting their ability to photosynthesise (McNeil & Waddington, 2003; Silvola, 1991; Titus *et al.*, 1983).

Several of the reference sites displayed a positive, albeit weak, association with Fe. This was thought to be caused by the legacy effects of metal extraction at these sites, combined with their similar floristic composition. Whilst Fe toxicity has been suggested as a cause of poor growth (Aerts *et al.*, 1992), *Sphagnum* appeared unaffected at these sites with dominant cover of typical ombrotrophic species, and tolerance demonstrated in *S. fallax* (Hájek *et al.*, 2014).

The Pennine sites were associated with a number of pollutant gradients: Al, SO_4^{2-}, Mo, V, NO_3^-, Cd and Zn. The biogeochemical drivers associated with the Pennine sites largely reflect the concentrations of elements and ions summarised in Section 3.4.2. However, interpretation of these influential gradients was confounded by the non-linear responses of some vectors (SO_4^{2-} and V) and strong influence of a small number of Bleaklow samples (Figure 34). This caused species and samples to be clustered around the plot origin. Despite this, it was still possible to distinguish vegetation communities of these degraded Pennine sites, and the biogeochemical characteristics associated with them; e.g. *S. denticulatum* and Al, and *S. fimbriatum* and *S. subnitens* and NO_3^-.

There is a wealth of literature covering the adverse effects of enhanced nitrogen deposition on *Sphagnum* (e.g. Berendse *et al.*, 2001; Bobbink & Hettelingh, 2011; Bragazza *et al.*, 2004; Gunnarsson *et al.*, 2004; Gunnarsson & Rydin, 2000; Limpens & Berendse, 2003; Paulissen *et al.*, 2004). In intact conditions, bogs are able to mitigate small increases in N availability by retaining and storing substantial amounts of N in *Sphagnum* biomass and peat (Lamers *et al.*, 2000; Moore *et al.*, 2005). This prevents N availability increasing in the soil layers (Fritz *et al.*, 2014) and becoming available to other plant species. However, there is a limit to how much N *Sphagnum* can filter in this way, beyond which N will become available to more vigorously growing species (Aerts, 1990; Steubing & Fangmeier, 1991). This can result in competition for light from vascular plants (Berendse *et al.*, 2001; Hautier *et al.*, 2009) or other mosses (Mitchell *et al.*, 2002), and subsequent reduced water availability (Fritz *et al.*, 2014). The critical load for *Sphagnum* in bog vegetation is 10 kg N ha^{-1} yr^{-1} (Gunnarsson, 2005).

Sphagnum can also be more directly affected by increased nitrogen deposition. Atmospheric N is absorbed by *Sphagnum* capitula (Williams *et al.*, 1999). However, like most plant species, *Sphagnum* has finite capacity to use N and a limited ability to control its uptake (Sheppard *et al.*, 2011), leading to N saturation (Lamers *et al.*, 2000; Rudolph *et al.*, 1993). This can cause a reduction in growth and productivity of *Sphagnum* and other bryophytes (Arroniz-Crespo *et al.*, 2008; Baxter *et al.*, 1992; Gunnarsson & Rydin, 2000), linked to increasing *Sphagnum* tissue N content (Limpens *et al.*, 2011). Other effects observed include adverse physiology and growth due to nutrient imbalances (Bragazza *et al.*, 2004; Gerdol *et al.*, 2007; Pearce *et al.*, 2003), and increased sensitivity to pests and pathogens (Wiedermann *et al.*, 2007). Additional factors further confound the responses observed in *Sphagnum*, such as temperature (Gunnarsson *et al.*, 2004), summer droughts (Carroll *et al.*, 1999; Gerdol *et al.*, 2007; Sheppard *et al.*, 2008a; 2008b), and P limitation (Aerts *et al.*, 2001).

Nitrate is known to have detrimental effects on *Sphagnum* species, including *S. capillifolium* (Sheppard *et al.*, 2011), *S. cuspidatum* (Press *et al.*, 1986), *S. fallax* and *S. magellanicum* (Twenhöven, 1992). However, responses are not always consistent, with positive effects recorded at NO_3^- concentrations greater than those which induced negative effects (e.g. Baker & Boatman, 1990; Rudolph & Voight, 1986). Under pristine conditions, *Sphagnum* obtains N from rainwater using the inducible enzyme, nitrate reductase (Press & Lee, 1982; Woodin *et al.*, 1985). Enzyme activity increases proportionally with NO_3^- concentration (Press *et al.*, 1986; Woodin & Lee, 1987a; Woodin *et al.*, 1985), which can lead to the accumulation of toxic NH_4^+ ions under high levels of N deposition (Limpens & Berendse, 2003). However, when exposed to long-term raised N deposition this association is lost, indicating *Sphagnum* can adapt to such conditions by limiting further N uptake (Jauhiainen *et al.*, 1998; Press & Lee, 1982; Press *et al.*, 1986; Woodin & Lee, 1987a; Woodin *et al.*, 1985). Thus, it would appear *S. fallax* and *S. papillosum* from the Pennine sites have successfully adapted to elevated concentrations of nitrate; concentrations which may have contributed to the initial failure of transplant experiments (Caporn *et al.*, 2006; Ferguson & Lee, 1983a).

Pollutant sulphur and its products are thought to have been a major cause of *Sphagnum* decline in northern England (Ferguson & Lee, 1983b; Lee & Woodin, 1988), affecting species directly through phytotoxicity, or indirectly by soil acidification (Lee, 1998). However, the apparent resistance of *S. fallax* to sulphur pollutants has been observed both experimentally and as the result of atmospheric pollution (Ferguson & Lee, 1980; Tallis, 1973). These effects are confounded by the different toxicity of sulphur products (sulphate vs. bisulphite (Ferguson & Lee, 1980)), and the ability of *Sphagnum* species to withstand their effects. The atmospheric deposition of transition metals in the southern Pennines and Peak District helped to reduce the effects of sulphur deposition, by catalysing the oxidation of highly toxic bisulphite (HSO_3^-) to the much less toxic sulphate (SO_4^{2-}), as observed in *S. fallax* and *S. cuspidatum* (Baxter *et al.*, 1991). Short exposure to low concentration (< 1 mM) sulphate was not thought to cause any damaging effect upon ombrotrophic *Sphagnum*. However, 5 mM produced marked reductions in *Sphagnum* growth (Ferguson & Lee, 1979).

Heavy metals have well known impacts upon vegetation, although most research has focused on vascular plants (e.g. Harmens *et al.*, 2013). *Sphagnum* is known to accumulate high levels of heavy metals (Brown, 1984), which can cause chlorosis, brown tips, and plasmolysis (Glime & Keen, 1984). Bryophyte protonemal growth can be inhibited by heavy metals, including Al and Zn (Kapur & Chopra, 1989). The phytotoxicity of metals in soil varies depending upon their oxidation state and mobility, as governed by properties such as redox potential, organic matter and pH (Blamey *et al.*, 2015; Rydin & Jeglum, 2013). For example, aluminium is most toxic as Al^{3+} in solution of pH < 4.5 (Parker *et al.*, 1988; Pavan & Bingham, 1982; Tanaka *et al.*, 1987). Thus, the behaviour of heavy metals in peatlands is complex, and therefore effects are difficult to predict (Ashmore *et al.*, 2007). Cadmium is known to be directly toxic to *Sphagnum* at low concentrations; 0.1 mM in *S. nemoreum*, and 112 ppm in *S. fimbriatum* (Simola, 1977a; Simola, 1977b). Vanadium is usually bound tightly to soil organic matter, hence little is known about its ecological effects (Harmens *et al.*, 2008; Poledniok & Buhl, 2003). At high rates of supply (10 – 20 mg l^{-1}), it is harmful to plants (Arnon & Wessel, 1953). Molybdenum phytotoxicity is rarely exhibited in the field, but can be induced experimentally, with wide variation in critical values between species; e.g. 135 mg kg^{-1} leaf tissue in barley, and > 600 mg kg^{-1} in *Brassica* and *Allium* without symptoms (Adriano, 1986; Davis *et al.*, 1978; Gupta *et al.*, 1978). Zinc caused reduced growth in *Marchantia polymorpha*; ~ 50 % at 100 ppm, and ~ 75 % at 500 ppm (Coombes & Lepp, 1974).

Thus, it appears the environmental tolerance of *Sphagnum*, and indeed the wider vegetation community, is dependent upon past exposure history, and current interacting factors, within the constraints of genetically controlled traits, as demonstrated in other bryophytes (Glime, 2007; Shaw, 1987). The biogeochemical gradients discussed here represent both direct physiological factors, and complex, indirect environmental factors (*sensu* Austin, 1980; Jansen & Oksanen, 2013).

Pennine sites

Barium, aluminium, phosphorus, magnesium, molybdenum, lead, iron and sulphur were identified as significant biogeochemical drivers of the vegetation at the Pennine sites. Variance inflation factors indicated that each variable was independent, with all values < 2.4. This constrained model accounted for 24.99 % of the variation, representing a reduction compared to the national comparison model. Despite fewer sample sites, highly variable vegetation composition in the Pennine samples, and fewer constraining variables could explain this reduction.

The ordination displayed some level of distinction between samples containing *Sphagnum* and those which did not. Samples without *Sphagnum* were generally found at lower values on CCA2, and those with *Sphagnum* at higher values (Figure 35). Most samples were located around -0.5 on CCA1, with the exception of 8 samples at ~ 3 or more. Of these, all but one were from Bleaklow and had significant influence upon the ordination. Indeed, of the eight constraining environmental variables, six demonstrated strong relationships with these samples. These samples originated from water-gathering features, such as pools and gullies, which act to collect and concentrate local solutes and fluvial matter. *S. cuspidatum* and *S. denticulatum* were found most frequently and at their greatest cover in these locations, reflecting their ecological niche (Atherton *et al.*, 2010; Hill *et al.*, 2007). Al, Pb and Ba demonstrated the strongest relationship with these outlying samples. Al is mobile in acidic conditions (Büscher *et al.*, 1990; Holden *et al.*, 2007b; NEGTAP, 2001), whilst Pb is known to be transported in eroded sediment from these peatlands (Rothwell *et al.*, 2005a, 2007a; 2008b), hence their elevated concentrations. This assessment was supported by the co-occurrence of Ba, which can be interpreted as a proxy measure for disturbance, as discussed in the national comparison. Mg, Mo and S were also associated with the outlying samples. These gradients may represent further examples of concentrated solutes and particulate matter, with Mg thought to be contained within the mineral additions applied during revegetation works (Caporn *et al*., 2007). Interpretation of S and Mo vectors was confounded by their non-linear nature. Both Pb and S are known to have direct toxic effects upon *Sphagnum*; 207 ppm Pb retarded growth in *S. nemoreum* (Simola, 1977a; 1977b), whilst products of S can be potently phytotoxic (Ferguson & Lee, 1980).

The majority of the samples, including both those with and without *Sphagnum*, were arranged virtually parallel to CCA2. Vectors of Fe and P related almost directly to this arrangement of samples on the ordination. Some forms of Fe are relatively soluble (Tipping, 2002) and so would be expected to be higher in areas of water movement and accumulation; areas frequently colonised by *Sphagnum*. Similarly, P is more soluble at lower pH (Verhoeven *et al.*, 1988), which could explain the similar behaviour of these gradients. *Sphagnum* is a highly efficient scavenger of nutrients and ions from its environment (e.g. Brown, 1984; Carpi *et al.*, 1994; Fritz *et al.*, 2014), thus it will retain elements and compounds to which it is exposed. Increased availability of Fe and P can also help *Sphagnum* to outcompete other species, however the mechanism is not known (Hájek *et al.*, 2002; Hájek *et al.*, 2014; Kooijman, 2012). In nature, P occurs almost exclusively as PO_4^{3-} (Allen, 1989), which in acid soils, is readily precipitated as highly insoluble Fe or Al phosphates (Boström *et al.*, 1982). This contradicts the behaviour of Fe and P in this study, perhaps due to the interacting effects of other metals and nutrients present (Barker & Pilbeam, 2015).

3.5.4 Vegetation, peat total, and comparative chemistry

Bryophytes, including *Sphagnum*, have much the same mineral requirements as higher plants in terms of essential elements. These can be separated into macronutrients (C, Ca, Fe, H, K, Mg, N, O, P and S) and micronutrients (Bo, Cl, Cu, Mn, Mo, Ni and Zn), derived from five main sources: soil, stream, water, atmospheric dust, precipitation and litter (Babb & Whitfield, 1977; Frego & Carelton, 1995; Parker, 1983). Within the plant cells, macronutrients are maintained at a relatively high and consistent concentrations, with any differences arising from what is bound to the cell surface (Glime, 2007). This uptake occurs through the use of cation exchange sites (Bates, 1997; Clymo, 1964; Craigie & Maass, 1966; Wells & Brown, 1990), of which *Sphagnum* is highly efficient due to the high concentrations of polyuronic acids within the cell walls (Clymo, 1963; Craigie & Maass, 1966). Under pristine conditions, this enables *Sphagnum* to grow in very nutrient poor conditions, where it can out compete other species by creating intense nutrient impoverishment, binding available nutrients (Van Breemen, 1995b). However, in polluted conditions, this can result in the accumulation of heavy metals because *Sphagnum* lacks the selectivity in binding and uptake of these pollutants (Brown, 1984; Brown & Bates, 1990). This is reflected in the concentrations of almost all heavy metals measured, which were significantly correlated with peat extractable values (Table 26). Within this relationship, there was considerable variation in the proportions of peat extractable and vegetation values. For example, peat extractable and vegetation concentrations of aluminium displayed a consistent pattern across most of the sites, with the vegetation displaying some level of Al accumulation (Figure 36). However, at Whixall, Migneint and Moidach, this pattern was different with Al concentrations broadly equal between peat extractable and vegetation values. This may be due to a number of potential interacting factors; namely, species composition, microtopography, and biogeochemical conditions. *Sphagnum* species have different cation exchange capacities, which correlates with their microtopographical niches (Clymo, 1963; Spearing, 1972). Those of drier locations, such as hummock species, have more exchange sites than those of wetter locations, found in hollows and pools (Brown, 1982). Biogeochemical conditions can influence the uptake of metals, with some being pH dependent; e.g. Zn and Cd (Gjengedal & Steinnes, 1990), whilst the presence of other elements may produce interferences by forming complexes. *Sphagnum* itself demonstrates preferences, such as accumulating Al and Mn, but excluding Cu and Zn (Glime, 2007). This preference is based on concentration, ionic radius and valency of the chemical species (Bates, 2000). Samples of *Sphagnum* from the Pennine sites have accumulated concentrations of pollutants similar to, or exceeding, those found in areas of intense industrial activity; e.g. As (Arafat & Glooschenko, 1982) and V (Shotyk *et al.*, 2014).

In pristine conditions, N is the primary limiting nutrient in bogs, with *Sphagnum* acquiring N, P and K in the upper parts of the plant through active uptake (Wojtun, 1994), where they are efficiently translocated to growing tissues (Aldous, 2002; Gerdol, 1990; Rydin & Clymo, 1989). In the presence of increased N availability, this uptake continues and tissue concentrations increase proportionally with deposition rates (Caporn, 1997; Woodin & Farmer, 1993); a relationship clearly demonstrated in the results (Table 26). Differences in N input are not the only source of variation in tissue N concentrations. *Sphagnum* species of wetter conditions are likely to have greater concentrations due to their contact with bog water containing nitrate and ammonium ions (Carroll *et al.*, 2009). These increases in tissue N can have implications for peat formation and carbon sequestration as *Sphagnum* with lower C:N ratio decomposes more rapidly (Aerts *et al.*, 1992; Clymo & Hayward, 1982; Coulson & Butterfield, 1978; Luken & Billings, 1983).

Prolonged N deposition can cause a shift to P limitation (e.g. Aerts *et al.*, 1992; Limpens *et al.*, 2004). Over time, high N levels of N deposition will increase the N:P ratio until phosphorus will become the primary limiting nutrient (Aerts *et al.*, 1992; Lee & Woodin, 1988; Malmer, 1988, 1990). Eventually, severe growth reduction and mortality of *Sphagnum* can occur (Ferguson *et al.*, 1984; Press *et al.*, 1986; Woodin & Lee, 1987b). Low N:P ratios (< 10 – 14) indicate N limitation, whilst high ratios (> 14 – 16) indicate P limitation (Aerts & Berendse, 1988; Lajtha & Klein, 1988; Rundel, 1982; Verhoeven & Schmitz, 1991; Vermeer, 1986a; b), and have been successfully used in the assessment of bryophytes (Aerts *et al.*, 1992; Bragazza *et al.*, 2004; Jiroušek *et al.*, 2011). *Sphagnum* tissue N:P ratio can be used to indicate N saturation as *Sphagnum* growth is thought to be limited by phosphate (Clymo & Hayward, 1982; Koerselman & Meuleman, 1996). The effect of N deposition on N:P ratio was found to be similar across *Sphagnum* species, with differences found to be regional, corresponding to differences in rates of N deposition (Malmer, 1988, 1990). Black Hill was the only site to demonstrate potential N limitation, with N:P ratio of 11.34, with the remaining sites > 20, indicating P limitation (Table 24). A critical N deposition threshold of 10 kg N ha^{-1} yr^{-1} was established, above which, *Sphagnum* growth shifted from N limited to co-limitation by P or K (Bragazza *et al.*, 2004; Gunnarsson & Rydin, 2000). Many areas of the UK receive inputs exceeding this threshold (RoTAP, 2012) and is reflected in N:P ratios. In northern Europe, where N deposition rates are 5 – 60 kg N ha^{-1} yr^{-1} (Wedin & Tilman, 1996), shifts from N to P limitation have also been observed (Aerts *et al.*, 1992; Bragazza *et al.*, 2004; Gunnarsson & Rydin, 2000; Jiroušek *et al.*, 2011). Concurrent increases in P input can buffer such increases in N:P ratio, as appears to be the case at Black Hill, thought to be the effect of fertiliser addition as part of revegetation works. P limitation may also have implications for the reproductive success of *Sphagnum*, with protonemata growth of several species limited by P availability (Boatman & Lark, 1971).

The upper layers of peatlands subjected to atmospheric pollution can contain significant quantities of deposited nutrients and heavy metals. In the southern Pennines and Peak District, this has been well documented (Hutchinson, 1995; Jones & Hao, 1993; Lee & Tallis, 1973; Livett *et al.*, 1979; Markert & Thornton, 1990), with Pb concentrations some of the highest in European peatlands (Rothwell *et al.*, 2005b). Problems arise when these stored pollutants become mobilised and therefore available to organisms. Heavy metals availability is influenced by a range of parameters, including pH and organic matter content of the substrate (Linton *et al.*, 2007). Metals such as Cd, Ni and Zn are weakly-sorbed to organic matter, whereas Al, Cu and Pb are strongly-sorbed (Tipping *et al.*, 2003). These relationships can be observed in the comparative assessments of extractable and total peat concentrations. For example, extractable Cu concentrations were considerably lower than total, whilst the difference between extractable and total Cd was noticeably less (Figure 36). There are two well defined mechanisms of releasing this store of pollutant metals: 1) erosion and transportation of contaminants in fluvial systems (e.g. Dawson and Macklin, 1998; Horowitz *et al*., 2001; Blake *et al*., 2003); a particular problem in the southern Pennines (Tallis, 1997b); and 2) mobilisation of contaminants at low pH, such as those generated by drought induced acidification (e.g. Lucassen *et al.*, 2002; Tipping *et al.*, 2003). Peatlands are also able to retain large amounts of nitrogen, with the peat itself acting as the major N sink (Chapman & Edwards, 1999; Nadelhoffer *et al.*, 1994). Whilst this may help to slow the rate of N saturation in these ecosystems, with such a store of N, the impacts are long-lived, with effects of experimental additions lasted for 20 years (Lee, 1998). *Sphagnum* is able to obtain N from soil depths of 3 – 8 cm, and thus able to access and be influenced by this nutrient store (McKane *et al.*, 1993). Despite a long history of N deposition, concentrations measured in both the Pennine and reference sites were not drastically different from isolated European reference sites (Bragazza & Gerdol, 2002). Whilst the Pennine sites demonstrate elevated concentration of numerous pollutants when compared to the reference sites, they are still considerably (sometimes orders of magnitude) lower than sites close to industrial activity, such as smelting; e.g. Cu, Fe and Ni (Barrett & Watmough, 2015; Juckers & Watmough, 2014).

Table 28 and Table 29 compares vegetation, and peat total values, respectively, from this study with available literature. Where possible, means or medians have been reported.

Table 28 – Summary values (mean ± SD, ppm) of vegetation chemistry variables for reference (R) and Pennine (P) sites, and those from literature for comparison.

Variable		*Study sites*	*Literature values*	*Details*
Al	R:	207.1 ± 158.7	378 ± 167	North and south regions of Finland (Malmer, 1988)
	P:	667.0 ± 768.0	430	*S. magellanicum* from Sweden (Damman, 1978)
As	R:	0.51 ± 1.37	0.11 – 0.25	Canadian smelting region (Arafat & Glooschenko, 1982)
	P:	1.18 ± 0.97		
Ba	R:	11.99 ± 8.55	6.02 – 13.00	Germany (Shotyk *et al.*, 2014)
	P:	46.20 ± 78.60	21.4 ± 10.4	Oil sands region, Canada (Shotyk *et al.*, 2014)
C (%)	R:	49.39 ± 1.78	43.08 ± 0.13	*S. capillifolium*, north Italy (Vingiani *et al.*, 2004)
	P:	48.23 ± 4.27		
Ca	R:	2,230 ± 1,612	1,400	*S. fallax* from north Pennines (Coulson & Butterfield, 1978)
	P:	3,590 ± 5,956	1,783 ± 1,230	Northern Finland (Pakarinen & Tolonen, 1977)
Cd	R:	0.26 ± 0.32	0.1 – 0.5	Northern Finland, Germany, and Sudety mountains, Poland (Pakarinen & Tolonen, 1976; Shotyk *et al.*, 2014; Wojtuń *et al.*, 2013)
	P:	0.47 ± 0.24	200	Near Pb-Zn smelter, UK (Cameron & Nickless, 1977)
Co	R:	0.17 ± 0.14	0.70 ± 0.34	New England, USA (Gotelli *et al.*, 2008)
	P:	0.80 ± 1.06		
Cu	R:	4.16 ± 1.70	2.3 – 22.2	Finland, and Sudety mountains, Poland (Malmer, 1988; Pakarinen & Tolonen, 1976; Wojtuń *et al.*, 2013)
	P:	7.62 ± 3.26	47	Near industrial area, UK (Goodman & Roberts, 1971)
Fe	R:	458.2 ± 510.1	230.9 ± 88.2	Northern Finland (Pakarinen & Tolonen, 1976)
	P:	911.0 ± 704.0	451.4 ± 398.5	Finland (Pakarinen & Tolonen, 1977)

Variable		*Study sites*	*Literature values*	*Details*
K	R:	2,255 ± 833	3,276 ± 1,822	Finland (Pakarinen & Tolonen, 1977)
	P:	3,719 ± 2,224	3,500	*S. magellanicum* from Sweden (Damman, 1978)
			2,762 – 4,928	*S. capillifolium* (*rubellum*) from Germany and Belgium (Kempter & Frenzel, 2007)
Mg	R:	1,073 ± 296	490	*S. magellanicum* from Sweden (Damman, 1978)
	P:	916.6 ± 290.9	1,197 ± 463	Finland (Pakarinen & Tolonen, 1977)
Mn	R:	113.2 ± 105.7	10 – 250	Finland, and Sudety mountains, Poland (Malmer, 1988; Pakarinen & Tolonen, 1976; Wojtuń *et al.*, 2013)
	P:	58.28 ± 41.48	35.1 – 137.0	*S. capillifolium* (*rubellum*) from Germany and Belgium (Kempter & Frenzel, 2007)
Mo	R:	0.13 ± 0.26	0.49 ± 0.57	Northern Finland (Pakarinen & Tolonen, 1976)
	P:	2.13 ± 2.12	0.31 – 0.39	Germany (Shotyk *et al.*, 2014)
N (%)	R:	0.99 ± 0.23	0.67	*S. fallax* from North Pennines (Coulson & Butterfield, 1978)
	P:	1.42 ± 0.46	0.67 ± 0.14	Finland (Pakarinen & Tolonen, 1977)
Na	R:	753.5 ± 292.7	1,537 ± 533	Finland (Pakarinen & Tolonen, 1977)
	P:	804.1 ± 423.0	590	*S. magellanicum* from Sweden (Damman, 1978)
Ni	R:	3.57 ± 3.46	1.21 ± 0.54	Northern Finland (Pakarinen & Tolonen, 1976)
	P:	2.70 ± 4.11	4.85 – 5.86	Germany (Shotyk *et al.*, 2014)
P	R:	342.8 ± 146.3	656.0 ± 248.1	Finland (Pakarinen & Tolonen, 1977)
	P:	804.4 ± 551.9	800 – 1,000	*S. fallax* from northern Pennines (Coulson & Butterfield, 1978)
Pb	R:	9.98 ± 11.61	37.3 ± 37.3	Finland (Malmer, 1988)
	P:	81.00 ± 91.50	10.9 – 13.7	*S. papillosum* from southern Pennines (Livett *et al.*, 1979)
S	R:	875.5 ± 197.2	930 ± 353	Finland (Malmer, 1988)
	P:	1,285 ± 360	852 – 967	*S. capillifolium* (*rubellum*) from Germany and Belgium (Kempter & Frenzel, 2007)

Variable		*Study sites*	*Literature values*	*Details*
Sn	R:	0.07 ± 0.31	< 0.3	*Hylocomium splendens*, Washington (Wiersma *et al.*, 1987)
	P:	0.02 ± 0.11		
Sr	R:	11.37 ± 4.71	25	*Hylocomium splendens*, Washington (Wiersma *et al.*, 1987)
	P:	13.83 ± 9.39		
Ti	R:	4.07 ± 3.14	16.9 – 43.3	*S. capillifolium* (*rubellum*) from Germany and Belgium (Kempter & Frenzel, 2007)
	P:	10.16 ± 6.99		
V	R:	0.55 ± 0.65	0.65 – 1.29	Germany (Shotyk *et al.*, 2014)
	P:	2.60 ± 2.04	2.67	Oil sands region, Canada (Shotyk *et al.*, 2014)
Zn	R:	44.58 ± 23.97	33.79 ± 6.95	Northern Finland (Pakarinen & Tolonen, 1976)
	P:	60.02 ± 18.82	11.4 – 37.7	*S. papillosum* from southern Pennines (Livett *et al.*, 1979)
C:N	R:	52.57 ± 12.48	25.3 ± 3.6	*S. fallax* from the Netherlands (Harpenslager *et al.*, 2015)
	P:	37.15 ± 11.28		
N:P	R:	32.71 ± 12.57	23 – 31	P limited sites (Boeye *et al.*, 1997)
	P:	23.74 ± 12.93	8 – 15	N limited sites (Boeye *et al.*, 1997)
			11.19 ± 3.78	Finland (Pakarinen & Tolonen, 1977)

Table 29 – Summary values (mean ± SD, ppm) of peat total variables for reference (R) and Pennine (P) sites, and those from literature for comparison.

Variable		*Study sites*	*Literature values*	*Details*
Al	R:	740.1 ± 378.2	375 – 1,960	Italian Alps (Bragazza & Gerdol, 2002)
	P:	1,658 ± 1,299	4,100 – 24,100	Canadian smelting region (Barrett & Watmough, 2015; Juckers & Watmough, 2014)
As	R:	3.65 ± 4.46	0.96	Jura Mountains (Steinmann & Shotyk, 1997)
	P:	4.57 ± 2.45	4.46 – 12.4	Southern Pennines (Rothwell *et al.*, 2008a; Rothwell *et al.*, 2009)
Ba	R:	17.04 ± 9.81	5.2 ± 2.6	Natural background for continental Europe (Krachler & Shotyk, 2004)
	P:	48.00 ± 82.00	86 – 107	Background concentration for western Siberia (Vodyanitskii *et al.*, 2012)
C (%)	R:	51.87 ± 2.05	50	North Pennines (Allen, 1989)
	P:	50.58 ± 3.90	12.4 – 46.2	Canadian smelting region (Barrett & Watmough, 2015; Juckers & Watmough, 2014)
Ca	R:	1,614 ± 492	1,600 – 4,753	Italian Alps (Bragazza & Gerdol, 2002)
	P:	3,344 ± 5,344	1,100 – 6,600	Canadian smelting region (Barrett & Watmough, 2015; Juckers & Watmough, 2014)
Cd	R:	1.09 ± 0.84	~ 1	Sweden (Pakarinen & Tolonen, 1976)
	P:	0.99 ± 0.36	1.19 – 1.31	Southern Pennines (Elliott *et al.*, 2015; Rothwell *et al.*, 2008a)
Co	R:	0.76 ± 0.53	0.54	Jura Mountains (Steinmann & Shotyk, 1997)
	P:	1.39 ± 1.17	5.1 – 28.2	Canadian smelting region (Barrett & Watmough, 2015; Juckers & Watmough, 2014)
Cu	R:	8.47 ± 8.72	6 – 20	Low background UK sites (Livett *et al.*, 1979)
	P:	22.50 ± 14.73	147 – 1,553	Canadian smelting region (Barrett & Watmough, 2015; Juckers & Watmough, 2014)
Fe	R:	2,339 ± 1,832	819 – 4,514	Italian Alps (Bragazza & Gerdol, 2002)
	P:	3,242 ± 1,867	7,040 ± 3,910	Canadian smelting region (Barrett & Watmough, 2015)

Variable		*Study sites*	*Literature values*	*Details*
K	R:	616.7 ± 273.1	258 – 753	Italian Alps (Bragazza & Gerdol, 2002)
	P:	665.4 ± 345.8	750 ± 190	Canadian smelting region (Barrett & Watmough, 2015)
Mg	R:	1,033 ± 278	447 – 697	Italian Alps (Bragazza & Gerdol, 2002)
	P:	577.4 ± 217.2	346 – 1,015	Southern Pennines (Rothwell *et al.*, 2009)
Mn	R:	47.40 ± 55.12	7 – 115	Italian Alps (Bragazza & Gerdol, 2002)
	P:	27.60 ± 17.78	56.9 ± 35.0	Canadian smelting region (Barrett & Watmough, 2015)
Mo	R:	3.61 ± 6.66	0.08 ± 0.02	Jura Mountains (Krachler & Shotyk, 2004)
	P:	14.86 ± 9.03	1.28 ± 0.47	Southern Pennines (Rothwell *et al.*, 2008a)
N (%)	R:	1.49 ± 0.36	0.4 – 1.5	Italian Alps (Bragazza & Gerdol, 2002)
	P:	1.55 ± 0.32	0.76 – 2.12	Canadian smelting region (Barrett & Watmough, 2015; Juckers & Watmough, 2014)
Na	R:	294.1 ± 91.2	52 – 184	Italian Alps (Bragazza & Gerdol, 2002)
	P:	213.3 ± 99.8	610 ± 190	Canadian smelting region (Barrett & Watmough, 2015)
Ni	R:	2.76 ± 3.08	17 – 32	Background concentration for western Siberia (Vodyanitskii *et al.*, 2012)
	P:	5.58 ± 4.18	153 – 1,304	Canadian smelting region (Barrett & Watmough, 2015; Juckers & Watmough, 2014)
P	R:	508.8 ± 214.3	155 – 622	Italian Alps (Bragazza & Gerdol, 2002)
	P:	734.4 ± 280.6	780 ± 187	Canadian smelting region (Barrett & Watmough, 2015)
Pb	R:	67.35 ± 53.85	0.28 ± 0.05	Natural background (Shotyk *et al.*, 1998)
	P:	207.6 ± 162.5	263 – 1,230	Southern Pennines (Elliott *et al.*, 2015; Jones & Hao, 1993; Rothwell *et al.*, 2008a; Rothwell *et al.*, 2009)
S	R:	2,467 ± 1,591	1,410	Jura Mountains (Steinmann & Shotyk, 1997)
	P:	2,695 ± 1,014	2,300 – 9,300	Canadian smelting region (Barrett & Watmough, 2015; Juckers & Watmough, 2014)

Variable		*Study sites*	*Literature values*	*Details*
Sn	R:	0.29 ± 0.61	2.42 – 2.55	Snowy Mountains, Australia (Marx *et al.*, 2010)
	P:	1.28 ± 2.50		
Sr	R:	18.55 ± 5.77	7.6	Jura Mountains (Steinmann & Shotyk, 1997)
	P:	15.42 ± 8.21	114 – 129	Background concentration for western Siberia (Vodyanitskii *et al.*, 2012)
Ti	R:	24.26 ± 20.54	96	Jura Mountains (Steinmann & Shotyk, 1997)
	P:	39.42 ± 23.39	145 ± 32.3	Southern Pennines (Rothwell *et al.*, 2008a)
V	R:	4.60 ± 3.00	1.66 – 8.33	Forested catchment, Ontario, Canada (Landre *et al.*, 2010)
	P:	11.26 ± 6.69	29.7 ± 4.44	Southern Pennines (Rothwell *et al.*, 2008a)
Zn	R:	75.82 ± 43.10	85 – 161	Low background UK sites (Livett *et al.*, 1979)
	P:	71.79 ± 60.67	119.7 – 139.0	Holme Moss (Elliott *et al.*, 2015; Rothwell *et al.*, 2008a)
C:N	R:	36.81 ± 9.22	21.8 ± 5.40	Canadian smelting region (Barrett & Watmough, 2015)
	P:	33.97 ± 6.65	29.2 – 33.9	Peak District (Rosenburgh *et al.*, 2013)
N:P	R:	32.92 ± 11.72	24 – 28	*S. magellanicum*, Scotland (Williams & Silcock, 1997)
	P:	23.35 ± 8.17		

3.6 Conclusion

This chapter aimed to elucidate those biogeochemical factors affecting the natural recovery of *Sphagnum* on degraded bog. A number of good quality sites with abundant *Sphagnum* were compared to highly degraded sites, where *Sphagnum* was scarce. By characterising differences in vegetation and biogeochemistry, influential biogeochemical drivers of the vegetation composition were identified, and the responses of *Sphagnum* species modelled along those environmental gradients. There was a stark contrast in vegetation composition between the reference and Pennine sites, representative of high quality bog vegetation, and severely modified, nutrient-enriched conditions, respectively. Within these reference sites, there was floristic distinction between sites, demonstrating the natural variability of even good quality bog habitats. The Pennine sites were characterised by species typical of enriched conditions, along with atypical species due to the application of lime and fertiliser as part of revegetation works.

Biogeochemical characteristics revealed the Pennine sites to be highly polluted, with elevated concentrations of a range of heavy metals and nutrients, reflecting their close proximity to the past industrial centres of northern England. Perhaps more surprising was the presence of some of these pollutants at a number of the reference sites, often exceeding levels found at the Pennine sites, as a result of historic local inputs, and atmospherically transported industrial pollution. Biogeochemical drivers of the vegetation were highlighted, providing a clear distinction between reference and Pennine sites. In general, reference sites were associated with base cation drivers, whilst Pennine sites were related to a number of pollutant metals and nutrients. Separate assessment of the reference sites revealed more subtle differences. Omitting the Pennine sites allowed these weaker gradients to be uncovered. The distinction between the Pennine sites was less well defined, however, there was some differentiation between samples containing *Sphagnum* and those which did not, reflecting the biogeochemical distinction between samples with and without *Sphagnum*.

Modelling *Sphagnum* responses to these gradients revealed several instances of tolerance, presumably the result of prolonged exposure to elevated pollutant levels. The mechanisms of this tolerance and adaptation is well established for some contaminants, such as nitrogen. However, species typical of high quality site, typically absent from Pennine sites, have also demonstrated their ability to persist and indeed flourish in the presence of potentially toxic heavy metals and nutrients. Thus, it would appear *Sphagnum* is regionally adapted to its local biogeochemical conditions, based on its past and current exposure to pollutants. The near eradication of *Sphagnum* from the Peak District and southern Pennines shows the effects of atmospheric pollution were greater than the sum of their individual parts, and that additional factors, such as erosion, over grazing and wildfire, played a pivotal role. This was supported by the relatively low proportion of variance accounted for by the explanatory biogeochemical models. The combined ecological stress of direct toxic effects from pollutant inputs, competition due to nutrient enrichment, and drought caused by erosion and hydrological disturbance, led to its widespread loss from the region. Where these stressors were less severe or reduced, such as in permanent pools, sheltered cloughs, and minerotrophic flushes, *Sphagnum* was able to survive. Therefore, it is likely that *Sphagnum* is able to tolerate moderate biogeochemical stress without succumbing, provided significant additional environmental stressors are not also present.

This study assessed the influence of biogeochemical variables upon *Sphagnum*, and so included no additional environmental factors, such as hydrology, and current and past management. Water availability was implicated as a potential driver of bog vegetation, despite moisture content only being chosen as an explanatory variable to differentiate between microtopographical niches (e.g. hummock and hollow). Similarly, Ba concentrations were considered a potential proxy measure for erosion. Without measurement of these additional, physical characteristics, considerable interpretation and ambiguity was involved. The addition of such data would require a longer term monitoring, not compatible with the one-off sampling procedure employed here. The sampling process itself could be improved by the inclusion of “intermediate” sites, such as those similar to Whim which have good quality bog vegetation but have been exposed to some level of pollution. The large differences in flora and biogeochemical characteristics between the reference and Pennine sites may have masked more subtle trends. A larger number of sample sites would provide data on *Sphagnum* species in a range of biogeochemical conditions, rather than some species only being found at one type of site, thus skewing any results. As with any modelling approach, the confidence placed in the conclusion will only match the quality of data being entered.

In summary, some *Sphagnum* species appear capable of developing tolerance to polluted biogeochemical condition, brought about by long-term exposure. In the presence of additional environmental stress, these pollutants can cause the regional loss of *Sphagnum*. In the past, atmospheric pollution was so severe that it was major factor in the near eradication of *Sphagnum*. However, whilst current biogeochemical conditions clearly reflect this legacy of industrial pollution, the wider success of *Sphagnum* is more likely to be limited by physical characteristics, such as water availability and erosion.

Chapter 4 – Discussion and Conclusion

4.1 General discussion and conclusions

The work presented here demonstrates both the opportunities for, and challenges facing blanket bog restoration in the Peak District and southern Pennines. These results and conclusions will contribute to the quantitative and qualitative underpinnings of best practice guidelines for the reintroduction of *Sphagnum* to degraded blanket peatlands.

This work was necessitated by the widespread absence of *Sphagnum* from the degraded blanket bogs of northern England. Following severe atmospheric pollution and poor land management, *Sphagnum* was all but eradicated from the region. Air quality was considered the primary driver of *Sphagnum* decline, therefore, commensurate increases in *Sphagnum* cover may have been expected in response to improvements in air quality. However, natural recolonisation by *Sphagnum* has been slow, appearing limited to expansion of remnant patches. Revegetation by other species, such as *Eriophorum* spp. and *Calluna vulgaris*, has occurred both naturally and as a result of restoration works. Comparative biogeochemical assessment of these degraded peatlands reflected their history of pollution deposition, when compared to better quality bogs from across the UK. This legacy was suggested as a limiting factor in the recolonisation and wider success of *Sphagnum*. Indeed, indoor trials of *Sphagnum* propagules grown on peat from Holme Moss demonstrated the detrimental effect of this polluted substrate. Analysis revealed which biogeochemical variables were significant drivers of vegetation composition, however, these accounted for a low proportion (< 30 %) of the observed variation. Both water availability and erosion status were implicated as additional significant factors, however, it was not possible to quantify these. The altered peat biogeochemistry of the degraded sites may be exerting a greater effect on the ability of *Sphagnum* to recolonise the region by preventing spores from establishing. The key limitation of *Sphagnum* dispersal by spore is the failure to establish rather than their production (Campbell *et al.*, 2003), with biogeochemical conditions proving critical (Sundberg & Rydin, 2002). Considerable quantities of pollutants are stored in both the vegetation and peat of the Peak District and southern Pennine region, making this is an issue which is likely to persist, resulting in the continued slow rate of *Sphagnum* recolonisation.

Thus, the introduction of vegetative propagules of *Sphagnum* is required to generate significant new cover. The recent development of a new propagule, *BeadaMoss*, allowed easy and accurate manipulation of *Sphagnum* material, including species identity and application rates. The tissue contained in these propagules was sourced locally, before being bulked up using micropropagation techniques, eliminating any concerns of sustainability and biosecurity associated with the use of harvested material. Field trials revealed *Sphagnum* could be successfully introduced to a range of substrate types, including vegetation communities significantly different from those where natural recolonisation had occurred. Non-metric multidimensional scaling (NMDS) was used to characterise the vegetation communities associated with *Sphagnum* in reintroduced and naturally occurring locations. Figure 39 shows NMDS ordination of vegetation data (using Bray-Curtis dissimilarity index) from *Sphagnum* bead field trials (Section 2.4), and survey data from Holme Moss and Black Hill (Section 3.4.1). Points have been grouped according to the *Sphagnum* present; from bead trials ("reintroduced"), or from the national survey data ("present" and "absent").

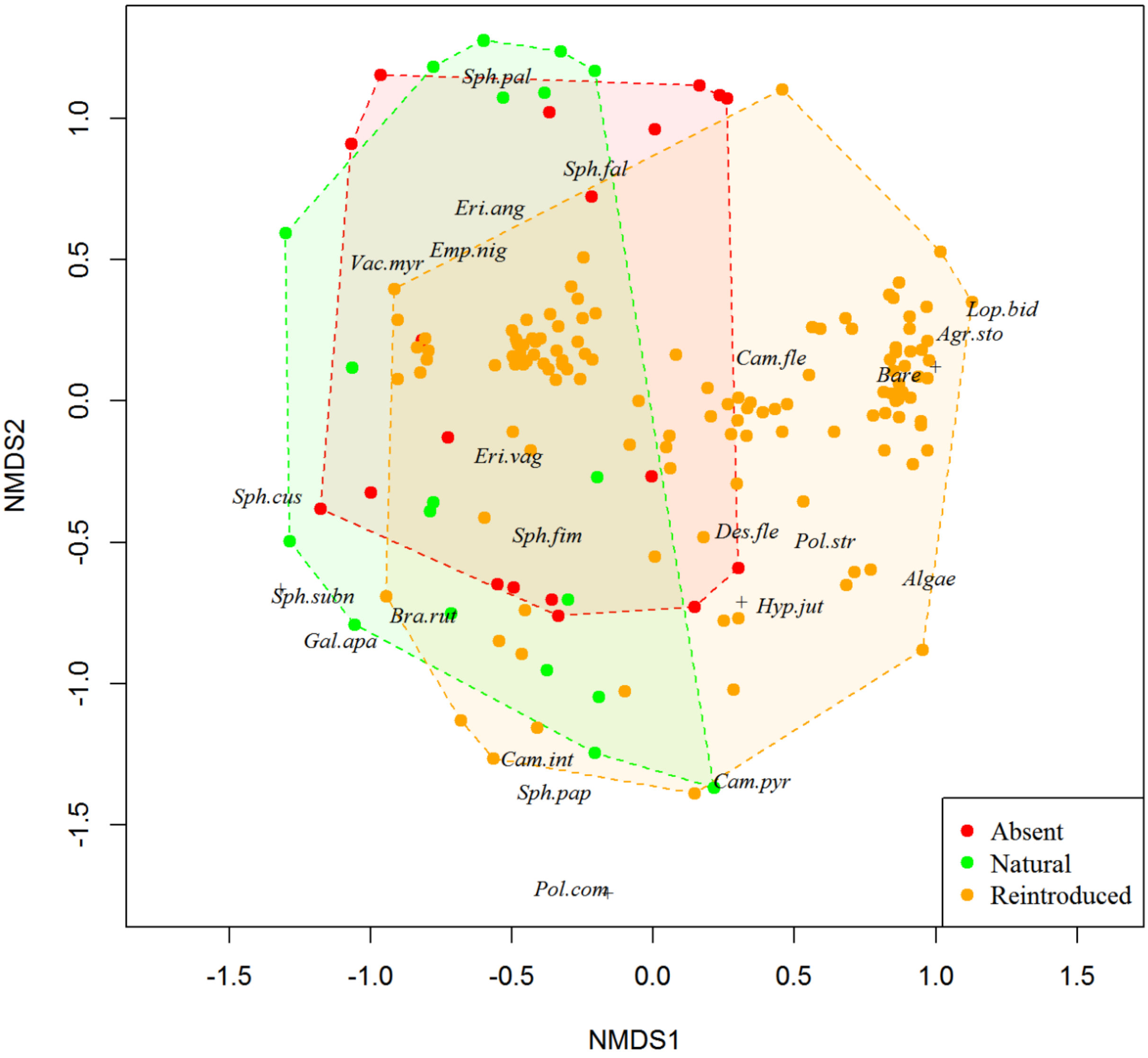


Figure 39 – Non-metric multidimensional scaling (NMDS) ordination of vegetation data from *Sphagnum* bead field trials ("reintroduced"), and survey data from Holme Moss and Black Hill ("present" and "absent"). Species labels can be found in Appendix 1. The most abundant species are added first and where species labels overlap, they have been omitted and the locations marked (+); all species labels are displayed in Appendix 14.

Vegetation composition was found to be different between these groups (PERMANOVA, P = 0.001), demonstrating that *Sphagnum* can be reintroduced to a wider range of substrate types than where it has managed to recolonise naturally. Propagule availability and dispersal can therefore be considered a limiting factor.

Almost all experimental plots failed to establish on bare peat, due to the harsh microclimatic conditions and mobility of the substrate. The success of vegetated plots appeared related to moisture availability, with successfully established *Sphagnum* found either in contact with the underlying peat, located in channels and depressions, or areas of near-surface water table. Concurrent research found natural *Sphagnum* recolonisation on a nearby degraded site (Bleaklow) was limited to gullies and other water gathering depressions (Rogers, 2014). Vegetation density was also thought to influence the success of *Sphagnum* for two reasons. Dense vegetation and a closed canopy prevented propagules from reaching the peat surface beneath, leading to desiccation and death, and where *Sphagnum* had established, plants appeared adversely affected by heavy shading and smothering. Mowing of the sward was suggested to be effective at reducing this effect. Whilst *Sphagnum* was able to establish on a range of substrate types, including previously bare peat, there were concerns surrounding the long term viability of such reintroductions. Many areas of the southern Pennines are characterised by lenses of revegetated bare peat, likely to be hydrologically isolated from the surrounding peat body. Despite high inputs from both rain and occult precipitation (Figure 40), it may be insufficient to support the growth and expansion of individual *Sphagnum* plants. Larger clumps of *Sphagnum* may be better able to survive in these locations as they will be more able to maintain their own microclimatic conditions, thus reducing the likelihood of complete desiccation (Schipperges & Rydin, 1998).

The ability of *Sphagnum* to improve its own conditions means that any success in reintroduction and natural recolonisation has the potential to generate more equable conditions and enhance the survival of further plants. This effect is not simply based around improved microclimatic conditions, and increased resilience to drought and/ or desiccation. *Sphagnum* is able to take up and retain large quantities of pollutant nutrients and heavy metals, whilst the successive growth of *Sphagnum* effectively isolates it further from the underlying substrate and any contaminants it may hold. However, the initial effect of this influx of pollutants is likely to have a considerable effect upon the growth of any *Sphagnum* propagules. These processes were observed in the indoor growth of chopped *Sphagnum* material. An initial phase of sickly growth with atypical *Sphagnum* morphology and colouration, followed by continued, substantial healthy growth by species characteristic of good quality bog. Field trials with transplanted material behaved similarly; originally thought to have failed, before becoming established and expanding significantly.

Figure 40 – Interception of occult precipitation by *Campylopus* spp.

Sphagnum fallax was the most successful species used in reintroduction trials, and its natural prevalence in the region indicates its suitability to the local conditions. *S. fallax* has demonstrable ability to withstand the legacy effects of industrial pollution, and is tolerant of periodic desiccation caused by disturbed hydrology and harsh microclimatic conditions. Whilst *S. fallax* alone is not recognised as indicative of “good condition” when assessed using Common Standards Monitoring (JNCC, 2009), its presence and expansion will improve hydrological and biogeochemical conditions, facilitating further reintroduction, recolonisation, and potentially, diversification to more typical ombrotrophic species (Barrett & Watmough, 2015; Rydin & Jeglum, 2013). To this end, *S. fallax* could represent the primary stage of *Sphagnum* succession, leading to the establishment of more desirable ombrotrophic species, such as *S. capillifolium* and *S. papillosum*. Records of such species in the region demonstrate the potential for diversification (Carroll *et al.*, 2009; Rogers, 2014), whilst surviving transplant experiments of regionally absent and/or scarce species have flourished in recent years (Caporn *et al.*, 2006; Ferguson & Lee, 1983a). The regional eradication of the most sensitive species, such as *S. austinii*, will require the use of propagules to be reintroduced; a further role for *BeadaMoss*.

This research suggested that success of *Sphagnum* reintroduction appears to be influenced by four potential factors: substrate stability, water availability, shading/ smothering, and substrate biogeochemistry. It should be noted that of these, only substrate biogeochemistry was actually quantified; the remaining three were implicated from field observations and interpretation of results in the context of existing literature. Success seemed to depend upon the cumulative stress exerted upon *Sphagnum* by these factors. For example, *Sphagnum* with a ready water supply and no shading will be better able to cope with the effects of polluted substrate, compared with a partially desiccated, shaded plant. Thus, areas of greatest reintroduction success are likely to be those which have begun to naturally recolonise (Figure 41). Target of these “easy win” locations will provide benefits to the wider bog area through improvements in hydrology, raising water table in surrounding peat bodies. This approach may restrict application of propagules to areas typical of improved conditions, omitting those atypical areas also capable of sustaining *Sphagnum* growth, such as those found in this work.

Figure 41 – Natural recolonisation of an erosion gully by *Sphagnum*.

4.2 Project impact

The applied nature of this research, and involvement of the Moors for the Future Partnership, has led to continual dialogue with land owners and conservation practitioners throughout its duration. A regional technical advisory group was formed, providing a platform for discussion and the dissemination of research. Members included stakeholders, land owners and conservation groups from the Peak District and southern Pennine region, and further afield. This proved essential, with numerous separate parties conducting restoration works on land they manage or own. By sharing knowledge and experience, advice could be sought and exchanged, preventing wasted time, effort and resources – a considerable issue in conservation with land managed by independent bodies. This research played a central role in the advisory group, offering quantitative evidence to support the decisions made in *Sphagnum* reintroduction, and wider restoration works. Research reports were produced and made available via the Moors for the Future Partnership website; an interim report on *Sphagnum* reintroduction trials, and reintroduction trials on *Molinia* grassland.

The Moors for the Future Partnership have since scaled up their landscape scale application of *Sphagnum* propagules, embracing new developments in the reintroduction of propagated moss. *Sphagnum* plug plants were developed by Micropropagation Services Ltd. to generate rapid cover, with increased resistance to desiccation because of their larger size. Another new product, SoluMoss™, incorporates longer *Sphagnum* strands suspended in solution. Over the past three years, *Sphagnum* beads have been applied to nearly 1000 ha over 6 different sites. In March 2015 alone, 400 ha worth of beads, 80,000 *Sphagnum* plugs and 500 l of SoluMoss™ were applied {Moors for the Future, 2015 #1578}. The knowledge gained from this pioneering landscape-scale *Sphagnum* reintroduction will be made available through publication of the upcoming “Practitioners guide to *Sphagnum* reintroduction”.

In response to growing interest from conservation agencies, an experimental protocol for field *Sphagnum* reintroduction trials was developed and distributed. This was produced to standardise the experimental approach, allowing results to be directly comparable. There is undoubtedly a wealth of knowledge surrounding blanket bog restoration, however, it is fragmented and not always formally recorded or accessible. Such a protocol was designed to address these issues and improve knowledge and understanding in the wider scientific and stakeholder community. The RSPB and National Trust adopted the protocol and have on going experimental trials. In an extension of this research and test of wider applicability, trials were established on cutover and previously forested raised bog in collaboration with Natural England.

Conferences provided an ideal opportunity to engage with the wider scientific and stakeholder community, develop new connections, and develop a greater understanding of contemporary issues surrounding peatland restoration. Table 30 provides a summary of conferences attended and contributions made.

Table 30 – Summary of events attended.

Date	*Event*	*Contribution*
28 – 29/09/2010	IUCN Peatland Programme – Investing in Peatlands	Poster
15 – 16/11/2010	Moors for the Future MoorLIFE Conference	Oral paper
15/12/2010	Manchester Metropolitan University Research Day	Poster
27/01/2011	Manchester Metropolitan University Annual Research Student Conference	Poster
27 – 28/04/2011	Association of Applied Biologists Vegetation Management Conference	Delegate
03 – 08/06 2012	International Peat Congress	Poster
17 – 20/12/2012	British Ecological Society Annual Meeting	Oral paper
25 – 27/03/2013	Committee on Air Pollution Effects Research Annual Meeting	Oral paper
02 – 04/09/2013	Society of Wetland Scientists European Chapter Meeting	Oral paper
10 – 12/09/2013	IUCN Investing in Peatlands Conference	Poster
11/06/2014	Moors for the Future *Sphagnum* Seminar	Oral paper
23 – 27/08/2015	Society of Ecological Restoration World Conference on Ecological Restoration	Delegate

4.3 Future research

Further research into blanket bog restoration should focus on better understanding the limiting factors surrounding *Sphagnum* reintroduction, along with the impacts of successful reintroduction for the wider ecosystem. Many of the pilot studies undertaken here could be expanded to include additional replicates across multiple sites, increasing the confidence and applicability of conclusions drawn. As trials continue, and knowledge and experience increases within the scientific and stakeholder community, it is essential that an open dialogue exists between these two parties to enable maximum benefit and success to be achieved, with future objectives likely to evolve in the face of new challenges, as they arise.

Moisture availability has been consistently implicated as a crucial factor in the success of *Sphagnum* reintroduction. However, this relationship remains to be quantified. Restoration of lowland raised bogs requires a stable water table at or near the surface of the peat. In the degraded blanket bogs of the Peak District and southern Pennines, both rainfall and occult precipitation are greater, and the network or erosion features can gather and channel available water. The presence of *Sphagnum* within areas of severely disturbed hydrology indicates water table, *per se*, may not be a constraining factor, but rather the availability of water. Assessment of such a relationship would require *in situ* monitoring of moisture conditions, making use of numerous probes and data loggers. The results could help to inform a more targeted approach to *Sphagnum* reintroduction, by focussing on those areas most likely to support new growth. This could be extended to include remote sensing, such as LiDAR (light detection and ranging) and hydrological modelling, helping to predict where conditions will be wet enough to sustain *Sphagnum*.

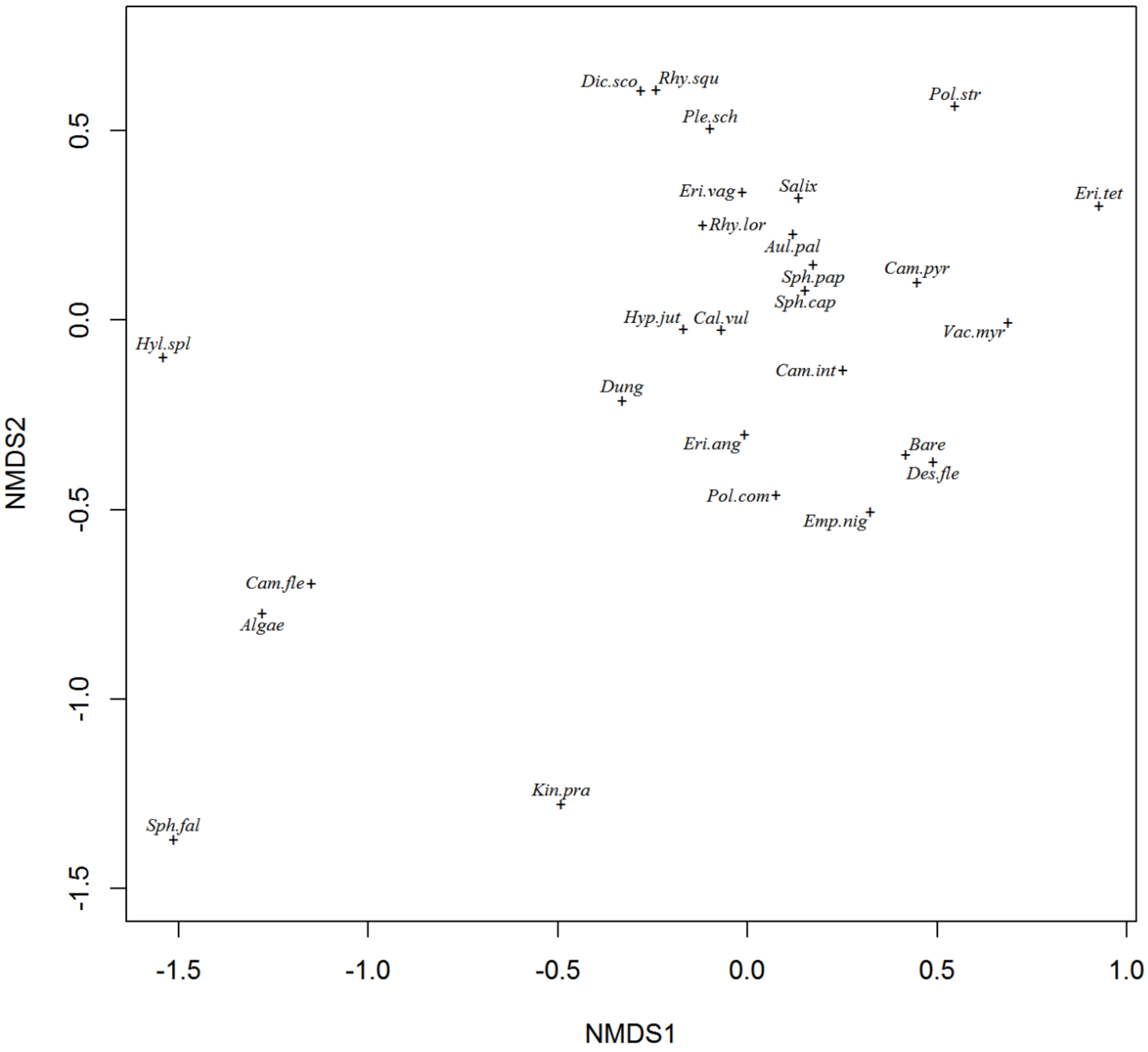
Long term monitoring of experimental plots is essential to determine their success and longevity. Realistically, regimes of five years or more are required to accurately assess the outcome of *Sphagnum* reintroductions. Vegetation cover data, along with fixed point quadrats, can be used to track the establishment, growth and expansion of reintroduced *Sphagnum*. These should include the wider bog surface, rather than just the immediate area targeted. Over longer time scales of decades, this will demonstrate the impact of significant *Sphagnum* cover on the wider vegetation community. Increases in water table will likely result in species shift from those typical of drier, heath-like, to those more typical of bog vegetation. Changes in the provision of ecosystem services are unlikely to occur in the short term, necessitating extended monitoring campaigns. Carbon sequestration and water quality are likely to be the greatest policy drivers of blanket bog restoration, both of which are readily quantifiable using existing methodologies.

Appendices

Appendix 1 – Abbreviated species names

Agr.sto	*Agrostis stolonifera*	Jun.squ	*Juncus squarrosus*
Algae	algae	Kin.pra	*Kindbergia praelonga*
And.pol	*Andromeda polifolia*	Lop.bid	*Lophocolea bidentata*
Aul.pal	*Aulacumnium palustre*	Mol.cae	*Molina caerulea*
Bare	bare ground	Myr.gal	*Myrica gale*
Bet.pen	*Betula pendula*	Nar.oss	*Narthecium ossifragum*
Betula	*Betula* spp.	Odo.sph	*Odontoschimsma sphagni*
Bra.rut	*Brachythecium rutabulum*	Pla.und	*Plagiothecium undulatum*
Cal.vul	*Calluna vulgaris*	Ple.sch	*Pleurozium schreberi*
Cam.fle	*Campylopus flexuosus*	Poh.nut	*Pohlia nutans*
Cam.int	*Campylopus introflexus*	Pol.com	*Polytrichum commune*
Cam.pyr	*Campylopus pyriformis*	Pol.str	*Polytrichum strictum*
Cha.ang	*Chamerion angustifolium*	Rhy.alb	*Rhynchospora alba*
Cla.por	*Cladonia portentosa*	Rhy.lor	*Rhytidiadelphus loreus*
Des.fle	*Deschampsia flexuosa*	Rhy.squ	*Rhytidiadelphus squarrosus*
Dic.sco	*Dicranum scoparium*	Rub.cha	*Rubus chamaemorus*
Dro.ang	*Drosera anglica*	Salix	*Salix* spp.
Dro.rot	*Drosera rotundifolia*	Sci.ces	*Scirpus cespitosus*
Dry.fil	*Dryopteris filix-mas*	Sph.cap	*Sphagnum capillifolium*
Emp.nig	*Empetrum nigrum*	Sph.cus	*Sphagnum cuspidatum*
Epi.ang	*Epilobium angustifolium*	Sph.den	*Sphagnum denticulatum*
Eri.tet	*Erica tetralix*	Sph.fal	*Sphagnum fallax*
Eri.ang	*Eriophorum angustifolium*	Sph.fim	*Sphagnum fimbriatum*
Eri.vag	*Eriophorum vaginatum*	Sph.mag	*Sphagnum magellanicum*
Gal.apa	*Galium aparine*	Sph.pal	*Sphagnum palustre*
Gal.sax	*Galium saxatile*	Sph.pap	*Sphagnum papillosum*
Gym.inf	*Gymnocolea inflata*	Sph.pul	*Sphagnum pulchrum*
Hyl.spl	*Hylocomium splendens*	Sph.subn	*Sphagnum subnitens*
Hyp.cup	*Hypnum cupressiforme*	Sph.ten	*Sphagnum tenellum*
Hyp.jut	*Hypnum jutlandicum*	Vac.myr	*Vaccinium myrtillus*
Jun.eff	*Juncus effusus*	Vac.oxy	*Vaccinium oxycoccos*

Appendix 2 – Non-metric multidimensional scaling (NMDS) ordination of the vegetation composition data for the *Sphagnum* source trial. Labels are arranged to minimise overlapping.



Appendix 3 – Details of all experimental *Sphagnum* bead plots

Zero
Greater than zero
Lower threshold (0.5 %)
Upper threshold (0.8 %)

Date	*Substrate*	*Replicate*	*Treatment*	*Sown*	*N*	*% Success*
Nov-09	Bare	1	*S. fallax*	1600	0	0
Nov-09	Bare	1	*S. fimbriatum*	1600	0	0
Nov-09	Bare	1	*S. papillosum*	1600	0	0
Nov-09	Bare	1	*S. cuspidatum*	1600	0	0
Nov-09	Bare	1	*S. palustre*	1600	0	0
Nov-09	Bare	1	Control	-	-	-
Nov-09	Bare	2	*S. fimbriatum*	1600	0	0
Nov-09	Bare	2	*S. fallax*	1600	0	0
Nov-09	Bare	2	*S. palustre*	1600	0	0
Nov-09	Bare	2	*S. cuspidatum*	1600	0	0
Nov-09	Bare	2	*S. papillosum*	1600	0	0
Nov-09	Bare	2	Control	-	-	-
Nov-09	Bare	3	*S. cuspidatum*	1600	0	0
Nov-09	Bare	3	*S. fimbriatum*	1600	0	0
Nov-09	Bare	3	*S. papillosum*	1600	0	0
Nov-09	Bare	3	*S. palustre*	1600	0	0
Nov-09	**Bare**	**3**	***S. fallax***	**1600**	**1**	**0.0625**
Nov-09	Bare	3	Control	-	-	-
Nov-09	Treated	1	*S. papillosum*	1600	0	0
Nov-09	Treated	1	*S. fallax*	1600	0	0
Nov-09	Treated	1	*S. cuspidatum*	1600	0	0
Nov-09	Treated	1	*S. fimbriatum*	1600	0	0
Nov-09	**Treated**	**1**	***S. palustre***	**1600**	**5**	**0.3125**
Nov-09	Treated	1	Control	-	-	-
Nov-09	Treated	2	*S. palustre*	1600	0	0
Nov-09	Treated	2	*S. papillosum*	1600	0	0
Nov-09	Treated	2	*S. fimbriatum*	1600	0	0
Nov-09	Treated	2	*S. fallax*	1600	0	0
Nov-09	Treated	2	*S. cuspidatum*	1600	0	0
Nov-09	Treated	2	Control	-	-	-
Nov-09	**Treated**	**3**	***S. fimbriatum***	**1600**	**4**	**0.2500**
Nov-09	**Treated**	**3**	***S. palustre***	**1600**	**9**	**0.5625**
Nov-09	Treated	3	*S. cuspidatum*	1600	0	0
Nov-09	**Treated**	**3**	***S. papillosum***	**1600**	**12**	**0.7500**
Nov-09	**Treated**	**3**	***S. fallax***	**1600**	**1**	**0.0625**
Nov-09	Treated	3	Control	-	-	-
Nov-09	**Vegetated**	**1**	***S. cuspidatum***	**1600**	**60**	**3.7500**
Nov-09	**Vegetated**	**1**	***S. fallax***	**1600**	**49**	**3.0625**
Nov-09	**Vegetated**	**2**	***S. fallax***	**1600**	**17**	**1.0625**
Nov-09	**Vegetated**	**3**	***S. fallax***	**1600**	**20**	**1.2500**

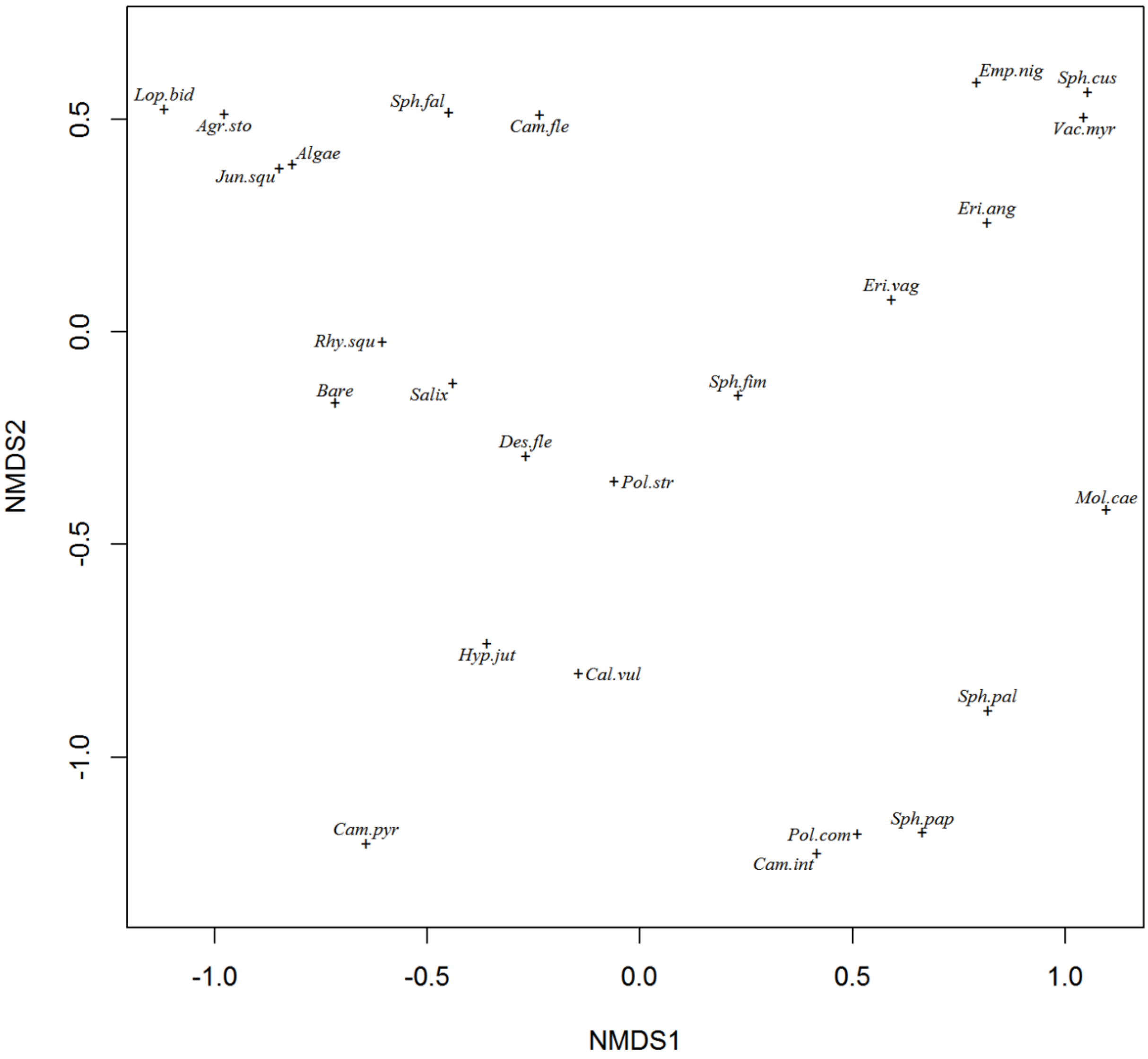
Date	***Substrate***	***Replicate***	***Treatment***	***Sown***	***N***	***% Success***
Apr-10	Bare	1	Control	-	-	-
Apr-10	Bare	1	*S. fallax*	1600	0	0
Apr-10	Bare	1	*S. papillosum*	1600	0	0
Apr-10	Bare	1	*S. fimbriatum*	1600	0	0
Apr-10	Bare	1	*S. palustre*	1600	0	0
Apr-10	Bare	1	*S. cuspidatum*	1600	0	0
Apr-10	Bare	2	Control	-	-	-
Apr-10	Bare	2	*S. fimbriatum*	1600	0	0
Apr-10	Bare	2	*S. papillosum*	1600	0	0
Apr-10	Bare	2	*S. cuspidatum*	1600	0	0
Apr-10	Bare	2	*S. fallax*	1600	0	0
Apr-10	Bare	2	*S. palustre*	1600	0	0
Apr-10	Bare	3	Control	-	-	-
Apr-10	**Bare**	**3**	***S. fimbriatum***	**1600**	**2**	**0.1250**
Apr-10	Bare	3	*S. fallax*	1600	0	0
Apr-10	Bare	3	*S. palustre*	1600	0	0
Apr-10	Bare	3	*S. cuspidatum*	1600	0	0
Apr-10	Bare	3	*S. papillosum*	1600	0	0
Apr-10	**Treated**	**1**	***S. cuspidatum***	**1600**	**2**	**0.1250**
Apr-10	**Treated**	**1**	***S. palustre***	**1600**	**3**	**0.1875**
Apr-10	Treated	1	*S. fimbriatum*	1600	0	0
Apr-10	**Treated**	**1**	***S. papillosum***	**1600**	**3**	**0.1875**
Apr-10	Treated	1	*S. fallax*	1600	0	0
Apr-10	Treated	1	Control	-	-	-
Apr-10	Treated	2	Control	-	-	-
Apr-10	Treated	2	*S. fallax*	1600	0	0
Apr-10	Treated	2	*S. cuspidatum*	1600	0	0
Apr-10	Treated	2	*S. fimbriatum*	1600	0	0
Apr-10	Treated	2	*S. papillosum*	1600	0	0
Apr-10	Treated	2	*S. palustre*	1600	0	0
Apr-10	Treated	3	Control	-	-	-
Apr-10	Treated	3	*S. fallax*	1600	0	0
Apr-10	Treated	3	*S. cuspidatum*	1600	0	0
Apr-10	Treated	3	*S. papillosum*	1600	0	0
Apr-10	Treated	3	*S. palustre*	1600	0	0
Apr-10	Treated	3	*S. fimbriatum*	1600	0	0
Apr-10	Vegetated	1	Control	-	-	-
Apr-10	Vegetated	1	*S. fallax*	1600	0	0
Apr-10	Vegetated	1	*S. cuspidatum*	1600	0	0
Apr-10	**Vegetated**	**1**	***S. palustre***	**1600**	**7**	**0.4375**
Apr-10	Vegetated	1	*S. papillosum*	1600	0	0
Apr-10	**Vegetated**	**1**	***S. fimbriatum***	**1600**	**1**	**0.0625**
Aug-10	Bare	1	*S. fallax*	1600	0	0
Aug-10	Bare	1	Control	-	-	-
Aug-10	Bare	1	*S. palustre*	1600	0	0
Aug-10	Bare	2	*S. palustre*	1600	0	0
Aug-10	Bare	2	*S. fallax*	1600	0	0
Aug-10	Bare	2	Control	-	-	-

Date	***Substrate***	***Replicate***	***Treatment***	***Sown***	***N***	***% Success***
Aug-10	Bare	3	*S. fallax*	1600	0	0
Aug-10	Bare	3	Control	-	-	-
Aug-10	Bare	3	*S. palustre*	1600	0	0
Aug-10	**Treated**	**1**	***S. fallax***	**1600**	**288**	**18.0000**
Aug-10	Treated	1	*S. palustre*	1600	0	0
Aug-10	Treated	1	Control	-	-	-
Aug-10	Treated	2	*S. palustre*	1600	0	0
Aug-10	Treated	2	Control	-	-	-
Aug-10	**Treated**	**2**	***S. fallax***	**1600**	**264**	**16.5000**
Aug-10	Treated	3	Control	-	-	-
Aug-10	**Treated**	**3**	***S. fallax***	**1600**	**33**	**2.0625**
Aug-10	Treated	3	*S. palustre*	1600	0	0
Sep-10	Bare	1	*S. fallax*	1600	0	0
Sep-10	Bare	1	*S. papillosum*	1600	0	0
Sep-10	Bare	1	*S. cuspidatum*	1600	0	0
Sep-10	Bare	1	*S. palustre*	1600	0	0
Sep-10	Bare	1	*S. fimbriatum*	1600	0	0
Sep-10	Bare	1	Control	-	-	-
Sep-10	Bare	2	*S. fallax*	1600	0	0
Sep-10	Bare	2	*S. cuspidatum*	1600	0	0
Sep-10	Bare	2	*S. papillosum*	1600	0	0
Sep-10	Bare	2	*S. fimbriatum*	1600	0	0
Sep-10	Bare	2	*S. palustre*	1600	0	0
Sep-10	Bare	2	Control	-	-	-
Sep-10	Bare	3	Control	-	-	-
Sep-10	Bare	3	*S. papillosum*	1600	0	0
Sep-10	Bare	3	*S. fimbriatum*	1600	0	0
Sep-10	Bare	3	*S. cuspidatum*	1600	0	0
Sep-10	Bare	3	*S. palustre*	1600	0	0
Sep-10	Bare	3	*S. fallax*	1600	0	0
Sep-10	Treated	1	Control	-	-	-
Sep-10	Treated	1	*S. cuspidatum*	1600	0	0
Sep-10	Treated	1	*S. fallax*	1600	0	0
Sep-10	Treated	1	*S. fimbriatum*	1600	0	0
Sep-10	Treated	1	*S. palustre*	1600	0	0
Sep-10	Treated	1	*S. papillosum*	1600	0	0
Sep-10	Treated	2	*S. papillosum*	1600	0	0
Sep-10	Treated	2	*S. cuspidatum*	1600	0	0
Sep-10	Treated	2	*S. fimbriatum*	1600	0	0
Sep-10	Treated	2	*S. palustre*	1600	0	0
Sep-10	Treated	2	*S. fallax*	1600	0	0
Sep-10	Treated	2	Control	-	-	-
Sep-10	Treated	3	Control	-	-	-
Sep-10	Treated	3	*S. fimbriatum*	1600	0	0
Sep-10	Treated	3	*S. cuspidatum*	1600	0	0
Sep-10	Treated	3	*S. palustre*	1600	0	0
Sep-10	Treated	3	*S. fallax*	1600	0	0
Sep-10	Treated	3	*S. papillosum*	1600	0	0

Date	***Substrate***	***Replicate***	***Treatment***	***Sown***	***N***	***% Success***
Sep-10	Vegetated	1	Control	-	-	-
Sep-10	**Vegetated**	**1**	***S. palustre***	**1600**	**1**	**0.0625**
Sep-10	**Vegetated**	**1**	***S. fallax***	**1600**	**3**	**0.1875**
Sep-10	Vegetated	2	*S. fallax*	1600	0	0
Sep-10	Vegetated	2	*S. palustre*	1600	0	0
Sep-10	Vegetated	2	Control	-	-	-
Sep-10	Vegetated	3	*S. palustre*	1600	0	0
Sep-10	Vegetated	3	*S. fallax*	1600	0	0
Sep-10	Vegetated	3	Control	-	-	-
May-11	Treated	1	*S. fallax*	1600	0	0
May-11	Treated	1	*S. capillifolium*	1600	0	0
May-11	Treated	1	*S. palustre*	1600	0	0
May-11	Treated	1	*S. fimbriatum*	1600	0	0
May-11	Treated	1	*S. cuspidatum*	1600	0	0
May-11	Treated	1	Control	-	-	-
May-11	Treated	1	*S. papillosum*	1600	0	0
May-11	Treated	2	*S. papillosum*	1600	0	0
May-11	Treated	2	Control	-	-	-
May-11	Treated	2	*S. cuspidatum*	1600	0	0
May-11	Treated	2	*S. fimbriatum*	1600	0	0
May-11	Treated	2	*S. palustre*	1600	0	0
May-11	**Treated**	**2**	***S. fallax***	**1600**	**9**	**0.5625**
May-11	Treated	2	*S. capillifolium*	1600	0	0
May-11	Treated	3	*S. palustre*	1600	0	0
May-11	Treated	3	*S. papillosum*	1600	0	0
May-11	Treated	3	*S. fallax*	1600	0	0
May-11	Treated	3	*S. capillifolium*	1600	0	0
May-11	Treated	3	Control	-	-	-
May-11	Treated	3	*S. cuspidatum*	1600	0	0
May-11	Treated	3	*S. fimbriatum*	1600	0	0
May-11	Vegetated	1	Control	-	-	-
May-11	Vegetated	1	*S. palustre*	1600	0	0
May-11	Vegetated	1	*S. fallax*	1600	0	0
May-11	Vegetated	2	*S. palustre*	1600	0	0
May-11	Vegetated	2	*S. fallax*	1600	0	0
May-11	Vegetated	2	Control	-	-	-
May-11	Vegetated	3	*S. palustre*	1600	0	0
May-11	Vegetated	3	Control	-	-	-
May-11	Vegetated	3	*S. fallax*	1600	0	0
Aug-12	Vegetated	1	*S. palustre*	1600	0	0
Aug-12	Vegetated	1	Control	-	-	-
Aug-12	Vegetated	1	*S. capillifolium*	1600	0	0
Aug-12	Vegetated	1	*S. fallax*	1600	0	0
Aug-12	Vegetated	1	*S. fimbriatum*	1600	0	0

Date	***Substrate***	***Replicate***	***Treatment***	***Sown***	***N***	***% Success***
Aug-12	Vegetated	2	*S. fallax*	1600	0	0
Aug-12	Vegetated	2	*S. palustre*	1600	0	0
Aug-12	Vegetated	2	Control	-	-	-
Aug-12	Vegetated	2	*S. fimbriatum*	1600	0	0
Aug-12	Vegetated	2	*S. capillifolium*	1600	0	0
Aug-12	Vegetated	3	*S. capillifolium*	1600	0	0
Aug-12	Vegetated	3	*S. fallax*	1600	0	0
Aug-12	Vegetated	3	*S. fimbriatum*	1600	0	0
Aug-12	Vegetated	3	*S. palustre*	1600	0	0
Aug-12	Vegetated	3	Control	-	-	-
Aug-12	Treated	1	Control	-	-	-
Aug-12	Treated	1	*S. capillifolium*	1600	0	0
Aug-12	Treated	1	*S. fallax*	1600	0	0
Aug-12	Treated	1	*S. fimbriatum*	1600	0	0
Aug-12	Treated	2	Control	-	-	-
Aug-12	Treated	2	*S. capillifolium*	1600	0	0
Aug-12	Treated	2	*S. fallax*	1600	0	0
Aug-12	Treated	2	*S. fimbriatum*	1600	0	0
Aug-12	Treated	3	Control	-	-	-
Aug-12	Treated	3	*S. capillifolium*	1600	0	0
Aug-12	Treated	3	*S. fallax*	1600	0	0
Aug-12	Treated	3	*S. fimbriatum*	1600	0	0

Appendix 4 – Non-metric multidimensional scaling (NMDS) ordination of the vegetation composition data for the *Sphagnum* bead trials. Labels are arranged to minimise overlapping.



Appendix 5 – Extractable (e) and total (t) biogeochemical values from Holme Moss reference material. Values in µg g^{-1} dry weight, unless indicated otherwise. Mean and relative standard deviation (RSD) reported for the 10 replicates.

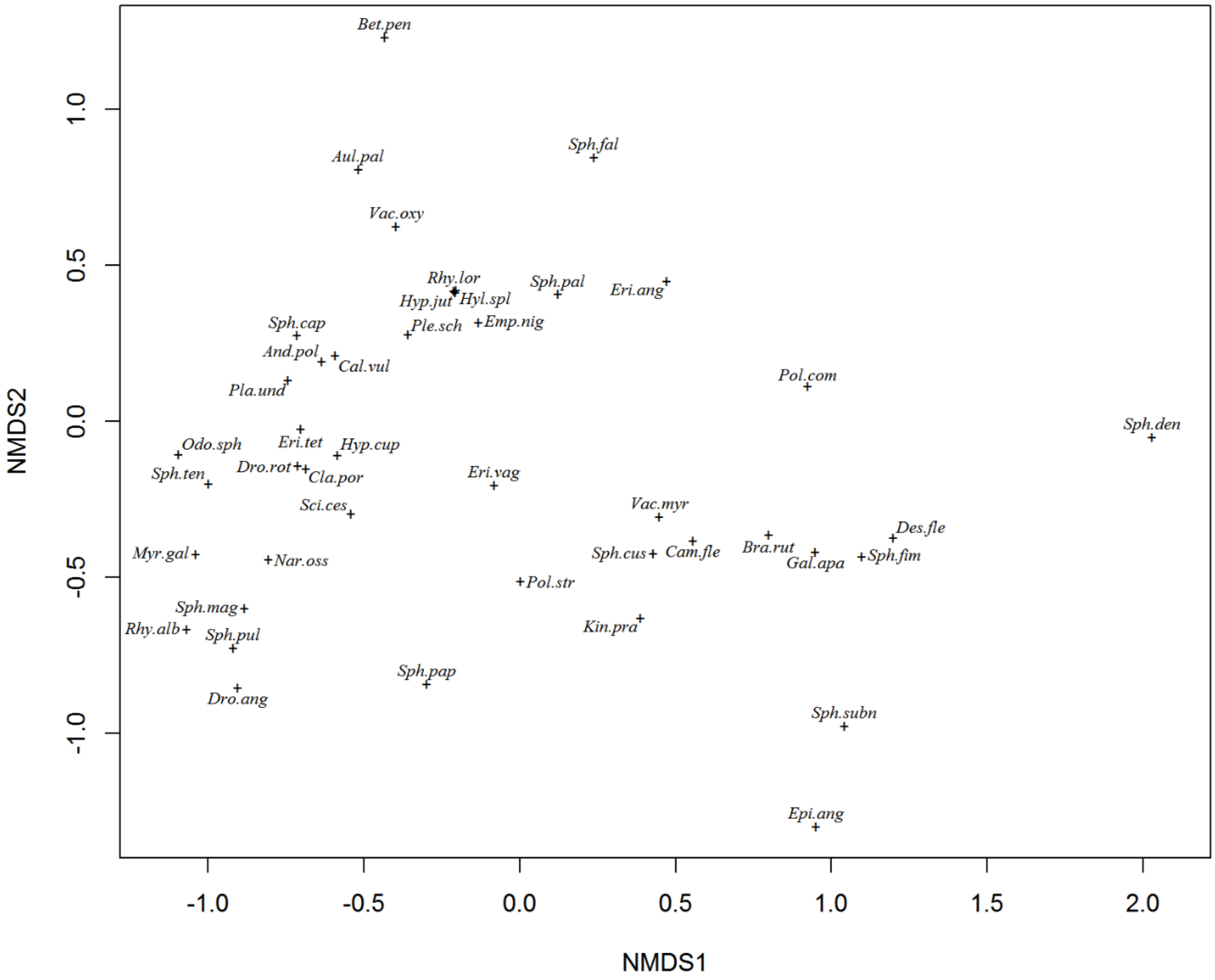
Sample	*MC (%)*	*pH*	*e Al*	*e As*	*e Ba*	*e Ca*$^{2+}$	*e Ca*	*e Cd*	*e Co*	*e Cu*	*e Fe*	*e Mn*	*e Mo*	*e Na*$^{+}$
Ref 1	85.05	3.80	147.3	0.332	3.00	516.8	42.0	0.257	0.382	2.92	67.0	0.112	0.278	223.7
Ref 2	84.28	3.79	277.5	2.190	23.86	463.8	124.6	0.373	0.294	6.70	226.0	0.553	0.349	159.4
Ref 3	85.08	3.85	307.0	2.343	21.43	523.6	142.5	0.433	0.367	7.01	209.6	0.664	0.365	163.2
Ref 4	85.25	3.82	292.2	2.585	19.52	501.5	135.8	0.426	0.361	6.72	256.8	0.658	0.389	163.1
Ref 5	85.56	3.97	313.5	3.290	7.73	530.3	135.8	0.446	0.366	8.22	321.2	0.652	0.524	171.0
Ref 6	86.15	3.95	333.8	2.520	13.00	554.9	148.3	0.490	0.383	7.49	221.5	0.697	0.403	182.5
Ref 7	86.23	3.99	321.8	2.523	1.66	529.0	139.3	0.431	0.329	9.37	231.1	0.643	0.499	191.0
Ref 8	86.35	3.94	333.9	2.923	23.81	517.6	136.7	0.459	0.375	10.84	272.9	0.663	0.576	169.6
Ref 9	86.59	3.86	359.8	2.452	21.02	555.6	149.7	0.482	0.380	11.08	199.3	0.718	0.444	171.4
Ref 10	85.50	3.93	310.7	2.336	19.86	530.2	134.8	0.419	0.315	7.79	220.8	0.636	0.390	165.1
Mean	85.60	3.89	299.8	2.349	15.49	522.3	129.0	0.422	0.355	7.82	222.6	0.600	0.422	176.0
RSD (%)	0.84	1.91	19.44	33.07	55.04	5.04	24.33	15.81	8.83	30.04	29.35	29.45	21.23	10.98

Sample	*e NH*$_4^{+}$	*e Ni*	*e NO*$_3^{-}$	*e P*	*e Pb*	*e PO*$_4^{3-}$	*e S*	*e Sn*	*e SO*$_4^{2-}$	*e Sr*	*e Ti*	*e V*	*e Zn*
Ref 1	139.4	1.481	126.2	0.306	111.6	3.138	3.06	0.000	181.7	0.316	0.000	0.000	13.28
Ref 2	128.9	2.963	120.9	1.398	255.0	3.168	10.77	0.032	187.0	1.095	0.516	0.000	42.85
Ref 3	139.2	3.372	132.1	1.058	269.8	3.284	9.91	0.035	185.5	1.294	0.624	0.149	48.29
Ref 4	140.8	3.192	124.5	1.481	253.1	4.251	11.35	0.045	193.1	1.233	0.731	0.081	50.09
Ref 5	141.4	3.426	139.6	2.272	290.2	3.659	12.36	0.068	210.5	1.151	1.338	0.080	52.58
Ref 6	148.5	3.666	134.8	1.215	320.2	2.689	11.93	0.036	208.0	1.309	0.571	0.137	47.50
Ref 7	145.5	3.609	126.8	1.378	310.4	2.652	11.01	0.048	213.1	1.188	0.885	0.104	48.11
Ref 8	146.1	3.757	130.4	1.937	338.3	2.987	11.45	0.067	211.1	1.187	1.592	0.134	38.78
Ref 9	151.8	4.172	127.6	1.214	360.2	3.320	10.95	0.033	222.7	1.307	0.514	0.191	38.35
Ref 10	140.3	3.453	126.2	1.308	296.7	2.438	10.69	0.033	202.1	1.187	0.412	0.103	36.40
Mean	142.2	3.309	128.9	1.357	280.5	3.159	10.35	0.040	201.5	1.127	0.718	0.098	41.62
RSD (%)	4.44	21.79	4.21	38.30	24.51	16.72	25.62	48.86	6.89	26.03	62.77	27.32	5.70

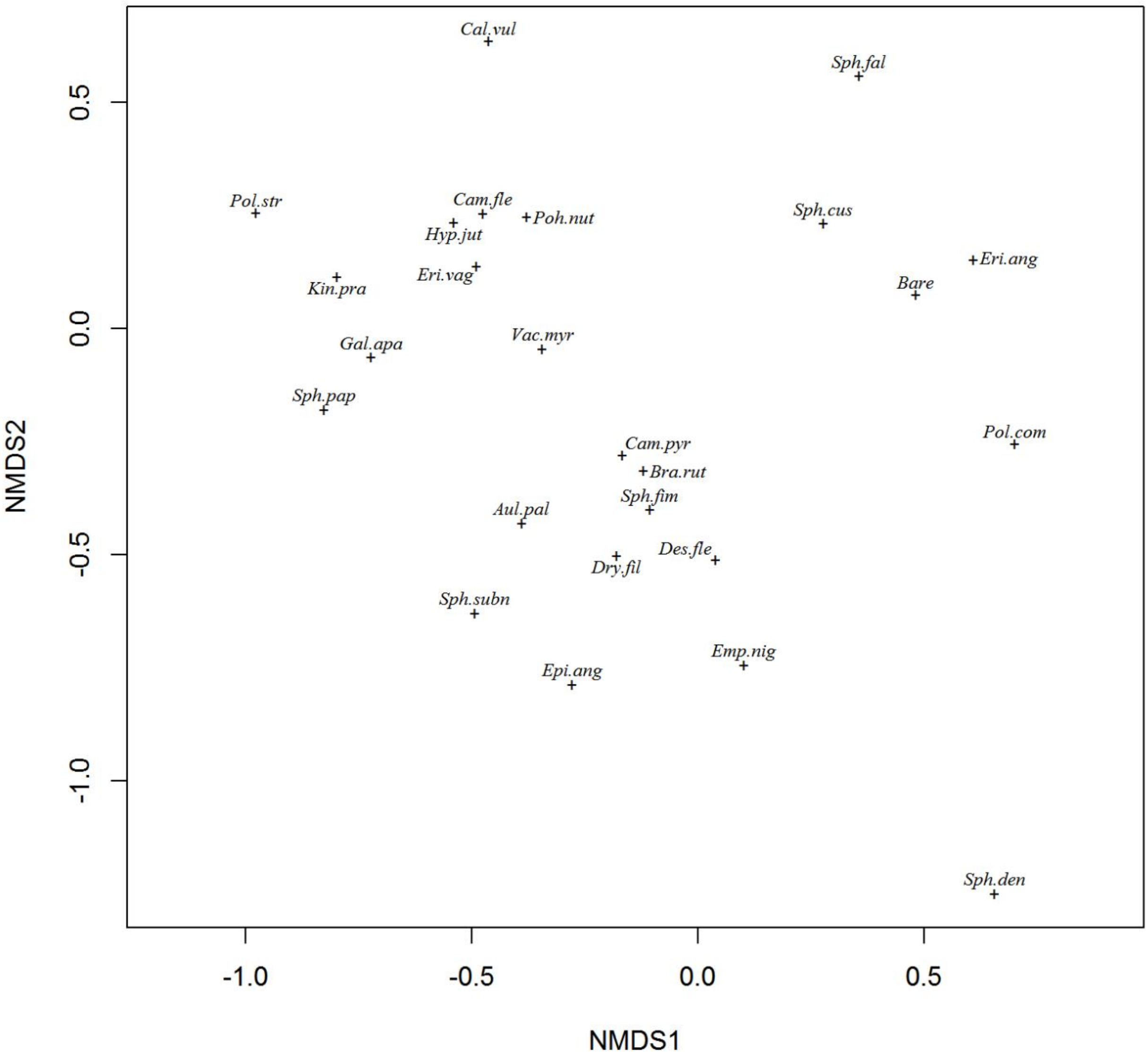
Sample	*t Al*	*t As*	*t Ba*	*t C (%)*	*t Ca*	*t Cd*	*t Co*	*t Cu*	*t Fe*	*t K*	*t Mg*	*t Mn*
Ref 1	2618	12.30	22.44	53.05	690.0	0.919	1.996	84.03	5407	272.7	341.8	14.38
Ref 2	3037	14.24	23.75	53.30	710.6	0.985	2.711	90.98	6736	393.8	391.0	18.23
Ref 3	2754	12.51	23.66	53.17	721.6	0.933	2.211	85.35	5551	300.4	363.0	15.45
Ref 4	2959	13.35	24.44	53.22	720.9	0.976	2.506	88.69	6403	348.1	377.2	16.34
Ref 5	2804	12.39	23.54	53.04	709.1	1.048	2.265	87.69	5758	298.9	350.7	15.92
Ref 6	2698	12.17	22.99	52.74	696.7	0.942	2.178	83.62	5666	287.7	347.4	15.23
Ref 7	2992	13.22	24.45	52.87	711.9	0.965	2.554	89.69	6513	373.6	376.5	17.09
Ref 8	2670	12.26	22.81	53.02	705.3	0.924	2.167	87.75	5849	307.2	357.3	15.01
Ref 9	2584	11.93	22.46	52.75	692.4	0.904	1.976	84.58	5696	270.6	343.4	14.23
Ref 10	2817	12.50	23.17	53.08	694.8	0.921	2.349	88.61	5893	346.3	366.3	16.03
Mean	2793	12.69	23.37	53.02	705.3	0.952	2.291	87.10	5947	319.9	361.5	15.79
RSD (%)	5.70	5.54	3.11	0.36	1.62	4.52	10.46	2.92	7.50	13.39	4.53	7.76

Sample	*t Mo*	*t N (%)*	*t Na*	*t Ni*	*t P*	*t Pb*	*t S*	*t Sn*	*t Sr*	*t Ti*	*t V*	*t Zn*
Ref 1	14.47	1.840	138.2	12.11	716.8	663.9	3987	3.684	8.352	163.0	31.98	57.28
Ref 2	11.80	1.858	156.7	13.43	801.3	693.8	4227	6.377	9.159	214.9	34.85	60.25
Ref 3	11.55	1.846	144.6	19.75	730.5	685.5	4050	3.837	8.871	178.1	32.09	59.31
Ref 4	21.38	1.805	148.3	15.56	759.2	693.0	4231	5.480	9.207	198.7	34.25	57.41
Ref 5	13.41	1.853	139.4	16.09	659.0	665.8	3837	4.461	9.120	176.6	31.50	53.75
Ref 6	17.51	1.848	140.1	11.03	675.3	643.3	3827	4.237	8.804	175.3	31.36	55.34
Ref 7	24.92	1.849	150.3	16.01	718.2	659.6	3933	6.316	9.337	206.9	33.91	57.80
Ref 8	24.28	1.772	149.5	14.31	715.7	643.1	3855	4.045	8.736	179.3	31.39	54.86
Ref 9	14.06	1.842	137.4	17.05	683.7	650.4	3759	3.893	8.556	163.5	30.98	52.30
Ref 10	19.95	1.824	151.8	19.34	723.7	655.3	3859	4.688	8.864	196.5	33.69	56.21
Mean	17.33	1.834	145.6	15.47	718.3	665.4	3956	4.702	8.901	185.3	32.60	56.45
RSD (%)	29.01	1.46	4.57	18.40	5.74	2.89	4.20	21.46	3.47	9.66	4.36	4.35

Appendix 6 – Non-metric multidimensional scaling (NMDS) ordination of the vegetation composition data for the reference and Pennine sites. Labels are arranged to minimise overlapping.



Appendix 7 – Non-metric multidimensional scaling (NMDS) ordination of the vegetation composition data for the Pennine sites. Labels are arranged to minimise overlapping.



Appendix 8 – Mean (and standard error) of biogeochemical variables from samples containing *Sphagnum*. Values in µg g^{-1} dry weight, unless indicated otherwise. Rank ANOVA (F) and Bonferroni-corrected pairwise comparisons are reported. Sites which do not share a letter are significantly different. (* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$)

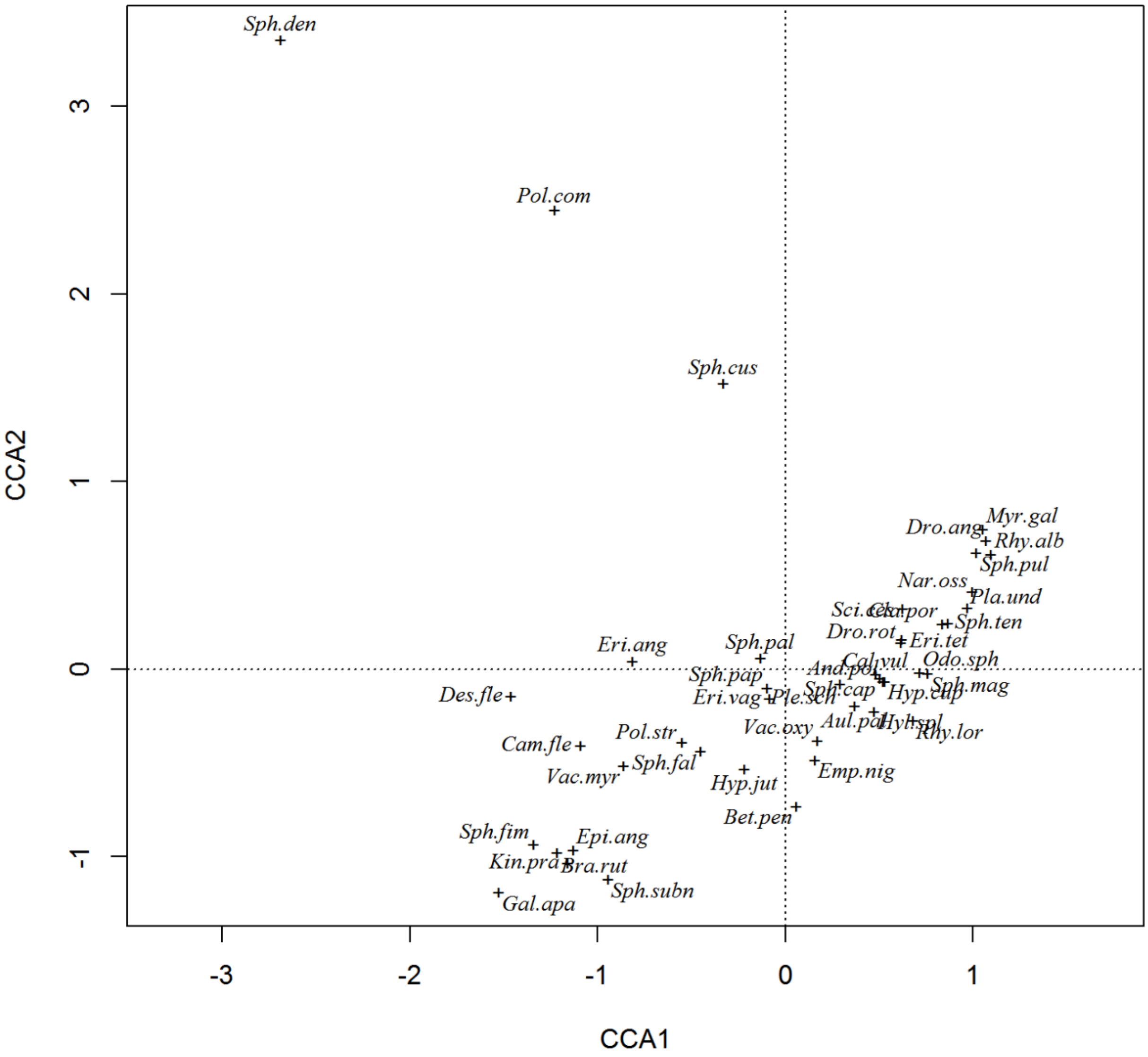
Variable	*Alport Moor*	*Black Hill*	*Bleaklow*	*Borth*	*Glasson*	*Holme Moss*	*Migneint*	*Moidach*	*Whim*	*Whixall*	*F*
MC (%)	91.65	92.29	92.20	92.32	92.44	91.73	92.65	92.80	90.19	92.54	0.93
	(0.87)	(0.91)	(1.34)	(0.65)	(0.64)	(1.13)	(0.53)	(0.72)	(0.81)	(0.79)	
pH	4.06	4.52	4.08	4.27	4.18	3.98	4.18	4.18	3.90	4.00	1.65
	(0.19)	(0.24)	(0.12)	(0.11)	(0.04)	(0.16)	(0.06)	(0.15)	(0.06)	(0.05)	
Al	195.5 $^{a b c}$	148.4 $^{b c d e}$	720.2 ^{a}	63.2 ^{f}	88.0 $^{d e f}$	336.7 ^{a}	186.3 $^{a b c d}$	106.0 $^{e f}$	222.5 $^{a b}$	99.5 $^{c d e f}$	13.93 ***
	(27.1)	(17.3)	(242.3)	(7.1)	(12.2)	(50.6)	(29.2)	(49.9)	(21.6)	(14.6)	
As	1.141 $^{a b c d}$	0.820 $^{b c d}$	4.169 $^{a b}$	0.411 $^{d e}$	0.117 ^{e}	2.443 ^{a}	1.238 $^{a b c d}$	0.548 $^{c d e}$	1.873 $^{a b c}$	0.575 $^{d e}$	13.19 ***
	(0.210)	(0.123)	(1.371)	(0.097)	(0.034)	(0.243)	(0.302)	(0.142)	(0.704)	(0.258)	
Ba	5.27 ^{a}	6.21 ^{a}	18.33 ^{a}	11.32 ^{a}	12.01 ^{a}	11.11 ^{a}	5.32 ^{a}	12.14 ^{a}	9.15 ^{a}	9.90 ^{a}	3.18 **
	(0.82)	(2.84)	(5.42)	(3.08)	(2.88)	(4.28)	(1.30)	(1.78)	(1.00)	(2.59)	
Ca	242.2 ^{c}	1988.9 ^{a}	292.3 ^{c}	1058.3 ^{a}	710.8 ^{a}	313.5 $^{b c}$	809.8 ^{a}	423.5 $^{b c}$	565.6 $^{a b}$	371.6 $^{b c}$	15.50 ***
	(25.9)	(568.4)	(51.4)	(151.0)	(41.5)	(34.0)	(63.7)	(53.6)	(96.6)	(35.2)	
Cd	0.698 $^{a b}$	1.274 $^{a b}$	0.774 $^{a b}$	0.293 ^{c}	0.435 $^{b c}$	0.623 $^{a b}$	1.348 ^{a}	0.250 ^{c}	1.204 ^{a}	0.679 $^{a b}$	12.14 ***
	(0.097)	(0.598)	(0.071)	(0.039)	(0.091)	(0.062)	(0.210)	(0.036)	(0.136)	(0.139)	
Co	0.522 $^{a b c}$	0.590 $^{b c}$	1.699 ^{a}	0.266 ^{c}	0.309 ^{c}	0.729 $^{a b}$	0.436 $^{a b c}$	0.424 $^{a b c}$	0.952 ^{a}	0.364 ^{c}	8.57 ***
	(0.083)	(0.199)	(0.491)	(0.014)	(0.061)	(0.079)	(0.043)	(0.047)	(0.135)	(0.050)	
Cu	9.163 ^{a}	5.102 $^{a b c}$	9.390 ^{a}	2.821 $^{c d}$	2.637 $^{b c d}$	5.868 ^{a}	4.260 $^{a b c}$	1.545 ^{d}	6.203 $^{a b}$	2.041 ^{d}	14.56 ***
	(1.320)	(0.682)	(1.180)	(0.750)	(0.450)	(0.821)	(0.391)	(0.171)	(1.412)	(0.356)	
Fe	434.9 $^{b c d e}$	259.4 $^{d e}$	329.8 $^{d e}$	362.3 $^{c d e}$	587.8 $^{a b c d}$	797.4 $^{a b c}$	2099.5 ^{a}	312.7 $^{c d e}$	1594.4 $^{a b}$	195.9 ^{e}	9.46 ***
	(102.0)	(38.3)	(97.9)	(66.6)	(97.7)	(148.6)	(435.5)	(65.8)	(569.1)	(24.6)	
K	198.5 $^{b c d}$	425.1 $^{a b}$	235.4 $^{b c d}$	465.6 ^{a}	361.6 $^{a b}$	278.9 $^{a b c}$	293.4 $^{a b c}$	289.7 $^{a b c}$	114.0 $^{c d}$	34.5 ^{d}	8.48 ***
	(56.8)	(96.0)	(68.3)	(45.0)	(48.4)	(69.3)	(29.9)	(45.4)	(25.6)	(18.7)	
Mg	478.2 ^{e}	643.9 $^{d e}$	731.7 $^{c d}$	1391.6 ^{a}	1075.6 $^{a b}$	456.0 ^{e}	1112.5 $^{a b}$	1070.9 ^{b}	927.2 $^{b c}$	618.5 $^{d e}$	31.63 ***
	(24.5)	(42.9)	(104.0)	(50.8)	(51.6)	(36.4)	(30.0)	(80.2)	(35.2)	(34.3)	
Mn	3.91 $^{b c d}$	4.81 $^{b c d}$	6.76 $^{b c d}$	29.89 $^{a b}$	10.52 $^{a b c}$	2.15 ^{d}	45.71 ^{a}	2.42 $^{c d}$	9.19 $^{a b c}$	2.93 $^{c d}$	8.04 ***
	(0.52)	(1.15)	(1.99)	(11.53)	(3.19)	(0.26)	(9.06)	(0.63)	(2.52)	(0.52)	

Variable	*Alport Moor*	*Black Hill*	*Bleaklow*	*Borth*	*Glasson*	*Holme Moss*	*Migneint*	*Moidach*	*Whim*	*Whixall*	*F*
Mo	1.028 ^{a}	0.459 ^{bc}	0.800 ^{ab}	0.088 ^{ef}	0.021 ^{g}	0.753 ^{ab}	0.155 ^{de}	0.145 ^{cde}	0.245 ^{cd}	0.038 ^{fg}	48.24 ***
	(0.114)	(0.105)	(0.110)	(0.007)	(0.007)	(0.071)	(0.027)	(0.011)	(0.069)	(0.010)	
Na^{+}	199.9 ^{b}	317.5 ^{ab}	190.3 ^{b}	434.2 ^{a}	372.2 ^{a}	385.5 ^{a}	303.2 ^{ab}	440.5 ^{a}	312.9 ^{ab}	366.9 ^{a}	7.00 ***
	(23.1)	(71.9)	(15.2)	(35.5)	(25.0)	(50.2)	(35.8)	(63.2)	(31.7)	(27.3)	
NH$_4^{+}$	384.1 ^{abc}	403.0 ^{abc}	226.3 ^{abc}	52.8 ^{cd}	30.6 ^{d}	1301.1 ^{a}	306.1 ^{ab}	28.5 ^{d}	33.7 ^{cd}	133.2 ^{bcd}	8.95 ***
	(153.9)	(143.4)	(69.1)	(20.0)	(11.3)	(260.4)	(68.3)	(20.9)	(8.5)	(48.6)	
Ni	2.185 ^{abc}	1.609 ^{abcd}	3.125 ^{ab}	0.613 ^{de}	0.944 ^{cde}	2.085 ^{abc}	1.054 ^{bcde}	0.470 ^{e}	2.579 ^{a}	0.993 ^{bcde}	9.73 ***
	(0.499)	(0.451)	(0.687)	(0.039)	(0.105)	(0.331)	(0.084)	(0.047)	(0.324)	(0.084)	
NO$_3^{-}$	446.0 ^{ab}	1368.5 ^{a}	250.6 ^{bc}	49.8 ^{bc}	3.9 ^{bc}	1996.1 ^{a}	2.7 ^{c}	2.3 ^{bc}	115.9 ^{bc}	3.9 ^{c}	11.77 ***
	(213.9)	(257.8)	(165.2)	(32.1)	(1.4)	(430.5)	(1.9)	(0.5)	(41.1)	(2.4)	
P	3.772 ^{bc}	18.373 ^{a}	6.197 ^{bc}	0.109 ^{e}	0.138 ^{e}	13.365 ^{ab}	3.043 ^{c}	0.537 ^{e}	2.992 ^{cd}	0.463 ^{de}	31.29 ***
	(0.727)	(2.810)	(3.147)	(0.082)	(0.056)	(3.027)	(0.867)	(0.159)	(1.011)	(0.071)	
Pb	184.69 ^{a}	88.08 ^{ab}	224.50 ^{a}	13.55 ^{e}	28.72 ^{cde}	108.20 ^{ab}	52.69 ^{bc}	14.26 ^{de}	87.24 ^{ab}	38.79 ^{cd}	24.31 ***
	(33.89)	(13.84)	(54.25)	(2.07)	(5.16)	(28.11)	(9.95)	(1.65)	(13.01)	(8.30)	
PO$_4^{3-}$	25.37 ^{ab}	207.22 ^{a}	11.41 ^{cd}	1.73 ^{cd}	3.41 ^{bcd}	186.34 ^{a}	10.54 ^{bc}	4.93 ^{d}	8.42 ^{bcd}	4.15 ^{d}	17.78 ***
	(6.51)	(40.75)	(6.27)	(0.39)	(0.45)	(46.19)	(2.54)	(3.29)	(2.65)	(2.74)	
S	9.99 ^{abc}	18.36 ^{a}	20.30 ^{a}	5.88 ^{c}	5.15 ^{c}	16.39 ^{a}	4.99 ^{c}	7.48 ^{bc}	10.76 ^{abc}	13.74 ^{ab}	10.81 ***
	(1.72)	(2.11)	(3.80)	(0.69)	(0.61)	(1.49)	(0.45)	(1.25)	(2.85)	(2.31)	
Sn	0.050 ^{abc}	0.014 ^{cd}	0.068 ^{ab}	0.000 ^{e}	0.000 ^{e}	0.090 ^{a}	0.000 ^{e}	0.017 ^{bc}	0.066 ^{abc}	0.002 ^{de}	26.32 ***
	(0.017)	(0.004)	(0.016)	(0.000)	(0.000)	(0.029)	(0.000)	(0.004)	(0.036)	(0.001)	
SO$_4^{2-}$	90.9 ^{bc}	209.0 ^{abc}	285.9 ^{abc}	96.5 ^{bc}	109.2 ^{bc}	545.3 ^{a}	68.5 ^{c}	183.5 ^{bc}	94.6 ^{bc}	278.8 ^{ab}	5.52 ***
	(19.6)	(57.3)	(74.1)	(16.8)	(15.5)	(78.5)	(18.2)	(60.3)	(12.8)	(61.2)	
Sr	2.066 ^{d}	4.489 ^{bc}	2.626 ^{cd}	8.489 ^{a}	7.210 ^{a}	2.365 ^{d}	7.758 ^{a}	7.456 ^{a}	6.501 ^{ab}	2.752 ^{cd}	25.21 ***
	(0.279)	(0.611)	(0.560)	(0.592)	(0.502)	(0.290)	(0.624)	(0.653)	(0.515)	(0.255)	
Ti	0.766 ^{a}	1.033 ^{a}	0.669 ^{ab}	0.218 ^{bc}	0.000 ^{c}	1.594 ^{a}	0.081 ^{c}	0.367 ^{bc}	2.584 ^{a}	0.000 ^{c}	20.66 ***
	(0.140)	(0.247)	(0.214)	(0.094)	(0.000)	(0.297)	(0.055)	(0.264)	(0.988)	(0.000)	
V	0.547 ^{a}	0.591 ^{a}	0.380 ^{a}	0.148 ^{b}	0.000 ^{b}	0.673 ^{a}	0.000 ^{b}	0.000 ^{b}	0.342 ^{a}	0.000 ^{b}	27.44 ***
	(0.133)	(0.113)	(0.121)	(0.071)	(0.000)	(0.180)	(0.000)	(0.000)	(0.065)	(0.000)	
Zn	67.24 ^{ab}	78.21 ^{ab}	46.81 ^{abc}	30.68 ^{c}	58.94 ^{ab}	42.39 ^{bc}	41.71 ^{abc}	27.74 ^{c}	52.77 ^{ab}	62.51 ^{a}	8.36 ***
	(8.46)	(14.85)	(4.09)	(2.41)	(8.18)	(6.21)	(2.75)	(3.81)	(5.37)	(4.64)	

Appendix 9 – Summary, permutation test and AIC values for the national comparison CCA model

```
> mod.sel01
Call: cca(formula = log10(veg+1)~ Mg + Al + Ba + Cd + NO3 + MC + SO4 + V +
Fe + Mo + Zn)

              Inertia Proportion Rank
Total          5.9572     1.0000
Constrained    1.7267     0.2898   11
Unconstrained  4.2305     0.7102   42
Inertia is mean squared contingency coefficient

Eigenvalues for constrained axes:
  CCA1   CCA2   CCA3   CCA4   CCA5   CCA6   CCA7   CCA8
0.4815 0.3789 0.2091 0.1788 0.1293 0.1072 0.0861 0.0644

Eigenvalues for unconstrained axes:
   CA1    CA2    CA3    CA4    CA5    CA6    CA7    CA8
0.4154 0.3847 0.3363 0.3012 0.2668 0.2261 0.1836 0.1679
(Showed only 8 of all 42 unconstrained eigenvalues)


> anova(mod.sel01,by="term")
Permutation test for cca under reduced model
Terms added sequentially (first to last)
Permutation: free
Number of permutations: 999

Model: cca(formula = log10(veg+1)~ Mg + Al + Ba + Cd + NO3 + MC + SO4 + V +
Fe + Mo + Zn)
         Df ChiSquare      F Pr(>F)
Mg        1    0.3749 7.7987  0.001 ***
Al        1    0.3331 6.9285  0.001 ***
Ba        1    0.1537 3.1969  0.001 ***
Cd        1    0.1491 3.1011  0.004 **
NO3       1    0.1350 2.8088  0.002 **
MC        1    0.1135 2.3616  0.004 **
SO4       1    0.1002 2.0836  0.003 **
V         1    0.1125 2.3409  0.002 **
Fe        1    0.0903 1.8784  0.024 *
Mo        1    0.0864 1.7974  0.015 *
Zn        1    0.0779 1.6211  0.031 *
Residual 88    4.2305


> mod.sel01$anova
      Df    AIC      F Pr(>F)
+ Mg   1 355.29 6.5819  0.005 **
+ Al   1 351.14 6.1551  0.005 **
+ Ba   1 350.17 2.8955  0.005 **
+ Cd   1 349.20 2.8632  0.005 **
+ NO3  1 348.43 2.6381  0.005 **
+ MC   1 348.04 2.2475  0.005 **
+ SO4  1 347.89 2.0043  0.005 **
+ V    1 347.41 2.2832  0.010 **
+ Fe   1 347.38 1.8492  0.025 *
+ Mo   1 347.39 1.7850  0.020 *
+ Zn   1 347.56 1.6211  0.015 *


---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

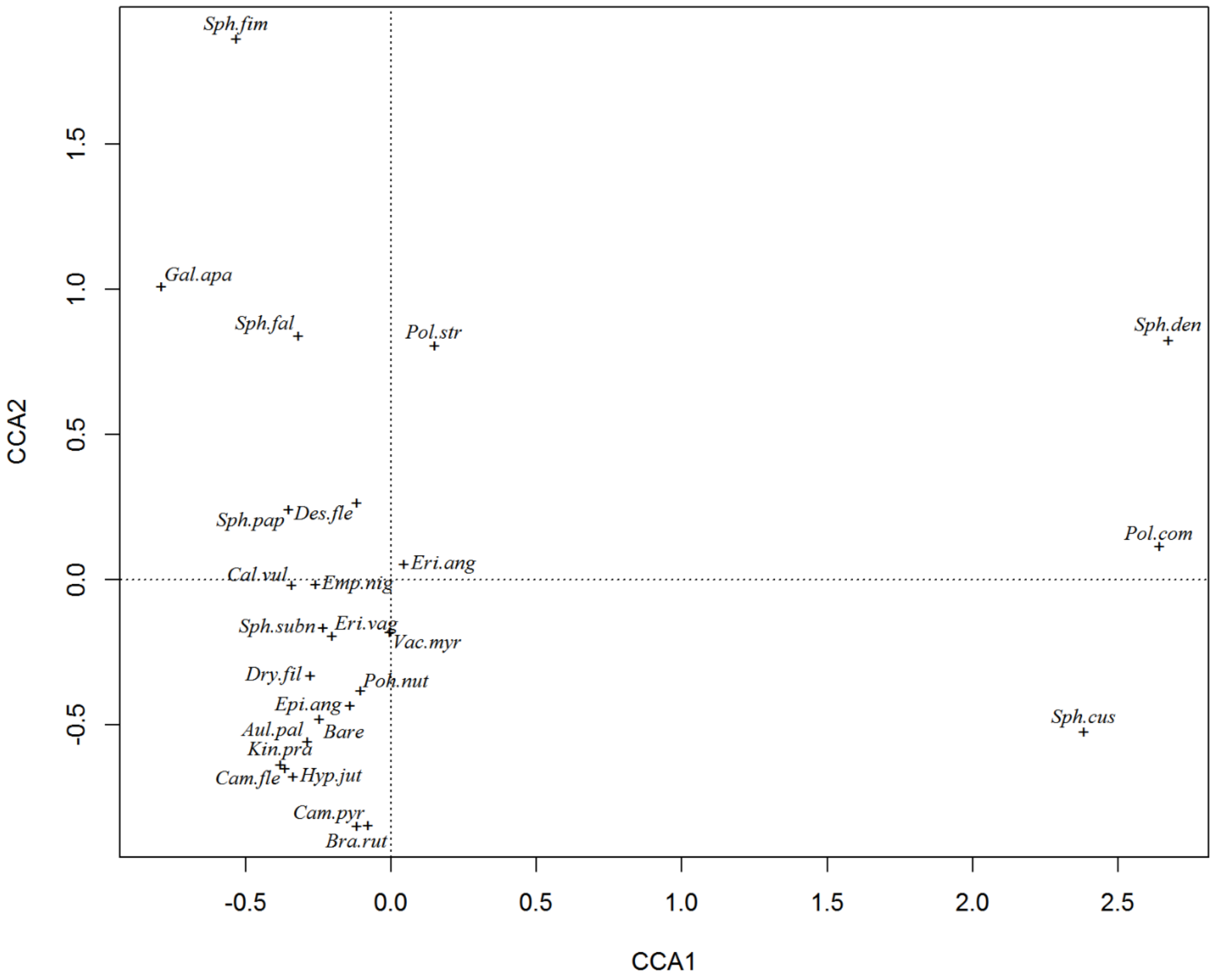
Appendix 10 – Canonical correspondence analysis (CCA) ordination of the vegetation composition data from all the sites, constrained by those environmental variables selected in the model building process (Mg + Al + Ba + Cd + NO_3^- + MC + SO_4^{2-} + V + Fe + Mo + Zn). Labels are arranged to minimise overlapping.



Appendix 11 – Summary, permutation test and AIC values for the Pennine sites CCA model

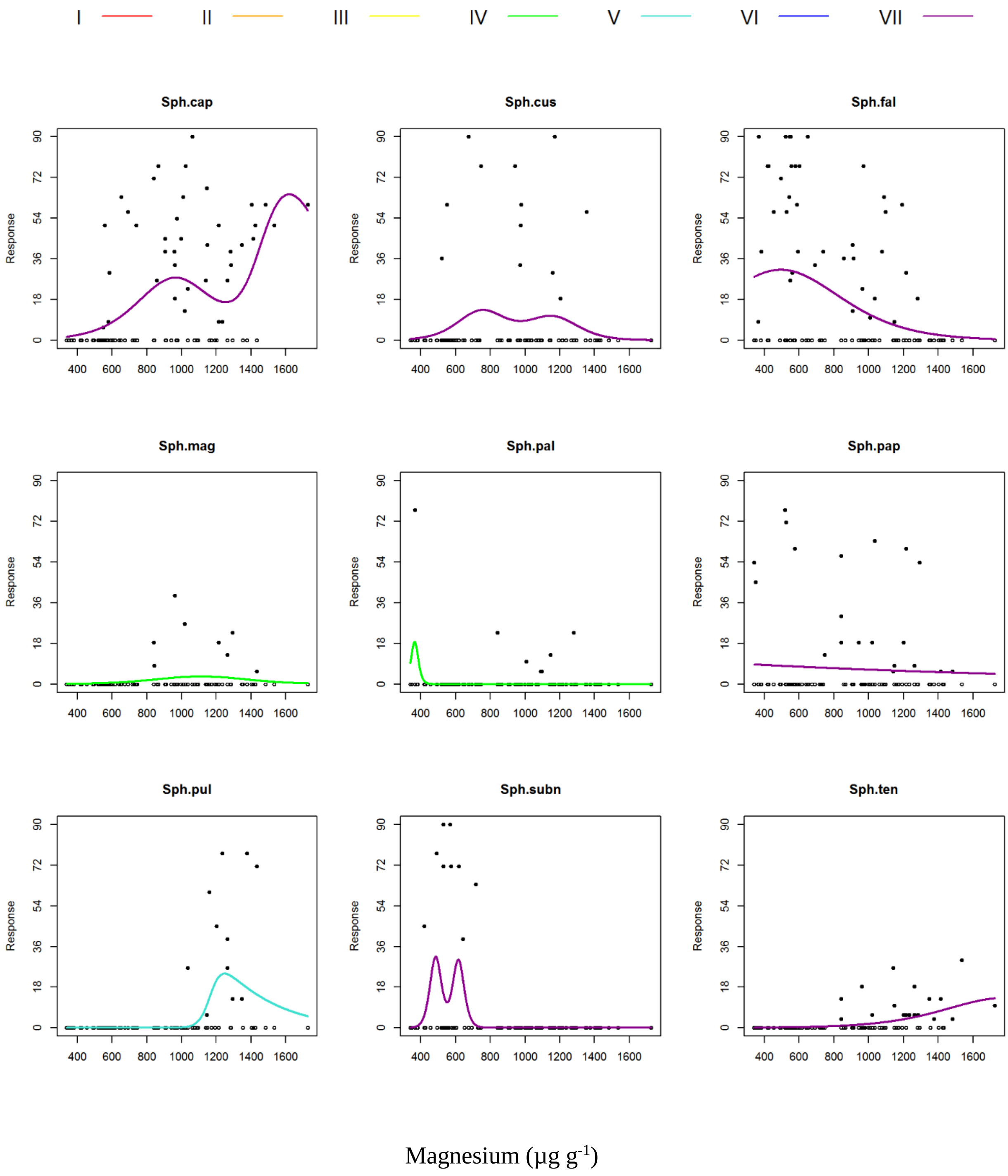
```
> mod.sel01
Call: cca(formula = log10(veg+1)~ Ba + Al + P + Mg + Mo + Pb + Fe + S)

              Inertia Proportion Rank
Total          5.7205     1.0000     
Constrained    1.4297     0.2499    8
Unconstrained  4.2908     0.7501   24
Inertia is mean squared contingency coefficient

Eigenvalues for constrained axes:
  CCA1   CCA2   CCA3   CCA4   CCA5   CCA6   CCA7   CCA8 
0.4865 0.2562 0.1734 0.1664 0.1385 0.1207 0.0673 0.0208 

Eigenvalues for unconstrained axes:
   CA1    CA2    CA3    CA4    CA5    CA6    CA7    CA8 
0.5373 0.4475 0.3979 0.3716 0.2877 0.2718 0.2378 0.2218 
(Showed only 8 of all 24 unconstrained eigenvalues)


> anova(mod.sel01,by="term")
Permutation test for cca under reduced model
Terms added sequentially (first to last)
Permutation: free
Number of permutations: 999

Model: cca(formula = log10(veg+1)~ Ba + Al + P + Mg + Mo + Pb + Fe + S)
         Df ChiSquare      F Pr(>F)    
Ba        1    0.3489 5.7740  0.001 ***
Al        1    0.2233 3.6958  0.001 ***
P         1    0.1703 2.8177  0.002 ** 
Mg        1    0.1585 2.6235  0.003 ** 
Mo        1    0.1633 2.7027  0.006 ** 
Pb        1    0.1137 1.8820  0.018 *  
Fe        1    0.1472 2.4356  0.005 ** 
S         1    0.1043 1.7264  0.040 *  
Residual 71    4.2908                  


> mod.sel01$anova
      Df    AIC      F Pr(>F)   
+ Ba   1 251.76 5.0669  0.005 **
+ Al   1 250.36 3.3406  0.005 **
+ P    1 249.67 2.5998  0.005 **
+ Mg   1 249.08 2.4673  0.010 **
+ NH4  1 249.18 1.7746  0.005 **
+ Mo   1 248.36 2.6202  0.010 **
+ Pb   1 248.35 1.8343  0.020 * 
+ Fe   1 248.15 1.9770  0.020 * 
+ S    1 247.78 1.7264  0.010 **



---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

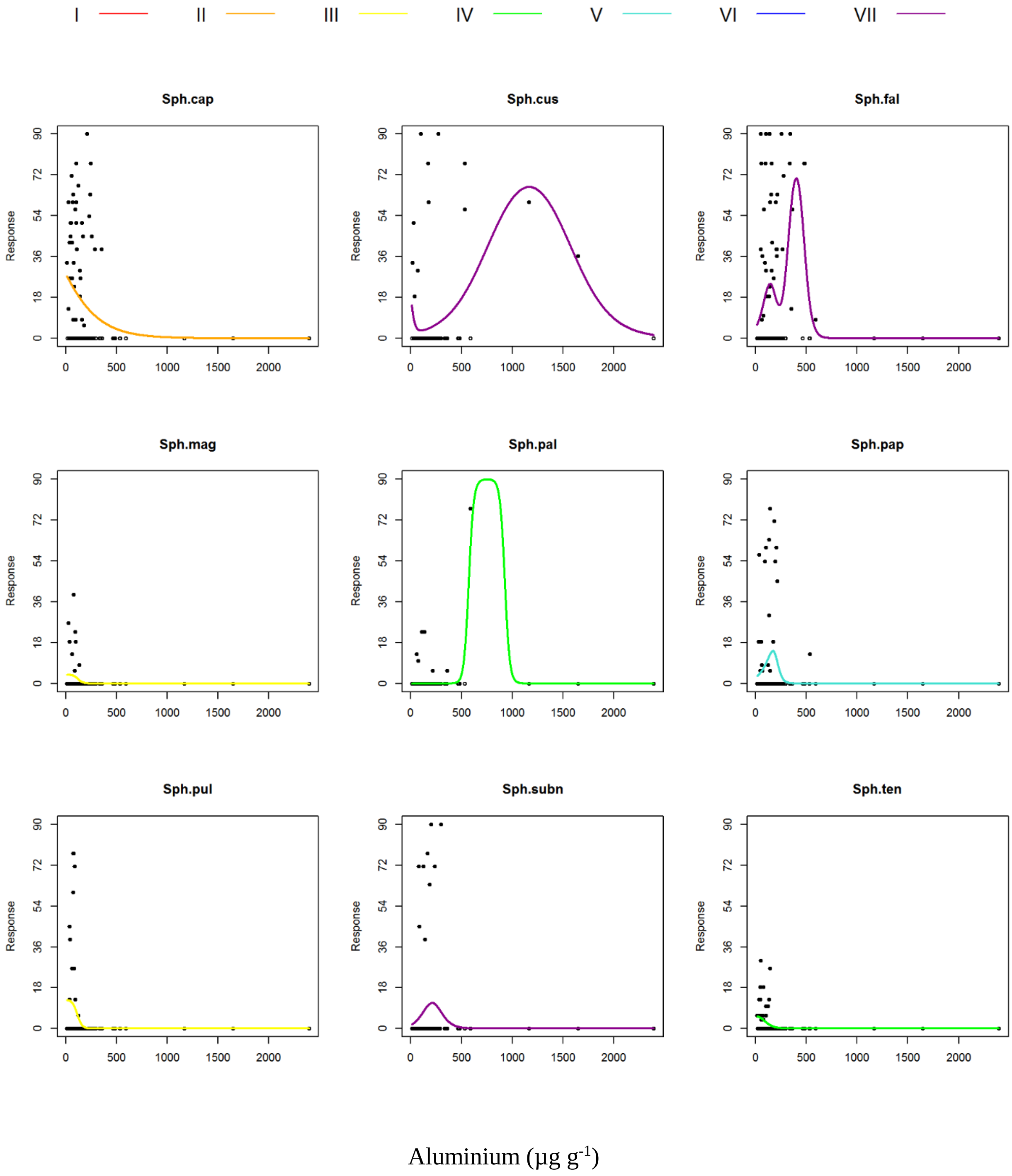
Appendix 12 – Canonical correspondence analysis (CCA) ordination of the vegetation composition data from the Pennine sites, constrained by those environmental variables selected in the model building process (Ba + Al + P + Mg + Mo + Pb + Fe + S). Labels are arranged to minimise overlapping.

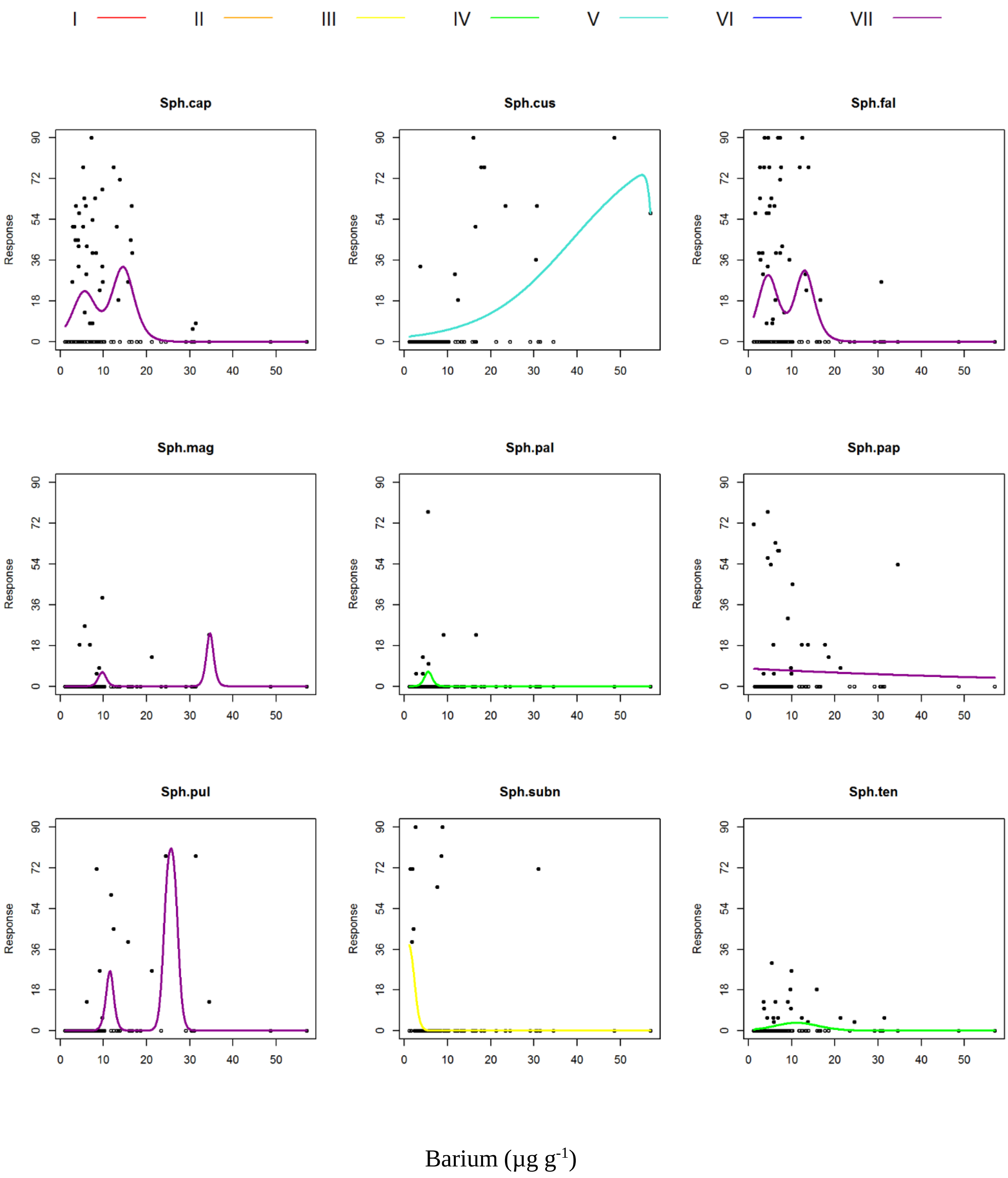


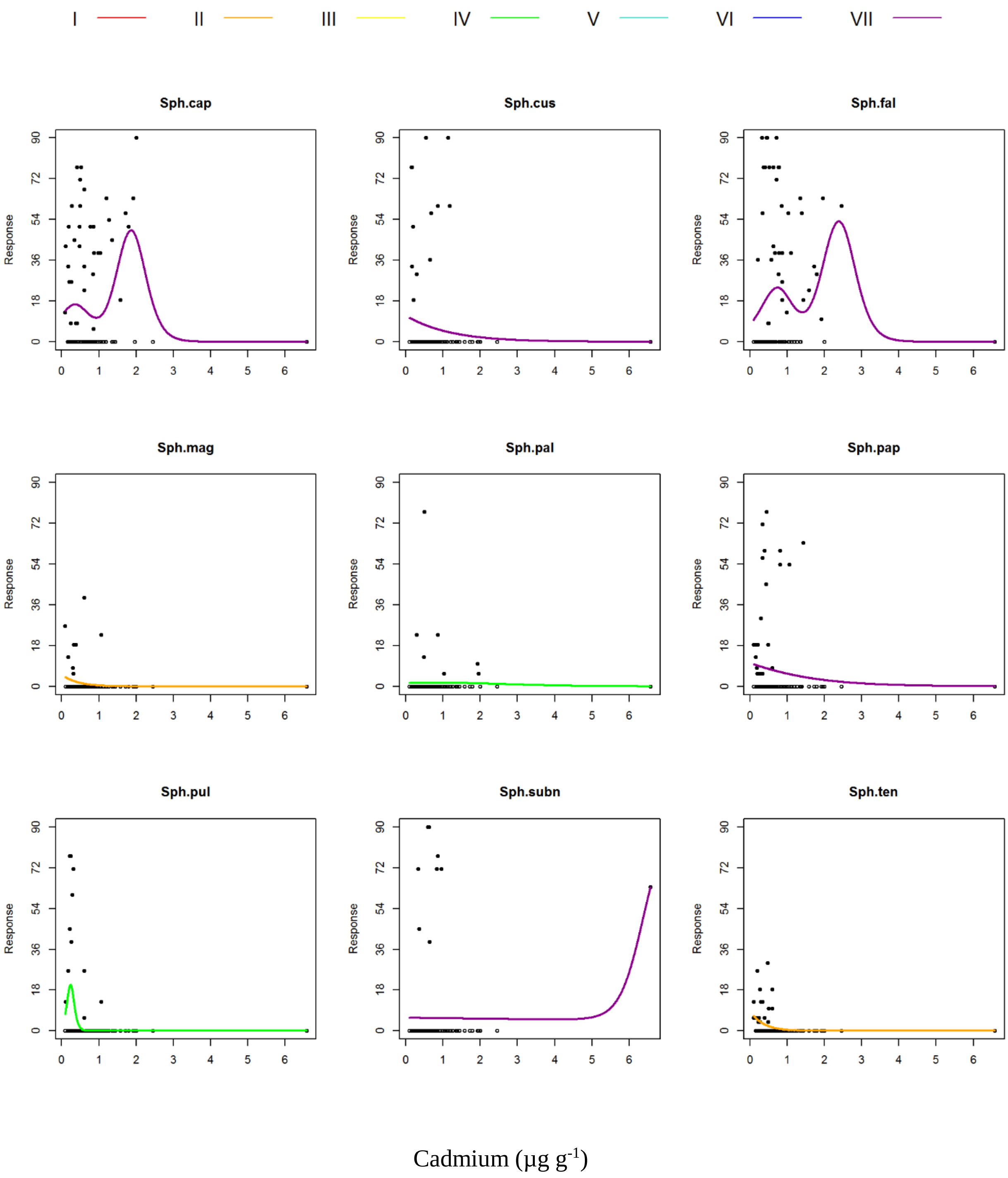
Appendix 13 – Results of HOF models for national comparison.

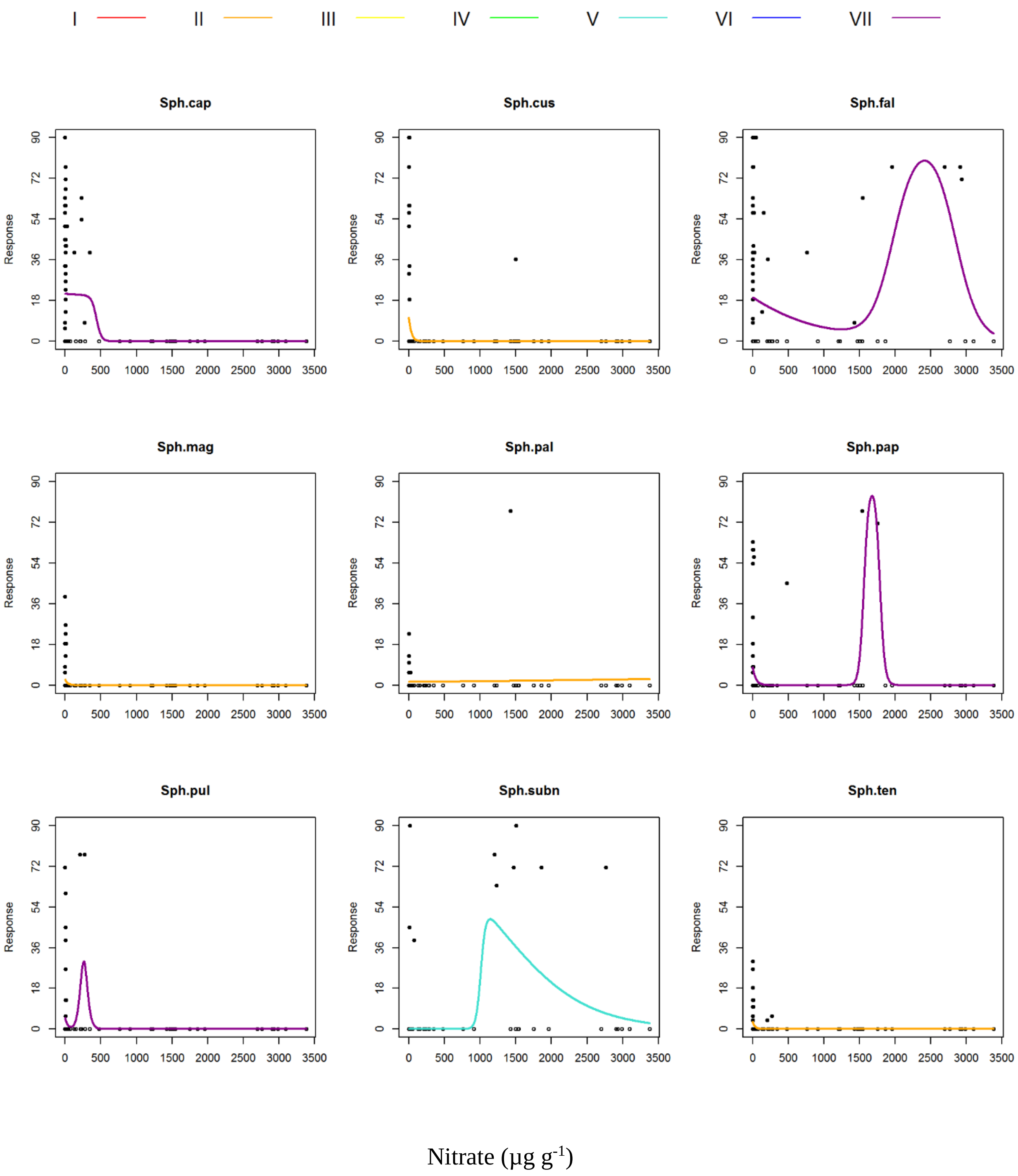
HOF model response curves for the most abundant species from all sites with respect to significant biogeochemical variables (Mg + Al + Ba + Cd + NO_3^- + MC + SO_4^{2-} + V + Fe + Mo + Zn). Species labels can be found in Appendix 1.

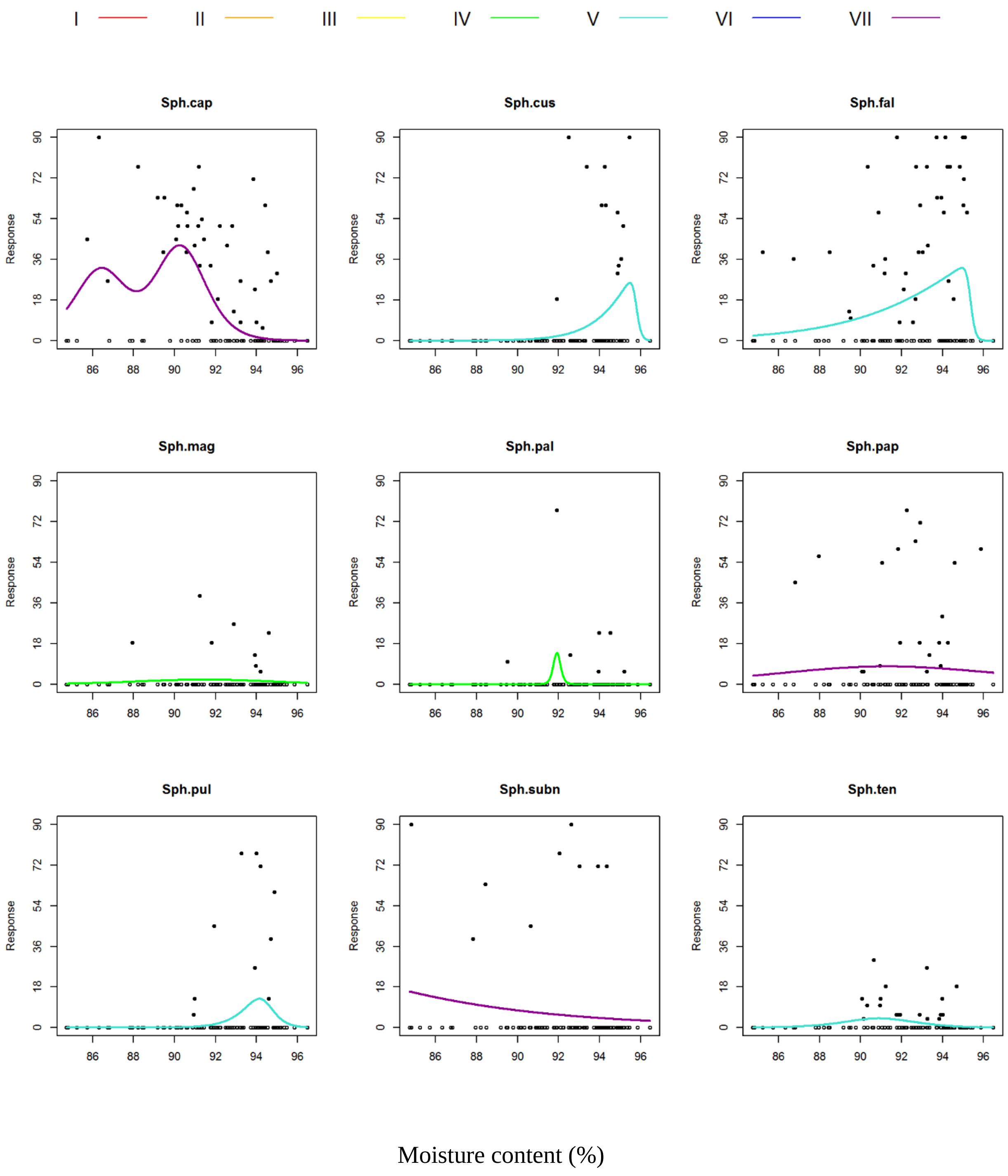


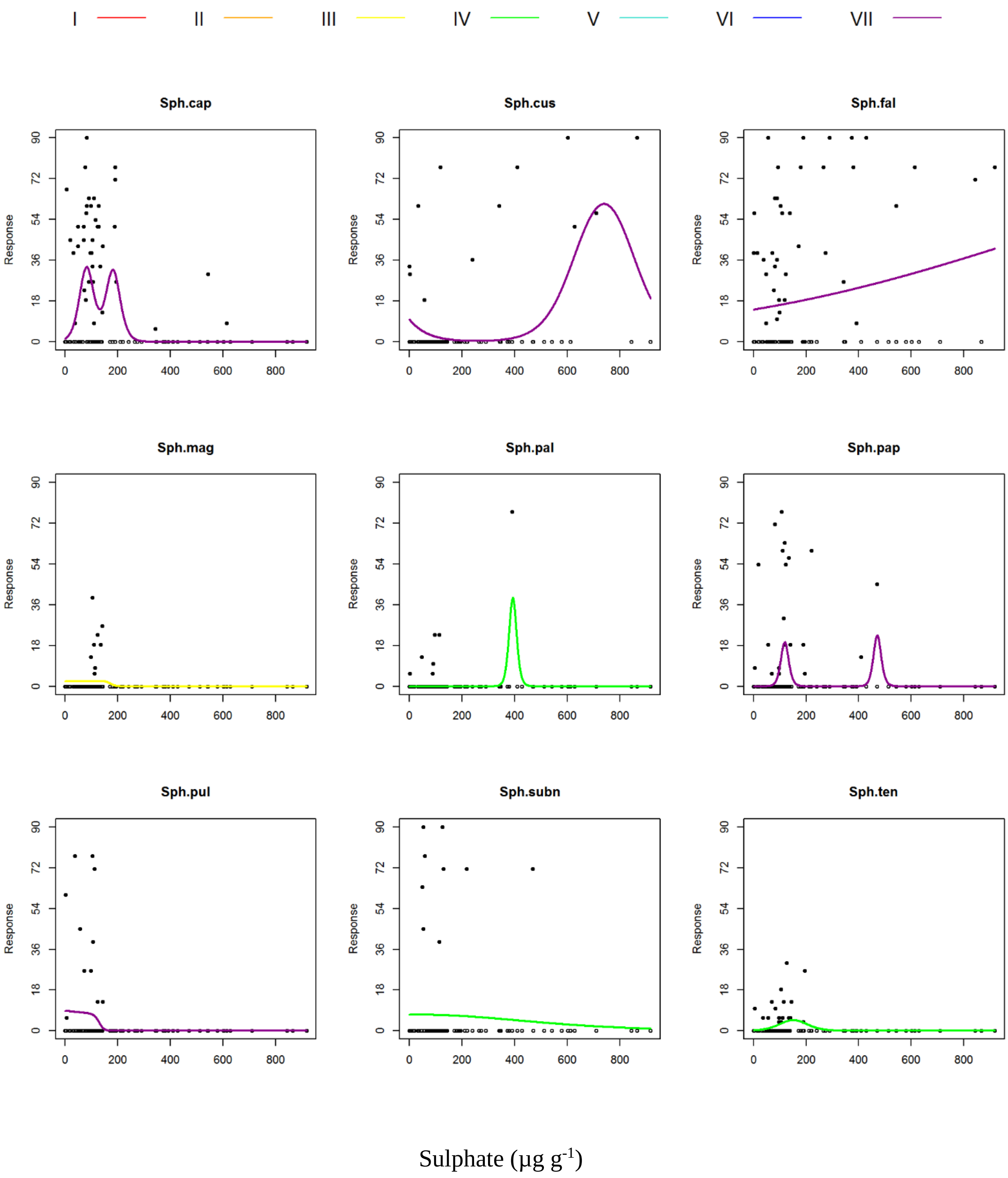

I
II
III
IV
V
VI
VII
Sph.cap
Sph.cus
Sph.fal
Sph.mag
Sph.pal
Sph.pap
Sph.pul
Sph.subn
Sph.ten
Response
0
18
36
54
72
90
0
500
1000
1500
2000
Aluminium (µg g-1)

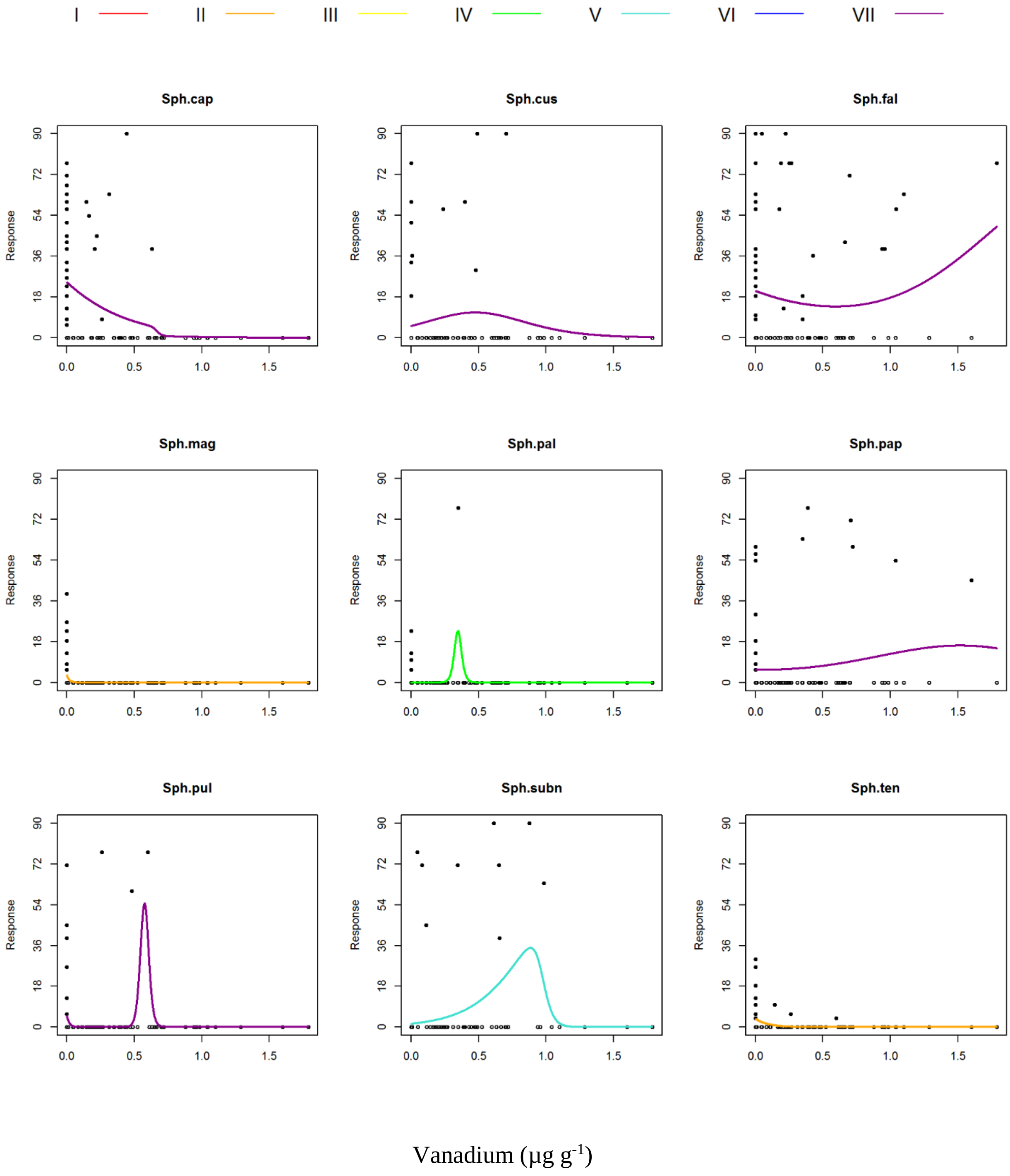

I
II
III
IV
V
VI
VII
Sph.cap
Sph.cus
Sph.fal
Sph.mag
Sph.pal
Sph.pap
Sph.pul
Sph.subn
Sph.ten
Response
0
18
36
54
72
90
0
10
20
30
40
50
Barium (µg g-1)

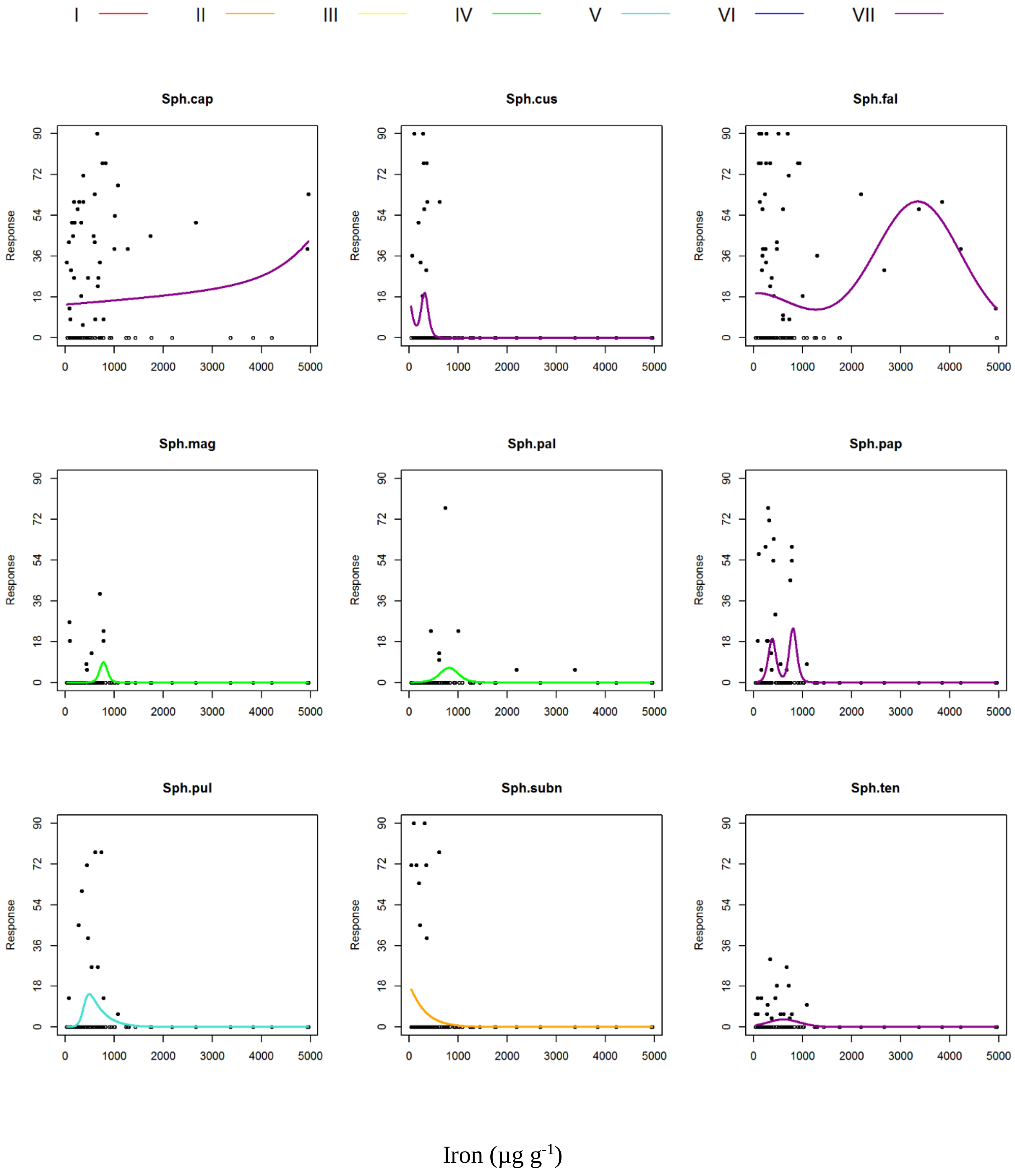

I
II
III
IV
V
VI
VII
Sph.cap
Sph.cus
Sph.fal
Sph.mag
Sph.pal
Sph.pap
Sph.pul
Sph.subn
Sph.ten
Response
0
18
36
54
72
90
0
1
2
3
4
5
6
Cadmium (µg g^{-1})

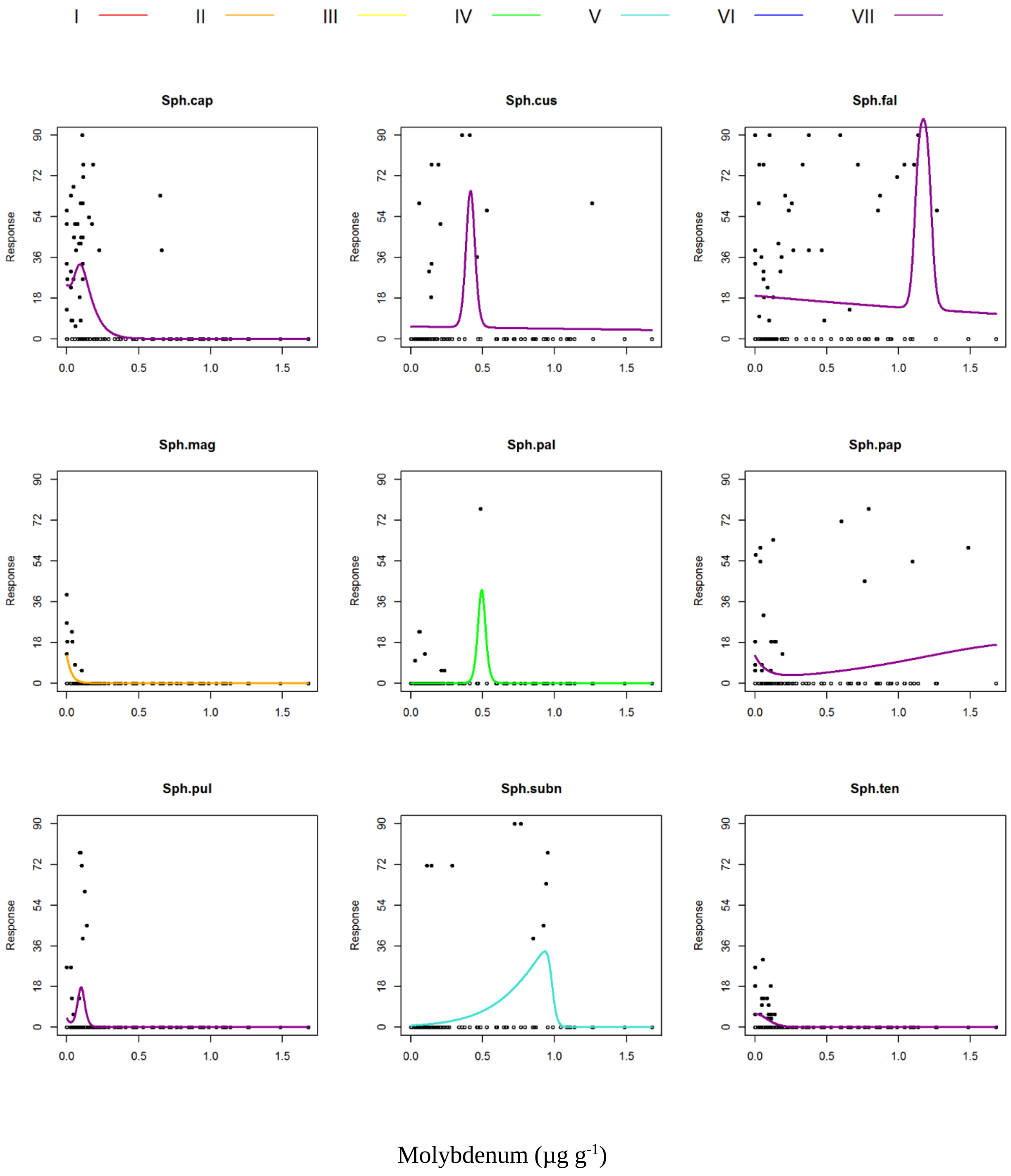

I
II
III
IV
V
VI
VII
Sph.cap
Sph.cus
Sph.fal
Sph.mag
Sph.pal
Sph.pap
Sph.pul
Sph.subn
Sph.ten
Response
0
18
36
54
72
90
0
500
1000
1500
2000
2500
3000
3500
Nitrate (μg g-1)

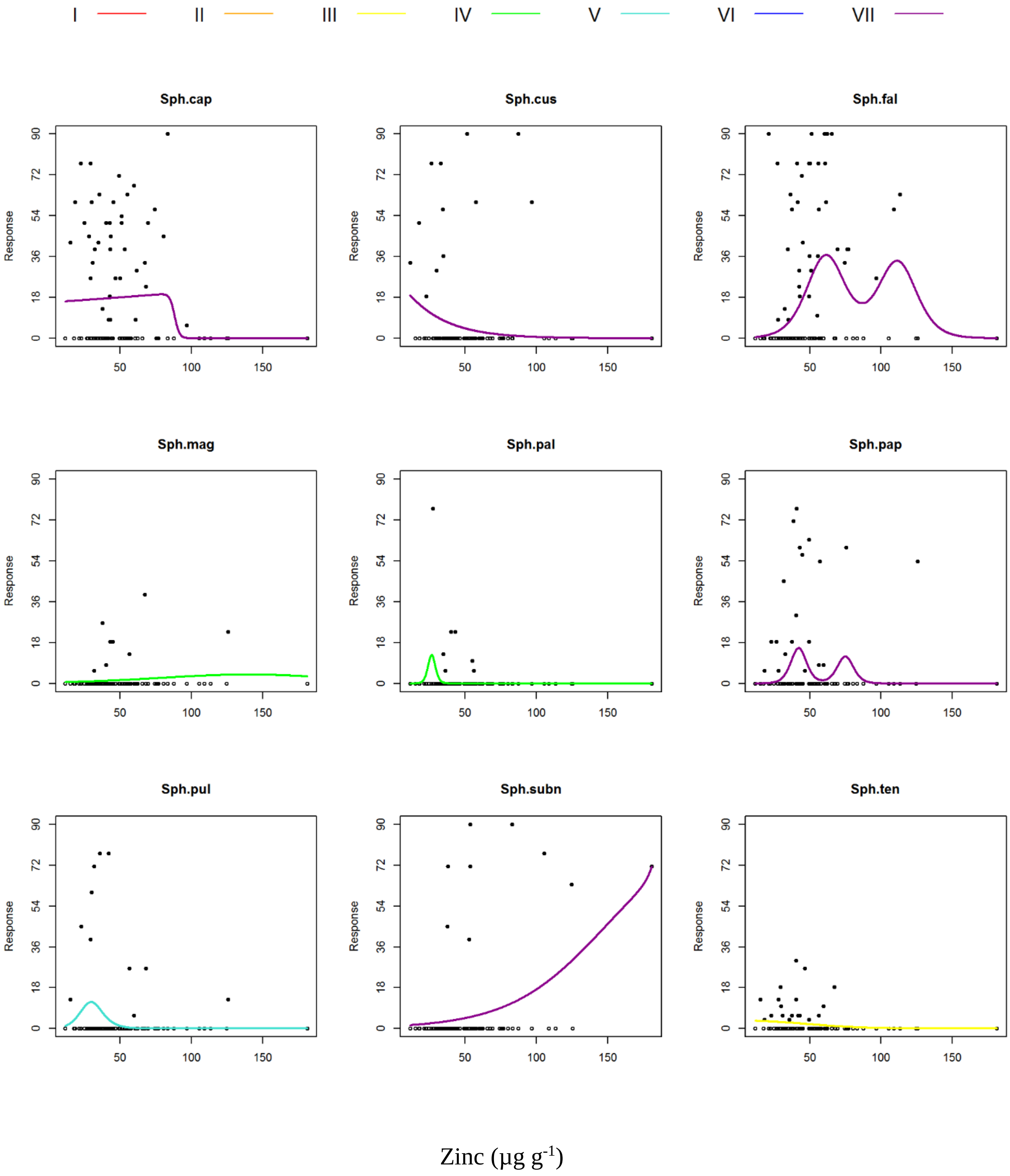

I
II
III
IV
V
VI
VII
Sph.cap
Sph.cus
Sph.fal
Sph.mag
Sph.pal
Sph.pap
Sph.pul
Sph.subn
Sph.ten
Response
0
18
36
54
72
90
86
88
90
92
94
96
Moisture content (%)


I
II
III
IV
V
VI
VII
Sph.cap
Sph.cus
Sph.fal
Sph.mag
Sph.pal
Sph.pap
Sph.pul
Sph.subn
Sph.ten
Response
0
18
36
54
72
90
0
200
400
600
800
Sulphate (µg g-1)

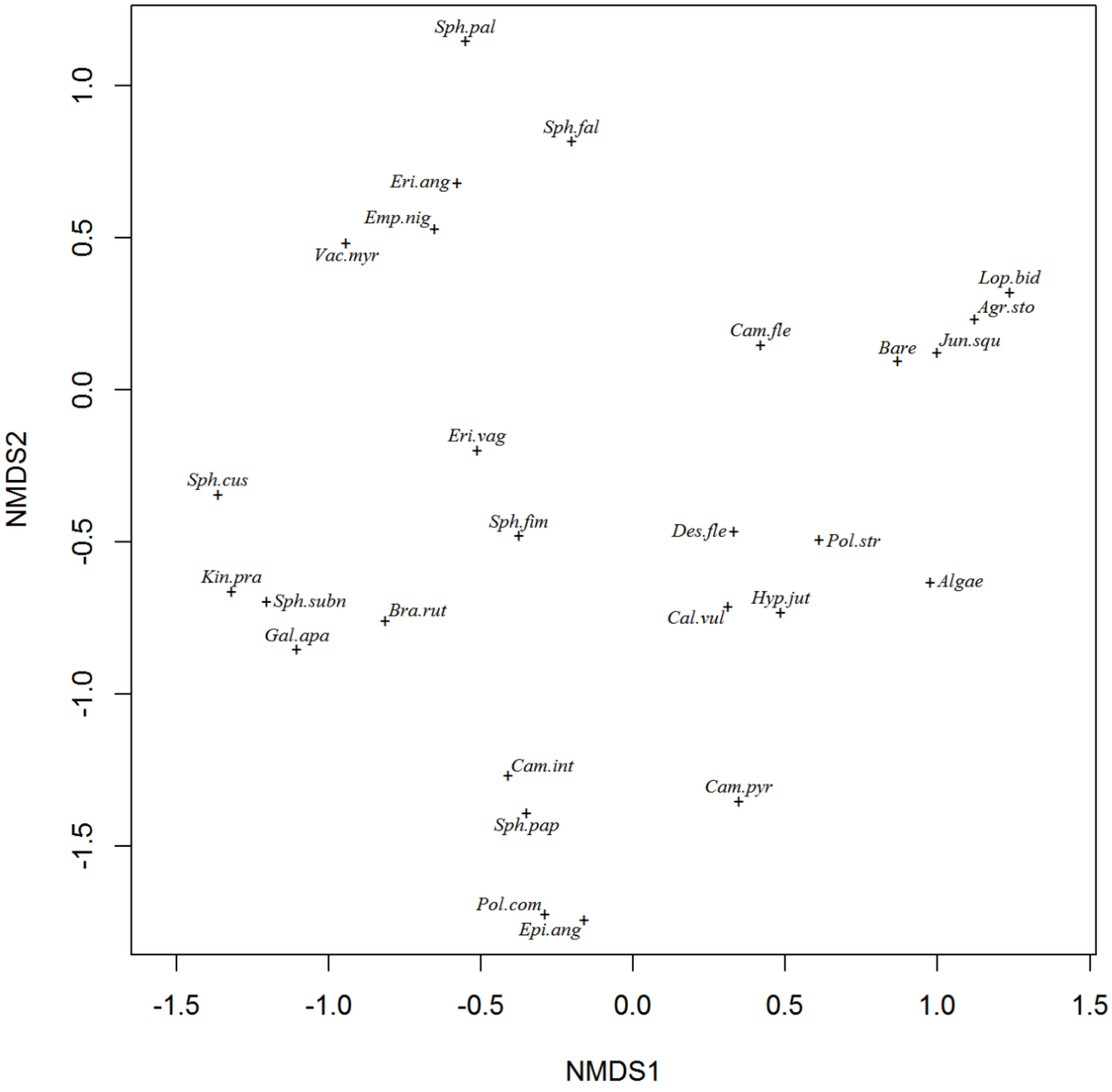

I
II
III
IV
V
VI
VII
Sph.cap
Sph.cus
Sph.fal
Sph.mag
Sph.pal
Sph.pap
Sph.pul
Sph.subn
Sph.ten
Response
0
18
36
54
72
90
0.0
0.5
1.0
1.5
Vanadium (µg g-1)


I
II
III
IV
V
VI
VII
Sph.cap
Sph.cus
Sph.fal
Sph.mag
Sph.pal
Sph.pap
Sph.pul
Sph.subn
Sph.ten
Response
0
18
36
54
72
90
0
1000
2000
3000
4000
5000
Iron (µg g-1)


I
II
III
IV
V
VI
VII
Sph.cap
Sph.cus
Sph.fal
Sph.mag
Sph.pal
Sph.pap
Sph.pul
Sph.subn
Sph.ten
Response
0
18
36
54
72
90
0.0
0.5
1.0
1.5
Molybdenum (µg g-1)


I
II
III
IV
V
VI
VII
Sph.cap
Sph.cus
Sph.fal
Sph.mag
Sph.pal
Sph.pap
Sph.pul
Sph.subn
Sph.ten
Response
0
18
36
54
72
90
50
100
150
Zinc (µg g⁻¹)

Appendix 14 – Non-metric multidimensional scaling (NMDS) ordination of the vegetation composition data from *Sphagnum* bead field trials, and survey data from Holme Moss and Black Hill. Labels are arranged to minimise overlapping.



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