The role of plant-soil interactions in peatland carbon cycling at a Scottish wind farm

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Abstract

Northern peatlands play an important role in the cycling of carbon (C) globally, and contain up to one third of the world's soil C despite only covering a small percentage of its land surface (Gorham, 1991). Changes in climate and land use are increasing the vulnerability of these vast C stocks, by altering the conditions favourable for peat accumulation and therefore C sequestration. The establishment of wind farms on peatlands is increasing in the UK, as a result of the growing need for sustainable energy and the suitably high wind speeds that are typical to these upland ecosystems (Smith et al., 2014). There is limited understanding of the impacts of operational wind farms on their host ecosystems, but evidence to suggest that wind farms create microclimate conditions by altering ground-level temperature is increasing (Armstrong et al., 2014a; Baidya Roy and Traiteur, 2010; L. Zhou et al., 2012). The sensitivity of peatland C cycling processes to wind farm-induced microclimatic changes represents a considerable gap in knowledge. Further, the role that aboveground and belowground peatland communities have in mediating the effects of wind farm microclimates on C cycling processes remains unknown. By examining plant-soil interactions across a peatland at Black Law Wind Farm and under a range of microclimate conditions in the laboratory, this thesis aimed to investigate the influence of plant functional type (PFT) and microclimatic conditions on physical, chemical and biological peatland properties, greenhouse gas (GHG) emissions and litter decomposition. Results show that a PFT legacy in peat plays a mediatory role in the response of CO_2 and CH_4 emissions to microclimatic differences in temperature and water table. Mass loss of litter is primarily driven by PFT differences in litter quality, with interactions between litter types controlling decomposition of litter mixtures via non-additive effects, and interactions between litter types and PFT legacies in peat affecting the likelihood of home-field advantage and disadvantage (HFA and HFD) litter mass loss. This thesis demonstrates that the direct effects of microclimatic changes in temperature and water table are important drivers of peatland C cycling processes; however the indirect effects of microclimate change on plant community composition e.g. the relative proportion of PFTs could influence these processes to a greater extent. Examining the importance of PFTs in C cycling processes at wind farm peatlands is important in improving predictions of peatland C sequestration under future climate change scenarios, and in calculating the C savings achieved by land-based renewable technologies.

Declaration

I declare that this thesis is the result of my own work. It has not been submitted for any other degree at the University of Glasgow or any other institution and all sources of information have been acknowledged explicitly.

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Abbreviations

ADD	Away Decomposition Difference
ADF	Acid Detergent Fibre
ADH	Additional Decomposition at Home
ADL	Acid Detergent Lignin
ANOVA	Analysis of Variance
BD	Bulk Density
C	Carbon
CH_4	Methane
CO_2	Carbon Dioxide
DL	Decomposition of Litter
db-RDA	Distance Based Redundancy Analysis
DECC	Department of Energy & Climate Change
DOC	Dissolved Organic Carbon
ECD	Electron Capture Detector
EDTA	Ethylenediaminetetraacetic Acid
$FeCl_3$	Ferric Chloride
FID	Flame Ionisation Detector
GC	Gas Chromatograph
HDD	Home Decomposition Difference
HFA	Home-Field Advantage
HFD	Home-Field Disadvantage
H_2SO_4	Sulphuric Acid

ICP-OES	Inductively Coupled Plasma-Optical Emission Spectroscopy
IPCC	Intergovernmental Panel on Climate Change
IRGA	Infrared Gas Analyser
K	Potassium
LCH	Lignin + Cellulose + Hemicellulose (total fibre content)
LME	Linear Mixed Effects (model)
N	Nitrogen
NDF	Neutral Detergent Fibre
NNR	National Nature Reserve
NS	Number of Species
OM	Organic Matter
P	Phosphorus
PFT	Plant Functional Type
PLFA	Phospholipid Fatty Acid
RCP	Representative Concentration Pathway
SIR	Substrate-Induced Respiration
TH	Total HFA

Chapter 1

Introduction

1.1 Northern peatlands and global change

Peatlands are areas of land covered by layers of incompletely decomposed organic matter (OM), rich in carbon (C), which have accumulated to depths greater than 30 cm (Rydin et al., 2006). Net primary production (NPP) has exceeded decomposition in these terrestrial ecosystems for millennia, under low oxygen (O_2) and waterlogged conditions (Charman, 2002). As a result, vast quantities of C have been sequestered into peat soils. Globally, the majority of peatlands are found at mid to high latitudes in the northern hemisphere, covering around 3 % of the world's land surface but containing up to 30 % of the world's soil C (Gorham, 1991). Thus, their C storage is much larger than their land surface area would imply (Wieder and Vitt, 2006). In the UK, peatlands occupy only 10 % of the land surface but yet again represent the largest terrestrial C store (i.e. 5162 x 10^9 kg of C), with the majority (i.e. 4523 x 10^9 kg of C) in Scotland (Dawson and Smith, 2007). Peatlands play a vital part in the global C cycle because they act as a sink and a source of carbon dioxide (CO_2) and methane (CH_4). CH_4 produces a short but intense greenhouse forcing because it is more effective as a greenhouse gas (GHG) than CO_2, whereas the release of CO_2 produces a weaker forcing per molecule, but does so over longer timescales due to its greater atmospheric lifetime (IPCC, 2013). Peat accumulation has been sufficiently large enough to exceed the warming effect of CH_4 emissions from these soils, such that northern peatlands have had a net cooling effect of -0.2 to -0.5 Wm^{-2} throughout the Holocene (Frolking and Roulet, 2007). The continuation of this cooling effect depends upon the preservation of peat C stores, and the amount of CO_2 uptake relative to the emission of CH_4.

Northern peatlands are vulnerable to climate change effects, as increases in temperature are predicted to be greatest in mid to high latitudes (IPCC, 2013). The uncertainty in future patterns of precipitation adds further pressure upon peatland C stores, with both increases and decreases in rainfall expected for the latitudinal range that they occupy (IPCC, 2013). There is mounting concern that changes in temperature and precipitation will destabilise peatland C stocks (Dise and Phoenix, 2011; Yu et al., 2011), resulting in a positive feedback to climate change by further increasing GHG concentrations in the atmosphere (Sirin and Laine, 2008). Moreover, peatland C losses are considered to be effectively permanent over timescales relevant to climate change mitigation policy, due to the excessively slow rates of C accumulation in these ecosystems (Frolking and Roulet, 2007).

Peatlands are also the basis for a variety of human activities, including peat extraction for horticulture and fuel, livestock grazing, game bird breeding, forestry and recreation

(Turetsky et al., 2002; Ward et al., 2007). These land use changes have resulted in the rapid loss of C, and together with climate change, represent an uncertain future for the fate of peatland C stocks (Ostle et al., 2009). In order to sustainably meet global energy demands, the establishment of land-based renewable technologies has increased (DECC, 2013). In particular, wind power has experienced the greatest growth worldwide (REN21, 2012). Onshore wind farms in the UK are often sited on peatlands, given the substantial wind resource common to these upland ecosystems. The construction of wind farms on undegraded peatlands introduces a higher risk of C loss than when constructed on mineral soils (Smith et al., 2014), with previous work indicating that when constructed on peatlands, the potential C savings from wind farm energy generation are small (Nayak et al., 2010). While there is some understanding, the impacts of an operational wind farm on the host environment are yet to be fully assessed (Millenium Ecosystem Assessment, 2005).

Knowledge of wind farm-induced changes in surface energy fluxes and microclimates is growing, effects on local air temperatures within and adjacent to wind farms have been observed. In west-central Texas, a 0.72 °C decadal increase in surface temperature was evident in eight years of satellite data for an area dominated by wind turbines, with the strongest warming during the night-time in summer months (L. Zhou et al., 2012). In California, the surface air temperature was significantly warmer downwind of the San Gorgonio wind farm at night-time (i.e. warmer by a maximum of 0.7 °C) and was significantly cooler during the daytime (i.e. with a maximum cooling of 3.5 °C) (Baidya Roy and Traiteur, 2010). In Scotland, air and soil temperature was measured across an area of peatland at Black Law Wind Farm. Operational wind turbines were found to increase the variability of air, surface and soil temperature diurnally, and raise night-time air temperature by 0.22 °C (Armstrong et al., 2014a). These observed wind farm-induced temperature changes are of an order of magnitude known to affect C cycling (Dorrepaal et al., 2009). Despite this, the effects of wind farm-induced temperature change in the short- and long-term are uncertain. Specifically, there still remains a considerable gap in knowledge on the effects of wind farm-induced microclimates on plant-soil processes and communities, and the implications for GHG emissions and soil C stocks (Armstrong et al., 2014b).

1.2 Carbon cycling in peatlands

The overall effect of climate change and land use change on peatland C stocks depends upon the balance between plant productivity and decomposition, which is mediated by

multiple abiotic and biotic factors and their feedbacks. The sequestration of C occurs via photosynthetic uptake of CO_2, inputs of senesced litter to soil, and deposition and turnover within the rhizosphere. On the other hand, the main routes of C release is the production of CO_2 and CH_4 through microbial respiration, and the loss of dissolved organic carbon (DOC) (Limpens et al., 2008).

The division of the peat profile into the acrotelm (i.e. near-surface O_2 rich layer above the water table) and catotelm (i.e. deeper O_2 poor layer below the water table), defines the nature of gas production with depth (Ingram, 1978).The upper acrotelm is aerated at least seasonally and is a more active environment for both growth and decay, and in particular the production of CO_2. CO_2 production occurs from the aerobic decay of organic matter (OM), plant respiration at the surface, root respiration within the peat and the oxidation of CH_4 (Bridgham, 1992). The majority of OM decomposition and related CO_2 production takes place in the acrotelm, due to higher oxygenation. There is lower potential for CO_2 production in the permanently saturated catotelm, although this zone is still important in terms of the total C budget of the peatland and the production of CH_4 by microorganisms specifically adapted to the limited availability of O_2 (Charman, 2002). CH_4 emissions are dependent on a complex balance between anaerobic CH_4 production and consumption, aerobic CH_4 consumption and transfer via ebullition, diffusion and plant root aerenchyma (Moore and Dalva, 1993).

Changes to the water table can influence the C balance of a peatland, through the complex effects of soil respiration, methanogenesis, and plant productivity (Aerts and Ludwig, 1997). A higher water table promotes peat accumulation (Weltzin et al., 2003), but increases CH_4 production (Roulet, 2000). Water table drawdown leads to a larger proportion of the peat profile being exposed to aerobic decomposition and can lead to short-term losses of C (Alm et al., 1999; Charman et al., 2008; Silvola et al., 1996). However, peatland drainage tends to increase C storage in the long-term because soil respiration is offset by increased primary production and reduced CH_4 emissions (Bubier, 1995; Holden et al., 2006). The height of the water table is dominated by the balance between precipitation and evaporation, with the latter being heavily controlled by temperature (Limpens et al., 2008). Consequently, fluctuations in temperature can drive fluctuations in the water table (Rydin et al., 2006). Furthermore, evidence suggests that lowering of the water table increases the sensitivity of peat decomposition to temperature, so that drier conditions are anticipated to accelerate warming-induced losses of peatland C (Ise et al., 2008).

Temperature is of key importance, not only because it influences the position of the water table, but because it drives plant productivity, OM decomposition rates and the uptake and release of CO_2 and CH_4 (Chivers et al., 2009; Dorrepaal et al., 2009; White et al., 2008). In arctic and boreal ecosystems, heterotrophic (soil organisms) and autotrophic (plant root) peat respiration has been observed to respond rapidly to raised temperatures (Dorrepaal et al., 2009). Temperature sensitivity is regularly represented by a Q_{10} value, which describes the response of decomposition process rates to a 10 °C change (Davidson and Janssens, 2006). Studies have shown that Q_{10} increases as soil temperature decreases (Kirschbaum, 1995; Lloyd and Taylor, 1994), with high temperature sensitivities observed by (Chapman and Thurlow, 1998) when peats were incubated at 0-15 °C (i.e. the temperature range representative of Scottish peatlands). However, the effects of temperature are commonly compounded by the effects of moisture availability and litter quality (Kirschbaum, 1995).

1.3 The role of aboveground and belowground communities in peatland C cycling

Abiotic factors (i.e. temperature, moisture availability and nutrient availability) are known to be the key controls of peatland C cycling processes, but it is apparent that other factors such as the composition of aboveground (i.e. plant) communities, and belowground (i.e. soil microbial) communities, are also important in driving the response of peatland ecosystems to climate change and land use change.

1.3.1 Peatland plant functional types

In blanket bog peatlands, plant communities are dominated by three plant functional types (PFTs): bryophytes (e.g. *Sphagnum* sp., feather mosses), graminoids (e.g. *Eriophorum vaginatum*, sedges and rushes) and shrubs (e.g. *Calluna vulgaris*, *Vaccinium* sp.). As a consequence of their environmental adaptation, there are similarities between PFTs but each group has a suite of specific functional traits. Plant functional traits influence the relative rate of productivity and decomposition, which in turn determines the net balance of C in the ecosystem (Ward et al., 2009). What is more, the physical presence of certain PFTs can affect the position of the water table (Robroek et al., 2010), which is known to govern the emission of CO_2 and CH_4 from peat to the atmosphere (Dinsmore et al., 2009). Small scale variation in the composition of peatland plant communities has been observed to influence C cycling processes (McNamara et al., 2008), by altering the physical and chemical characteristics of the peat, and the proliferation of particular microorganisms. Therefore, the dominance of different plant functional types (PFTs) within a peatland plant community is important (De Deyn et al., 2008).

Bryophytes, such as *Sphagnum* mosses, dominate productivity in peatlands and influence nutrient and C cycling unlike any other plant type (Aerts, 2003). *Sphagnum* moss species typically found in blanket bog hollows, such as *Sphagnum cuspidatum*, contribute to the accumulation of peat by retarding rates of decomposition (i.e. moss litters decay slower than vascular plant litters in blanket bog) (Bragazza et al., 2007; Moore et al., 2006). *Sphagnum* litter can be highly recalcitrant, despite the lack of lignin, because it contains a high proportion of phenolic compounds that provide chemical protection from the activity of decomposer enzymes (Freeman et al., 2001; van Breemen, 1995). Furthermore, moss litters have very low nutrient concentrations; the absence of a vascular root system means nutrients can only be acquired from the atmosphere (Aerts, 1999; Ward et al., 2009). Thus, mosses act as a strong filter for nutrient fluxes to other plants and thereby introduce a delay in the flux of nutrients through peat (Pastor et al., 2002). However, mosses are highly adapted to bog environments (Shaw and Goffinet, 2000). Mosses trap water and can re-hydrate quickly after drought stress, so can affect other plants by influencing soil moisture (Turetsky, 2003). Sphagnum can also form symbiotic associations with highly specific bacterial communities that control CH_4 cycling (Kip et al., 2010). Graminoids, such as the sedge *Eriophorum vaginatum*, are responsible for a large proportion of the total CH_4 fluxes from peatlands. Their deep-rooted systems are known to supply labile substrates to the soil, stimulating the activity and abundance of methanogenic bacteria (Ström et al., 2012). In addition, their aerenchymous tissues serve as direct conduits for the transfer of CH_4, from root tips in the catotelm to the atmosphere, bypassing the oxidative acrotelm (Greenup et al., 2000; Marinier, 2004). In comparison to bryophyte and shrub species, graminoids have a short leaf life span and a high leaf nitrogen (N) content, which increases the potential decomposability of their plant tissues (Ward et al., 2009). Ericoid shrubs, such as *Calluna vulgaris*, maximise nutrient uptake through associations with mycorrhizal fungi (Read et al., 2004), and also restrict the photosynthetic ability of the understory by shading out other peatland plant species (Grace and Marks, 1978). The decomposition of shrub litter is inhibited, with the retention of C in long-lived, lignin-rich and phenolic-rich tissues (Ward et al., 2009).

1.3.2 Peatland soil microorganisms

There is growing evidence for linkages between aboveground and belowground communities, particularly regarding functional feedbacks between plants and soil microbes (Wardle *et al.* 2004; Bardgett 2005; Bardgett & Wardle 2010; de Vries *et al.* 2012). Microbial communities are an essential component of decomposition, regulating both C

and nutrient cycling within peat and influencing peatland C sequestration and storage. In turn, the effects of environmental change on the amount and availability of C and nutrients is determined by the response seen in the structure of the soil microbial community (Allison et al., 2010; J. Zhou et al., 2012).

The two most abundant groups of microorganisms are fungi and bacteria (Bardgett, 2005). Fungi and bacteria are both responsible for decomposition of OM (Ayres et al., 2006; Bardgett, 2005), but have different functional roles in peat biogeochemical cycling (Myers et al., 2012) because of their differing capacities to degrade available and complex forms of C and N (McGuire et al., 2010). Fungi are known to have high C:N biomass stoichiometry, broad enzymatic capabilities and slower biomass turnover rates than bacteria (de Boer et al., 2005; Rousk and Bååth, 2007; Wallenstein et al., 2007). As a result, fungi have potentially higher C use efficiency than bacteria (Six et al., 2006) and perform the majority of recalcitrant C degradation by breaking down cellulose and lignin into simpler C compounds through the production of extracellular enzymes (de Boer et al., 2005; Thormann, 2006). However some fungi, the mycorrhizae, develop mutualistic relationships with plant roots that can be characterised by the transfer of plant-derived C to fungi and fungal-acquired nutrients to the plant (Read et al., 2004; Van Der Heijden, 1988). Bacteria are generally faster-growing and target labile C sources (i.e. hemicellulose and root exudates) that are easy to degrade (de Boer et al., 2005), although bacterial production of hydrolytic enzymes also contributes to the decomposition of cellulose (Berg and Laskowski, 2005). Broad functional groups of bacteria (e.g. gram-positive and gram-negative) also have different capacities to mineralise C; gram-positive bacteria can mineralise recalcitrant organic compounds whilst gram-negative bacteria target labile C compounds (Treseder et al., 2011). In summary, bacteria maintain a significant role in the degradation of simple substrates whereas fungi are the major decomposers of recalcitrant OM (de Boer et al., 2005). In peatlands, fungal biomass and production commonly dominates that of bacteria due to their higher tolerance of acidity (Latter et al., 1998). Aerobic bacteria and fungi are the most important and effective decomposers of OM above the water table, in oxic conditions, since they are responsible for the final mineral release from even the most chemically recalcitrant components (Moore et al., 2006; Myers et al., 2012; Thormann, 2006). Below the water table, anaerobic bacteria are better suited to compete for C resources under anoxic conditions (Myers et al., 2012).

Although microbial biomass is relatively low in peatlands, significant differences in both microbial diversity and functional activity have been found. Physical, chemical and biological parameters vary across peatlands, and are closely linked with changes in the composition of soil microbial communities (Andersen et al., 2013; Fisk et al., 2003; Jaatinen et al., 2007; Myers et al., 2012). The availability of O_2 (i.e. water table level) in peat has proven to be a powerful determinant of differences in the soil microbial community (Bru et al., 2011; Fierer, 2003; Sundh et al., 1997), together with OM content, nutrient concentrations and pH (Artz, 2009; Jaatinen et al., 2007). Increasing pH and nutrient concentrations have been shown to increase the relative proportions of bacteria and bacterial diversity in peatlands (Hartman et al., 2008; Jaatinen et al., 2007; Opelt et al., 2007), while the high OM content and low nutrient availability of peatlands generally favours a fungal dominated community (Artz, 2009; Van Der Heijden, 1988).

The height of the water table controls the ratio of aerobic to anaerobic microbial processes that lead to the production and consumption of CO_2 and CH_4, and has been identified as the strongest determinant of bacterial abundances (Mäkiranta et al., 2009; Sundh et al., 1997). Temperature also plays a part in determining the CO_2 and CH_4 flux rates by governing evapotranspiration (therefore water table height), chemical reactions and growth and activities of biota in and above soil (Bardgett et al., 2008). Higher temperatures have been observed to increase bacterial growth rates, with fungi more adapted to low temperatures than bacteria (Høj et al., 2006; Pietikåinen et al., 2005; Thormann, 2006). Changes in the soil microbial community composition could also arise from plant-mediated differences in soil temperature and water table level (McNamara et al., 2008).

Plant succession can stimulate shifts in microbial community composition (Artz et al., 2007). The composition of the soil microbial community may adapt in order to optimise variations in the quality of the C resource and to optimise the efficiency of decomposition (Hooper et al., 2000; Yuste et al., 2007). Thus, the proportion of different plant species aboveground will condition the composition of the microbial community belowground, in that soil microorganisms are likely to receive varying ratios of labile to recalcitrant compounds from different types of plant litter and root exudates (Grayston, 1998; Pendall et al., 2008). In addition, mutualistic relationships can exist between aboveground and belowground organisms, whereby the host plant is supplied with nutrients made available by microbes in the soil (Fisk et al., 2003; Hooper et al., 2000; Orwin et al., 2006). For example, methanogen communities have been found in association with tussock tundra and mycorrhizal fungi with ericoid shrubs (Galand et al., 2003; Read et al., 2004). Fungi

dominate the peat underlying shrub species due to plant-root symbioses, and because of the increased C:N and concentrations of phenolic compounds associated with this PFT (Freeman et al., 2001; Myers et al., 2012). In contrast, bacteria thrive in moss- and sedge-derived peat (Winsborough and Basiliko, 2010) due to the presence of more labile C substrates (Myers et al., 2012; Ström et al., 2012). Therefore, the identity of plants at the PFT group level could be used to predict what lies beneath: the abundance and activity of specific soil microorganisms (Hooper et al., 2000; Mitchell et al., 2010). As a result, shifts in the structure and function of peatland microbial communities are to be expected with local to global changes in climate, due to the interactions between air and soil temperature, soil moisture availability (i.e. water table level) and plant community composition (Bardgett and Wardle, 2010).

One of the most commonly used techniques for characterising soil microbial communities is phospholipid fatty acid (PLFA) analysis. Due to their presence in microbial cell walls, phospholipids are used as biomarkers to provide a metric of the relative abundance of broad microbial groups, such as bacteria, fungi, gram-positive and gram-negative bacteria (Frostegård and Bååth, 1996). The advantages of this method are that phospholipids are relatively simple to extract and interpret, making this a convenient process for distinguishing soil microbial community composition and size. Nevertheless, the popularity of procedures that use DNA or RNA to identify microorganisms, such as the analysis of terminal restriction fragment length polymorphisms (TRFLPs), is increasing.

1.3.3 Plant-soil interactions and decomposition processes

Litters of different plant species and functional types vary greatly in their decomposability, for example due to differences in lignin and nutrient concentrations (Artz, 2009; Ayres et al., 2006; Bardgett, 2005; Winsborough and Basiliko, 2010). These differences influence the composition and activity of microbial communities, which mediate litter decomposition rates, the release of GHGs and the accumulation of OM to form peat (Moore et al., 2006; Ward et al., 2009).

Sugars, amino acids and other water-soluble compounds are metabolised easily by microorganisms, which allows the initial decomposition of plant OM to occur rapidly. The decomposition of celluloses, hemicelluloses and waxes occurs more slowly. These slower to decompose OM fractions require enzymatic breakdown prior to uptake and utilisation by microorganisms, which depends on oxygen and nutrient availability and the level of inhibitory compounds (i.e. phenolics) (Bragazza et al., 2012b; Freeman et al., 2004).

Decomposition of lignins and polyphenols is restricted by the requirement for specialised oxidative enzymes. Therefore, decomposition of more resistant C compounds occurs at slow rates and is dependent on the degree of aeration in soil (Freeman et al., 2001). Therefore decomposition is often, but not always, faster for litters with higher nutrient availability and labile compound concentrations in an aerobic environment, but slower for litters with greater lignin and phenolic concentrations (Aerts, 1999; Blodau, 2002).

It has been hypothesised that some plants may encourage the development of microbial communities suited to the rapid decomposition of their own litter (Wardle, 2002). There is mounting evidence that litter decomposition rates are greater beneath the plant species the litter derived from, than beneath a different plant species. This effect is referred to as home-field advantage (HFA) (Ayres et al., 2006; Vivanco and Austin, 2008). Microbial communities are known to locally adapt to the plant species above them, therefore there is potential for HFA decomposition to occur (Artz, 2009; Carney and Matson, 2005; Trinder et al., 2009). However, differences in plant litter traits could create differences in the magnitude of HFA. For example, high quality litter that contains compounds relatively easy to degrade might be expected to have little or no HFA, since most microbial communities are able to decompose those compounds rapidly (Ayres et al., 2009a). Whilst HFA decomposition has been examined in other terrestrial ecosystems, such as forests and grasslands (Ayres et al., 2009b; St. John et al., 2011), its influence on peatland C cycling dynamics remains unexplored.

Most litter decomposition studies in peatlands have dealt mainly with the decomposition of single litter types (Belyea, 1996; Dorrepaal et al., 2005; Laiho, 2006; Latter et al., 1998; Moore et al., 2007). However, some peatland decomposition studies, such as (Ward et al., 2010), acknowledge that these ecosystems, along with most other terrestrial ecosystems, are characterised by multiple plant types and a mixed litter layer. Some studies show that when litter species are mixed, the properties relating to decomposition appear to be additive, such that a mixture behaves as expected based on the average influence of the individual species involved (Ball et al., 2008; Wardle et al., 1997). Yet, more frequently, the observed decomposition of litter mixtures is different from that expected from the additive decomposition of the component litters in the mixture. These differences arise from synergistic and antagonistic interactions between different litter types (Ball et al., 2008; Chapman and Newman, 2010; Gartner and Cardon, 2004; Hättenschwiler et al.,

2005; Hoorens et al., 2010; Marco et al., 2011); but understanding of the mechanisms behind non-additive decomposition is limited, especially in peatlands.

Physical, chemical and biological processes, individually or in combination, can drive the interactions that occur among litters from different species during decomposition (Bragazza et al., 2007). Mixing litters of different quality and structure can also change the physicochemical conditions of the decomposition environment (Aerts, 2003; Ward et al., 2010), which can influence decomposition rates directly, and indirectly via the response of the microbial community (Bragazza et al., 2007). Litter chemistry can influence the overall decomposition rate and the individual decay rates of litters within a mixture, as a result of nutrient transfer or the activity of specific decomposer organisms (Gartner and Cardon, 2004). Rapidly decaying litter releases nutrients, which can stimulate the decay of nearby recalcitrant litters (Ayres et al., 2009a; Vivanco and Austin, 2008). On the contrary, litter decay can be inhibited by the release of phenolics and tannins (Gartner and Cardon, 2004; Hector et al., 2000).

Litter decomposition rates are often estimated using measurements of litter mass loss for different plant species; however this can prove difficult due to the mixing of litters from many species growing in close proximity, and idiosyncratic interactions among those litters. In order to overcome species level problems in estimating litter mass loss, studies opt to investigate litter mixing effects on litter decomposition rates at the PFT level (Hoorens et al., 2010; Ward et al., 2010). To improve ecosystem-level estimates of decomposition rates and their sensitivity to local to global climate change, more information on interactions amongst litters from different PFTs is needed. The temperature sensitivity of decomposition processes can be influenced by the quality of the decomposing OM (Conant et al., 2008b; Craine et al., 2010; Davidson and Janssens, 2006; Jones et al., 2003). Therefore, effects of litter mixing on litter quality have the potential to influence the sensitivity of decomposition to changes in temperature. However, at the PFT level, the potential for synergistic and antagonistic interactions between litters to balance each other has been proposed (Hoorens et al., 2010); therefore an overall additive effect could arise (Hoorens et al., 2010). It has become clear that single litter decomposition rates may not adequately represent natural ecosystems (Gartner and Cardon, 2004; Hättenschwiler et al., 2005). Studies that have investigated the response of single litter decomposition to climate change may report dynamics different to those observed for litter mixtures (Gartner and Cardon, 2004; Hättenschwiler et al., 2005; Hoorens et al., 2010).

It is evident that aboveground and belowground communities play a role in regulating decomposition rates, the release of GHGs and the formation of peat. Peatlands are C-rich ecosystems subject to changes in climate and land use. These changes are expected to affect ecosystem C cycling and GHG emissions by influencing biogeochemistry, plant and soil ecology. There is considerable uncertainty regarding the nature and magnitude of interactions between wind farm-induced microclimatic conditions and peatland plant-soil properties and C cycling processes. So, in this PhD research I have aimed to address this uncertainty by examining microclimate-peatland interactions across a blanket bog located under a wind farm, and in controlled laboratory conditions.

1.4 Thesis aims and outline

The role of abiotic and biotic factors, and their interactions, in regulating peatland C cycling is critical. Changes in land use and climate are key determinants of these interactions. Specifically, there is a significant gap in knowledge regarding how peatland ecosystem function is affected by the establishment and operation of wind farms.

The overarching hypothesis of this thesis was that peatland PFTs and their interactions with a wind farm-induced microclimate explain abiotic and biotic peatland properties and C cycling processes. The overall aim of this thesis was to examine the contribution of PFTs to differences in physicochemical properties, microbial communities, GHG emissions and litter decomposition, at a wind farm.

To achieve this, field sampling to characterise differences in physicochemical properties and microbial communities between plant functional types and across a wind farm was conducted, followed by an in situ examination of short-term litter decomposition. Alongside, laboratory incubation experiments were used to examine GHG emissions and litter decomposition rates under controlled abiotic conditions.

Specific aims were:

1. To determine the regulatory role of PFTs on peat properties including microbial community abundance and composition (Chapter 2)

2. To investigate the interactive effects of PFT and microclimate on GHG emissions from peat (Chapter 3)

3. To examine the importance of abiotic and biotic peatland properties and home-field advantage as determinants of PFT litter decomposition (Chapter 4)

4. To test the interactive effects of peatland PFT and microclimate on litter decomposition and heterotrophic respiration rates (Chapter 5)

The following four chapters examine the interactions between peatland PFTs and microclimatic conditions, in order to understand peatland C cycling processes at a wind farm. Chapter 2 describes a spatio-temporal survey of soil microbial community abundance and composition, and physicochemical properties of peat and plant material at Black Law Wind Farm. The influence of PFT on abiotic and biotic parameters is identified, and relationships between those parameters examined in order to determine factors influencing plant-soil interactions at a peatland under a wind farm (Aim 1). Chapter 3 investigates the influence of PFT and small-scale differences in temperature and water table on CO_2 and CH_4 emissions from peat, through a mesocosm experiment. The effects of microclimatic manipulations, and their interactions with PFT, were examined in order to explore the driving factors for peat GHG emissions under controlled conditions (Aim 2). The influence of abiotic and biotic peatland parameters, and the roles of peat and litter PFT in regulating litter decomposition at Black Law Wind farm were assessed in Chapter 4, in order to examine the influence of home-field advantage on litter mass loss, and with a view to improve understanding of the factors controlling peatland litter decomposition at a wind farm (Aim 3). The interactive effects of PFT and small-scale differences in temperature were investigated through a mesocosm experiment in Chapter 5, to determine the influence of litter mixing and home-field advantage on litter mass loss and CO_2 emissions under manipulated microclimate conditions (Aim 4).

In summary, this thesis examines the regulatory role of PFTs in peatland C cycling processes, and investigates the influence of PFT and hypothesised wind farm-induced microclimate interactions on the functioning of a peatland ecosystem. Field and laboratory experiments are expected to reveal the importance of microclimate changes in temperature and water table level on GHG emissions and litter mass loss in peatlands. PFT differences in peat and litter quality are likely to play a part in mediating the effects of microclimatic change, as a result of interactions between abiotic and biotic factors. This research provides important insights into the ecosystem functioning of a peatland hosting a wind farm, specifically the response of peatland C cycling processes to microclimatic conditions.

1.5 Introduction to study site

This study was conducted at Black Law Wind Farm, near Forth in Lanarkshire, Scotland (55°46′01″N 03°44’20”W) (Figure 1). Black Law Wind Farm is one of the largest in the UK, with 54 turbines and the capacity to produce up to 124 megawatts of energy. It has been operational since 2005 and covers 18.6 km^2. The wind farm primarily comprises of blanket bog peatland, but there are also areas of grassland and plantation forestry within the wind farm. The thickness of the peat layer is variable, ranging from 0.5 – 6 metres thick, but typically less than 4 metres. The blanket bog peatland has accumulated since the end of the last ice age on an underlying stratum of glacier boulder clay. The boulder clay deposits cover the solid geology, known to consist predominantly of limestone coal formations and extrusive igneous rock. The elevation of the wind farm ranges from 250 to 320 metres above sea level, and the climate is described as temperate. The mean annual maximum temperature is 10.7 °C, the minimum 4.4 °C, and the mean annual precipitation is 1092.7 mm (data from nearest Met Office weather station at Salsburgh). The blanket peatland plant community is predominantly classified as National Vegetation Community (NVC) M19: *Calluna vulgaris – Eriophorum vaginatum* blanket mire (Rodwell, 1998). *Calluna vulgaris* and *Eriophorum vaginatum* form the bulk of the vegetation, with the addition of *Sphagnum* and *Polytrichum* and *Pleurocarpous* mosses. *E. vaginatum* is usually tussocky, with *C. vulgaris* commonly found on hummocks and moss species in hollows. Other existing land uses at Black Law Wind Farm comprise of mineral extraction, forestry, low density sheep grazing and recreational activities.

Four sites, coded 1 to 4, were established along a transect that was oriented with the principal axis of the wind farm and the dominant wind direction (i.e. SW to NE) (Figure 1.2). The orientation of the transect was chosen in order to detect a potential wind turbine-induced microclimate effect, as found in other studies (Baidya Roy and Traiteur, 2010; Baidya Roy et al., 2004; Zhou et al., 2012). It was hypothesised that the wind turbine-induced microclimate effect would increase along the transect, with site 4 having the greatest accumulated effect of wind turbines wakes on ground-level atmospheric conditions. The sites were selected to be similar, despite differences in micro-topography and percentage cover of each PFT between sites, together with the expected spatial variation in peat physicochemical properties. Sites 1 and 2 had thinner peat and litter layers, featured less hummock-hollow structures and were covered in more shrub than sites 3 and 4. Each site consists of four replicate blocks and each block is comprised of three

plots, one of each plant functional type: bryophyte (*Sphagnum cuspidatum*), graminoid (*Eriophorum vaginatum*) and shrub (*Calluna vulgaris*) (Figure 1.3).

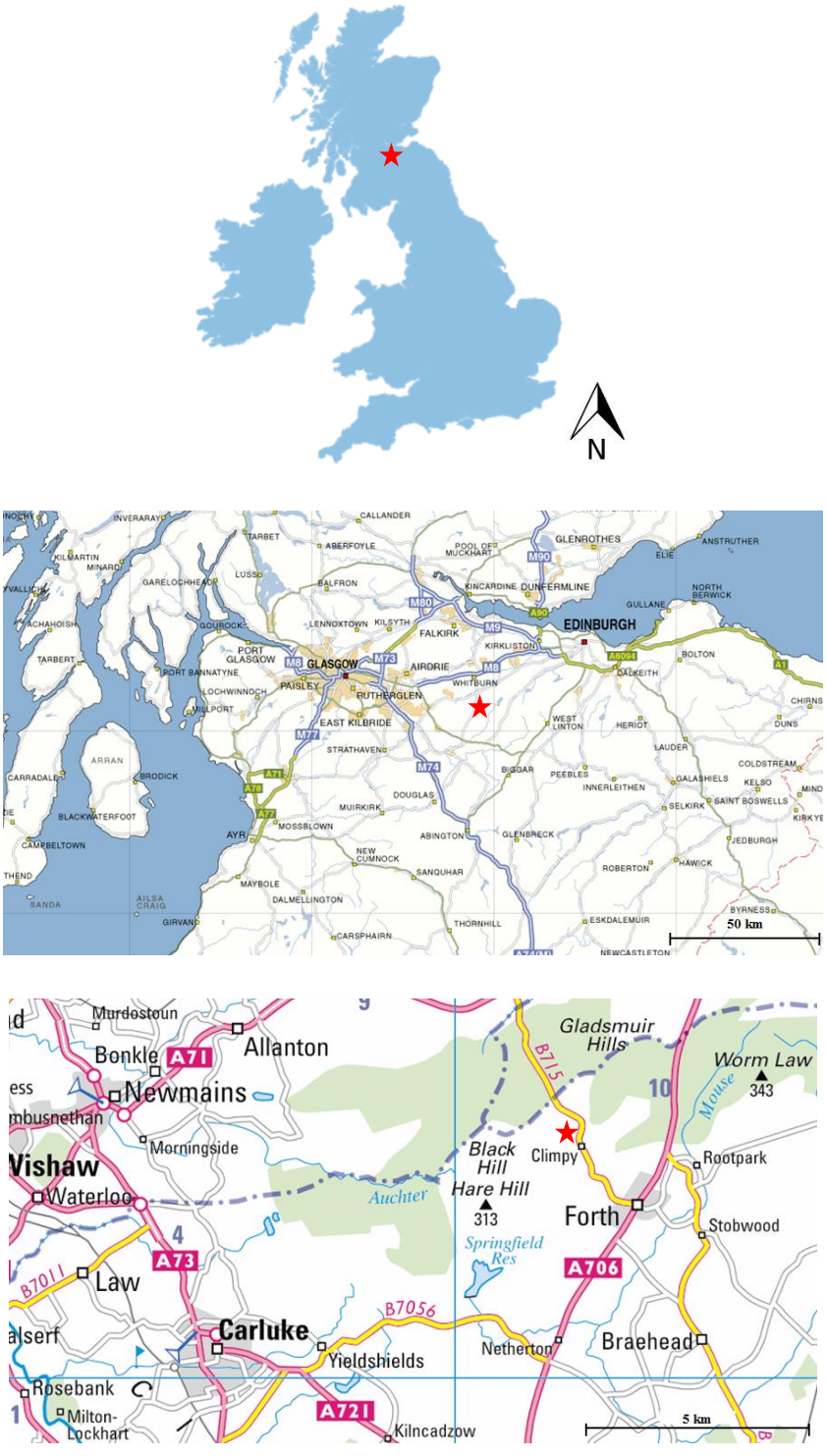

Figure 1.1: Maps to show the location of Black Law Wind Farm in the context of Great Britain and within its immediate surroundings. Red stars indicate the approximate location of Black Law Wind Farm.

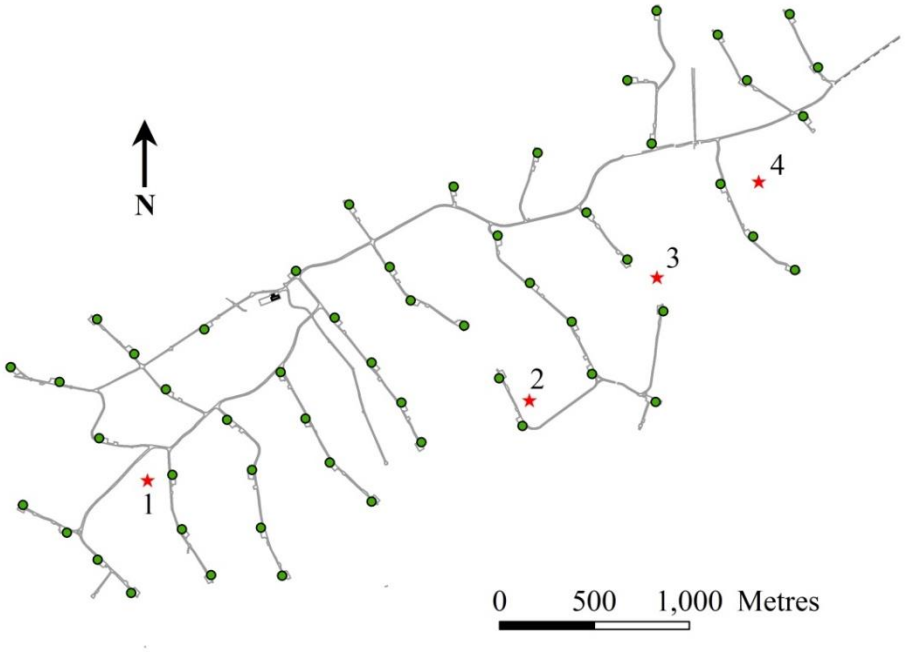

Figure 1.2: Map of Black Law Wind Farm. Lines represent the road network, green dots the wind turbines and red stars labelled 1 to 4 the sampling sites.

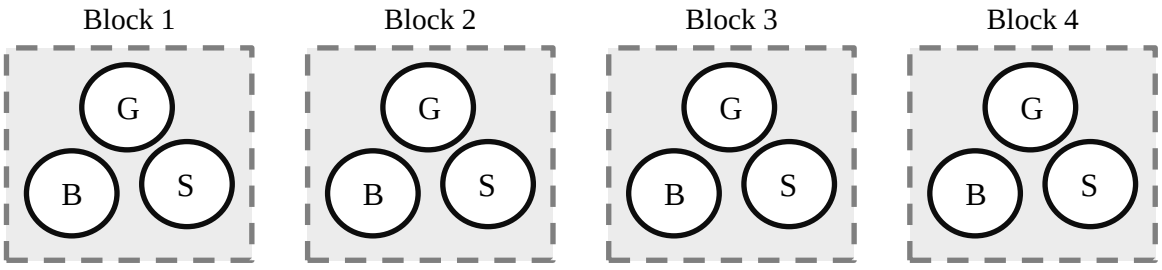

Figure 1.3: Block and plant functional type plot layout at each sampling site at Black Law Wind Farm (see Figure 1.2). B = bryophyte, G = graminoid, S = shrub.

Spatio-temporal variability of abiotic and biotic properties in a wind farm hosting northern peatland

2.1 Introduction

Northern peatlands play an important part in global carbon (C) cycles (Limpens et al., 2008; Sulman et al., 2013), but both climate change and land use change pose a significant threat to the future security of peatland C stocks (Armstrong et al., 2014b; Ostle et al., 2009; Ward et al., 2013). Warming, shifting patterns of precipitation and extreme weather events, such as drought, together with changes in the distribution and type of land use, could affect the capacity for C sequestration in peatlands (Ostle et al., 2009). In the UK, peatlands have been used for forestry, livestock grazing, game bird breeding and recreation, and have been exploited as a source of fuel or horticulture medium (Turetsky et al., 2002; Ward et al., 2007). There is evidence to show that these activities affect the C sink function of peatlands, with increased C loss caused by alterations to the abiotic and biotic components of the ecosystem (Maljanen et al., 2003; Strack et al., 2004; Wardle, 2002). It is well-known that peatland C dynamics are controlled by climate (Davidson and Janssens, 2006; Dorrepaal et al., 2009; Freeman et al., 2004), with rates of decomposition, photosynthesis and methane (CH_4) emissions likely to increase with rising temperatures. However, such effects are also likely to be strongly overshadowed by changes in water table level (Gorham, 1991; Moore and Knowles, 1989).

More recently, to address the need for electricity production from renewable sources (DECC, 2013), onshore wind farms are increasingly being constructed on peatlands, owing to limited agricultural value and high wind speeds (Clarke, 2009; Ostle et al., 2009). While there is some understanding of the impacts of wind farm construction on peatlands (Grieve and Gilvear, 2009; Smith et al., 2012; Waldron et al., 2009), knowledge of effects of wind farm operation are limited (Baidya Roy et al., 2004; L. Zhou et al., 2012). For example, there is no published research on the effects of wind farms on microclimates or peatland C cycling. Microclimate effects caused by wind farm land use have the potential to alter plant-soil C cycling processes: (1) directly through changes in ground-level temperature and soil moisture; (2) indirectly as a result of climate-induced changes in plant and soil microbial communities (Armstrong et al., 2014b). There remains, however, considerable uncertainty as to the magnitude and timescale of their effects on peatland abiotic and biotic properties.

It is important to consider aboveground and belowground peatland communities (Bardgett, 2005; Myers et al., 2012) because together they play a part in controlling the C source – C sink status of a peatland (De Deyn et al., 2008; Ward et al., 2009) and can vary across different spatial and temporal scales (Artz et al., 2007; Riutta et al., 2007; Schadt et al.,

2003; Schmidt et al., 2007; Weltzin et al., 2003). Peatland plant communities are dominated by three plant functional types (PFTs): bryophytes (e.g. *Sphagnum* sp., feather mosses), shrubs (e.g. *Calluna vulgaris*, *Vaccinium* sp.) and graminoids (e.g. *Eriophorum vaginatum*, sedges, and rushes) (Ward et al., 2009). PFTs are defined by their functional traits: bryophytes are slow growing and have low N litters, graminoids are faster growing, have high root biomass and litter quality, whilst shrubs have woody tissues rich in lignin and phenolic compounds (De Deyn et al., 2008; Dorrepaal et al., 2005; Turetsky, 2003). These traits can influence physical and biochemical properties of the underlying peat (Artz et al., 2007; Jobbágy and Jackson, 2000; Pendall et al., 2008) such as soil moisture, peat C:N and microbial community composition and size (Carrillo et al., 2012; Laiho et al., 2003; Weltzin et al., 2001).

Microbial communities are an essential component of biogeochemical cycling in peatlands, with fungi and bacteria responsible for degrading different available and complex forms of C and N (Bardgett, 2005; McGuire et al., 2010; Myers et al., 2012). Fungi have slower biomass turnover rates and broader enzymatic capabilities than bacteria (de Boer et al., 2005; Rousk and Bååth, 2007), which results in fungi having greater carbon use efficiency (Six et al., 2006). Fungi are known to dominate shrub-derived peat, due to their ability to degrade complex organic substrates (i.e. lignin) and litter with high C:N and concentrations of phenolic compounds (Freeman et al., 2001; Myers et al., 2012; Read et al., 2004). In contrast, bacteria are faster growing and target easily degraded substances composed of labile C (de Boer et al., 2005), which means that they thrive in moss- and sedge-derived peat because litter from those PFTs contains a higher proportion of less recalcitrant C compounds (Myers et al., 2012; Winsborough and Basiliko, 2010). In peatlands, significant differences in both microbial diversity and functional activity have been found in relation to the quality and quantity of plant litter, soil temperature, water table and nutrient concentrations (Bragazza et al., 2007; Fisk et al., 2003; Jaatinen et al., 2007; Myers et al., 2012). Therefore, the composition and function of peatland microbial communities are expected to shift with direct effects of climate and indirectly as a result of climate-induced effects upon abiotic soil properties and plant species composition (Bardgett and Wardle, 2010).

A significant gap in knowledge is how wind farms will affect peatland plant-soil interactions and the processes that they govern. Specifically, improved understanding of the influence of variation in PFTs upon peat properties and soil microbial communities is important to predict peatland biogeochemical functions. To address this, the spatial and

seasonal controls on abiotic and biotic peatland properties were examined at Black Law Wind Farm (Lanarkshire, Scotland). It was hypothesised that (1) peatland plant functional types and their traits will relate to differences in the abiotic and biotic properties of surface peat and litter; (2) these properties will vary spatially across the wind farm; (3) microbial community composition will vary seasonally due to interactions between water table depth and PFT-derived differences in peat properties.

2.2 Methods

This study was conducted using a fully factorial experimental field design comprising four blocks of three PFT plots (bryophyte, graminoid and shrub), at four sites across a blanket bog peatland at Black Law Wind Farm (Lanarkshire, Scotland), in February 2011 (Figures 1.1, 1.2 and 1.3, Chapter 1). Peat, litter and vegetation samples were collected from each of the 48 plots. At each sampling area, litter depth was measured three times within a 400 cm^2 quadrat before removing plant material. Vascular plant litter samples comprised of senesced, undecomposed leaves. Leaves that were not shed were only selected if they had already lost their green colour. *Calluna vulgaris* leaves were harvested with brown shoots to which they were attached. *Eriophorum vaginatum* leaves were collected by loose shaking of the plant and gentle separation by hand. The decomposition of Sphagnum litter can be hard to identify (Hogg, 1993), therefore in accordance with previous studies (Aerts et al., 2001; Bragazza et al., 2007) the stem section 2-4cm beneath the capitulum (i.e. growing tip) was used to represent freshly deposited *Sphagnum* litter stored in the acrotelm. Vegetation samples consisted of all above-ground live plant shoot material. Within each 400 cm^2 sampling area, a peat core (5 cm diameter, 15 cm depth) was extracted manually. In total, 144 samples (48 peat, litter and vegetation) were collected and analysed for total C and total N in February 2011. An additional 192 peat cores were similarly collected to assess seasonal and spatial variability of microbial community composition: 48 peat cores were collected throughout 2011 in February (winter), April (spring), July (summer) and October (autumn) 2011. Peat was then homogenised and a sub-sample was taken and stored at -20°C prior to extraction of microbial biomarkers.

The total C and nitrogen (N) content of peat, litter and vegetation were evaluated from 0.1 g homogenised and oven-dried (105 °C) sub-samples. Samples were analysed using a LECO Truspec CN Analyser (LECO, USA), with furnace temperature at 950 °C. Results were calibrated against three Ethylenediaminetetraacetic acid (EDTA) standard samples that were run every twenty peat, litter or vegetation samples. Peat pH was measured using a ratio of 1:2.5 (v:v) fresh peat at room temperature to deionised water, and a Hanna 211

pH meter with a two-point calibration (Emmett et al., 2008). Dry bulk density (BD) was measured (Carter, 1993) and used, together with the dry weight and total C and N contents of peat, to calculate the amount of C and N (g m^{-2}) for the surface 15 cm layer of peat. Litter C and N stocks (g m^{-2}) were also calculated, by using the litter dry weight, total C and N contents and depth of the litter layer. Water table level (mm) was measured at each PFT plot at one block at each site, recorded every 30 minutes, using a Level TROLL 500 (Insitu, USA) from the end of March 2011 onwards. The mean water table level for all plots at each time point was subtracted from the water table level for each plot at each time point, in order to calculate the deviation from the mean water table level. Water table level deviation was calculated for each PFT and site, in each season: spring (April 2011), summer (July 2011) and autumn (October 2011).

Soil microbial community composition was assessed by extraction of phospholipid fatty acids (PLFAs) from 0.5 g sub-samples of ground freeze-dried peat, using procedures based on the Bligh and Dyer (1959) method modified and described by Bardgett et al. (1996), Frostegård et al. (1991) and White et al. (1979). Extracted PLFAs were quantified by gas chromatography using an Agilent Technologies 6890N GC with a flame ionisation detector. An external standard containing 0.1 µg each of the following compounds in 1 µl of hexane: C16:0 (Methyl palmitate), C18:0 (Methyl stearate), C21:0 (Methyl heneicosanoate) and C23:0 (Methyl tricosanoate), was run once per day and compared with previous chromatograms to ensure consistency in instrument performance. Identification of PLFAs was achieved by first identifying peaks by gas chromatography mass spectrometry (GC-MS) and then using relative retention times, which were compared to an internal standard of C19:0 (Methyl nonadecanoate) to calibrate between peak areas and PLFA concentrations. As described by (Frostegard, 1993), fatty acid nomenclature was used. A number of the 23 identified fatty acids were assigned to different microbial groups, as described below. PLFAs of terminal and mid-chain branched, cyclopropyl saturated and monosaturated fatty acids (i15:0, a15:0, 15:0, i16:0, 16:1ω9, 16:1ω7 t, i17:0, a17:0, 17:0, cy17:0, 18:1ω7 and cy19:0) were considered indicative of bacteria where i15:0, a15:0, i16:0, i17:0 and a17:0 were gram-positive bacteria (gram +ve) and 16:1ω7 t, cy17:0, 18:1ω7 and cy19:0 were gram-negative bacteria (gram -ve). The PLFAs 18:1ω6 and 18:2ω6, 9 were taken to represent saprotrophic and ectomyhorrhizal fungi (Kaiser et al 2010, De Deyn et al 2011). Total PLFA concentration was calculated from all identified PLFAs (those listed above and 14:0, 16:1, 16:1ω5, 16:0, 17:1ω8, 7Me-17:0, br17:0, br18:0, 18:1ω5, 18:0, 19:1). The ratio of fungal to bacterial PLFAs (F:B) and the ratio of gram-positive bacterial PLFAs to gram-negative bacterial PLFAs (gram +ve:gram -ve)

were taken to represent the relative abundance metrics of these groups. The ratio of fungal biomass C to bacterial biomass C (F:B biomass C) was calculated by applying a conversion factor of 27.4 to F:B (Waring et al., 2013). The conversion factor was calculated from an average of empirically determined conversion factors from five studies (Bezemer et al., 2006; Bouillon et al., 2004; Joergensen and Wichern, 2008; Keinänen et al., 2002; Klamer and Bååth, 2004) and used to convert fungal and bacterial PLFA concentrations to their biomass C equivalents. The conversion of fungal and bacterial PLFA concentrations to their biomass C equivalents facilitates the comparison of PLFA data with SIR (substrate-induced respiration with specific inhibitors) and microscopy (i.e. quantification of strained hyphae and bacterial cells) data sets.

2.2.1 Statistical analysis

Two-way ANOVA was performed using SAS V9.1, Enterprise Guide 4.0 and followed by Tukey's test *post-hoc* analyses to test the hypotheses that abiotic and biotic peatland properties would vary spatially and relate to differences in PFT. The significance of site and PFT was tested on: (1) total C, total N, C:N, C stock, N stock, dry bulk density and pH in peat; (2) total C, total N, C:N, litter layer depth, C stock, N stock of litter and (3) total C, total N and C:N of vegetation. Normality of data was checked before analysis and appropriate transformations were applied if necessary. A linear mixed-effects (LME) model and Tukey's test *post-hoc* analysis was performed to detect if season, site and PFT significantly controlled water table level, using the R language and environment for statistical computing (R Development Core Team 2011) and several contributed packages (Hothorn et al., 2008; Pinheiro et al., 2011). Plot ID was used as a random effect to account for the repeated measures.

Repeated measures ANOVA was performed using SAS V9.1, Enterprise Guide 4.0 and followed by Tukey's test *post-hoc* analyses to test the hypothesis that microbial community composition would vary with season, location within the wind farm and PFT-derived differences in physical and chemical peat properties. The significance of site, season and PFT was tested on total PLFAs, total fungal, total bacterial, F:B, F:B biomass C, gram-positive bacteria, gram-negative bacteria, gram-positive bacteria:gram-negative bacteria in peat. Plot ID was used as a random effect to account for the repeated measures. All PLFA data were log-transformed before final analysis, except for F:B, F:B biomass C and gram-positive bacteria. The Pearson's correlation coefficient was calculated to give a measure of the relationship between C:N of peat and F:B biomass C. Data was log-transformed before analysis.

To further test the extent to which the entire profile of identified PLFAs for each peat sample were explained by abiotic variables (water table, pH, bulk density, litter depth, peat N, peat C, peat C:N, litter N, litter C, litter C:N, veg N, veg C, veg C:N) for each season was determined using distance-based redundancy analysis (db-RDA), a form of regression analysis that is used to model multivariate response data (Borcard et al., 2011a). Hellinger transformation was chosen as the most appropriate (Borcard et al., 2011b) and applied to each individual PLFA value, for use as the response variable in db-RDA. Variance partitioning followed each db-RDA in order to elucidate the relative effects of the abiotic variables on the identified PLFAs for each peat sample. Abiotic variables used to explain winter, spring, summer and autumn PLFA data were pH, bulk density, litter depth, peat N, peat C, peat C:N, litter N, litter C, litter C:N, veg N, veg C, veg C:N. Water table data was only available for spring, summer and autumn; therefore a separate db-RDA using deviation from mean water table level and the aforementioned abiotic variables was used to explain PLFA data for those three seasons. Correlation, db-RDA and variance partitioning was performed using the R language and environment for statistical computing (R Development Core Team 2011) and several contributing packages (Dray et al., 2009; Oksanen et al., 2006)

Throughout the text, 'significant' is referred to if $p < 0.05$.

2.3 Results

2.3.1 Peat properties

ANOVA analyses show that total C content, C:N, bulk density, pH and C stocks varied significantly across the peatland (Table 2.1). Total C content was significantly lower at site 1 than at sites 2, 3 and 4 (Figure 2.1). There was no overall effect of site on total peat N content (Table 2.1). Peat C:N ratios were significantly higher at site 4 than at site 1 (Figure 2.1). Bulk density was significantly greater at site 1 than at sites 2, 3 and 4, with no differences between sites 2 and 4 (Figure 2.2); whilst site 4 had significantly higher peat pH than site 3 (Figure 2.2). Peat C stock and N stocks were greater at sites 1 and 3 than at sites 2 and 4 (Figure 2.3). Peat properties did not vary with PFTs, with the exception of N stock (Table 2.1) which was significantly greater in peat sampled beneath graminoids than bryophytes (Figure 2.3). There were no statistically significant interactions between sampling site location and PFTs. Together these results show that there were spatial differences in the peat physicochemical properties and that PFTs were only related to peat N stocks of the parameters studied.

2.3.2 Litter properties

There was an overall effect of site on litter depth, total C content and C stock (Table 2.1). The litter layer was significantly deeper at site 1 than at sites 2 and 3 (Figure 2.5). Total C content was significantly greater at sites 3 and 4 than at sites 1 and 2 (Figure 2.4), but litter C stocks were significantly lower at site 2 that at site 3 (Figure 2.5). Total litter N content, C:N and N stocks did not vary with site (Table 2.1), but post-hoc testing indicated that C:N was higher at site 4 than at site 2 (Figure 2.4). PFT was found to influence all litter measurements, and there was a significant interactive effect of PFT and site on litter depth (Table 2.1). The litter layer was significantly deeper beneath areas of shrub and graminoid, than bryophyte; with differences between PFTs more evident at sites 2 and 4 (Figure 2.5). Total C content was greatest in shrub litter, less in graminoid, and lowest in bryophyte (Figure 2.4). Total N content was higher and C:N ratio lower in shrub litter, than graminoid and bryophyte litters (Figure 2.4). Graminoid litter C stock was greater than in both bryophyte and shrub litters, whilst graminoid N stock was only significantly higher than bryophyte (Figure 2.5). These results show that all litter properties measured here were influenced by PFT, whereas only some spatial differences and interactions between sampling site location and PFTs were observed.

2.3.3 Vegetation properties

Variability in plant total C content, total N content and C:N was related to both PFT and site (Table 2.1). Total C content was significantly higher at site 2 than at sites 1 and 3, and in shrub vegetation compared to bryophyte and graminoid vegetation (Figure 2.6). Total N content of plant samples was lowest at site 3 and highest for site 1, with significantly greater graminoid N content than bryophyte and shrub (Figure 2.6). The variability in plant C:N with site and PFT was dissimilar to both C and N concentrations separately, with greatest C:N in plants at site 3 and smallest C:N in graminoids (Figure 2.6). Overall, variability in plant properties was related to both PFT and location across the peatland, but no statistically significant interactions were observed between them (Table 2.1).

Table 2.1: Two-way ANOVA results showing site, PFT and site*PFT effects on BD = bulk density (g cm^{-3}), C% = total C content, N% = total N content, C:N = ratio of total C and total N, C stock (g C m^{-2} to 15 cm), N stock (g N m^{-2} to 15 cm) and LD = litter depth (cm).

Two-way ANOVA:		Site		PFT		Site * PFT	
		$F_{(3,48)}$	*p*	$F_{(2,48)}$	*p*	$F_{(6,48)}$	*p*
	BD	46.57	<.0001	1.17	0.3229	0.51	0.7987
	pH	4.84	0.0122	1.25	0.3091	1.00	0.4574
	C%	27.92	<.0001	1.95	0.1665	0.61	0.7172
Peat	N%	2.20	0.1050	1.29	0.2873	0.56	0.7586
	C:N	22.84	<.0001	1.07	0.3536	0.65	0.6886
	C stock	19.42	<.0001	2.16	0.1301	0.74	0.6229
	N stock	39.50	<.0001	4.17	0.0235	0.84	0.5447
	C%	112.09	<.0001	25.18	<.0001	1.50	0.2058
	N%	0.95	0.4253	4.88	0.0133	1.43	0.2303
Litter	C:N	1.99	0.1327	3.67	0.0354	1.33	0.2677
	LD	6.99	0.0002	25.07	<.0001	2.40	0.0310
	C stock	3.66	0.0197	10.22	0.0002	1.56	0.1865
	N stock	1.57	0.2134	5.51	0.0072	0.68	0.6698
	C%	8.28	0.0003	46.94	<.0001	0.33	0.9193
Vegetation	N%	11.09	<.0001	10.94	0.0002	1.19	0.3343
	C:N	10.97	<.0001	12.16	<.0001	1.26	0.2995

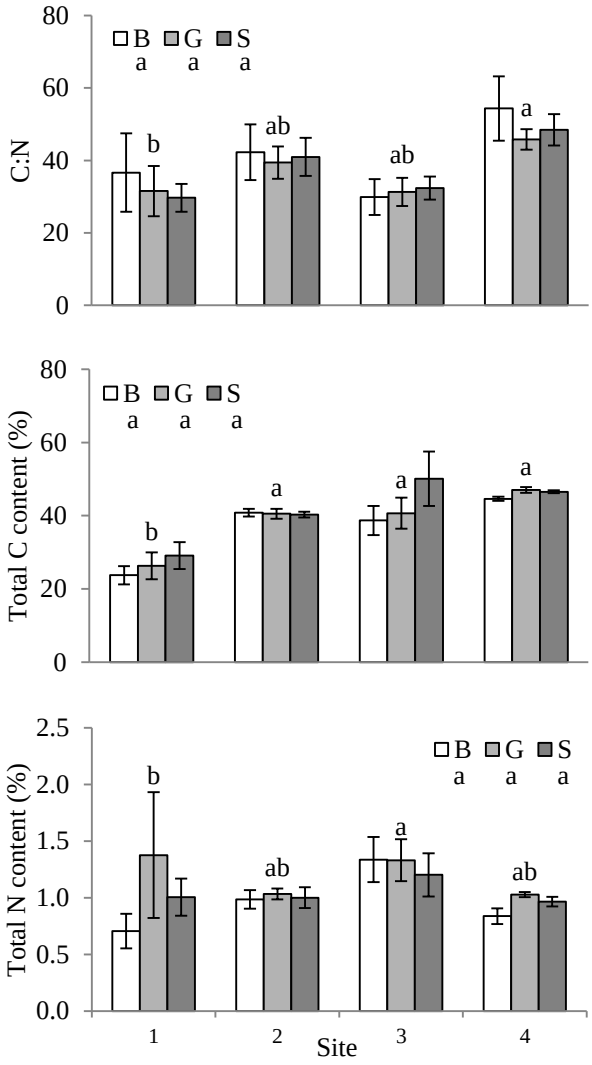

Figure 2.1: C:N, total C content and total N content for peat from each site and PFT. Data are means ± standard error. B = bryophyte, G = graminoid, S = shrub. Letters below legends denote pair-wise significant differences between PFT. Letters on graphs indicate pair-wise significant differences between sites.

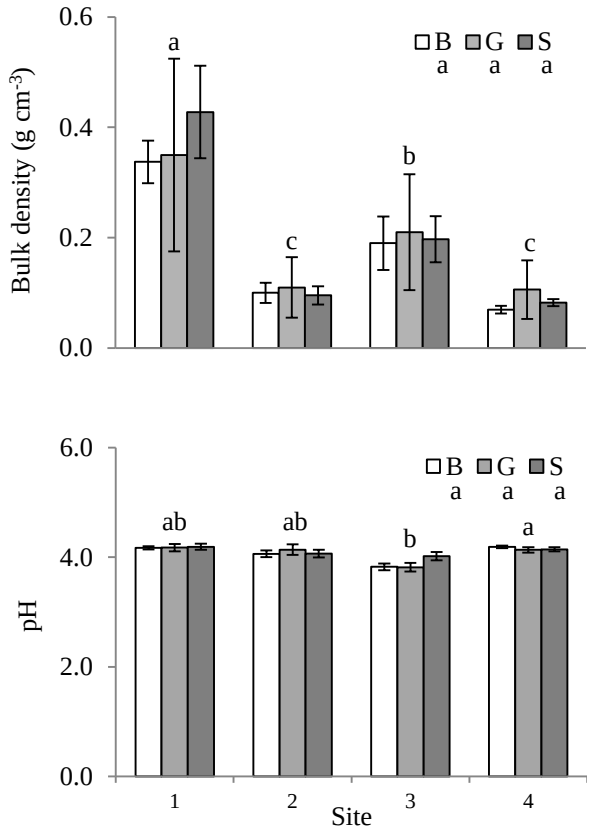

Figure 2.2: Peat bulk density and pH from each site and PFT. Data are means ± standard error. B = bryophyte, G = graminoid, S = shrub. Letters below legends denote pair-wise significant differences between PFT. Letters on graphs indicate pair-wise significant differences between sites.

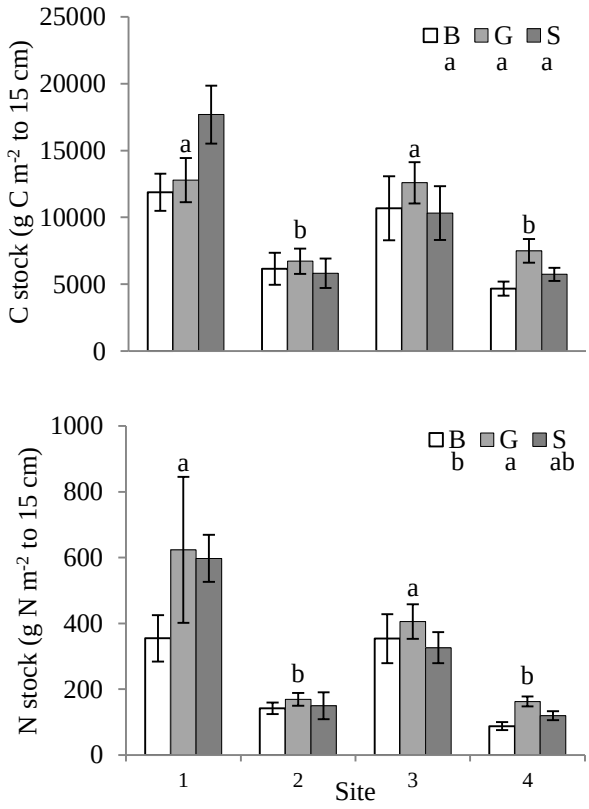

Figure 2.3: C stock and N stock for peat from each site and PFT. Data are means ± standard error. B = bryophyte, G = graminoid, S = shrub. Letters below legends denote pair-wise significant differences between PFT. Letters on graphs indicate pair-wise significant differences between sites.

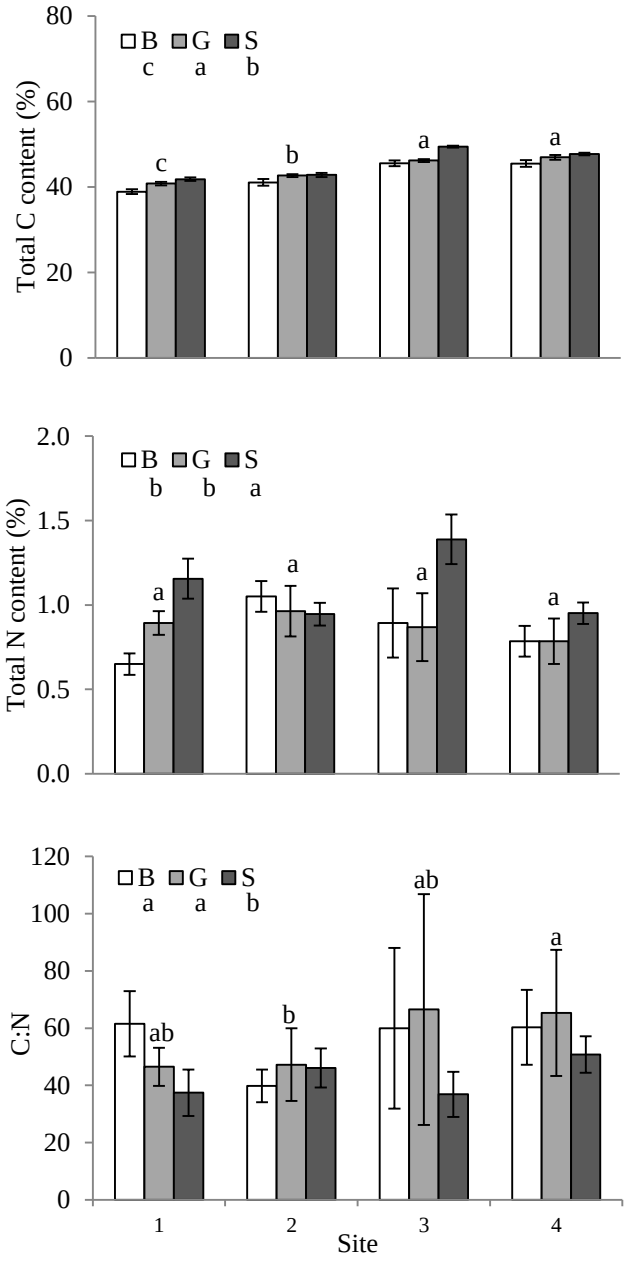

Figure 2.4: Total C, total N and C:N of litter from each site and PFT. Data are means ± standard error. B = bryophyte, G = graminoid, S = shrub. Letters below legends denote pair-wise significant differences between PFT. Letters on graphs indicate pair-wise significant differences between sites.

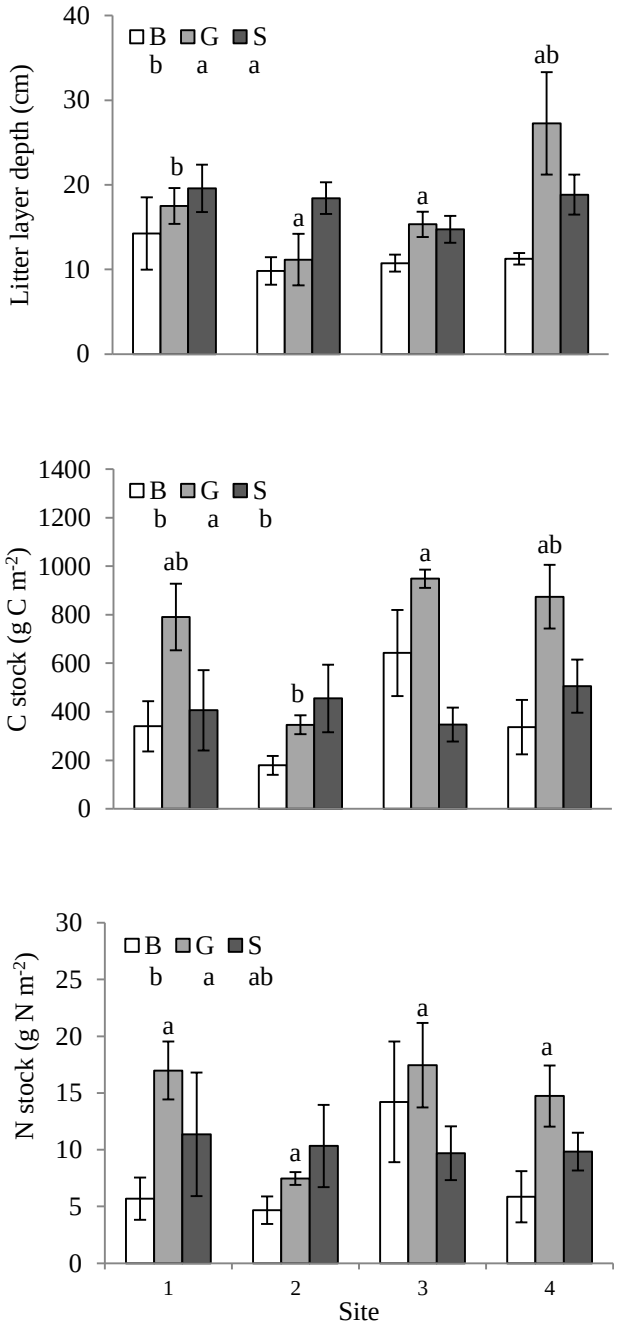

Figure 2.5: Litter depth, C stock and N stock for litter from each site and PFT. Data are means ± standard error. B = bryophyte, G = graminoid, S = shrub. Letters below legends denote pair-wise significant differences between PFT. Letters on graphs indicate pair-wise significant differences between sites.

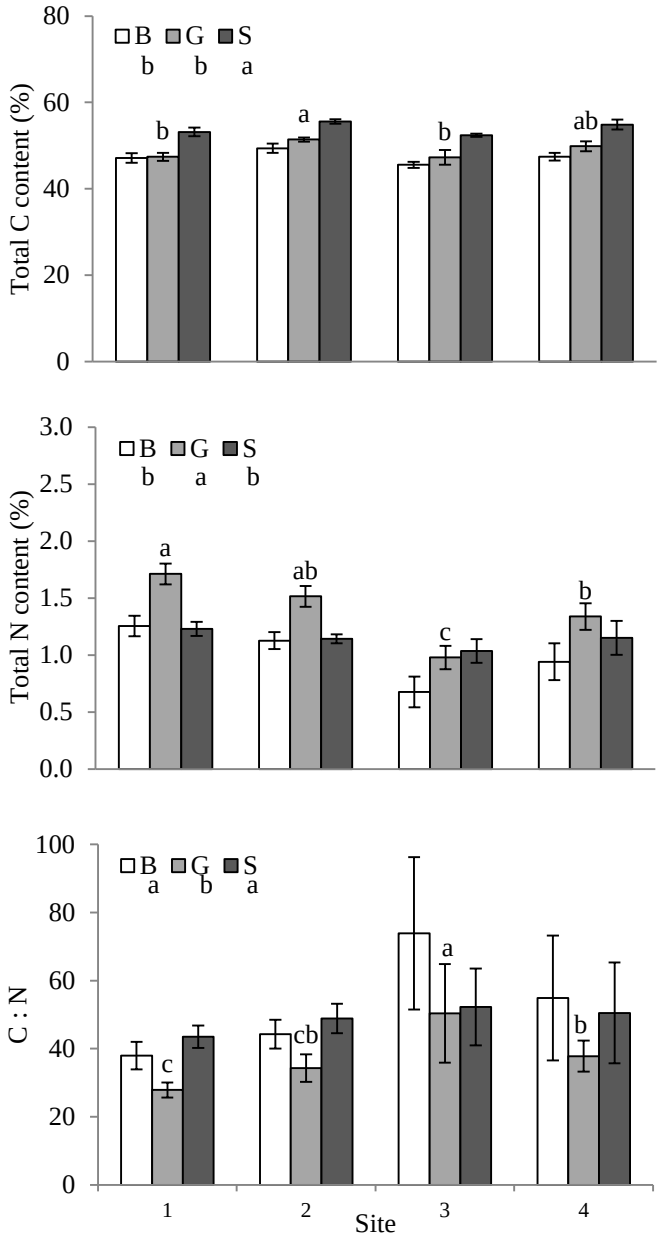

Figure 2.6: Total C, total N and C:N of vegetation from each site and PFT. Data are means ± standard error. B = bryophyte, G = graminoid, S = shrub. Letters below legends denote pair-wise significant differences between PFT. Letters on graphs indicate pair-wise significant differences between sites.

2.3.4 Water table level

Repeated measures ANOVA analyses showed that season and site had a significant effect on the water table, as did PFT, which had the greatest influence overall (Table 2.2). Significant interactions between season, site and PFT also had effects on the water table, which were equivalent in order of magnitude to the main effects of season and site (Table 2.2). Post-hoc tests revealed seasonal variability in water table level, observed as high water tables in autumn, lower water tables in spring and then summer (Figure 2.7). The position of the water table was different across the peatland, being lowest at site 2, and rising towards the surface at site 4, then site 3, to reach its highest overall position at site 1 (Figure 2.1). The biggest change in water table was observed with PFTs, with lowest and highest water tables measured in peat beneath shrub and bryophyte, respectively (Figure 2.7).

The mean water table at sites 1 and 3 was at or above the peat surface in summer and autumn, whilst in spring it remained below the surface at all sites (Figure 2.7). However, the position of the water table in spring was more variable across the peatland, than later in the year (Figure 2.7). For example, the variability in water table position was approximately three times larger in spring, than in summer and autumn, and was observed to deviate by approximately 150 mm above and below the mean water table level across the peatland. In summer and autumn, the water table in peat beneath shrub at each site, apart from site 2, was lower than the overall average i.e. drier, whereas bryophyte and graminoid water tables were often wetter (Figure 2.7). However, variability between PFTs was not the same in spring, as graminoid water tables were lower than those below shrub at sites 1 and 2 (Figure 2.7).

These results show that there were strong spatial and seasonal controls on water table, with significant interactions between time of year and location across the peatland affecting the amount of variation observed. PFTs had the strongest effect on the water table, and contributed to the variability in water table levels seen across the peatland through interactions with both site and season.

Table 2.2: Repeated measures ANOVA results showing season, site, PFT and their interactive effects on depth to water table (mm).

Repeated measures ANOVA:	df	F	*p*
Season	3	4079.0	<.0001
Site	3	7992.8	<.0001
PFT	2	763874.4	<.0001
Season*Site	9	7529.2	<.0001
Season*PFT	6	6285.1	<.0001
Site*PFT	6	1137.2	<.0001

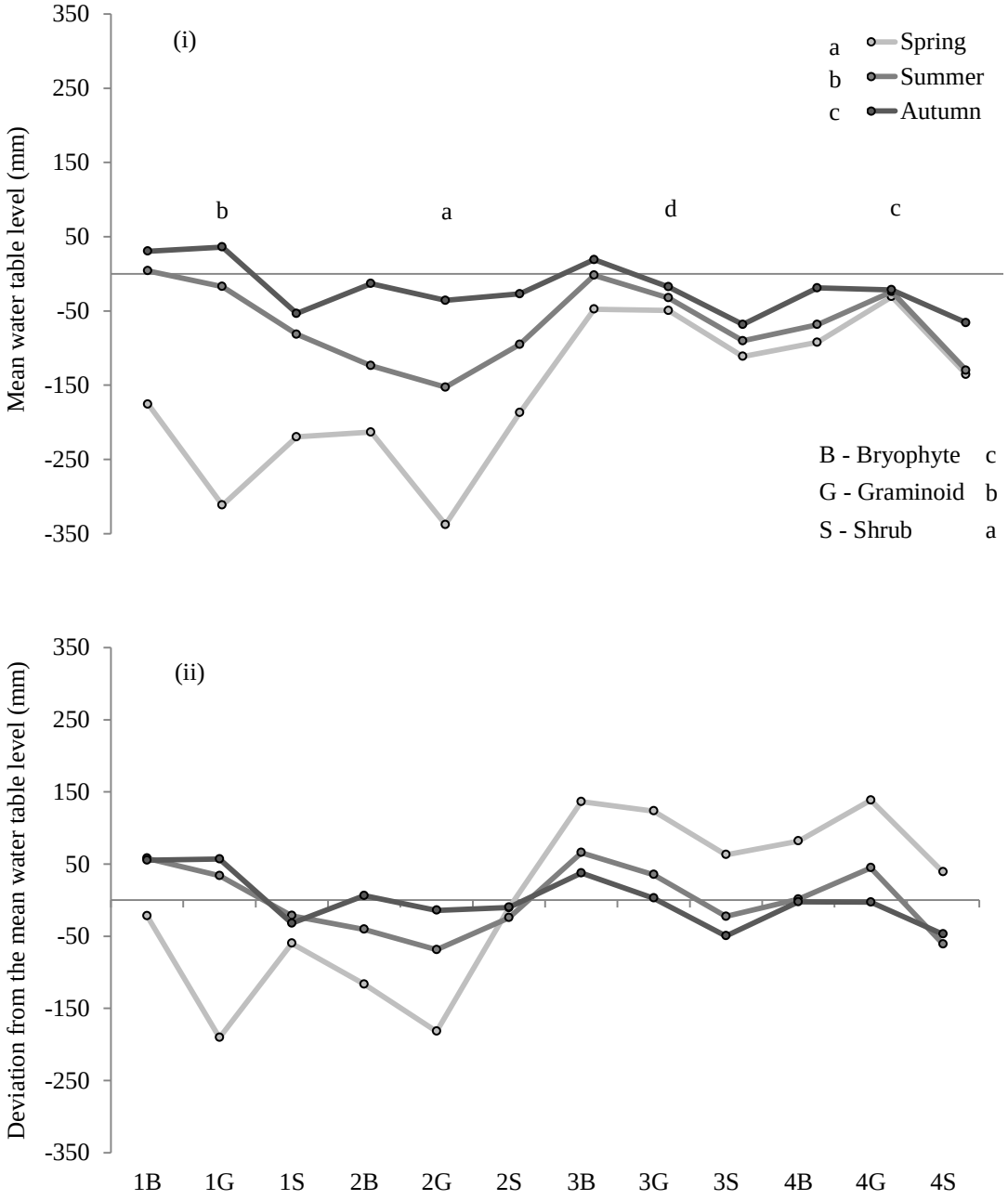

Figure 2.7: Mean water table level (mm) (i) beneath each PFT at each site (1, 2, 3 and 4) in spring, summer and autumn 2011. Average deviation from the mean water table level (ii), for each PFT, site and season. Legend letters indicate pair-wise significant differences between seasons, and separately for PFT. Letters on graph (i) indicate pair-wise significant differences between sites.

2.3.5 Peat microbial community

Results from repeated measures ANOVA analyses of microbial community abundance and composition (i.e. from PLFAs) show that both site and season had a significant effect on all measures (Tables 2.3, 2.4 and 2.5), and, that PFTs accounted for differences in variance of peat fungal to bacterial (F:B) ratios (Tables 2.3 and 2.6). There were significant interactions between site and season with effects on F:B and ratios of gram +ve to gram –ve bacteria (Tables 2.3, 2.7 and 2.8). No significant interactive effects of site and season were observed upon other PLFA groups (Table 2.3), and there were no significant interactions with PFT (Table 2.3).

The concentration of total PLFAs was significantly higher at site 4 than at sites 3, 2 and 1, the latter of which exhibited the lowest average total PLFA concentration in autumn and winter (Figure 2.8). Bacterial and fungal PLFAs showed a similar spatial variability to total PLFAs, and on average, site 4 had the highest abundance of fungal and bacterial PLFAs in spring (Tables 2.9 and 2.10). The ratio of fungi to bacteria was significantly lower at sites 1, 2 and 3 than at site 4 (Figure 2.9), a pattern most strongly observed in spring and autumn, and broadly reflected in the total concentrations of gram positive bacteria, gram negative bacteria, and ratio of gram +ve to gram -ve bacteria across all seasons (Tables 2.11, 2.12 and 2.13).

Total PLFAs were significantly more abundant in spring than in summer and winter (Figure 2.8). Bacterial PLFAs showed the same pattern as total PLFAs, with abundance in autumn also greater than when measured in summer and winter (Table 2.9). Similarly, the concentrations of fungal PLFAs in autumn were significantly greater than in summer (Table 2.10). A different pattern emerged for F:B, with increased dominance of fungi over bacteria in winter compared to spring and summer (Figure 2.9). There was evidence of a significant interaction between site and season for F:B (Table 2.3), observed as a greater proportion of fungal to bacterial PLFAs at site 2 in winter, compared with site 3 in winter and sites 1, 2 and 3 in spring, summer and autumn (Figure 2.9 and Table 2.7). Concentrations of gram +ve PLFAs were significantly greater in spring and autumn than in winter (Tables 2.5 and 2.11), whereas the abundance of gram -ve PLFAs was significantly lower in summer and autumn than in spring (Tables 2.5 and 2.12). The interactive effect of site and season was significant for the ratio of gram +ve to gram -ve bacteria (Table 2.3). In winter the dominance of gram +ve bacteria over gram -ve bacteria was significantly lower than in spring, summer and autumn (Tables 2.8 and 2.13), with the most marked differences observed between seasons for sites 1 and 2.

The ratio of fungal to bacterial PLFAs was significantly different with PFT (Table 2.3), being greater in shrub-derived peat than both graminoid- and bryophyte-derived peat (Figure 2.9 and Table 2.6). F:B biomass C also varied significantly with PFT, being greater in shrub-derived peat than graminoid-derived peat (Tables 2.3 and 2.6), together with the main and interactive effects of site and season (Table 2.3).

Across the peatland and for each PFT, ratios of fungal biomass C to bacterial biomass C were consistently above 4.0 in winter and autumn; but were as low as 0.5 in spring and summer (Figure 2.10). F:B biomass was higher in winter than in spring, summer and autumn (Figure 2.10 and Table 2.5), and at site 4 compared to sites 1 and 3 (Figure 2.10 and Table 2.4), with the same interaction between season and site observed as F:B PLFAs (Table 2.7). There is more variability in F:B biomass C at sites 1, 2 and 4 than at site 3, which shows bryophyte, graminoid and shrub F:B biomass C to be closely clustered with similar ratios of C and N (Figure 2.11). A moderate positive correlation between F:B biomass C and peat C:N was observed ($r = 0.51$, $p = 0.0002$, $n = 46$) (Figure 2.11).

PFT did not influence the variability of any other microbial measures and there were no significant interactive effects of PFT with site or season (Table 2.3). These results show that the overall trends were: (1) greater abundance of PLFAs at site 4 and in spring; (2) increased dominance of fungi in winter, at site 4 and beneath shrub; (3) larger gram +ve bacterial communities at site 4 with respect to gram -ve bacteria, with overall dominance diminishing in winter.

Table 2.3: Repeated measures ANOVA showing season, site, PFT (plant functional type) and their interactive effects on peat biotic characteristics: total PLFA (total PLFA concentration) = µg g^{-1} dwt soil, fungi = total fungal PLFA, bacteria = total bacterial PLFA, F:B = ratio of fungal to bacterial PLFA, F:B biomass C = ratio of fungal biomass C to bacterial biomass C, gram +ve bacteria = gram-positive bacteria PLFA, gram –ve bacteria = gram-negative PLFA, gram +ve:gram –ve = ratio of gram-positive bacterial to gram-negative bacterial PLFA.

Repeated measures ANOVA:	Season		Site		PFT		Season*Site		Season*PFT		Site*PFT	
Community	F	*p*	F	*p*	F	*p*	F	*p*	F	*p*	F	*p*
Total PLFA	6.35	0.0005	16.50	<.0001	0.88	0.4203	0.67	0.7387	0.98	0.4397	10.5	0.4024
Fungi	4.35	0.0060	22.65	<.0001	3.02	0.0570	1.01	0.4372	0.54	0.7792	0.90	0.4987
Bacteria	9.10	<.0001	14.19	<.0001	0.60	0.5237	0.75	0.6648	1.14	0.3458	1.00	0.4336
F:B	13.88	<.0001	11.65	<.0001	5.63	0.0057	5.22	<.0001	1.09	0.3706	0.60	0.7324
F:B biomass C	13.78	<.0001	11.38	<.0001	5.75	0.0068	5.16	<.0001	1.00	0.4323	0.58	0.7444
Gram +ve bacteria	12.57	<.0001	13.96	<.0001	0.84	0.4381	1.20	0.3047	1.06	0.3884	1.12	0.3607
Gram –ve bacteria	7.99	<.0001	18.37	<.0001	0.59	0.5599	0.98	0.4636	1.08	0.3806	1.11	0.3685
Gram +ve:gram –ve	24.07	<.0001	7.15	0.0004	0.01	0.9874	8.19	<.0001	1.18	0.3208	0.24	0.9623

Table 2.4: Pair-wise comparisons of microbial community composition (PLFAs) between each site, analysed by one-way ANOVAs and Tukey's test *post-hoc* analyses.

Measure of microbial community	Site			
	1	2	3	4
Total PLFA	a	a	a	b
Fungi	a	ab	b	c
Bacteria	a	a	a	b
F:B	a	bc	ab	c
F:B biomass C	c	ab	ac	b
Gram +ve bacteria	a	a	a	b
Gram –ve bacteria	a	a	a	b
Gram +ve:gram –ve	a	a	a	b

Table 2.5: Pair-wise comparisons of microbial community composition (PLFAs) between each season, analysed by one-way ANOVAs and Tukey's test *post-hoc* analyses.

Measure of microbial community	Season			
	Winter	Spring	Summer	Autumn
Total PLFA	b	a	b	ab
Fungi	ab	ab	a	b
Bacteria	a	b	a	b
F:B	a	b	b	ab
F:B biomass C	b	a	a	a
Gram +ve bacteria	a	b	ac	bc
Gram –ve bacteria	ab	a	b	bc
Gram +ve:gram –ve	a	bc	b	c

Table 2.6: Pair-wise comparisons of microbial community composition (PLFAs) between each peat PFT, analysed by one-way ANOVAs and Tukey's test *post-hoc* analyses.

Measure of microbial community	Peat PFT		
	B	G	S
Total PLFA	a	a	a
Fungi	a	ab	b
Bacteria	a	a	a
F:B	a	a	b
F:B biomass C	ab	a	b
Gram +ve bacteria	a	a	a
Gram –ve bacteria	a	a	a
Gram +ve:gram –ve	a	a	a

Table 2.7: Pair wise comparisons between site and season, for F:B and F:B biomass C.

		Season			
		Winter	Spring	Summer	Autumn
Site	1	ab	c	cd	bcd
	2	a	bcd	bcd	bcd
	3	bcd	bcd	bcd	bd
	4	ab	ab	ab	ab

Table 2.8: Pair wise comparisons between site and season, for gram +ve:gram -ve.

		Season			
		Winter	Spring	Summer	Autumn
Site	1	ab	cdefg	g	cdefg
	2	a	cfg	fg	bcdef
	3	bcdef	cfg	cdfg	cdfg
	4	abde	bcde	abe	abde

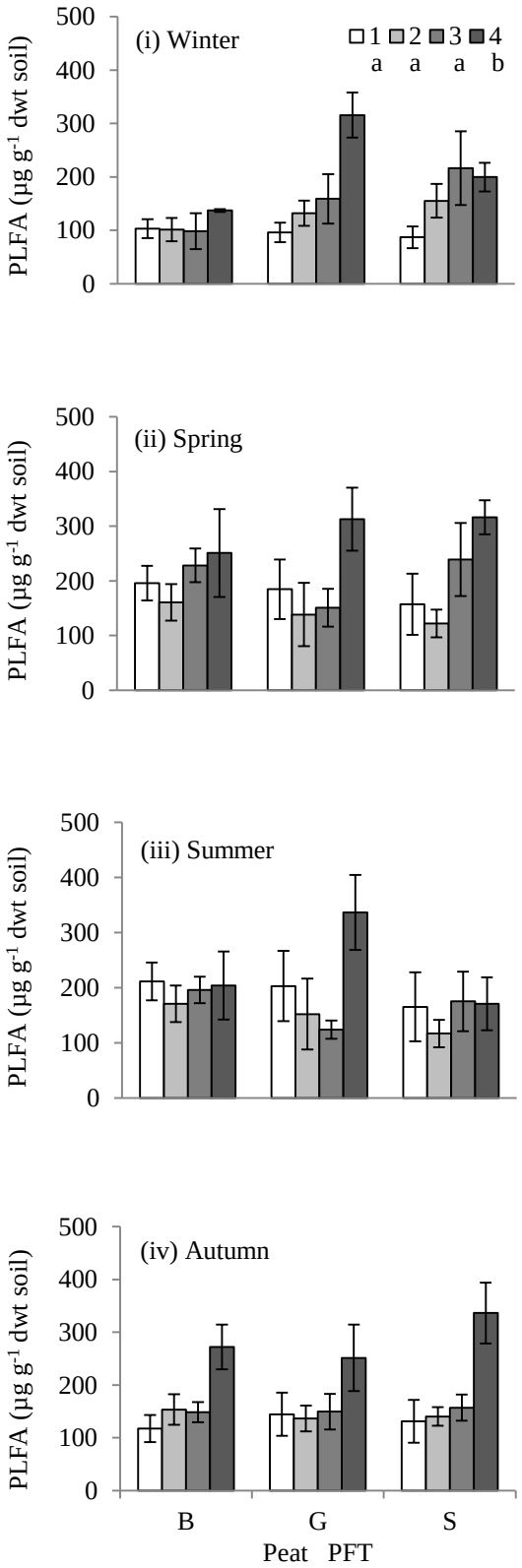

Figure 2.8: Seasonal total PLFAs at each site (1, 2, 3 and 4) and peat PFT (B = bryophyte, G = graminoid, S = shrub). Letters below legends denote pair-wise significant differences between sites. Pair-wise comparisons between season and peat PFT for total PLFAs are shown in Tables 2.5 and 2.13. Data are means ± standard error.

Table 2.9: Total bacterial PLFA concentration (µg g^{-1} dwt soil) at each peat PFT plot (B = bryophyte, G = graminoid, S = shrub) at each site. Mean values ± standard error.

Site	PFT	Total Bacterial PLFAs			
		Season			
		Winter	Spring	Summer	Autumn
1	B	46.74±9.04	102.87±18.17	40.57±7.10	60.90±14.11
	G	42.88±8.37	98.16±29.94	66.67±16.69	76.55±22.85
	S	37.55±9.23	81.92±32.22	50.54±0.87	67.54±21.98
2	B	43.40±9.92	82.76±19.00	44.37±6.21	78.84±15.97
	G	59.54±10.27	69.20±29.13	55.31±11.14	71.95±13.73
	S	60.35±11.66	61.56±13.29	49.67±7.58	70.21±8.46
3	B	44.99±16.69	117.28±16.97	68.83±3.23	73.81±8.81
	G	76.24±22.05	78.37±15.41	42.89±13.71	73.53±16.22
	S	103.90±32.85	113.51±31.01	76.30±4.60	77.99±10.77
4	B	66.23±2.60	127.17±46.42	75.96±18.17	137.99±23.93
	G	154.76±24.04	152.46±25.59	120.37±19.25	125.32±33.94
	S	91.54±9.38	141.08±16.04	103.93±11.15	160.04±34.33

Table 2.10: Total fungal PLFA concentration (μg g^{-1} dwt soil) at each peat PFT plot (B = bryophyte, G = graminoid, S = shrub) at each site. Mean values ± standard error.

Site	PFT	Total Fungal PLFAs			
		Season			
		Winter	Spring	Summer	Autumn
1	B	14.97±3.57	13.83±5.70	7.57±1.45	13.49±2.90
	G	14.09±3.22	9.37±3.08	11.89±2.81	17.08±5.33
	S	14.54±4.35	13.01±2.89	9.91±0.36	15.96±5.26
2	B	16.96±5.22	16.40±2.72	12.95±4.55	19.79±4.69
	G	21.13±4.27	16.64±7.73	11.51±3.09	15.67±1.67
	S	33.66±8.59	13.54±3.69	10.20±2.01	20.80±2.83
3	B	12.06±4.87	24.31±6.76	19.54±2.75	21.44±3.22
	G	20.74±8.37	17.70±6.14	11.88±4.31	23.54±5.75
	S	28.18 ±12.44	37.07±10.69	21.34±1.38	22.93±5.02
4	B	21.04±1.79	25.92±11.83	24.12±7.03	39.10±6.58
	G	48.25±4.28	46.12±11.40	46.25±8.35	36.76±8.57
	S	32.85±6.08	58.52±6.89	35.05±5.59	55.38±4.55

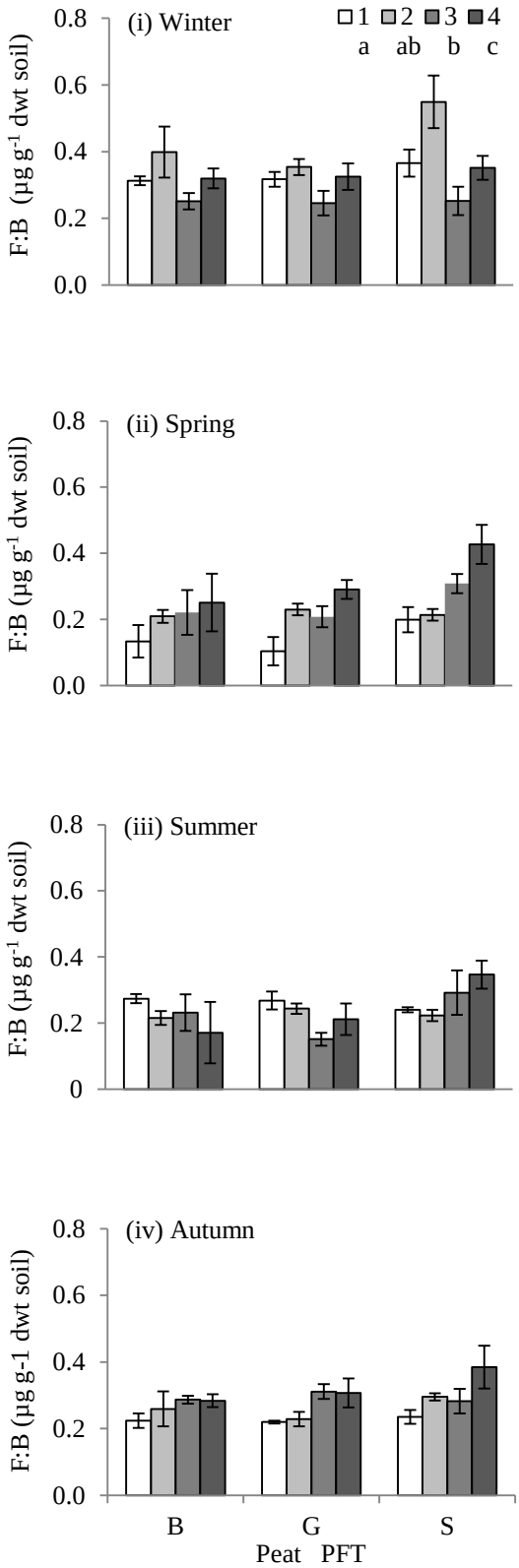

Figure 2.9: Seasonal F:B at each site (1, 2, 3 and 4) and peat PFT (B = bryophyte, G = graminoid, S = shrub). Letters below legends denote pair-wise significant differences between sites. Pair-wise comparisons between season, peat PFT and the interaction of season and site for F:B are shown in Tables 2.4, 2.5 and 2.11. Data are means ± standard error.

Table 2.11: Total gram +ve bacterial PLFA concentration (µg g^{-1} dwt soil) at each peat PFT plot (B = bryophyte, G = graminoid, S = shrub) at each site. Mean values ± standard error.

Site	PFT	Total Gram Positive Bacterial PLFAs			
		Season			
		Winter	Spring	Summer	Autumn
1	B	18.82±2.96	48.27±7.55	23.45±3.72	29.96±6.34
	G	18.04±3.52	49.36±14.77	37.82±8.45	37.36±10.36
	S	16.02±4.46	42.33±16.22	29.12±0.65	33.99±10.22
2	B	17.94±5.03	44.87±10.68	25.72±4.11	39.44±7.93
	G	24.82±6.83	37.26±14.46	31.52±6.79	35.99±6.71
	S	24.53±5.49	32.69±6.37	28.75±477	34.01±4.87
3	B	21.94±8.66	66.26±12.44	37.26±0.58	39.35±5.41
	G	38.62±10.78	45.12±7.56	23.20±9.00	35.93±7.95
	S	51.83±15.44	56.01±14.69	43.57±4.80	39.43±4.72
4	B	31.63±2.76	56.70±16.85	34.18±10.22	66.91±13.22
	G	69.55±8.69	77.58±10.73	48.87±6.49	58.24±15.34
	S	42.20±5.24	62.05±5.59	44.81±2.83	73.93±17.02

Table 2.12: Total gram -ve bacterial PLFA concentration (µg g^{-1} dwt soil) at each peat PFT plot (B = bryophyte, G = graminoid, S = shrub) at each site. Mean values ± standard error.

Site	PFT	Total Gram Negative Bacterial PLFAs			
		Season			
		Winter	Spring	Summer	Autumn
1	B	27.29±5.97	52.98±10.51	16.44±3.15	30.02±7.80
	G	24.17±4.94	47.54±14.76	28.08±8.30	38.25±12.32
	S	20.89±5.45	38.21±15.48	20.32±0.32	32.60±11.66
2	B	24.82±5.21	36.82±6.01	18.21±2.06	38.29±7.94
	G	33.90±3.86	30.94±14.15	23.05±4.35	34.91±7.09
	S	34.90±7.21	27.63±7.04	20.49±2.96	35.25±4.09
3	B	22.42±7.89	48.58±5.06	31.57±2.65	33.40±3.77
	G	36.61±11.23	31.79±7.55	19.62±5.94	36.59±8.70
	S	50.73±17.11	55.91±16.32	32.63±3.20	37.37±6.13
4	B	33.83±0.52	70.03±30.41	41.78±8.23	69.50±11.32
	G	83.08±16.48	72.69±14.08	71.50±12.76	65.65±18.89
	S	48.13±4.49	76.55±11.59	59.12±8.45	84.63±17.63

Table 2.13: Ratio of gram +ve and gram -ve bacterial PLFA at each peat PFT plot (B = bryophyte, G = graminoid, S = shrub) at each site. Mean values ± standard error.

		Gram Positive:Gram Negative Bacterial PLFAs			
Site	PFT	Season			
		Winter	Spring	Summer	Autumn
1	B	27.29±5.97	52.98±10.51	16.44±3.15	30.02±7.80
	G	24.17±4.94	47.54±14.76	28.08±8.30	38.25±12.32
	S	20.89±5.45	38.21±15.48	20.32±0.32	32.60±11.66
2	B	24.82±5.21	36.82±6.01	18.21±2.06	38.29±7.94
	G	33.90±3.86	30.94±14.15	23.05±4.35	34.91±7.09
	S	34.90±7.21	27.63±7.04	20.49±2.96	35.25±4.09
3	B	22.42±7.89	48.58±5.06	31.57±2.65	33.40±3.77
	G	36.61±11.23	31.79±7.55	19.62±5.94	36.59±8.70
	S	50.73±17.11	55.91±16.32	32.63±3.20	37.37±6.13
4	B	33.83±0.52	70.03±30.41	41.78±8.23	69.50±11.32
	G	83.08±16.48	72.69±14.08	71.50±12.76	65.65±18.89
	S	48.13±4.49	76.55±11.59	59.12±8.45	84.63±17.63

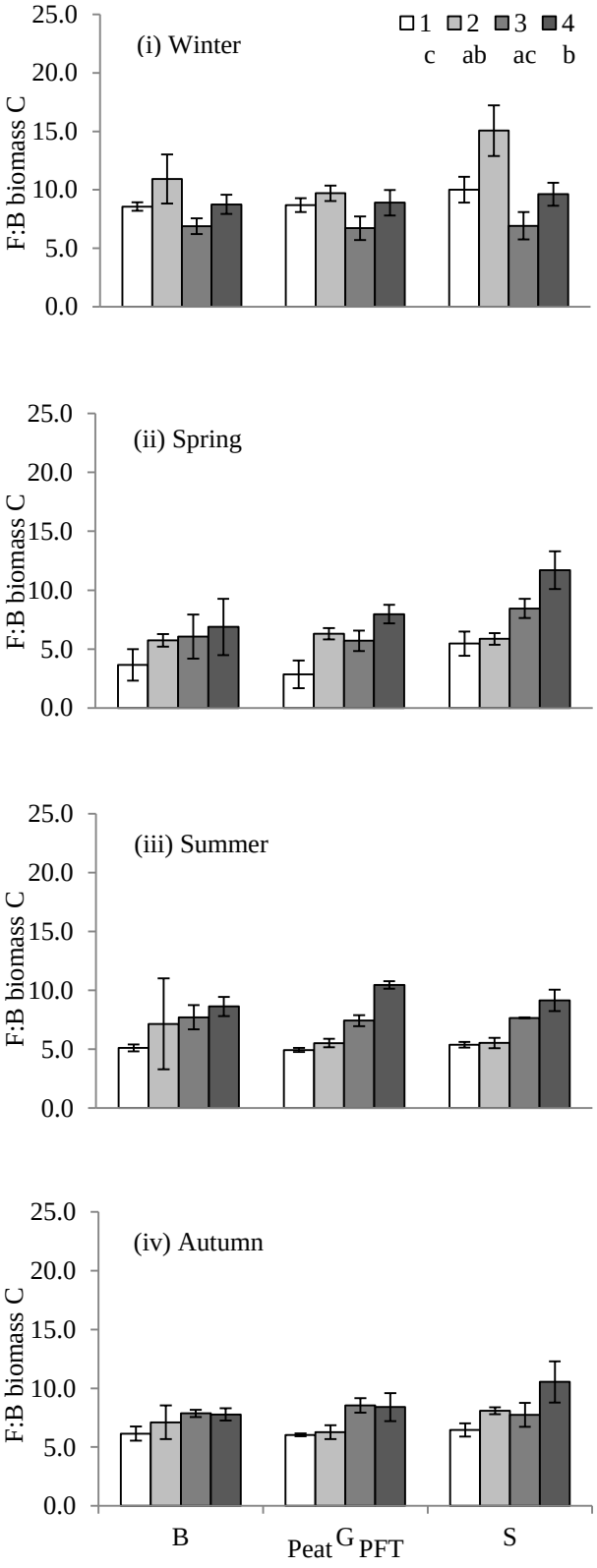

Figure 2.10: Seasonal F:B biomass C for each PFT (B = bryophyte, G = graminoid, S = shrub) and site (1, 2, 3 and 4). Letters below legends denote pair-wise significant differences between sites. Pair-wise comparisons between season, peat PFT and the interaction of season and site for F:B biomass C are shown in Tables 2.4, 2.5 and 2.11. Data are means ± standard error.

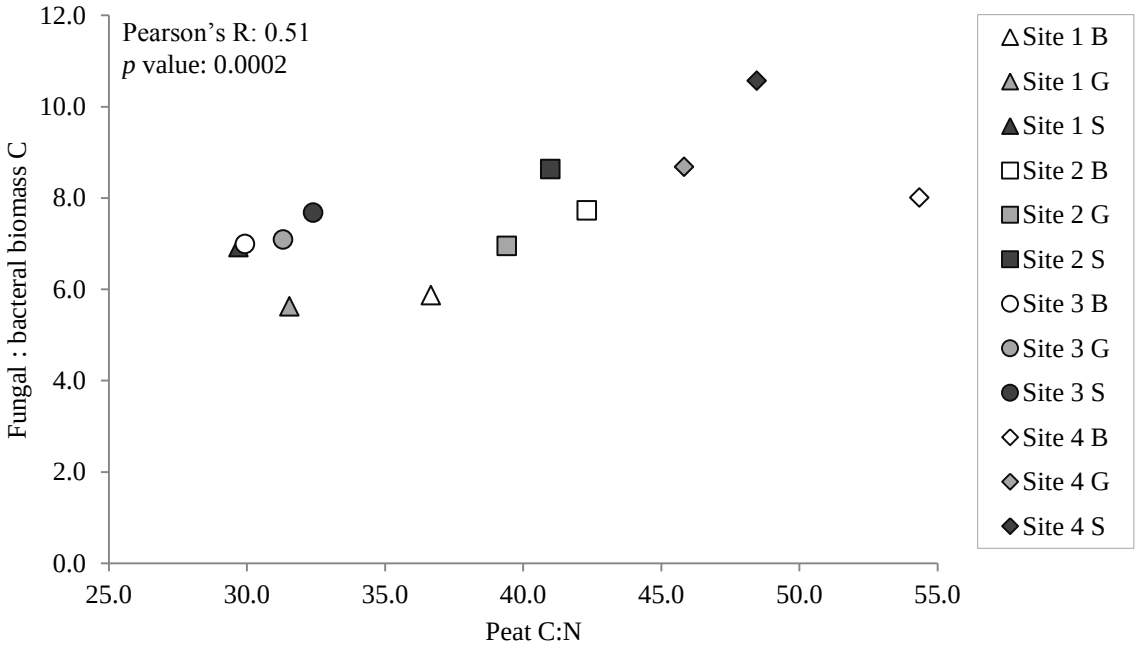

Figure 2.11: Mean F:B biomass C and mean peat C:N for each site and PFT (B = bryophyte, G = graminoid, S = shrub).

The db-RDA models of microbial community composition in winter ($F_{(12, 35)} = 3.898$, $p < .001$) and autumn ($F_{(12, 35)} = 3.2148$, $p < .001$) showed that a combination of peatland properties explained just over half of the modelled variance. Variance partitioning indicated that 59% of the modelled variation in the winter model (57%) was explained by a combination of peat properties (bulk density, pH, peat C%, peat N% and peat C:N) (Table 2.14), with bulk density, peat C:N and pH determined to be significant by forward selection (Table 2.15). In describing microbial community composition in autumn, peat properties explained 82% of the modelled variation (52%), with peat C:N the most significant explanatory variable (Table 2.14). The model which explained the greatest proportion of variance was the summer model ($F_{(12,28)} = 13.14$, $p < .001$), with variance partitioning and forward selection indicating that 83% of the modelled variance (85%) was explained by peat properties, of which peat C% and bulk density were significant (Table 2.15). The spring model ($F_{(12, 35)} = 2.2151$, $p < .001$) explained less modelled variation (43%) than winter, summer and autumn models. Variance partitioning showed that litter properties (litter depth, litter C%, litter N% and litter C:N) explained 77% of the modelled variation in the spring db-RDA (Table 2.14), and forward selection identified litter C% to be the sole significant explanatory variable of spring microbial community composition (Table 2.15).

To investigate the explanatory power of water table in addition to chemical peat, litter and vegetation properties in predicting seasonal and spatial microbial community composition, db-RDA models for spring, summer and autumn were repeated with the addition of water table deviation data. Deviation from the mean water table was not selected as a strong predictor of seasonally and spatially changing PLFA concentrations (Table 2.16). However, total C content of litter and vegetation and C:N of peat were consistently selected as the most significant variables for explaining the variation in seasonal microbial community composition across all wind farm sites (Table 2.16). This echoes the results from the first set of db-RDA models (Table 2.15). A db-RDA modelling approach demonstrated that the most commonly identified peatland properties selected to explain variation in the size and composition of the soil microbial community were total C content of litter and the ratio of C to N in peat. However, the peatland properties that explained the most variation in the measured microbial metrics changed with season: peat bulk density, litter total C content, peat total C content and peat C:N were shown to be the strongest predictors of the microbial community in winter, spring, summer and autumn, respectively.

Table 2.14: Results of variance partitioning carried out on individual PLFA concentration data following redundancy analysis (Table 2.9) to determine the proportions of variance explained by biochemical peat, litter and plant properties.

Season	PLFA community	Proportion of variance explained		
		Peat	Litter	Plant
Winter	Total PLFA	0.242	0.115	0.050
	Bacteria	0.087	0.154	0.051
	Fungi	0.043	0.122	0.108
Spring	Total PLFA	0.025	0.125	0.013
	Bacteria	0.005	0.111	0.016
	Fungi	0.025	-0.049	0.009
Summer	Total PLFA	0.283	0.055	0.003
	Bacteria	0.304	0.042	0.001
	Fungi	0.297	0.056	-0.016
Autumn	Total PLFA	0.125	0.041	-0.014
	Bacteria	0.089	0.083	0.008
	Fungi	0.006	-0.006	-0.052

Table 2.15: Redundancy analysis results showing the biochemical peatland properties which cause significant differences in individual PLFA concentrations for all sites and PFT plots in winter (February 2011), spring (April 2011), summer (July 2011) and autumn (October 2011). Water table data was not available for winter (February 2011) and therefore was not included in this analysis.

Season	Variable	F	*p*
Winter	Bulk density	13.58	0.001
	Litter C%	3.82	0.002
	Litter C:N	3.37	0.011
	Veg C%	3.98	0.007
	Peat C:N	3.13	0.012
	pH	2.09	0.044
Spring	Litter C%	12.32	0.001
	Peat C:N	2.69	0.014
	Veg C:N	2.47	0.018
Summer	Peat C%	59.90	0.001
	Bulk density	15.48	0.001
	Litter C%	7.39	0.002
Autumn	Peat C:N	14.71	0.001
	Litter C%	12.54	0.001

Table 2.16: Redundancy analysis results showing the biochemical and physical peatland properties which cause significant differences in individual PLFA concentrations for all sites and PFT plots in spring (April 2011), summer (July 2011) and autumn (October 2011). Water table data was included in this analysis because it was available for spring, summer and autumn (April, July and October 2011).

Season	Variable	F	*P*
Spring	Litter C%	12.32	0.001
	Peat C:N	2.68	0.008
	Veg C%	2.46	0.020
Summer	Litter C%	12.01	0.001
	Veg C%	3.41	0.007
	Peat C:N	2.68	0.022
Autumn	Litter C%	21.38	0.001
	Peat C:N	6.12	0.001
	Veg C%	5.22	0.001

2.4 Discussion

The aim of this study was to determine the spatio-temporal variability in abiotic and biotic properties of a blanket bog peatland at Black Law Wind Farm. Given the anticipated site and PFT-induced variability in physicochemical peat properties (hypotheses 1 & 2) and the known influence of these properties on C cycling processes, it was expected that the seasonal soil microbial community composition and size would also differ across Black Law Wind Farm (hypothesis 3). These results demonstrate that all peat physicochemical characteristics and microbial groups (Tables 2.1, 2.2 and 2.3) were significantly affected by site, with the exception of peat and litter total N contents, litter C:N and litter N stock (Table 2.1). The variables soil pH, bulk density, peat, litter and vegetation C contents, peat C:N and vegetation C:N were not only significantly different with site (Table 2.1) but also explained the most variation in the size and composition of the soil microbial community (Table 2.15). PFT was a strong driver of differences in peatland physicochemical characteristics (Tables 2.1 and 2.2), but also played a small role in determining differences in spatially and seasonally changing PLFA concentrations, owing to increased dominance of fungi relative to bacteria in in shrub-derived peat (Figure 2.9). Season was also a key control over water table and microbial community size and composition (Tables 2.2 and 2.3), with water tables nearer the peat surface in autumn (Figure 2.7), a spring-time increase in microbial community concentration (Figure 2.8) and a greater proportion of fungi relative to bacteria in winter (Figure 2.9).

2.4.1 Spatial and seasonal effects

The strongest driver of change in the peat properties studied was site, relative to the effects of season (Tables 2.2 and 2.3); this supports the principle that peatland C cycling varies more spatially than over time (Waddington and Roulet, 2000). For example, Waddington and Roulet (2000) observed a six-fold difference in CO_2 and CH_4 exchange between years, but there was up to 25 times difference in the net fluxes from areas of contrasting topography (i.e. hummocks and hollows). Nevertheless, seasonal changes in soil microbial communities are still central to the cycling of C in peatlands (Bardgett et al., 2005; Dinsmore et al., 2009; Fenner et al., 2005). Dinsmore et al. (2009) observed a clear temporal effect on CH_4 emissions but no consistent changes between sites dominated by different PFTs, and attributed seasonal differences to the activities of aerobic and anaerobic microbes in the growing season and winter season. Fenner et al. (2005) also found that there was a pronounced seasonality, and observed the optimum activity of C cycling enzymes to shift with soil temperature.

There were significant differences in the physicochemical properties of surface peat, litter and vegetation between sites across the peatland (Table 2.1), which confirmed the second hypothesis. Peat C:N and pH were highest at site 4, whereas bulk density, peat C and N stocks and litter layer depth were greatest at site 1 (Figures 2.1, 2.2, 2.3 and 2.5). Litter C content and C stocks were lowest at site 1 and site 2, respectively (Figures 2.4 and 2.5). Vegetation C was higher at sites 2 and 4, whilst vegetation N and C:N were lowest and greatest at site 3, respectively (Figure 2.6).

The peat bulk density, pH, total C and N contents at this wind farm peatland are comparable to those reported in studies investigating land use effects on peatlands, as well as peatlands that are neither developed nor disturbed. Across a range of undisturbed, drained and tree/shrub-dominated ombrogenous bogs in Finland, total N content was 0.5 – 1.0% and soil pH measured 3.7 – 3.9 (Silvola et al., 1996); these values are similar to those shown in Figures 2.1 and 2.2. In the surface 25 cm of peat at a bog in Minnesota, the overall average pH was the same as in this study i.e. 4.1 (Keller et al., 2004). Keller et al. (2004) also report peat total C content to be 42.2%, which falls within the range of values observed across the bog at Black Law Wind Farm (Figure 2.1). In Lower Saxony, Germany, the bulk density of peat ranged from: 0.06 – 0.21 g cm^3 in undisturbed peatlands, 0.08 – 0.15 g cm^3 in forested peatlands and 0.21 – 0.28 g cm^3 in peatlands converted to grasslands (Brake et al., 1999); these values are most similar to the peat bulk density at sites 2, 3 and 4 (Figure 2.2).

However, at a peatland in northern England with a long history of grazing and burning, the mean C stocks in the surface peat (20 cm deep) ranged from 3000 g C m^{-2} in grazed and burnt areas, up to 5500 g C m^{-2} in grazed and unburnt sites (Garnett et al., 2000). A later study, also at the same peatland in the Moor House National Nature Reserve (NNR), observed C stocks of a similar size as Garnett et al. (2000), an average C:N of ~37 and N stocks of ~1300 g N m^{-2} (Ward et al., 2007). Despite similar C:N ratios at Black Law (Figure 2.1), C stocks were higher and N stocks were lower than those observed by Ward et al. (2007) (Figure 2.3). Not only were there differences in the biochemical properties of the peat, but litter C:N was up to 1.5 times larger at the Black Law peatland than at Moor House NNR (Figure 2.4), and the C and N stocks in the litter layer were of an order of magnitude larger (Figure 2.5) (Ward et al., 2007). As for vegetation C:N, grazed and burnt peatland sites had slightly higher values than those reported in this study for the same PFTs (Figure 2.6) (Ward et al., 2007).

The breakdown of the microbial community into broad functional groups, determined by PLFAs, also revealed some strong spatial and seasonal patterns (Table 2.3) to support hypothesis 3. Site 4 was characterised by higher total concentrations of PLFAs than sites 1, 2 and 3 (Figure 2.8). The soil microbial community changed with fungi increasing in relative abundance compared to bacteria, notably in spring, from site 1 to 4 (Figure 2.9). Spring is characterised by higher total PLFA concentrations than summer and winter (Figure 2.8). However, in Swedish boreal peatlands, the variation in PLFA composition was found to be negligible over the growing season (Sundh et al., 1997). In other studies, microbial communities have been known to acclimate to prevailing external conditions and shift with changing environmental parameters associated with season (Fenner et al., 2005; Freeman et al., 2001). In northern upland peatlands, Fenner et al. (2005) found that a thermal optimum in microbially-mediated C cycling processes coincided with the highest ambient soil temperatures, and Freeman et al. (2001) observed increased enzyme activity in more aerated peat. However, some microbes can survive in a dormant state when conditions are outside of their normal range for growth (Atlas, 1988), and can then proliferate once optimum conditions return (Ranneklev and Bååth, 2001). Peat may therefore possess a 'microbial memory', to allow growth and activity to prevail when possible. The adaptation to seasonal shifts in environmental conditions, together with the potential for 'microbial memory', could explain why a spring-time maximum in total PLFA concentrations is observed. Therefore, this may reflect environmental conditions that are favourable for microbial communities i.e. a deeper spring-time water table (Figure 2.7) could promote increased activity of the soil decomposer community (Freeman et al., 2001). However, in forested peatlands in Finland, a spring-time increase in bacterial biomass was observed but total microbial biomass decreased with a drop in the average water tables (Mäkiranta et al., 2009). Nevertheless, spatio-temporal shifts in total microbial biomass and the relative abundance of microbial functional groups are also likely to be a result of differences in temperature (Pietikåinen et al., 2005; Ranneklev and Bååth, 2001), C and nutrient availability (Bossio et al., 1998; Schadt et al., 2003) or even predation of microbes (Wynn-Williams, 1982).

Many studies observe temperature to be the main driver of microbial activity (Lipson et al., 2002; Mäkiranta et al., 2009; Pietikåinen et al., 2005) and community composition change (Bossio et al., 1998; Lipson et al., 2002; Pregitzer et al., 1997). In this study, higher F:B in the winter microbial community relative to the summer community was observed, and has been reported previously, owing to the adaptation of fungi to colder temperatures (Pietikåinen et al., 2005), the utilisation of more complex structures (i.e. cellulose) (de

Boer et al., 2005) and the reduction in root exudates (Mäkiranta et al., 2009). In dry alpine meadow and tundra ecosystems, the soil microbial biomass reached its annual peak in winter, under snow, with fungi accounting for most of that increase in biomass (Lipson et al., 2002; Schadt et al., 2003). The availability of C substrates has also been linked to seasonal changes in the relative size of microbial groups in soil communities (Bossio et al., 1998), with increases in fungi due to a greater abundance of dead plant material in winter (i.e. harder to decompose litter material) while live roots and the supply of their exudates (i.e. easier to utilise substrates) increase in summer and favour bacteria (Schadt et al., 2003). Soil respiration rates have also been associated with differences in soil microbial community in spring, due to the decreasing importance of readily available organic matter as a determinant of the soil microbial community later in the growing season (Bossio et al., 1998) and due to a post-spring increase in predation of microbes by nematodes and protozoans (Wynn-Williams, 1982). These are possible explanations for the spring to summer decrease in soil microbial community size observed in this study (Figure 2.8).

Bulk density, pH, total C and C:N of peat, litter and vegetation were selected to best predict the variation within PLFA profiles of each peat sample (Table 2.15). The proportion of variance explained by peat, litter and vegetation variables was different for total PLFAs, fungal PLFAs and bacterial PLFAs in each season (Table 2.14), so it is difficult to identify which of the selected variables would consistently predict microbial community composition throughout the year. Other studies have also shown the effects of soil chemical characteristics on microbial community structure. At a cutover peatland undergoing restoration, redundancy analysis found peat bulk density, pH and water table to be significant in explaining seasonal variation in PLFAs (Andersen et al., 2010), whereas total N content and total C content were also used to best explain variability in the microbial community at a successional peatland gradient (Mitchell et al., 2010). A large proportion of the variation in bacterial community composition was also found to be caused by pH (Fierer et al., 2009; Lauber et al., 2008), and changes in fungal community composition were most closely correlated with nutrient status (Lauber et al., 2008) and C:N (Fierer et al., 2009). The moderate positive correlation between peat C:N and F:B biomass C across the peatland at Black Law Wind Farm (Figure 2.11), supports the relationships between soil C:N and F:B observed in other studies. For example, C:N declined along a successional gradient from shrub moorland to birch woodland, which coincided with a decrease in soil F:B (Mitchell et al., 2010). F:B has also been observed to increase from rich to poor fens, with fungal activity differing by more than a factor of five and bacterial activity by less than a factor of two (Myers et al., 2012). There are a number

of possible mechanisms that may explain this: (1) C:N could directly constrain the soil microbial community owing to the different nutrient demands of the fungal and bacterial energy channels (Bardgett and Wardle, 2010; De Deyn et al., 2008) i.e. the production of extracellular enzymes and transport proteins by recalcitrant C users (fungi) demands more N than the activities of labile C users (bacteria), and means that fungi are less common in more N-limited soils (Allison et al., 2011; Treseder et al., 2011), (2) fungal activity is likely to be low in rich peatland sites i.e. with low C:N, due to increased competitive ability of bacteria (Myers et al., 2012), (3) C:N may serve to represent the combined effects of multiple drivers such as pH and the quantity and quality of organic matter inputs from plant litter and root exudates (Fierer et al., 2009) and (4) higher F:B may lead directly to higher soil C:N, given the wider C:N of fungal biomass (Guggenberger et al., 1999).

Water table is often studied, due to its spatial and seasonal effects on C cycling and response to land use change and local to global scale climate change (Ise et al., 2008; Lafleur et al., 2005; Weltzin et al., 2000). Site and season were significant factors for water table depth (Table 2.2), with the position of the water table highest in autumn and for sites 1 and 3 (Figure 2.7). However the change in water table depth i.e. the deviation in water table level from the mean across all PFTs, sites and seasons, was not identified as a significant control over spatially and seasonally changing soil microbial communities (Table 2.16). Contrary to this study, water table depth or soil moisture has previously been identified as an important driver of differences in the size and composition of the soil microbial community (Andersen et al., 2010; Dinsmore et al., 2009; Jaatinen et al., 2007; Mäkiranta et al., 2009; Mitchell et al., 2010), with fungi generally better adapted to low moisture conditions. At this wind farm peatland, other factors such as soil temperature or the availability of substrates to microorganisms could be stronger than the effect of water table upon the soil microbial community size and structure. Another explanation could be that PFTs buffer the effect of the water table upon the soil microbial community by responding differently to water table change. *Sphagnum* mosses have been reported to be most sensitive to the short-term draw-down of the water table, with almost complete cessation of their physiological activities (Riutta et al., 2007). On the other hand, shrub CO_2 exchange hardly changed, but contributed twice as much to the CO_2 exchange than sedges, under lower water table levels (Riutta et al., 2007). This demonstrates that water table position affects PFT-induced differences in CO_2 exchange, and therefore has the potential to influence other plant processes (i.e. production of root exudates) that would affect the overall size and relative proportion of microbial groups within the soil community (Schadt et al., 2003). Therefore, the indirect effects of water table-induced

changes in PFTs might be stronger determinants of differences in the microbial community than direct effects of water table position.

2.4.2 Plant functional type effects

As confirmation of hypotheses 1 and 3, PFT was a significant factor in determining differences in the physicochemical properties of peat, litter and vegetation (Tables 2.1 and 2.2) and changes within the soil microbial community (Table 2.3). The total concentrations of microbes were not significantly different between PFTs, but shifts in the relative abundance of fungi and bacteria were detected i.e. more fungi beneath shrub (Table 2.3). Ward et al. (2007) found that the peat decomposer community was not as sensitive to land use-induced changes in vegetation community composition as expected, whereas previous studies in boreal ecosystems have shown measures of microbial community to respond to the manipulation of PFTs i.e. the removal of shrubs and mosses (Wardle and Zackrisson, 2005). However, whilst PFT does not affect the overall abundance of microbes, PFTs do play an important role in the composition of the microbial community at this wind farm peatland. In turn, PFT-induced changes in the microbial community composition might influence C cycling, due to altering the dominance of particular functional groups (de Boer et al., 2005; Fisk et al., 2003; Waring et al., 2013). For example, Fisk et al. (2003) measured greater microbial activity in sites dominated by shrubs and *Sphagnum* moss than in sedge-dominated sites. Furthermore, patterns of substrate utilisation differed between shrub/*Sphagnum* and sedge sites, and this suggests that different assemblages of microorganisms mediated C fluxes in shrub/*Sphagnum* peat. In this study there were higher ratios of fungal to bacterial PLFAs in shrub-derived peat (Figure 2.9), possibly owing to the greater C content of shrub litter and vegetation observed (Figures 2.1 and 2.6) (McGuire et al., 2010; Treseder et al., 2011) and possibly greater abundance of mycorrhizae (Talbot et al., 2008). Another explanation could be that there were higher concentrations of lignin and phenolic compounds in shrub litter (Ward et al., 2009), which would select for microbes with a greater ability to utilise recalcitrant soil organic matter, and generate a bias towards the more conservative, fungal-based energy channel (Bardgett and Wardle, 2010). As seen by (Bardgett and Wardle, 2010), greater inputs of graminoid litter and rhixoexudates to peat can promote a bacteria-dominated microbial community, which might explain the relatively low F:B ratios observed in graminoid peat (Figure 2.9). Whereas symbiotic relationships between bryophyte mosses (i.e. *Sphagnum*) and N-fixing cyanobacteria (DeLuca et al., 2002) might be one mechanism that could lead to a relatively low abundance of fungi to bacteria in bryophyte peat (Figure 2.9).

Plants are a major source of C substrate for the soil microbial community, the form of which will vary with PFT (Ward et al., 2009). PFT-induced differences in litter and vegetation properties (Table 2.1) were found to explain variation within the soil microbial community (as tested by db-RDA) (Tables 2.14, 2.15 and 2.16), which indicates that the differences in the quality of plant inputs to the soil (i.e. C and N content) between each PFT might be one mechanism behind differences in the soil microbial community. In a study of a cutover peatland, Artz et al. (2007) acknowledged that such changes in below-ground C availability can drive differences in the diversity of fungal communities. However, because the original plant PFT signature can become progressively weaker as decomposition occurs i.e. from litter to peat (Grayston, 1998; Orwin et al., 2006), this might account for the minimal effects of PFT on biochemical peat properties and the soil microbial community (Tables 2.1 and 2.3). Furthermore, the influence of PFT on the soil microbial community could be obscured by other stronger controls on the microbial community i.e. soil chemistry, temperature and moisture (Mäkiranta et al., 2009; Mitchell et al., 2010). By measuring the soil microbial community in the surface 15 cm of peat, it is possible that the portion of soil microbial community that is most likely to be affected by small-scale variation in soil chemistry and climate was sampled. Therefore, the effects of soil chemistry and climate may exceed those of PFT. The lack of PFT effects on PLFA groups (apart from F:B) and chemical peat properties could also be a result of greater patchiness in vegetation at Black Law than at other blanket bogs such as Moor House, Upper Teesdale, where PFT modulated the response of GHG fluxes to climatic change (Ward et al., 2013).

Research was undertaken on a wind farm site, to study the effects of a new land use change for peatlands. This work revealed spatio-temporal differences in peat, litter and vegetation physicochemical properties and the soil microbial community across a wind farm hosting peatland, which were comparable with those in undisturbed peatlands and peatlands subjected to other more common land uses i.e. drainage and forestry, but less so with grazed and burnt peatlands. The bulk density and pH of peat, together with the total C content and C:N of peat, litter and vegetation were identified as the strongest controls over the soil microbial community. However, PFT may be better suited to predicting the soil microbial community than one-off measurements of soil properties and chemicals, because relatively slow growing vegetation types represent a better long term proxy of climate, soil chemistry and land use, than soil characteristics alone (Mitchell et al., 2010). The differences in the peatland properties observed here cannot be directly attributed to a wind farm microclimate effect, but do suggest that wind farm-induced changes in the plant

community composition could have important implications for surface storage and flux of C in peatlands hosting wind farms.

2.5 Conclusions

This research aimed to assess the spatio-temporal variation in aboveground and belowground peatland properties for each PFT, at a peatland hosting a wind farm. As expected, site was a dominant factor for changes in peat, litter and plant physicochemical properties, while PFT effects were found for all measured litter and vegetation properties, but only peat N stock. The position of the water table and the size and composition of soil microbial communities did vary seasonally, but there were stronger spatial differences observed i.e. between PFTs or across the peatland. Peat variables were strongly correlated with soil microbial community composition across all sites in winter, summer and autumn, whereas litter variables explained the most variation in spring-time soil microbial communities. This supports the interpretation that variation in microbial community composition for each PFT and across all sites and seasons was primarily related to peat characteristics: bulk density, pH, total C content and C:N (Table 2.15). While PFT did affect the composition of the microbial community, there were no PFT-induced differences in microbial abundance. However, litter and vegetation total C content and C:N were selected to explain a significant amount of variation within the seasonally and spatially changing soil microbial community. Therefore, peat, litter and vegetation chemical characteristics can all serve as key determinants of soil microbial communities, but the observed interactions of site with season and PFT suggest that complex feedbacks to environmental change are to be expected. Furthermore, the causes and consequences of these results need more consideration. Studying wind farm-induced microclimate effects of small-scale temperature change on peatland C cycling and understanding how plant functional traits influence decomposition rates are important.

The variation found in aboveground and belowground peatland properties across Black Law Wind Farm supports the need for spatially distributed designs that incorporate PFTs and seasonal sampling, when understanding peatland C cycling and storage. In order to improve the capacity to predict ecosystem response to global climate change, land use change and even land use-induced microclimate change, future field studies should control for PFT and spatio-temporal variability in physical, chemical and biological peatland properties.

Microclimate and plant functional type controls on peat greenhouse gas fluxes

3.1 Introduction

Northern peatlands play an important part in global carbon (C) cycles (Sulman et al., 2013), however climate change (Ward et al., 2013) and land use change (Armstrong et al., 2014; Ostle et al., 2009) increase the vulnerability of currently vast peatland C stores. The principal consequences of climate change and land use change in peatlands include alterations in air and soil temperature and water table depth, which are known to strongly regulate the release of greenhouse gases (GHG) and determine rates of C sequestration in peatlands (Davidson and Janssens, 2006; Sulman et al., 2013). In addition, changes in plant community composition have also been observed which are likely to mediate C cycle responses to climate and land use change (Gallego-Sala and Prentice, 2012; Ward et al., 2013), but the relative importance and mechanisms underlying these effects are unclear (Carney and Matson, 2005; Ward et al., 2013; Weltzin et al., 2000). Northern peatlands are subjected to natural cycles of temperature and moisture conditions (seasonal, diurnal and inter-annual). For example, soil temperatures have been found to range from -4°C to 16°C (Fenner et al., 2005; Worrall et al., 2004) and water tables can fluctuate between the peat surface and up to 45 cm below (Bubier et al., 2003; Holden and Burt, 2003) across a range of tundra and temperature peatlands. The relatively small microclimate changes predicted as a result of global climate change (i.e. 1.7 – 4.4°C rise in air temperature, together with fluctuating precipitation) (IPCC, 2013) and land use change (i.e. water table >50 cm below the surface in drained sites) (Price et al., 2003) are likely to affect C cycling, but effects could be relatively small. However, this has not been tested experimentally, and the direct effects of microclimatic change and interactions with typical peatland plants are poorly understood.

Temperature and water table level regulate peat respiration and decomposition processes (Briones, 2009; Clark et al., 2009; Rydin et al., 2006), and resultant carbon dioxide (CO_2) and methane (CH_4) emissions (Bardgett et al., 2008; Ward et al., 2009). Relatively small temperature and water table changes have been observed to significantly affect ecosystem functioning, for example a mean 1°C annual increase in temperature raised respiration by up to 60% in Arctic blanket peatland (Dorrepaal et al., 2009), whilst a warming of 1^oC increased CH_4 fluxes by 80%, 8% and 75% under raised, control and lowered water tables respectively (Turetsky et al., 2008). Greater GHG emissions with warming (4 to 24^oC) in peat cores with high and low water table levels (near surface to 36 cm below) are also observed under controlled laboratory conditions (Aerts and Ludwig, 1997; Blodau et al., 2004; McKenzie et al., 1998; Scanlon and Moore, 2000; Waddington et al., 2001). Shifts in

peatland water table levels alter the balance between aerobic and anaerobic conditions influencing biological processes in the peat. Aerobic conditions favour peat CO_2 emissions and inhibit CH_4 emissions (Estop-Aragonés, 2011; Öquist and Sundh, 1998), whilst anaerobic conditions decrease CO_2 emissions and increase CH_4 emissions (Glatzel et al., 2004; Moore and Dalva, 1997).

Plant community composition effects on C cycling are less understood. In blanket peatlands dominant plant functional types (PFTs) are bryophytes (e.g. *Sphagnum* sp., feather mosses), shrubs (e.g. *Calluna vulgaris, Vaccinium* sp.) and graminoids (e.g. *Eriophorum vaginatum,* sedges, and rushes). The regulatory roles of PFTs in peatland C dynamics (Ward et al., 2012). These functional traits determine the quality and quantity of C inputs entering the soil (Bardgett et al., 2013), resulting in changes to the chemical composition of peat (Ward et al., 2009) and the form and function of the soil microbial community (Artz, 2009; Read et al., 2004). Ultimately, PFT-induced differences in soil microbial composition will modulate the magnitude of GHG emissions (De Deyn, 2011; Hector et al., 2000; Ward et al., 2010, 2007).

Effects of PFT on GHG emissions have been observed in the field and laboratory. Areas occupied by graminoids had higher GHG fluxes than adjacent shrub dominated blanket peat (Greenup et al., 2000; McNamara et al., 2008; Ward et al., 2013) and mesocosms containing sedges had significantly higher fluxes of CH_4 compared to those without (Green and Baird, 2013). It is known that graminoids and shrubs differ in the rate that they allocate C belowground (Ward et al., 2012, 2009). These differences are expected to affect the quality and quantity of root exudates released to the soil and thereby alter the composition and activity of microbial communities (Bardgett et al., 2013; De Deyn et al., 2008), for example peat beneath shrub is likely to have a greater abundance of mycorrhizal fungi than under graminoids (Read et al., 2004). Plant root symbioses and the presence of recalcitrant litter (which has increased C:N and concentrations of phenolic compounds) have been found to explain the association of fungi with shrubs (Freeman et al., 2001; Myers et al., 2012; Smith and Read, 2010). Bacteria dominate in moss- and sedge-derived peat (Winsborough and Basiliko, 2010) due to more easily decomposed litter (Ward et al., 2010) and peat containing smaller proportions of recalcitrant material (Myers et al., 2012). Bryophyte mosses play an important role in peatland CH_4 cycling, through their close association with methanotrophic bacteria (Kip et al., 2010) whereas graminoids provide conduits for passive gas transfer from the peat to the atmosphere with their aerenchymous tissues (Artz et al., 2007; McNamara et al., 2008; Moore et al., 2007; Pietikåinen et al.,

2005) and stimulate methanogenic bacteria due to the provision of labile substrates (i.e. acetate) through their deep roots (Ström et al., 2012). Fungi are known to have slower and more efficient use of C than bacteria (Rousk and Bååth, 2007; Six et al., 2006), so the ratio of fungi to bacteria in the soil microbial community beneath dominant PFTs can affect the storage and flux of C in peatlands (Waring et al., 2013). As a result of PFT-induced changes in abiotic and biotic soil conditions, a plant legacy effect can therefore exist within the soil and play an important role in regulating GHG emissions.

Rarely are the effects of temperature, water table and PFT on GHG fluxes examined together (Couwenberg et al., 2011; Green and Baird, 2012; Ward et al., 2009) and PFT interactions with microclimatic changes in temperature and water table remain unknown. This represents a significant gap in knowledge that needs to be addressed to improve understanding of the mechanisms that regulate peatland biogeochemical cycling. The objective of this study was, therefore, to assess the sensitivity of peat GHG fluxes to small-scale changes in temperature and interactions with water table level and PFT to enable better predictions of the role of microclimate change and plant community composition on peatland C cycling. A multi-factorial microcosm experiment was designed to test the interactive effects of temperature and water table, on CO_2 and CH_4 fluxes from peat sampled from under three different PFTs. In this study, the hypotheses were: (1) small-scale changes in temperature and water table level would interact to differentially affect peat CO_2 and CH_4 fluxes, with effects being more pronounced at high and low temperature and water table levels, (2) the legacy of plant species traits upon peat abiotic and biotic properties would result in differences in GHG fluxes, with greater CH_4 fluxes from graminoid peat due to the supply of labile C substrates into the peat, (3) the influence of PFT on peat GHG fluxes would be strongest at the start of the incubation, with temperature and water table treatments dominating PFT legacy effects as labile C substrate depletion occurred over time.

3.2 Methods

To address the hypotheses of this study, peat cores were taken in May 2011 from a blanket bog at Black Law Wind Farm, Lanarkshire, Scotland (Figure 1.1, Chapter 1). One hundred and eight intact cores (PVC pipe, 11 cm diameter, 30 cm depth) were taken from beneath three dominant plant species (i.e. *Calluna vulgaris*, *Eriophorum vaginatum* and *Sphagnum capillifolium*) each being representative of shrub, graminoid or bryophyte PFTs. Vegetation was removed from the core surface area prior to collection to control for differences in initial plant biomass and future growth. Instead, this study examined the

legacy of PFT effects within the upper layer of peat - the portion of depth profile most sensitive to abiotic change and most productive of GHGs (Strack et al., 2008). To reduce the influence of spatial variation, cores were all collected within an area of approximately 10 m^2. Whilst minimising disturbance to the peat, cores were extracted manually, wrapped in polythene and transported to the laboratory. Bases were fixed to all of the cores using silicone adhesive sealant. A drainage tube was inserted near the base of each cylinder and fixed up the length of the microcosm to facilitate water table measurements. Cores were kept at 4°C prior to the commencement of the experiment. Supplementary peat samples (PVC pipe cores, 5 cm diameter, 15 cm depth) were taken from the sampling location to quantify peat bulk density, pH, total C content, total nitrogen (N) content, C:N, C stock, N stock and soil microbial community composition beneath each PFT (see section 2.2, Chapter 2).

A fully factorial experiment was established comprising three temperatures, three water table levels, three PFTs replicated four times. Incubation temperatures were above mean annual temperature (8°C) at Black Law wind farm and within a 4°C range (12, 14, and 16°C). The temperature range was chosen in order to simulate conditions at the field site during summer (i.e. a period of increased GHG uptake and release), as well as small-scale temperature changes which could result from global climate change and land use change. The global mean surface temperature is projected to rise by 2-4 °C by the end of the 21st century, according to the Representative Concentration Pathway (RCP) 8.5 (IPCC, 2013). Wind farm microclimate effects have also been observed to change surface air temperature by 0.7-3.5 °C (Armstrong et al., 2014b; Baidya Roy and Traiteur, 2010).

Thirty six peat cores were placed into each of three controlled temperature rooms. At each temperature, 12 peat cores from each PFT were randomly assigned a water table level treatment. Water table levels were adjusted to below the surface of each core with depth ranges chosen that are typical of the water table dynamic range at this site (Waldron *et al*., unpublished raw data): low (25 cm depth), intermediate (15 cm depth) or high water table level (5 cm depth).

Water table levels were manipulated with the addition of deionised water during a two week adjustment period, and maintained throughout the experiment. Deionised water was used in preference to rainwater to control for variable nutrient inputs. Peat cores were incubated for 322 days, with CO_2 and CH_4 emissions measured six times at 7, 35, 154, 223 and 322 days after the start of the experiment. To measure CO_2 and CH_4 flux rates, an opaque chamber (12 cm diameter, 10 cm height) was attached to the top of each core with

silicone adhesive sealant (mean headspace volume was 642.14 cm^3). Headspace gas samples (10 ml) were collected through a rubber septum in each chamber lid, using a 20 ml syringe fitted with a 0.5 mm needle, flushed three times with headspace gas before filling. Gas sampling was at four time points, immediately after sealing the lid and then at three 10 minute intervals. All gas samples were stored in pre-evacuated 3 ml exetainers (Labco, UK) and analysed for CO_2 and CH_4 concentration on a Perkins Elmer AutosystemXL GC with FID and methaniser. Full details of GC conditions are described in (Case et al., 2013). Results were calibrated against two certified gas standards of 500 and 4000 ppm CO_2, 1 and 10ppm CH_4. Gas fluxes (CO_2 and CH_4) were calculated from the change in chamber concentration, air temperature and chamber volume and area measurements (Holland et al., 1999).

3.2.1 Statistical analysis

One-way ANOVA was performed using SAS V9.1, Enterprise Guide 4.0 to test the significance of PFT on biochemical characteristics of peat, followed by Tukey's test *post-hoc* analyses. Normality of data was checked before analysis and appropriate transformations were applied if necessary. This analysis was conducted in order to test the hypothesis that a plant functional type legacy in peat can affect biochemical properties, and in turn influence GHG fluxes.

Repeated measures ANOVA was performed using SAS V9.1, Enterprise Guide 4.0 to test the hypotheses that PFT legacy effects in peat and small-scale changes in temperature and water table would result in differences in GHG fluxes over the incubation period. The significance of temperature, water table level and PFT over time was tested on CO_2 and CH_4 fluxes, followed by Tukey's test *post-hoc* analyses. Data were checked for normality, with natural log transformations applied to CO_2 and CH_4 data before final analysis.

Throughout the text, 'significant' is referred to if $p < 0.05$.

3.3 Results

3.3.1 Biochemical peat properties

Bulk density, pH, total C content, total N content, C:N, C stock, N stock and measures of microbial community composition and size are shown in Table 3.1. One-way ANOVA analyses show that these peat properties were not significantly different with PFT at the sampling site (Table 3.1).

3.3.2 CO_2 fluxes

Average CO_2 flux response to temperature, water table and PFT ranged between 0.05 and 1.96 CO_2 – C g m^{-2} d^{-1}. Temperature and water table significantly affected CO_2 fluxes, with an interaction between them (Table 3.2). CO_2 fluxes increased with rising temperature and lowering of the water table, with this response being strongest at the warmest temperature (Figure 3.1).

PFT did not significantly affect CO_2 fluxes analysed across the 11 month experiment (Table 3.2), but there were significant positive interactions between temperature and PFT at day 0 ($F_{(2,626)} = 3.75$, $p = 0.0076$), day 7 ($F_{(2,626)} = 3.10$, $p = 0.0198$) and day 35 ($F_{(2,626)} = 3.82$, $p = 0.0067$), with additional interactions between water table and PFT at day 7 ($F_{(2,626)} = 4.64$, $p = 0.0020$) (data not shown). Interactive effects of temperature, water table and PFT had the greatest impact upon CO_2 fluxes from graminoid and bryophyte cores, which increased by a greater magnitude than shrub CO_2 fluxes at the warmest temperature and lowest water table.

There was a significant interaction between time and temperature (Table 3.2), with CO_2 fluxes decreasing over time by a larger extent at lower temperatures. For instance, at day 0 average CO_2 fluxes at the lowest temperature were approximately 26% greater than at day 322, whereas emissions at the warmest temperature were approximately 10% greater at day 0 than at day 322 (data not shown). Effects of water table varied significantly over the course of the experiment, with the effect of time decreasing CO_2 fluxes by a greater degree under high water tables. Average CO_2 fluxes were approximately 60% greater with high water tables at day 0 than at day 322, while emissions at day 0 from low water tables were approximately 17% greater than at day 322 (data not shown).

Table 3.1: Biochemical peat properties for each PFT (B = bryophyte, G = graminoid, S = shrub). BD = dry bulk density (g cm^{-3}), C% = total C content, N% = total N content, C:N = ratio of C% and N%, C stock = g C m^{-2} to a depth of 15 cm, N stock = g N m^{-2} to a depth of 15 cm, total PLFAs = total PLFA concentration (µg g^{-1} dwt soil), fungi = total fungal PLFAs, bacteria = total bacterial PLFAs, F:B = ratio of fungal to bacterial PLFAs, gram +ve = gram-positive bacterial PLFAs, gram –ve = gram-negative bacterial PLFAs, G +ve:G –ve = ratio of gram-positive bacterial to gram-negative bacterial PLFAs. Data are means ± standard error. One-way ANOVA results showing the effect of PFT: *ns* = not significant, * = $p < 0.05$, ** = $p < 0.01$ and n = 4 per PFT.

	PFT		
	B	G	S
BD	0.10 ± 0.02 ns	0.11 ± 0.05 ns	0.10 ± 0.02 ns
pH	4.06 ± 0.06 ns	4.14 ± 0.10 ns	4.07 ± 0.07 ns
C%	40.84 ± 1.06 ns	40.51 ± 1.36 ns	40.30 ± 0.79 ns
N%	0.99 ± 0.08 ns	1.03± 0.05 ns	1.00 ± 0.09 ns
C:N	42.32 ± 3.85 ns	39.42 ± 2.23 ns	40.99 ± 2.63 ns
C stock	6159.15 ± 1190.45 ns	6719.40 ± 950.10 ns	5812.33 ± 1101.10 ns
N stock	141.92 ± 17.83 ns	169.67 ± 19.60 ns	149.61 ± 40.83 ns
Total PLFAs	101.61 ± 21.85 ns	132.23 ± 23.66 ns	155.18 ± 31.64 ns
Fungi	16.96 ± 5.22 ns	21.13 ± 4.27 ns	33.66 ± 8.59 ns
Bacteria	43.40 ± 9.92 ns	59.54 ± 10.27 ns	60.35 ± 11.66 ns
F:B	0.40 ± 0.08 ns	0.35 ± 0.02 ns	0.55 ± 0.08 ns
Gram +ve	17.94 ± 5.03 ns	24.82 ± 6.83 ns	24.53 ± 5.49 ns
Gram –ve	24.82 ± 5.21 ns	33.90 ± 3.86 ns	34.90 ± 7.21 ns
G +ve:G -ve	0.72 ± 0.14 ns	0.70 ± 0.17 ns	0.73 ± 0.11 ns

3.3.3 CH_4 fluxes

Temperature, water table and PFT all significantly affected CH_4 emissions with interactions between these parameters and also with time (Table 3.3). At low water tables, increasing temperature had no effect upon CH_4 fluxes. However, CH_4 fluxes at intermediate and high water tables did vary with temperature, but there was no consistent trend. CH_4 fluxes were low in all PFT treatments at 14°C, whereas CH_4 fluxes did vary significantly with PFT at 12°C and 16°C. A greater magnitude of change from low to intermediate to high water tables in graminoid and bryophyte CH_4 fluxes was observed at 16°C (Figure 3.2), but the largest degree of change in shrub CH_4 fluxes with each 10 cm increase in water table level occurred at 12°C (Figure 3.2).

CH_4 fluxes were low in all PFT treatments, but overall were greater for graminoid than bryophyte and shrub (Figure 3.2). CH_4 fluxes at intermediate and high water tables were significantly higher than those measured at low water tables, with a greater magnitude of change in graminoid CH_4 fluxes from low to intermediate to high water tables compared with bryophyte and shrub (Figure 3.2).

Overall, average CH_4 fluxes decreased significantly over time with significant interactions between temperature, water table and PFT (Table 3.3 and Figure 3.3). CH_4 fluxes at the beginning of the experiment varied significantly with temperature, water table and PFT. However, a significant reduction in CH_4 fluxes was observed after day 7, a trend which was seen across all treatments (Figure 3.3). The effect of time decreased graminoid CH_4 fluxes by a greater magnitude at 16°C, 12°C and at high water table levels (Figure 3.3). For bryophyte and shrub, time had little effect upon CH_4 emissions across all temperature and water table treatment ranges, as CH_4 emissions overall were very low in these PFT treatments (Figure 3.3).

Table 3.2: Main and interactive effects of time, temperature, water table and PFT on CO_2 fluxes (CO_2 -C g m^{-2} d^{-1}) analysed by repeated measures ANOVA. D = sampling days within the 322 day experimental period, T = temperature (°C), WT = water table position (cm below the surface of peat core) and PFT = plant functional type. Df = degrees of freedom, F = F value and *p* = *p* value.

Repeated measures ANOVA:	df	F	*p*
D	5	21.49	<0.0001
T	2	64.00	<0.0001
WT	2	30.34	<0.0001
PFT			*ns*
D*T	10	4.30	<0.0001
D*WT	10	3.28	0.0004
D*PFT			*ns*
T*WT	4	4.97	0.0008
T*PFT			*ns*
WT*PFT			*ns*

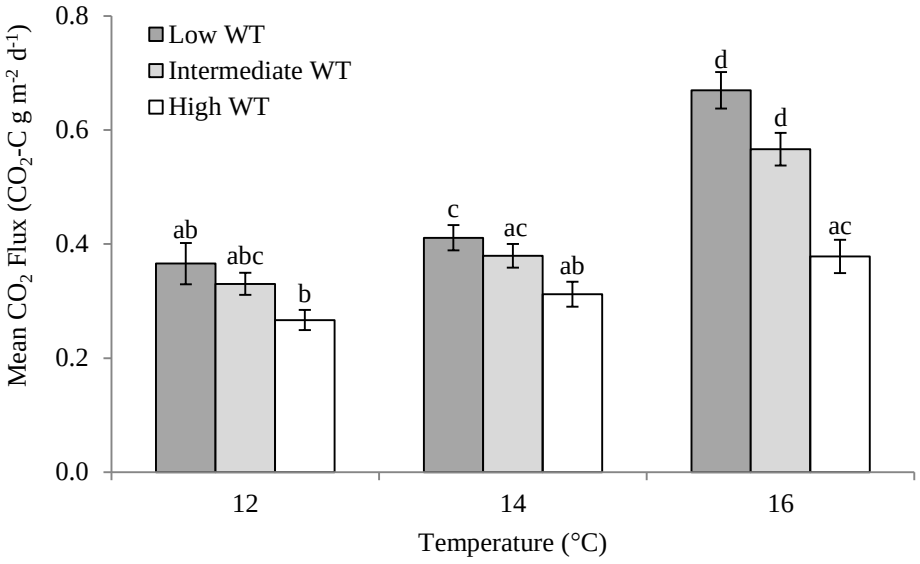

Figure 3.1: CO_2 fluxes from all cores across the 4°C temperature range for each water table (WT) level treatment: low = -25 cm, intermediate = -15 cm, high = -5 cm. Letters indicate pair-wise significant differences between temperature and water table level treatments. Data are means (averaged for PFT) ± standard error. CO_2 flux expressed as CO_2 - C in g m^{-2} d^{-1}.

Table 3.3: Main and interactive effects of time, temperature, water table and PFT on CH_4 fluxes (CH_4-C g m^{-2} d^{-1}) analysed by repeated measures ANOVA. D = sampling days within the 322 day experimental period, T = temperature (°C), WT = water table position (cm below the surface of peat core) and PFT = plant functional type. Df = degrees of freedom, F = F value and *p* = *p* value.

Repeated measures ANOVA:	df	F	*p*
D	5	14.64	<0.0001
T	2	8.74	0.0003
WT	2	17.81	<0.0001
PFT	2	10.32	<0.0001
D*T	10	2.98	0.0013
D*WT	10	7.25	<0.0001
D*PFT	10	3.12	0.0008
T*WT	4	3.24	0.0146
T*PFT	4	3.01	0.0210
WT*PFT	4	3.99	0.0046

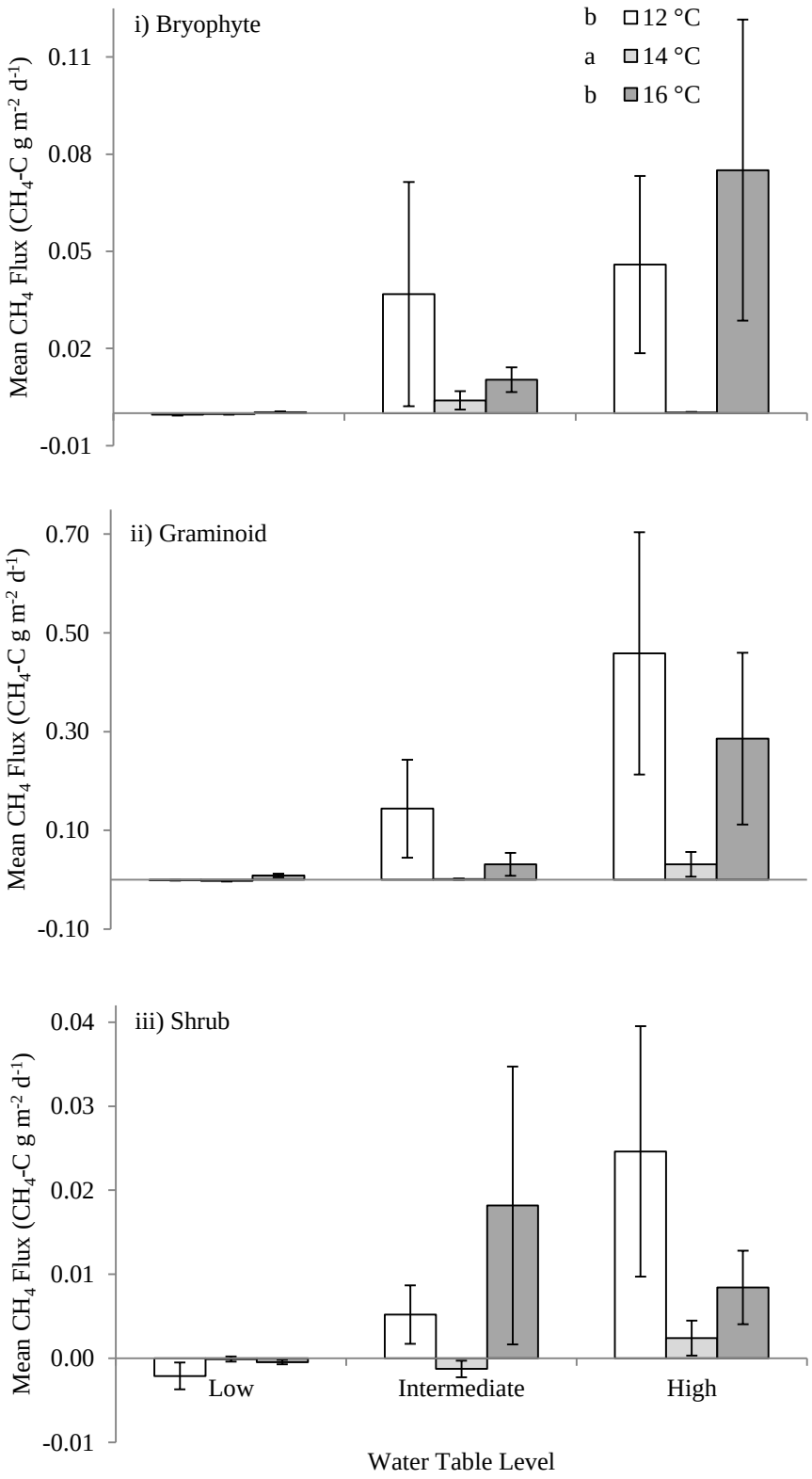

Figure 3.2: CH_4 fluxes from cores of each PFT: i) bryophyte, ii) graminoid and iii) shrub, across the 4°C temperature range for each water table level treatment: low = -25 cm, intermediate = -15 cm, high = -5 cm. Letters indicate pair-wise significant differences between temperature treatments. Data are means ± standard error. CH_4 flux expressed as CH_4 - C in g m^{-2} d^{-1}.

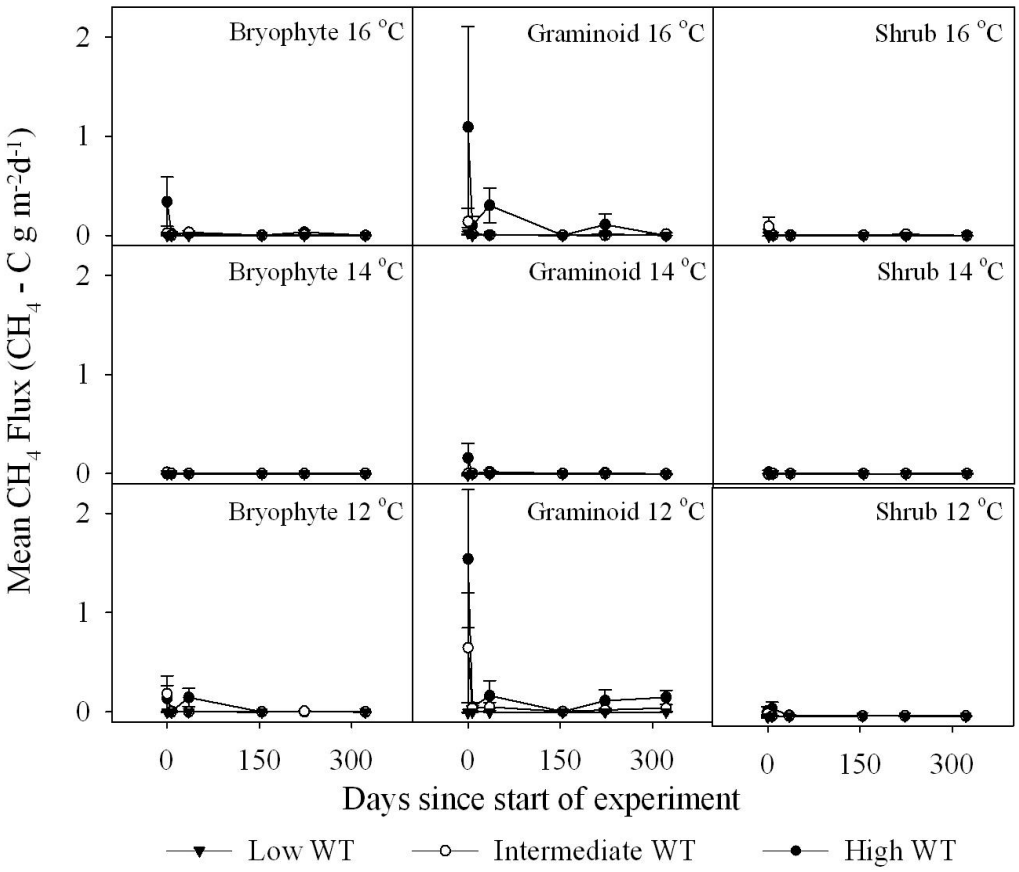

Figure 3.3: Mean CH_4 flux over 322 day experimental period, showing effects of temperature (°C), water table (WT) position (low = -25 cm, intermediate = -15 cm, high = -5 cm) and PFT (bryophyte, graminoid and shrub). Error bars are standard error. CH_4 flux expressed as CH_4 - C in g m^{-2} d^{-1}.

3.4 Discussion

This multi-factorial microcosm experiment elucidates the effects of changes in peatland microclimates on C cycling, by investigating the interactive effects of temperature, water table and PFT on both CO_2 and CH_4 emissions from peat. Results demonstrate that small changes in temperature and water table were the dominant controls on CO_2 fluxes (Table 3.2), whereas CH_4 fluxes reflected significant interactions between PFT, temperature and water table (Table 3.3).

3.4.1 Microclimate effects

In support of the first hypothesis, significant differences in both CO_2 and CH_4 fluxes were found between each 2°C change in temperature and 10 cm decrease in water table (Figures 3.1 and 3.2), with significant interactions between temperature and water table affecting both CO_2 and CH_4 fluxes.

Temperature and water table were shown to be major controls for CO_2 (Figure 3.1), with larger increases in CO_2 flux occurring at the highest temperature and lowest water table, than at lower temperatures and higher water tables. CO_2 fluxes at 16°C were 1.8 times greater under low water tables than under high water tables. This magnitude of change is similar to the 2.5 times greater CO_2 production observed at warmer temperatures, under aerobic conditions compared to anaerobic (Moore and Dalva, 1997). At 12°C, and with water table depths ranging from 0 – 30 cm, CO_2 fluxes at drained and forested ombrogenous and minerogenous bogs also increased with lower water table levels, but were of an order of magnitude greater than measured in this study (Silvola et al., 1996).

An increase in soil microbial activity with lowered water tables is a common response in previously saturated soils (Kirschbaum, 2004), with the stimulation of heterotrophic decomposition and hydrolytic enzyme activity (Bubier et al., 2003; Freeman et al., 2001). Water table position has previously been found to be the strongest control on peat CO_2 fluxes (Laine et al., 2007). However, in this study small differences in temperature had the greatest relative effect on CO_2 fluxes (Figure 3.1), which is in agreement with the effects on peat respiration observed with an average 1°C rise in temperature (Dorrepaal et al., 2009; Ward et al., 2013). However, whilst respiration may rise with small-scale increases in temperature under controlled conditions, the net effect on CO_2 flux may not be the same under field microclimate conditions due to reduced oxygen availability caused by high water tables or CO_2 uptake by the living plant surface (Chivers et al., 2009; Ward et al., 2013).

Temperature was also a principal driver of differences in CH_4 fluxes (Figure 3.2), however there was no linear relationship between temperature and net methane fluxes observed in some studies (Dunfield et al., 1993). The response of CH_4 emissions to the small increases in temperature imposed here, were more complex than initially hypothesised, with greater graminoid CH_4 fluxes at 12°C than at 14°C and 16°C on average (Figure 3.2). CH_4 fluxes are expected to increase with atmospheric warming under a range of water table scenarios, as a result of the heightened temperature sensitivity of CH_4 production compared with methanotrophy (Dunfield et al., 1993). Therefore, CH_4 production is expected to increase proportionately more than CH_4 oxidation under a warmer climate. However, this study suggests that this may not always be the case.

Differences in CH_4 fluxes were observed between high and low water tables. Peat cores with the largest water-logged, anaerobic zone produced average CH_4 fluxes (0.1037 CH_4-C g m^{-2} d^{-1}) three orders of magnitude higher than those from cores with a larger aerated zone (0.0002 CH_4-C g m^{-2} d^{-1}) (Figures 3.2 and 3.3). The observation that highest CH_4 flux rates are found with minimal aerobic zones is not unusual (Bellisario et al., 1999; White et al., 2008), yet the magnitude of this effect is lower than previously observed (Moore and Dalva, 2001).

CH_4 fluxes from low water tables were inhibited and less sensitive to changes in temperature and PFT (Figure 3.2). Under aerobic conditions the inhibition of CH_4 production is caused by the restricted activity of anaerobic methanogens, an expected effect of prolonged oxygen exposure (Estop-Aragonés, 2012). Although higher temperatures support increased methanogenesis (Dunfield et al., 1993), this study shows that low water tables have the ability to offset increased emissions through a greater capacity for oxidation. As a result, the interacting strengths of these responses can cause variability in emissions (Dijkstra et al., 2012).

The mechanism of increased substrate use at warmer temperatures and the important interaction with water table level may explain why CH_4 fluxes here are greater at 12°C than 16°C for graminoid and shrub cores with high water tables (Figure 3.2). This partially supports the first hypothesis and suggests that an increase in water table can have a greater effect on CH_4 fluxes than warming (Dijkstra et al., 2012; Turetsky et al., 2008). However, temperature is an important factor in regulating the activity of methanogens (Frenzel and Karofeld, 2000; Williams and Crawford, 1984) and is also strongly interrelated with water table level because heat diffusion in peat is controlled by water (Bubier and Moore, 1994). Therefore, the significant interaction between water table and small-scale temperature

change reported here is important, indicating that these relationships can exist and exert influence over GHG production under microclimate changes (i.e. 2°C temperature change and 10 cm water table adjustment).

3.4.2 Plant functional types

Changes in climate and vegetation are known to independently exert control over ecosystem C dynamics (De Deyn et al., 2008; Dorrepaal et al., 2009), but rarely are PFT effects on CO_2 and CH_4 emissions examined in conjunction with environmental variables such as water table or temperature (Hooper et al., 2000; Kardol et al., 2010; Ward et al., 2013), and seldom are the sub-surface PFT effects on GHG fluxes considered instead of the living plant surface.

Peat abiotic and biotic properties were not significantly different between the three PFTs at the start of the experiment (Table 3.1). Graminoid cores emitted CO_2 fluxes of a greater magnitude than bryophyte and shrub, but these differences were not significant overall (Table 3.2). However, the second hypothesis is partially confirmed because graminoid peat emitted significantly more CH_4 than other PFTs across all water table and temperature treatments (Figure 3.2). Furthermore, this study revealed that CH_4 fluxes were more strongly regulated by PFT than small-scale warming (i.e. increases of 2°C or 4°C) (Table 3.3), an observation also noted with a 1°C warming in the field (Ward et al., 2013). Graminoid cores emitted 17 and 5 times more CH_4 than shrub and bryophyte cores respectively, with no significant difference between CH_4 fluxes from bryophyte and shrub cores (Figure 3.2). Strong relationships between graminoid species and CH_4 emissions have been observed previously by (Couwenberg et al., 2011; Greenup et al., 2000), with greater CH_4 fluxes from graminoid>bryophyte>shrub dominated peat (Green et al., 2011; Moore and Dalva, 1997; Waddington et al., 1996; Whiting and Chanton, 1993). Higher CH_4 fluxes from graminoids may be explained by the functional traits of this species. Graminoids have more easily decomposed litter and increased quality and quantity of root exudates that will enhance methanogenic bacterial activity, whilst the presence of aerenchymous tissue in graminoids will provide a by-pass for CH_4 through the methanotrophic 'processing' of the aerobic peat layer (Green and Baird, 2012). Despite no significant PFT-induced differences in C:N and total PLFAs in peat (Table 3.1), it is possible that the quality of C compounds (Cornwell et al., 2008) and detailed differences in microbial composition and diversity (Artz et al., 2007) could result in abiotic and biotic conditions that also control GHG fluxes. CH_4 fluxes have also been affected by PFT outside of the growing season (Ward et al., 2013), which indicates that PFT-induced

differences in microbial activity and peat physicochemical conditions determine differences in GHG emissions during periods of inactive growth: evidence to support the existence of plant legacy effects in peat that are observed in this study.

In support of the third hypothesis, some significant interactions of PFT with temperature and water table were observed to affect initial CO_2 (data not shown) and CH_4 fluxes (Figure 3.3). The supply of root exudates might be the mechanism behind the short-lived PFT-induced differences in GHG fluxes observed at the start of the experiment, due to providing a pool of labile C that is rapidly respired (Bradford et al., 2008; Freeman et al., 2004). Without living plants to replenish the labile C pool (Davidson and Janssens, 2006), microbial activity will be limited by the quality and quantity of root exudates that remain in the peat from beneath each PFT.

Atmospheric warming, as a result of climate change, is expected to be greatest at northern latitudes (Weltzin et al., 2000), with significant effects on ecosystem function mediated through climate-driven changes in plant community composition (Walker et al., 2006; Weltzin et al., 2000). Higher CH_4 emissions are expected with climate change, from the loss of oxidising peat produced by the *Sphagnum* methanotroph consortium in favour of vascular plants i.e. graminoids and shrubs (Gallego-Sala and Prentice, 2012). However, the increased sensitivity of graminoid GHG fluxes to the interactive effects of temperature and water table observed in this study implies a resilience of bryophyte and shrub peat to changes in abiotic environmental variables. These results confirm the second hypothesis that the legacy of plant species traits on peat will result in differential GHG fluxes from peat. It is now important to improve the fundamental understanding of these responses by investigating the relationship between plant species traits and peat abiotic and biotic properties. For example, by investigating the litter chemistry and nutrient stoichiometry of peat under different PFTs alongside more detailed analysis of microbial community composition and diversity. This will enable us to understand how changes in above-ground plant community composition will interact with longer-term legacy effects on peat abiotic and biotic properties to determine soil C cycling under future climate change.

3.5 Conclusions

Peatland microclimates are expected to alter as a consequence of climate change and land use change (Armstrong et al., 2014b; Ward et al., 2013). Given the capacity for GHG fluxes to be affected by small-scale changes in temperature and water table depth as shown here, future monitoring of peatland microclimatic changes is essential to understanding C

cycling processes. The known variability in C cycling between PFTs during active growth (Ward et al., 2013), together with the PFT legacy effect on peat GHG emissions observed in this study, demonstrate that future studies should also control for both above and belowground PFT effects. Whilst the underlying causes of the results reported in this study require further investigation, the findings indicate that peat microclimate changes and the relative proportion of each PFT within the plant community can act as independent or interactive modulators of peatland GHG fluxes. Better evidence of the magnitude of direct and indirect microclimate change effects on peat C cycling is required in order to predict the size and direction of C storage change, especially as long term changes in relative abundance of PFT groups might become more important.

Plant functional type controls on litter decomposition rates in peatlands

4.1 Introduction

The rate of litter decomposition affects the balance and storage of carbon (C) in terrestrial ecosystems, and ultimately influences the cycling of C at the global scale (Wang et al., 2014). In view of this, factors affecting litter decomposition have been studied extensively (Aerts, 1997; Butenschoen et al., 2011; Clarkson et al., 2014; Couteaux et al., 1995). Three main factors govern decomposition dynamics: (1) conditions of the decomposition environment, such as soil temperature, aeration and moisture availability (Clarkson et al., 2014), (2) litter quality characteristics, such as initial nutrient concentrations, lignin content and C:N (Hoorens et al., 2002), (3) composition and abundance of the decomposer community e.g. the ratio of fungi to bacteria (F:B) and total microbial biomass (Myers et al., 2012).

In northern peatlands, the formation of blanket bog peat is a direct result of very low rates of decomposition (Belyea, 1996). The accumulation of large organic C stocks in these ecosystems is attributed to the inhibition of soil microbial activity, caused by the combination of cool temperatures, high water tables and slow to decompose plant litters and organic matter substrates (Moore et al., 2007). The plant species that produce these litters have distinct functional traits, which are used to classify the species by 'plant functional type' (PFT) groups (Chapin et al., 1996; Cornwell et al., 2008; De Deyn et al., 2008). There is a well-established relationship between plant litter species identity and its decomposition (Aerts, 1997), a relationship that can also be applied to litters from different PFTs (Cornwell et al., 2008). Bryophytes (e.g. *Sphagnum* sp., feather mosses), shrubs (e.g. *Calluna vulgaris*, *Vaccinium* sp.) and graminoids (e.g. *Eriophorum vaginatum*, sedges and rushes) are three dominant peatland PFTs that determine differences in C cycling due to their functional dissimilarities (Ward et al., 2009). Bryophytes produce litter with poor organic matter quality and low N concentrations, shrub litter has high C:N and is rich in lignin, and both litter types contain phenolic compounds that are known to inhibit decomposition (Hättenschwiler and Vitousek, 2000; Read et al., 2004; Turetsky, 2003). Relative to shrubs and bryophytes, graminoids have a high leaf nitrogen (N) content and contain less recalcitrant C compounds, increasing the decomposability of their tissues (Dorrepaal et al., 2005).

Litter PFT can also influence the underlying peat, along what is increasingly known as the decomposition continuum across the litter-soil interface (Ball et al., 2014; Clymo et al., 1998; Wardle et al., 2004). The PFT of litter to which the peat is exposed to has the

potential to influence the quality and quantity of C inputs entering the soil (Bardgett et al., 2013), resulting in changes to the chemical composition of peat (Orwin et al., 2006; Ward et al., 2009) and the form and function of the soil microbial community (Ayres et al., 2006; Read et al., 2004; Wardle, 2002). Therefore, as a function of surface litter resources, a PFT legacy effect can exist within the soil and determine rates of decomposition (Ayres et al., 2006; Ball et al., 2014; Carrillo et al., 2012). It has been proposed that the legacy effect of a PFT and its litter in soil can favour the decomposition of that litter type, an effect referred to as 'home-field advantage' (HFA). HFA decomposition has been observed in a number of studies (Ayres et al., 2009b; Freschet et al., 2012; Gholz et al., 2000; Perez et al., 2013; Vivanco and Austin, 2008), but rarely are the effects of HFA on litter decomposition explored in peatlands. The aforementioned studies suggest that it is the selection of a soil microbial community, most efficient at decomposing a particular PFT litter, which produces the positive feedback on decomposition i.e. greater rates of litter mass loss at 'home'. If microbial communities are indeed more efficient at decomposing litter from the plant species above them, microbial community composition should vary spatially with the location of specific plant types, a pattern that has already emerged in peatlands (Artz, 2009; Trinder et al., 2009). Differences in plant litter traits could also affect the likelihood of HFA decomposition. HFA is likely to be more important for low quality litters with reduced nutrient availability (Osanai et al., 2012; Vivanco and Austin, 2011), whereas high quality litter containing compounds relatively easy to degrade might be expected to have little or no HFA, since most microbial communities will contain biota capable of decomposing those compounds rapidly (Ayres et al., 2009a). However, studies that have found no evidence of HFA support the view that HFA decomposition is highly dependent on the experimental system, the presence of living plants and the time given for effects to manifest (Gießelmann et al., 2011; St. John et al., 2011).

Mean global temperatures are expected to increase with climate change, with affects most evident at high latitudes and high altitudes (IPCC, 2013). Warming has often been found to increase litter decomposition (Hobbie, 1996; Kirwan and Blum, 2011; van Meeteren et al., 2008), due to an increase in microbial activity (Aerts, 2006; Allison and Treseder, 2011). However, some studies suggest that the acceleration of decomposition caused by warming may be offset under drier conditions (Butenschoen et al., 2011; Gavazov, 2010) or by altered plant community composition and litter quality inputs (Cornelissen et al., 2007). Decomposition processes in northern peatlands are therefore likely to be affected by climate change, through direct shifts in soil temperature or moisture availability (van

Meeteren et al., 2008), and indirect impacts on the soil microbial community (Aerts and Ludwig, 1997; Hobbie, 1996), or the relative abundance of PFTs (Aerts, 2006; Hobbie, 1996). Land use pressures on peatlands are also important to consider when assessing litter decomposition rates. The effects of common peatland activities such as forestry, sheep grazing, game bird breeding and extraction for fuel have been analysed at length, with evidence showing that development and disturbance can increase C loss from these ecosystems (Garnett et al., 2000; Maljanen et al., 2003; Nieminen, 2004; Turetsky et al., 2002; Ward et al., 2007). Wind farms are a relatively new peatland land use, due to the growing demand for renewable electricity generation and the typically high wind speeds experienced in these upland areas. Lower C stocks and capacity for C sequestration are unavoidable effects of wind farm construction on peatands (Ostle et al., 2009; Smith et al., 2014), due to peat excavation and drainage (Freeman et al., 2001; Silvola et al., 1996). The impacts of wind farm construction on Scottish peatlands have been calculated (Nayak et al., 2010), however the operational effects of wind farms still need to be considered in order to construct a full C life cycle analysis of this peatland land use (Armstrong et al., 2014b; Ostle et al., 2009). There is evidence to suggest that wind farms can alter near surface temperatures (Baidya Roy and Traiteur, 2010; L. Zhou et al., 2012), which could manifest changes in soil temperature and water table level (Armstrong et al., 2014b). But currently, wind farm microclimates and their effects on peatland C cycling remain unknown.

A spatial assessment of litter decomposition at Black Law Wind Farm (Lanarkshire, Scotland) was conducted, with the aim of understanding the effects of PFT legacies on litter mass loss at a peatland hosting a wind farm, and with the broader view to determine how PFTs might play a significant part in mediating effects of climate change in peatlands. Assuming that PFT legacy affects litter quality and soil microbial community composition and activity, it was hypothesised that (1) decomposition of PFT litters will be greater in peat under the same PFT (HFA). Moreover, HFA will be greater for more recalcitrant shrub-derived litter compared to more labile graminoid litter (hypothesis 2). In addition, it was hypothesised (3) that whilst environmental controls (i.e. water availability and temperature) will strongly influence litter decomposition, measures of litter and peat chemistry will explain more variation in litter decomposition rates. To test these hypotheses, litter bags containing litter from each PFT were buried across the peatland and retrieved after one year. The relatively short duration of this study means that only early stages of decomposition i.e. the loss of most labile compounds from litters would be observed. Therefore, findings cannot be used reliably to inform predictions of long-term

litter mass loss i.e. during the breakdown of more recalcitrant compounds (Latter et al., 1998; Prescott, 2005).

4.2 Methods

4.2.1 Determining litter decomposition

A fully factorial experimental field design comprising four blocks and three PFT plots (bryophyte, graminoid and shrub) was replicated at four sites across blanket bog peatland at Black Law wind farm (Figures 1.1, 1.2 and 1.3, Chapter 1). At each of the 48 PFT plots, litter bags comprised of litter from each PFT (144 in total) were placed beneath the litter layer in March 2012. Litter bags were retrieved after 386 days, in April 2013.

Litter decomposition was determined using mass loss determinations (Graças et al., 2005). Litter from each PFT was collected in October 2012 within a sampling area of approximately 10 m^2 to reduce the influence of spatial variation. *Calluna vulgaris* leaves that had already lost their green colour were collected, together with brown shoots to which they were loosely attached. Senesced *Eriophorum vaginatum* leaves were collected by loosely shaking and raking the plant by hand, to gently separate the leaves that were no longer green. Identification of decomposed *Sphagnum* litter can prove difficult (Hogg, 1993), therefore in accordance with previous studies (Aerts et al., 2001; Bragazza et al., 2007) the stem section 2-4cm beneath the growing tip (i.e. capitulum) was harvested and used to represent *Sphagnum* litter that had been freshly deposited and subsequently stored in the acrotelm.

Litter was air-dried to remove excess surface moisture and sub-samples were oven-dried at 105°C to ascertain the moisture content and dry weight equivalent of each PFT. Litter bags were prepared by putting 0.50 g of air-dried litter in polyethylene litter bags (5 mm wide, 5 mm long) with a mesh width of 1 mm, a mesh size chosen to reduce loss of litter from the bags (Aerts et al., 2012). In addition, this mesh size was selected to ensure that decomposer micro-organisms and micro-invertebrates could access the litter samples in the bags (Aerts et al., 2012; Swift et al., 1979). After retrieval, soil particles and extraneous litter and roots were removed from the litter bags. Litter bags were dried at 105°C until there was no further weight loss and the final weight noted. The actual weight loss over the experimental period was calculated as a percentage of the initial mass of air-dried litter, calibrated to oven-dried mass. Litter decomposition is reported as percentage litter mass remaining (% of initial dry mass) and percentage litter mass loss (% initial dry mass) is used for the calculation of home field advantage.

4.2.2 Calculating home field advantage and disadvantage

Home field advantage (HFA) and disadvantage (HFA) of litter decomposition is calculated using a method developed by (Clarke and Norman, 1995) and adapted by Ayres *et al*. (2009). A HFA or HFD value is calculated for each PFT and is expressed in the units of measurement (% mass loss). HFA and HFD are calculated using the following equations:

$$HDD_b = \left(DL_{bB} - DL_{gB}\right) + \left(DL_{bB} - DL_{sB}\right) \quad \text{Eqn. 1}$$

$$ADD_b = \left(DL_{bG} - DL_{gG}\right) + \left(DL_{bS} - DL_{sS}\right) \quad \text{Eqn. 2}$$

$$TH = \frac{HDD_b + HDD_g + HDD_s}{NS - 1} \quad \text{Eqn. 3}$$

$$ADH_b = HDD_b - ADD_b - TH \quad \text{Eqn. 4}$$

Lowercase letters (b, g, s) indicate bryophyte, graminoid and shrub litters. Uppercase letters (B, G, S) indicate bryophyte, graminoid and shrub peat. ADH is the additional decomposition at home for the species indicated by the lowercase letter. HDD and ADD refer to home and away decomposition differences, respectively. DL is a measure of decomposition (in this case % mass loss of litter). TH represents the total HFA for all species combined. NS indicates the number of species. If $ADH_b > 0$, bryophyte litter decomposed faster than expected when at home (i.e. HFA); if $ADH_b = 0$, bryophyte litter decomposition at home occurred at the expected rate (i.e. no HFA); if $ADH_b < 0$, bryophyte litter decomposition at home occurred slower than expected (i.e. home field disadvantage, HFD). The ADH for each PFT was calculated at each site (with block replicates).

4.2.3 Peat and litter properties

Water table depth and soil temperature at 5 cm depth were recorded from March 2012 to April 2013. Water table depth (mm) was recorded every 30 minutes at each PFT plot at one block at each site, using Level TROLL 500 (Insitu, USA). Soil temperature (°C) at 5 cm depth was recorded every 30 minutes, beneath each PFT plot at three blocks at each site using Onset Hobo Pendant temperature loggers (Onset, USA). The mean water table level for all plots at each time point was subtracted from the water table level for each plot at each time point, in order to calculate the deviation from the mean water table level. Water table level deviation was calculated for each PFT and site, over 1 year (March 2012

– April 2013). The same method was used to calculate the deviation in soil temperature from the mean.

The initial biochemical composition of each PFT peat and litter was assessed. Peat total C content, total N content, C:N, pH and dry bulk density data from section 2.3.1, Chapter 2 will be used here in the statistical analysis of percentage remaining litter, in order to test the influence of physical and chemical peat properties on litter decomposition. Total C content, total N content and C:N were measured in four litter samples from each PFT, using the same method for peat samples described in section 2.2, Chapter 2. Total phosphorus (P) content was determined after ashing and acid digestion, using ICP-OES (Inductively Coupled Plasma – Optical Emission Spectroscopy; Sciantec Analytical, UK) (Boss and Fredeen, 1999). Phytate P content was determined after ferric chloride ($FeCl_3$) precipitation and acid digestion, using ICP-OES (Sciantec Analytical, UK). Available P content was determined by subtracting phytate P content from total P content. From this data, C:P and N:P were determined using the total content of C, N and P.

Stepwise chemical digestion in an Ankom 220 Fibre Analyser (Sciantec Analytical, UK) was used to quantify hemicellulose, cellulose and lignin litter fractions (Van Soest, 1994). Hemicellulose-like substances were extracted from the Neutral Detergent Fibre (NDF; comprised of hemicellulose, cellulose, lignin and mineral ash) with hot acid detergent solution to leave the Acid Detergent Fibre (ADF; comprised of cellulose, lignin and mineral ash) (Van Soest and Wine, 1967). Cellulose-like substances were extracted by cold digestion with 72% sulphuric acid (H_2SO_4), with the remaining residues representing the Acid Detergent Lignin (ADL; comprised of lignin and mineral ash) (Van Soest and Wine, 1967). Hemicellulose content was determined by subtracting the ADF from the NDF, and cellulose content was determined by subtracting the ADL from the ADF. From this data, lignin:N was calculated as a traditional indicator of litter quality (Cadisch and Giller, 1997). The total fibre content of litter (LCH = lignin + cellulose + hemicellulose) was also calculated, as it has previously been shown to be a powerful predictor of decomposition dynamics (Vaieretti et al., 2005).

4.2.4 Statistical analysis

All statistical analysis in this chapter was performed using the statistical package R, version 2.14.0 (The R Project, 2012), with the exception of data used from section 2.2.1, Chapter 2. All data were checked for normality before final analysis. Throughout the text, ‘significant’ is referred to if $p < 0.05$.

Two-way ANOVAs were performed using SAS V9.1, Enterprise Guide 4.0 to test the hypothesis that chemical properties of peat would vary with location within the wind farm and with PFT (see section 2.2.1, Chapter 2). Linear mixed-effects (LME) models were performed to detect if environmental peat properties i.e. soil temperature and water table level varied with month, site and PFT. LME models used plot ID as a random effect to account for the repeated measures and were followed by Tukey's test *post-hoc* analyses. Soil temperature and water table level data was used from April 2012 to March 2013, on account of missing data in March 2012 and April 2013.

In order to test the hypotheses that litter decomposition would vary with peat and litter PFT, one-way ANOVAs were used to test the significance of PFT on the chemical properties of litter used in litter bags and followed by Tukey's test *post-hoc* analyses. In addition, three-way ANOVA was performed to test the significance of site, peat PFT and litter PFT on percentage litter mass remaining, followed by Tukey's test *post-hoc* analyses. The Pearson's correlation coefficient was calculated to give a measure of the linear dependence between the litter mass remaining and all peat and litter physicochemical properties.

In order the test the hypothesis that home-field advantage would occur i.e. decomposition of PFT litters would be greater in peat under the same PFT, a two-way ANOVA was used. The significance of site and PFT on additional mass loss at home (HFA) and away (HFD) was tested, followed by Tukey's test *post-hoc* analyses. T-tests were used to test if additional mass loss at home and away was significantly different to zero.

To test the hypothesis that environmental, physical and chemical peatland properties would influence litter decomposition, a linear mixed effects (LME) model was used to investigate how properties of peat and litter improved predictions of percentage litter mass remaining. A LME model of litter mass remaining was constructed, including data from all four sites across the peatland. Block was included as a random effect and peat and litter properties were specified as fixed effects. Properties of peat included in the model were: total C content, total N content, C:N, pH, bulk density (data used from section 2.3.1, Chapter 2), deviation from mean soil temperature and deviation from mean water table level. Properties of litter used were: total C content, total N content, C:N, total P content, available P content, C:P, N:P, hemicellulose, cellulose, lignin, lignin:N and LCH. The initial model, including all fixed effects, could not be used due to the presence of co-linear variables and complexity induced by the number of variables. To determine the fixed effects that were the source of these problems, each fixed effect variable was removed

from the model in turn. The following fixed effect variables were removed permanently from the model: litter C:N, total P content, available P content, C:P, C:N, hemicellulose, cellulose, lignin, lignin:N and LCH. All remaining variables were included in the initial model with non-significant variables removed manually in a systematic, step-wise process to achieve the best goodness of fit with fewest factors, assessed by selecting the model with the lowest Akaike's Information Criterion (AIC). If removal of a non-significant variable increased the AIC value, the variable was retained in the refined model. Peat total C content, peat total N content, bulk density, deviation from mean soil temperature and deviation from mean water table level were removed during model refinement. Once the final model was reached a liner model was fitted, removing random effects, in order to assess the significance of each term in the model. The adjusted R^2 of the fitted model was calculated and compared with the adjusted R^2 of models fitted with each variable removed in turn. The relative contribution of each variable in explaining the variance of the model was then calculated as a percentage of the total variance explained.

4.3 Results

4.3.1 Peat chemistry

For total C content, total N content, C:N, pH and bulk density of peat across the peatland see section 2.3.1, Chapter 2.

4.3.2 Water table

Water table varied significantly across the wind farm, and beneath each PFT (Table 4.1). There were statistically significant interactions between site and PFT, together with time, but these were not as large as the individual influence of PFT. The position of the water table (reported as mm below the peat surface, data not shown), in 2012 decreased significantly each month from April (~35 mm) to June (~70 mm) and then rose significantly each month to December (~9 mm), with the exception of August. In 2013, depth to the water table increased significantly from January (~40 mm), to February and then March (~62 mm). Water table position varied across the wind farm transect, and was significantly lower at site 2 (50.68 ± 67.78 mm) than at sites 3 (46.30 ± 38.14 mm), 4 (31.73 ± 32.36 mm) and 1 (29.82 ± 78.61 mm): water table level increased towards the peat surface in that order. At all sites, apart from site 3, the standard deviation of the water table level was larger than the mean, which suggests that the water table at those sites was more variable with PFT and over time. The mean water table level was nearer to the surface of the peat beneath bryophytes (26.11 ± 59.45 mm), and was significantly lower

beneath graminoids (30.05 ± 64.56 mm) and shrubs (62.73 ± 41.13 mm). As with site, the standard deviation of the water table level beneath bryophytes and graminoid was greater than the mean, indicating that shrub water table levels were less variable across the wind farm and study period. The water table level remained below the surface of the peat throughout most of the year, but did reach the surface on occasion. For example, pools of water up to ~73 mm deep on average were measured at site 1 beneath graminoid in November.

At sites 1, 3 and 4, the water table beneath bryophytes was either above i.e. wetter or the same as the mean water table level across all sites for the duration of the experiment (Figure 4.1). Peat beneath bryophytes at site 2 tended to be drier than the mean water table level in the summer of 2012 i.e. by ~76mm in June, with the exception of July, and in January-April 2013 (Figure 4.1). The water table level beneath graminoids was more variable than beneath bryophytes and shrubs (Figure 4.1), with water table levels at site 1 observed to be ~100 mm above and ~150 mm below the mean (Figure 4.1). Graminoid water table levels at site 2 were also drier than average in spring and summer, with the difference most evident in August 2012 (Figure 4.1). Deviation from mean water table level beneath graminoids at sites 3 and 4 followed the same pattern throughout the study period, and were wetter i.e. above average in spring and summer, and got progressively drier towards the end of 2012, before rising again in January-April 2013. The water table beneath shrub was much less variable than beneath graminoid and bryophyte, with sites 1, 3 and 4 remaining lower than the mean water table level from April 2012-2013 (Figure 4.1). At site 2, the shrub water table level was generally similar to, or wetter (i.e. in June-July 2012 and the first three months of 2013) than the mean (Figure 4.1).

These results show that the level of the water table was (1) highest in winter and beneath bryophytes, (2) lowest in summer months and beneath shrubs, (3) the position of the water table was nearest the peat surface at site 1, and furthest from it at site 2, owing to the variability in water table beneath bryophytes and graminoids.

Table 4.1: Linear mixed effects model results showing month, site, PFT and their interactive effects on soil temperature and depth to water table (mm).

Repeated measures ANOVA:		df	F	*p*
Temperature	Month	11	289034.17	<0.0001
	Site	3	336.24	<0.0001
	PFT	2	226.53	<0.0001
	Month*Site	33	671.92	<0.0001
	Month*PFT	22	25.26	<0.0001
	Site*PFT	6	199.24	<0.0001
Water table	Month	11	3852.80	<0.0001
	Site	3	3071.56	<0.0001
	PFT	2	15432.12	<0.0001
	Month*Site	33	568.26	<0.0001
	Month*PFT	22	222.08	<0.0001
	Site*PFT	6	5174.71	<0.0001

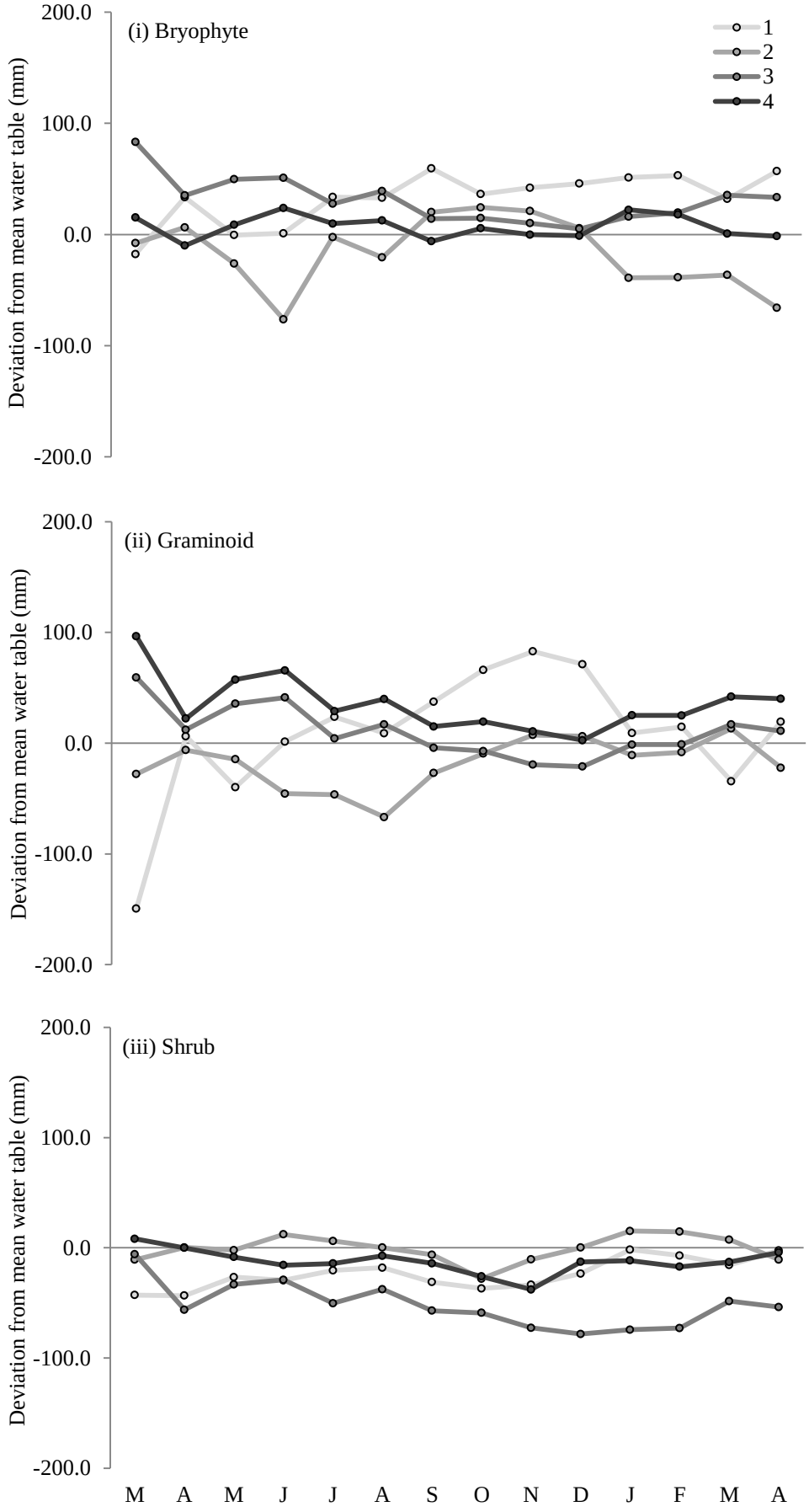

Figure 4.1: Deviation from mean monthly water table level (mm) beneath each PFT, at each site, from March 2012 to April 2013.

4.3.3 Soil temperature

Soil temperature varied significantly between sites and PFTs, but the largest influence was attributed to that of time (Table 4.1). Interactive effects of site, PFT and time were also observed, but their influence was relatively small compared to the individual effect of time (Table 4.1). Soil temperature (data not shown) increased significantly every month from April 2012 (~6.3°C) to August 2012 (~14.0°C), after which it decreased significantly every month until December 2012 (~1.6°C), with temperatures in early 2013 being slightly but significantly warmer (by up to ~1.2°C). Soil temperature was significantly higher at sites 1 and 4, than at sites 2 and 3, but only by ~0.2 °C. A similar magnitude of temperature change was observed between PFTs, with ~0.13°C higher soil temperatures beneath bryophytes than beneath shrubs.

In bryophyte peat, the soil temperature at site 1 was observed to be ~1°C cooler than the mean soil temperature of all sites in summer and ~1.1°C warmer than the mean for all sites in winter (Figure 4.2). Bryophyte soil temperature at sites 3 and 4 followed a similar pattern to each other, and were ~0.4°C warmer and cooler in the summer and winter months, respectively (Figure 4.2). At site 2 the temperature of bryophyte peat was not as variable, but did remain warmer than the mean for most of the year, apart from in November 2012 (Figure 4.2). For graminoid peat, the same trends in deviation from mean soil temperature in bryophyte peat were observed for sites 1, 3 and 4 over the study period (Figure 4.2), but were slightly smaller i.e. +0.6°C in winter and -0.8°C in summer at site 1 for graminoid, rather than ±1°C for bryophyte at site 1 (Figure 4.2). Deviation in graminoid and bryophyte peat temperature at site 2 was of a similar size, but was ~0.2°C cooler in spring-summer 2012 for graminoid rather than +0.2°C for bryophyte over the same time period (Figure 4.2). Deviation from the mean soil temperature across all sites and months for shrub peat reflected the patterns observed for graminoid and bryophyte, but the range in variability was reduced and site 2 was ~0.4°C cooler in spring-summer 2012 rather than -0.2°C and +0.2°C for graminoid and bryophyte peat, respectively (Figure 4.2).

In summary, soil temperature was highest beneath bryophyte and lowest beneath shrub, reaching a maximum in summer and minimum in winter. However, beneath each PFT, the soil temperature at site 1 was cooler than the overall mean in summer and warmer in winter. The opposite was observed for the soil temperature at sites 3 and 4, whilst the soil temperature at site 2 tended to not be as variable.

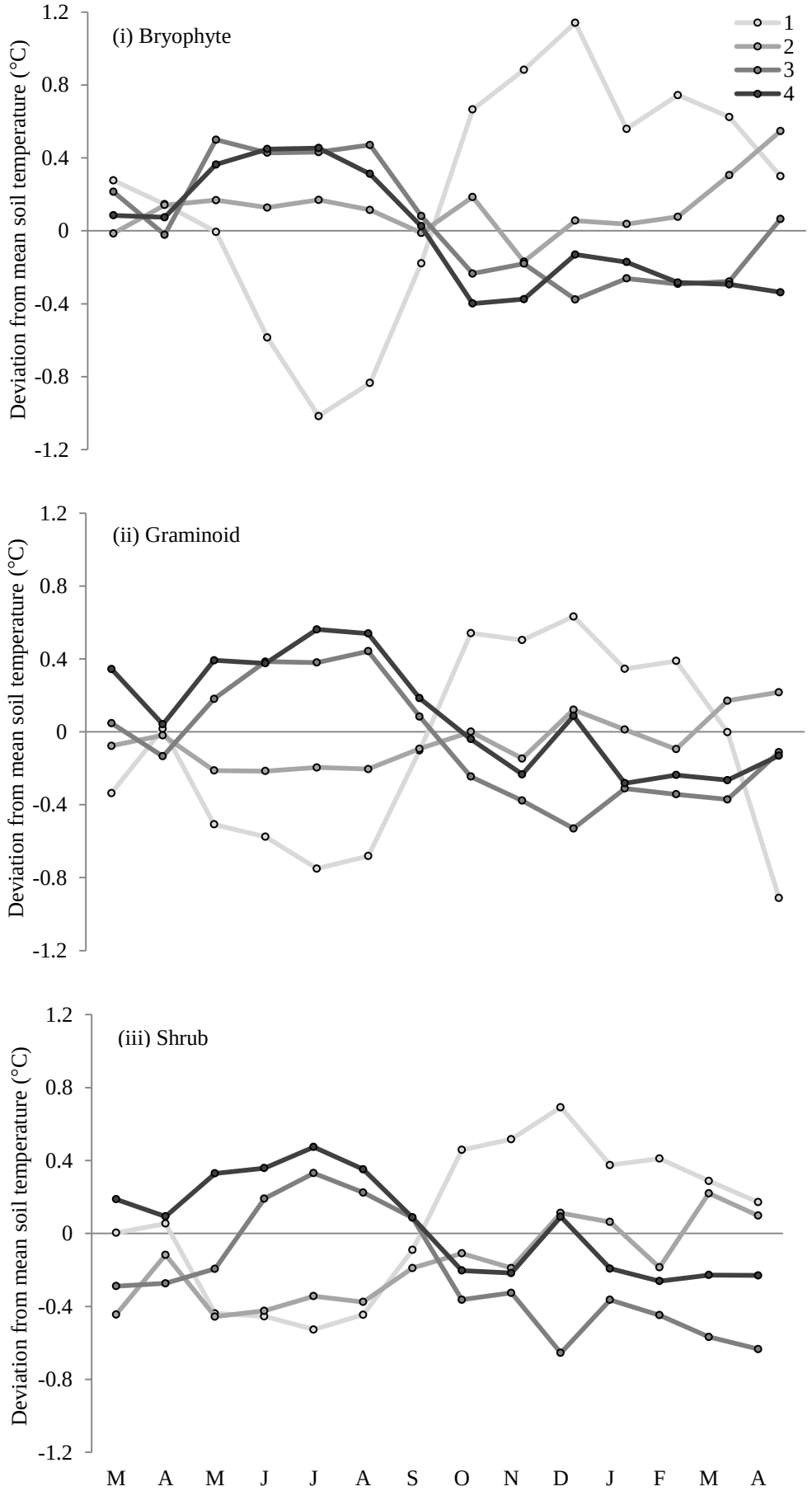

Figure 4.2: Deviation from mean monthly soil temperature (°C) beneath each PFT, at each site, from March 2012 to April 2013.

4.3.4 Chemical properties of litter

All litter properties varied significantly between PFTs, apart from litter lignin:N (Table 4.2). Total C content of litter increased from bryophyte to graminoid litter, and was highest in shrub (Table 4.3). Graminoid litter N content was significantly higher in bryophyte and shrub litters (Table 4.3). The opposite was observed for C:N, with bryophyte litter C:N significantly higher than both shrub and graminoid (Table 4.3). Graminoid litter also had highest concentrations of total P, greater than shrub but not bryophyte; whereas available P was higher in graminoid litter than in both shrub and bryophyte litters (Table 4.3). C:P and N:P were both significantly higher for shrub litter, but were lowest for graminoid and bryophyte litters, respectively (Table 4.3). Hemicellulose, cellulose and lignin content were highest in graminoid, bryophyte and shrub, respectively (Table 4.3). The total fibre content (LCH) was lowest in graminoid, increasing in shrub and highest in bryophyte (Table 4.3), a trend that was reflected in lignin:N. The lignin:N of bryophyte and shrub litters indicate that they are slower to decompose, as more recalcitrant litters have lignin:N close to 40 (Kirschbaum, 2013) (Table 4.3). Whereas litters of intermediate decomposability are characterised by a lignin:N of 15 (Kirschbaum, 2013), which suggests that graminoid litter is more labile than shrub and bryophyte (Table 4.3). However, differences in lignin:N between PFTs were not significant (Table 4.2).

4.3.5 Litter decomposition

The amount of decomposition varied between litters from different PFTs, but there were no overall or interactive effects of site and peat PFT (Table 4.4). Significantly more litter remained in bryophyte litters bags after one year of decomposition, than both shrub and graminoid litter bags (Figure 4.3). Graminoid litter bags contained the least amount of litter at the end of the experiment (Figure 4.3), owing to increased decomposition of this litter PFT compared to bryophyte and shrub. The differences in decomposition observed between litters of different PFT origin were consistent, regardless of peat PFT (Figure 4.3) and site. There were no significant interactions between litter PFT and peat PFT, but the interaction with site was close to significant, suggesting that there may be some spatial variability within litter decomposition (Table 4.4).

Table 4.2: Differences in litter properties between each PFT. Litter properties were analysed by one-way ANOVA with PFT as the main factor. Pair-wise comparisons were performed by Tukey's HSD (shown in Table 4.3).

	Property	One-way ANOVA		
		df	F	*p*
Litter	Total C	2	1118.53	<0.0001
	Total N	2	364.37	<0.0001
	C:N	2	112.30	<0.0001
	Total P	2	32.25	<0.0001
	Available P	2	24.68	0.0002
	C:P	2	38.68	<0.0001
	N:P	2	62.85	<0.0001
	Cellulose	2	14.16	0.0016
	Hemicellulose	2	71.32	<0.0001
	Lignin	2	9.43	0.0062
	Lignin:N	2	1.93	0.2010
	LCH	2	95.35	<0.0001

Table 4.3: Properties of each PFT litter. B = bryophyte, G = graminoid and S = shrub. LCH = total fibre content (lignin + cellulose + hemicellulose). Data are means ± standard error. Pair-wise comparisons of litter properties for each litter PFT, analysed by one-way ANOVAs and Tukey's HSD tests (all one-way ANOVAs were significant at $p < 0.01$, with the exception of Lignin:N, see Table 4.2).

Litter property	Litter PFT					
	B		G		S	
	Mean ± SE	Tukey HSD	Mean ± SE	Tukey HSD	Mean ± SE	Tukey HSD
Total C	43.49±0.07	c	47.64±0.15	a	51.79±0.14	b
Total N	0.61±0.03	c	1.61±0.03	a	1.30±0.02	b
C:N	71.84±3.48	c	29.64±0.42	a	39.92±0.80	b
Total P	0.05±0.05	a	0.08±0.00	a	0.05±0.00	b
Available P	0.05±0.01	b	0.08±0.00	a	0.04±0.00	b
C:P	807.83±62.72	c	562.54±20.07	a	1035.76±2.72	b
N:P	11.43±1.29	c	19.00±0.79	a	25.98±0.48	b
Hemicellulose	13.80±0.98	c	20.08±0.82	a	7.03±0.40	b
Cellulose	44.60±5.30	b	23.42±1.93	a	23.25±0.31	a
Lignin	20.81±5.45	a	23.16±1.69	a	39.44±0.44	b
Lignin:N	34.14±8.94	-	14.40±1.05	-	30.36±0.34	-
LCH	79.24±0.75	c	66.66±0.68	a	69.71±0.58	b

Table 4.4: Three-way ANOVA results showing significant factors and their interactions for mass of litter remaining (% initial dry mass) after 1 year of decomposition. PFTP = plant functional type of peat and PFTL = plant functional type of litter. Df = degrees of freedom, F = F value and *p* = *p* value.

Three-way ANOVA:	df	F	*p*
Site	3	0.40	0.7500
PFTP	2	0.20	0.8188
PFTL	2	131.02	<0.0001
Site*PFTP	6	0.86	0.5270
Site*PFTL	6	2.06	0.0634
PFTP*PFTL	4	0.25	0.9065

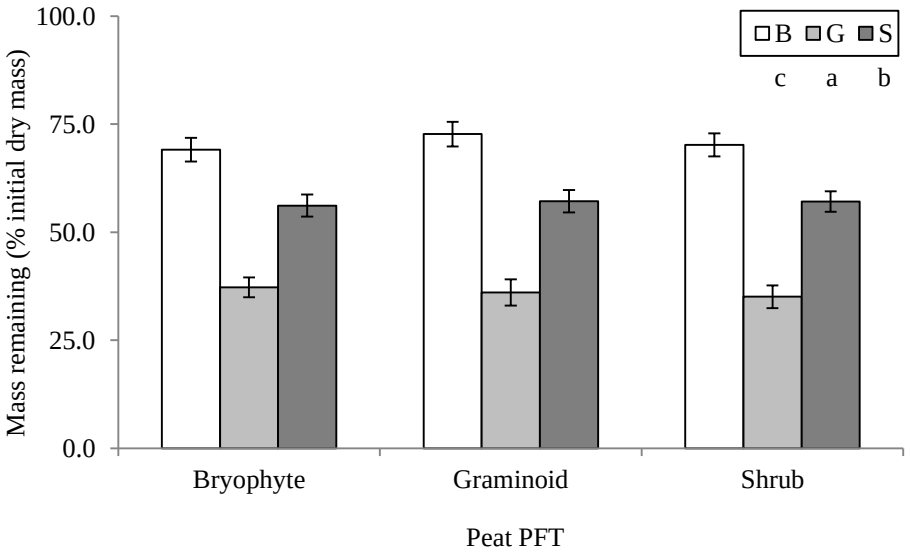

Figure 4.3: Litter mass remaining after 1 year for each litter PFT and peat PFT. B = bryophyte litter, G = graminoid litter, S = shrub litter. Letters indicate pair-wise significant differences between mass remaining of each PFT litter, tested by one-way ANOVA with Tukey's HSD test. Data are means (averaged for site) ± standard error.

4.3.6 Litter decomposition and properties of peat and litter

Percentage litter mass remaining was significantly correlated with chemical properties of litter but not peat (Table 4.5). Litter decomposition increased with increasing litter total C and N contents, hemicellulose, C:P, N:P and available P, as indicated by the negative correlations with remaining litter mass (Table 4.5). The opposite was observed for litter C:N, cellulose, total fibre (LCH), lignin:N and total P, which were positively correlated with litter mass remaining (Table 4.5). The strongest relationships were observed with litter total C content and lignin:N, with more litter mass loss with high C and low lignin:N.

The linear mixed effects model showed that chemical properties of litter improved predictions of litter decomposition more so than peat chemistry (Table 4.6). Peat pH, peat C:N and litter total N content explained 0.58%, 1.76% and 5.54% of the model variance (Table 4.6), whilst the contribution of litter total C content was much higher at 65.40% (Table 4.6). The best fit model indicates that both peat and litter chemical properties influence percentage remaining litter mass at Black Law Wind Farm, but it is litter total C content which has the greatest influence on spatial and PFT-induced differences in litter decomposition.

4.3.7 Home-field advantage and disadvantage of litter decomposition

A significant interaction between litter PFT and site was observed for HFA and HFD litter decomposition (Tables 4.7 and 4.8), but the main effect of litter PFT was stronger (Table 4.7). Additional mass loss of bryophyte litter on bryophyte peat was observed, with significant differences from zero at sites 1, 2 and 3 suggesting that HFA did occur in bryophyte litter bags across the peatland (Figure 4.4). In contrast, HFD was observed in graminoid litter bags, with significantly lower percentage mass loss of graminoid litter on graminoid peat than expected at all sites (Figure 4.4). Positive values of additional mass loss of shrub litter on shrub peat were observed, but they were not significantly different from the amount of decomposition expected (Figure 4.4). In summary, HFA was observed for bryophyte litter but not for shrub or graminoid, graminoid litter had HFD decomposition and additional mass loss of litter was only significantly different between each PFT at site 3 (Table 4.8 and Figure 4.4).

Table 4.5: Pearson's correlation between the mass of litter remaining (% initial dry mass) and peat and litter properties. Temp = deviation from mean soil temperature over the year, water table = deviation from mean water table level over the year, df = degrees of freedom and r = Pearson's correlation coefficient.

	Variable	df	r	*p* value
Peat	pH	142	0.03	0.5923
	Bulk density	142	0.04	0.3734
	Total N	142	0.06	0.6899
	Total C	142	-0.03	0.6338
	C:N	142	-0.09	0.3177
	Temp	142	0.08	ns
	Water table	142	-0.04	ns
Litter	Total N	142	-0.46	<0.0001
	Total C	142	-0.77	<0.0001
	C:N	142	0.38	<0.0001
	Lignin	142	0.04	0.9915
	Cellulose	142	0.58	<0.0001
	Hemicellulose	142	-0.43	<0.0001
	LCH	142	0.70	<0.0001
	Lignin:N	142	0.77	<0.0001
	C:P	142	-0.47	<0.0001
	N:P	142	-0.75	<0.0001
	Total P	142	0.30	<0.0001
	Available P	142	-0.64	<0.0001

Table 4.6: Linear mixed effects model to determine the relationship between litter mass remaining (% initial dry mass) and peat-litter abiotic properties across Black Law Wind Farm. Temperature = deviation from mean soil temperature over the year, water table = deviation from mean water table level over the year and - = variable not present in refined model. The relative contribution (%) of each variable in explaining model variance was calculated as % difference in adjusted R^2 comparing the full refined model and the model with each variable removed.

Variable		Mass remaining	
		%Adj.R^2	*p*
Peat	Temperature	-	-
	Water Table	-	-
	pH	0.58	0.2313
	Bulk density	-	-
	Total N	-	-
	Total C	-	-
	C:N	1.76	0.0382
Litter	Total N	5.54	0.0003
	Total C	65.40	<0.0001
	C:N	-	-
	Lignin	-	-
	Cellulose	-	-
	Hemicellulose	-	-
	LCH	-	-
	Lignin:N	-	-
	C:P	-	-
	N:P	-	-
	Total P	-	-
	Available P	-	-

Table 4.7: Two-way ANOVA results showing significant factors and their interactions for additional mass loss at home and away (% initial dry mass) after 1 year of decomposition. PFTL= plant functional type of litter. Df = degrees of freedom, F = F value and *p* = *p* value.

ANOVA:	df	F	*p*
Site	3	0.60	0.6196
PFTL	2	73.29	<0.0001
Site*PFTPL	6	2.89	0.0209

Table 4.8: Pair-wise comparisons of additional mass loss at home and away for the interaction between litter PFT and site.

Litter PFT	Site			
	1	2	3	4
B	ab	a	ab	abc
G	de	d	d	cde
S	bce	abce	bce	bce

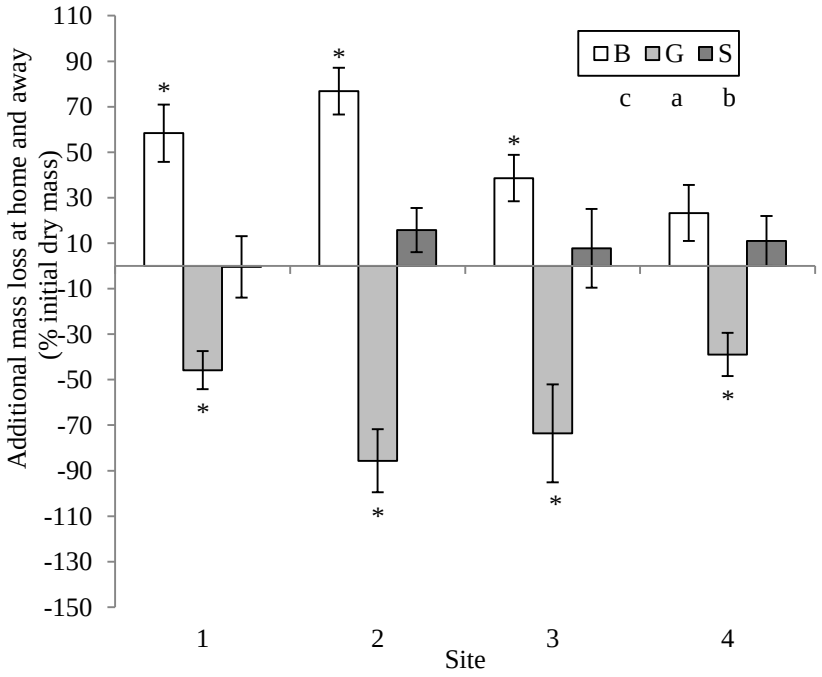

Figure 4.4: Additional litter mass at home and away for each litter PFT at each site across the wind farm transect. Positive values correspond to greater than expected litter mass loss at home (i.e. HFA), while negative values correspond to lower than expected litter mass loss at home (i.e. HFD), and asterisks indicate significant differences from zero ($p < 0.05$). B = bryophyte litter, G = graminoid litter, S = shrub litter. Letters indicate pair-wise significant differences between the additional mass loss of each PFT litter, tested by one-way ANOVA with Tukey's HSD test. Pair-wise comparisons of additional mass loss at home for each PFT for interaction between site and PFT are shown in Table 4.8. Data are means ± standard error.

4.4 Discussion

4.4.1 Controlling factors for litter decomposition

Litter PFT was a significant factor in determining differences in the amount of litter decomposition, which supports the third hypothesis and the common view that litter traits are the predominant controlling factor for litter decomposition (Aerts, 1997; Butenschoen et al., 2011; Cornwell et al., 2008; Pérez-Harguindeguy et al., 2000).

Bryophyte litter decomposed more slowly than shrub and graminoid litters, the latter decomposing the most in 1 year (Figure 4.3). These findings reflect those of other short term peatland ecosystem studies that observed low rates of decomposition in bryophyte communities. For example, in temperate fens and bogs, shrub and graminoid litter decomposition rates were faster than *Sphagnum* moss litter (Aerts et al., 1999). Similar results were observed in a peat microcosm experiment, which compared the decomposition rates of litters derived from the same PFTs, in the Alaskan tundra: 90% *Sphagnum* litter mass remained after 21 weeks, whereas 75% litter mass remained for *Eriophorum vaginatum* (Hobbie, 1996). The findings of this study showed a similar trend to that reported by Hobbie (1996) (Figure 4.3), but mass loss was greater on account of the study duration (i.e. 55 weeks instead of 21 weeks). A long-term litter bag experiment conducted on the Moor House National Nature Reserve in the Northern Pennines focussed on the decay rates of *Eriophorum vaginatum* and *Calluna vulgaris* litters. After 1 year, *Eriophorum* had 74% remaining leaf litter mass and the shoots and stems of *Calluna vulgaris* had 84% and 92%, respectively (Latter et al., 1998). While shrub litter was slower to decompose than graminoid litter, the amount of mass remaining in this study (i.e. ~36% for graminoid and ~57% for shrub) was smaller (Figure 4.3).

Graminoid plant material is typically reported to have a higher N content and proportion of labile C (Myers et al., 2012; Ström et al., 2012). In agreement, graminoid litter in this study had higher total N and P contents, available P content and proportion of hemicellulose compared to other PFT litters (Table 4.3). These chemical litter properties increase litter decomposability by providing a source of nutrients and simple C compounds for soil decomposers to utilise, selecting for a faster C cycling, more bacterial-dominated microbial community (Myers et al., 2012). Conversely, litters with high lignin:N and low hemicellulose content i.e. shrub (Table 4.3) are more recalcitrant and decompose more slowly (Cornwell et al., 2008; Trinder et al., 2009). The presence of secondary metabolites in high concentrations and the low quality (i.e. high C:N) of bryophyte litter, as seen here

(Table 4.3), are often recognised as the underlying causes for low bryophyte litter mass loss (Aerts et al., 1999; Cornelissen et al., 2007). The observed PFT effects upon litter quality and decomposition (Tables 4.2 and 4.4) indicate that PFT can influence and therefore determine short-term litter decay rates. However, Latter et al. (1997) found that the differences observed between the mass loss of graminoid and shrub litters after 1 year were not evident 22 years later; therefore caution must be taken when interpreting the findings of this study, because short-term observations will differ from longer-term responses.

Litter decomposition did not differ between sites across the peatland at Black Law Wind Farm (Table 4.4), despite spatial differences in environmental variables known to affect decomposition, such as water table level (Figure 4.1 and Table 4.1), soil temperature (Figure 4.2 and Table 4.1) and peat chemistry (see section 2.3.1, Chapter 2). Instead, spatially-consistent measures of litter chemistry (i.e. litter C and N contents) were found to be more important than spatially variable peat properties (i.e. peat pH and C:N) to best explain the differences in litter decomposition (Table 4.6).

Temperature can be used to predict litter decomposition (Butenschoen et al., 2011; Hobbie, 1996; Osono et al., 2011). In this study, however, soil temperature neither correlated significantly nor explained variation in percentage litter mass remaining (Tables 4.5 and 4.6). During the decomposition period, soil temperature varied significantly between sites and in the peat beneath different PFTs, by less than 1.2°C on average (Figure 4.2). Soil temperature was highest beneath bryophytes, but litter from that PFT decomposed the slowest. However, bryophyte litter decomposed more rapidly in its home environment, which could be attributed to warming effects enhancing soil microbial decomposition of more recalcitrant C sources (Hilasvuori et al., 2013). Responsiveness of litter decomposition to temperature increases of between 0.7 and 1.2°C has been observed previously, with significantly higher litter mass loss (~50%) with warming than without (~45%) after 4 years of field incubation (Aerts et al., 2012). In other studies with larger temperature increases (>4°C), higher decomposition rates of 5 - 18% more mass loss were recorded (Cornelissen et al., 2007; Hobbie, 1996). This implies that the decomposer community was not insensitive to the small-scale temperature changes observed across the peatland at Black Law Wind Farm, but that the response size reflected the magnitude of the temperature increase. Alternatively, the response to temperature could be masked by soil moisture availability due to changes in water table depth.

Water table was spatially variable, across the peatland and with PFT, but its relationship with the amount of litter mass loss was not significant (Tables 4.5 and 4.6). However, clear correlations with water table and litter decomposition rates have been observed previously, with a more saturated environment generally slowing the rate of litter decomposition in northern peatlands (Moore et al., 2006; Moore, 2007). However, in drained peatlands, both Laiho et al. (2004) and Lieffers (1988) attributed relatively slow decomposition rates to lowered water tables and therefore moisture stress. Whereas, at a Swedish raised bog, species decayed more rapidly in the unsaturated layer of peat compared to the intermittently or permanently saturated layers (Johnson and Damman, 1991), owing to greater potential for litter mass loss with increased peat aeration (Belyea, 1996). More recently in New Zealand, a 5 year litter bag study examining the decomposition rates at a restiad peatland found that the water table had varying effects on different litters at different sites (Clarkson et al., 2014). Litter decomposition rates decreased with increased saturation, irrespective of site, species or litter chemistry (Clarkson et al., 2014). Another study also found water table to be the principal factor controlling decomposition rates (Bridgham and Richardson, 2003), although litter chemistry was also important. On the basis of observations at other peatland sites, it is surprising that the water table at Black Law wind farm did not significantly affect litter decomposition.

Decomposition rates measured in another 1 year peatland litter bag study were found to be dependent on the combination of litter quality, abiotic conditions and decomposer activity (Belyea, 1996). Whereas, Scheffer et al. (2001) and Szumigalski and Bayley (1996) observed litter type to exert a greater effect on decomposition than the variation in environmental conditions among or within peatland. In this study, litter decomposition was found to be almost entirely dependent on litter quality, with few effects of peat chemistry (Tables 4.5 and 4.6). Differences in litter quality and nutrient availability are known to be important for the decomposition of different PFT litters in peatlands (Ward et al., 2010), and their influence upon litter mass loss rates has been examined widely. Litter decomposition of different PFTs in a peat microcosm experiment had a stronger relationship with litter C quality than with litter N concentrations (Hobbie, 1996), and also explained the most variability in litter decomposition at Black Law Wind Farm (Table 4.6). Similarly, Wang et al. (2014) found litter quality to be of significant importance, but with litter N and P concentrations affecting litter decomposition rates the most; other studies have used initial N and lignin litter concentrations to predict litter decomposition (Butenschoen et al., 2011; Hobbie, 1996; Osono et al., 2011). Lignin:N showed the strongest positive relationship with the percentage remaining litter mass (Table 4.5),

indicating the likelihood that litters with low N or high lignin contents would decompose more slowly. Although lignin:N was not significantly different between PFTs (Table 4.2), it was higher for bryophyte and shrub litters than graminoid (Table 4.3). Futhermore, litter bags containing litter with lower lignin:N were lighter at the end of the experiment (i.e. graminoid), than those containing litters with higher lignin:N (i.e. shrub and bryophyte) (Figure 4.3). However, there are limitations to using measures of litter quality to predict litter decomposition. Prescott et al. (2004) showed the initial nutrient concentrations of litter to be closely related with the first year decomposition rate of litter, but found that as litter decomposition progressed, the relationship weakened. Another more recent study also suggests that in the early stages of litter decomposition (i.e. loss of labile litter compounds), the initial litter quality controls the rate of litter decomposition (Bray et al., 2012). In the later stages of decay (i.e. loss of recalcitrant litter compounds), the composition of the microbial community will play a greater role in controlling litter decomposition rate than litter quality (Bray et al., 2012).

Despite there being no significant influence of peat PFT on litter decomposition observed after 1 year (Table 4.4), it might be expected to become more important with time via PFT legacy effects on physicochemical characteristics of the peat and in turn, the composition and size of the microbial community. Carrillo et al. (2012) found strong short-term (i.e. within 28 days) plant legacy effects on N dynamics and early stage C dynamics, owing to the litter input history to soil. Therefore, the effects of peat PFT (i.e. peat chemistry, temperature and moisture) could have contributed to differences in litter decomposition at the start of this experiment, but were not evident after 1 year due to the overriding effects of litter chemistry. Moreover, this might explain how HFA and HFD decomposition was observed despite the absence of an interaction between peat PFT and litter PFT.

4.4.2 PFT determines home-field advantage and disadvantage

The occurrence of home-field advantage (HFA) and disadvantage (HFD) decomposition was controlled by the composition of the litter bags, but not by the decomposition environment. HFA decomposition was only observed for bryophyte litter, an effect seen across the peatland, at sites 1, 2 and 3. Unlike bryophyte litter, shrub litter did not decompose more when buried ‘at home’ in peat beneath shrub plants, neither did it experience greater mass loss when ‘away’, as was the case for graminoid litter. As a result of its recalcitrant characteristics (i.e. high lignin concentration), it is surprising that shrub litter did not experience greater mass loss at home. However, bryophyte litter did have lower N content than shrub, so was more likely to experience HFA as a result of increased

competition for resources within the microbial community (Osanai et al., 2012; Vivanco and Austin, 2011).

HFA decomposition was limited to just one PFT group, therefore this study's findings only partially uphold the expectations that (1) HFA can occur in peatlands (hypothesis 1), (2) HFA will be evident for more recalcitrant litters (hypothesis 2). Higher decomposition rates have been observed when litters decompose in their native environment (Ayres et al., 2009b; Vivanco and Austin, 2008), but strong positive HFA effects are not common (Ayres et al., 2006; Carrillo et al., 2012), such as those shown in this study for bryophyte litter. In agreement with other studies, this study found that decomposition of high quality litter (e.g. graminoid with low C:N) did not show any HFA effects. However, it was not hypothesised that graminoid litter decomposition would have HFD. Greater mass loss for a high quality litter in a low quality environment (i.e. high C:N in the surrounding peat and litter) might arise from nutrient transfer and exposure to more favourable decomposition conditions (Gartner and Cardon, 2004; Hättenschwiler et al., 2005). At Black Law Wind Farm there were no PFT-induced differences in peat chemistry, which suggests that graminoid HFD decomposition could be attributed to (1) the warmer soil temperatures beneath bryophytes, (2) the lower water table levels beneath shrubs and (3) increased microbial activity as a result of graminoid litter N inputs to a more nutrient-deprived decomposer community.

Ayres et al. (2006) found that plant species did not encourage the development of soil microbial communities that specialised in decomposing their litter rapidly. It is possible that the importance of microbial community composition in decomposition increases as labile substrates are lost, with HFA and HFD effects becoming more clear and consistent over longer timescales. By measuring decomposition rates for longer than 1 year, the additional breakdown of more recalcitrant substrates (i.e. lignin) could reveal HFA and HFD effects that were not evident during earlier stages of litter decomposition. Observed differences in HFA suggest that the chemical properties of litter can affect the magnitude of preferential litter decomposition upon peat of the same PFT origin. Furthermore, the interaction between litter PFT and site suggests that the control of litter chemistry over HFA decomposition is spatially variable, perhaps due to wind farm-induced changes in the peat i.e. soil temperature and water table. However, the absence of an interaction between litter PFT and peat PFT indicates that HFA is driven primarily by the litter inputs, and not by PFT induced differences in soil chemistry.

Overall, these results show that despite HFA, bryophyte litters still decompose slowly. Graminoid litter decomposition was faster than the other PFTs over 1 year, particularly when placed in an environment different to its origin (HFD). Predicted shifts in plant community composition as a result of climate change are likely to favour the growth of vascular plant species (Gallego-Sala and Prentice, 2012). Therefore, if graminoids were to establish themselves on peat that had previously received litter inputs from shrubs or bryophytes, rates of litter decomposition and associated soil C losses to the atmosphere might be expected to increase. If the proportion of shrubs within the plant community was to increase instead, rates of shrub litter decomposition in areas previously dominated by graminoids or bryophytes are likely to remain the same i.e. no HFA or HFD.

Climate- and land use-induced changes in plant community composition could have important implications for litter decomposition rates in peatland ecosystems, by altering litter inputs, the decomposition environment and likelihood of HFA and HFD effects. Thus, despite the absence of a temperature effect on litter decomposition in this study, the influence of temperature on the future composition of each PFT within the plant community may in turn have an impact on litter decomposition and peat formation.

4.5 Conclusions

This study highlights the importance of plant functional traits in short-term decomposition processes in peatlands and demonstrates that HFA and HFD effects have the potential to influence litter mass loss. The work reported here also provides further evidence that graminoid litter decomposes faster than that of shrub and bryophyte, and that bryophyte communities are important in maintaining low rates of decomposition. This is important as the relative proportions of dominant PFTs in peatland plant communities are expected to shift with climate change, with vascular species such as graminoids predicted to dominate as bryophytes decline in blanket bogs (Gallego-Sala and Prentice, 2012). Climate and land use change effects on plant community composition could therefore have important implications for litter decomposition rates in peatland ecosystems, by altering litter inputs, the decomposition environment and the likelihood of HFA and HFD.

Other studies have examined the importance of PFT litter type (Cornwell et al., 2008; Trinder et al., 2009; Ward et al., 2009) and HFA on rates of decomposition (Ayres et al., 2009b, 2006; Freschet et al., 2012). This study uniquely investigates PFT quality, HFA, HFD and the interactions between them in a northern peatland. The results demonstrate that peatland C cycling is strongly influenced by biotic controls, which will interact with

climate to promote the decomposition of more labile litter types. Further examination of PFT, HFA and HFD effects under both field and laboratory conditions is required, over timescales that encompass later stages of decay and with the incorporation of PFT litter mixing to better represent realistic conditions within the ecosystem (Harguindeguy et al., 2008).

Chapter 5

Plant functional type and microlimatic controls on litter decomposition

5.1 Introduction

Northern peatlands are a particularly important component of the global carbon (C) cycle, accumulating vast quantities of C due to low rates of litter decomposition (Limpens et al., 2008). Decomposition in these ecosystems is limited by low pH, low temperatures, functionally limited decomposer communities, oxygen limitation and chemically complex substrates with generally low nitrogen (N) content (Freeman et al., 2001; Moore et al., 2006). However, any changes that alleviate the current constraints on decomposition could result in peatlands becoming a net source of C, rather than remaining as a net C sink (Gorham, 1991; Moore et al., 2006). Climate change due to greenhouse gas (GHG) emissions is predicted to raise mean global temperatures by 1-3.5°C in the next 50-100 years with above-average increase at high latitude and high altitude regions (IPCC, 2013). Wind farm-induced microclimate change can also have similar effects on ground-level temperature, by increasing night-time temperatures (Armstrong et al., 2014a; Zhou et al., 2012), which is of particular concern due to the ever-increasing construction of wind farms upon peatlands (Smith et al., 2014). Increases in temperature associated with climate change and wind farm microclimate change may affect rates of decomposition in peatlands (Armstrong et al., 2014b), through direct and indirect effects upon the soil environment and the quality and quantity of litter inputs (Aerts, 1997; Fierer et al., 2005), resulting in increased litter mass loss and emissions of CO_2 from the soil to the atmosphere (Cox et al., 2000; Fierer et al., 2005).

Peatland plant species are often grouped by functional similarity, to capture plant type differences at the ecosystem level (Chapin et al., 1996). Bryophytes (e.g. *Sphagnum* sp., feather mosses), shrubs (e.g. *Calluna vulgaris, Vaccinium* sp.) and graminoids (e.g. *Eriophorum vaginatum,* sedges, and rushes) are the three dominant plant functional type (PFT) groups in peatland ecosystems, with litters that differ in their decomposability due to low concentrations of N (i.e. bryophyte), high C:N and lignin content (i.e. shrub), the presence of phenolics (i.e. bryophyte and shrub) and labile C compounds (i.e. graminoid) (Dorrepaal et al., 2005; Read et al., 2004; Ward et al., 2009). The functional traits of these three PFT groups may establish a legacy within the soil over time, by conditioning the biochemical properties of the underlying peat to the PFT of the surface litter resources (Ball et al., 2014; Carrillo et al., 2012; Wardle et al., 2004). As a result, PFT legacies have the potential to change soil C dynamics by altering rates of litter mass loss and CO_2 emissions through facilitating a home-field advantage (HFA) or home-field disadvantage

(HFD) (Ayres et al., 2009b; de Toledo Castanho and de Oliveira, 2008; Vivanco and Austin, 2008).

Soil community composition has been observed to vary among areas dominated by different PFTs (Ayres et al., 2006; Ward et al., 2009). In shrub-derived peat, fungi dominate due to the presence of recalcitrant organic matter (OM), whereas bacteria thrive in moss- and sedge-derived peat as a result of labile C provision (Myers et al., 2012; Ström et al., 2012; Ward et al., 2009; Winsborough and Basiliko, 2010). Therefore, the ratio of fungi to bacteria (F:B) beneath dominant PFTs can affect the rate of litter decomposition and resultant release of CO_2 (Waring et al., 2013), with local adaptation of microbial communities resulting in faster rates of decomposition. Greater rates of respiration, a measure of decomposition, have been reported when soil microbes and litter from the same 'home' ecosystem were incubated together, indicating that differences in soil community composition among ecosystems can cause decomposition-related HFA (Strickland et al., 2009). Differences in plant litter traits could create differences in the magnitude of HFA, with high quality litter experiencing little or no HFA since being readily decomposed by most microbial communities (Ayres et al., 2009). In support of this, relatively labile litter has been found to decompose to a similar degree between different ecosystems, but recalcitrant litter decomposes substantially faster at home than away (Hunt et al., 1988). Microclimate may also have an interactive effect with litter quality and adaptation of microbial communities (de Toledo Castanho and de Oliveira, 2008; Vivanco and Austin, 2008), resulting in greater HFA with small-scale increases in temperature.

Relatively small increases in temperature have been observed to have significant effects on ecosystem functioning, with an average 1°C annual increase in temperature rising rates of respiration by up to 60% in Arctic blanket peatland (Dorrepaal et al., 2009) and greater GHG emissions from warmed peat cores under controlled laboratory conditions (Aerts and Ludwig, 1997; Blodau et al., 2004; McKenzie et al., 1998; Scanlon and Moore, 2000; Waddington et al., 2001). Research on single species litter decomposition dynamics has shown correlations with temperature (Blair, 1990; Hättenschwiler et al., 2005; Hector et al., 2000), but the effects of small-scale temperature changes on litters of different quality, in monoculture or in mixture, requires further investigation. Most ecosystem C models assume that the temperature sensitivity of decomposition is identical for all types of soil OM (Burke et al., 2003).

Temperature sensitivity is often reported as a Q_{10}, the factor by which respiration rates (i.e. rates of decomposition) will alter in response to a 10°C change. Lloyd and Taylor (1994)

predicted that soil respiration in regions where temperatures are low would be more sensitive to changes in temperature, as a result of large quantities of OM previously inaccessible to microorganisms becoming available under warmer conditions. In support of this, soil and litter respiratory Q_{10} values were reported to be ~4.5 at 10°C and ~2.5 at 20°C (Kirschbaum, 1995) and the temperature sensitivity of peat respiration was high (i.e. 4.8) when incubated at typical temperatures experienced in the Scottish uplands (0 – 15°C) (Chapman and Thurlow, 1998). Furthermore, Hamdi et al. (2013) found significantly higher temperature sensitivities for tundra and peatland soils, than those associated with forest and grassland soils. However, the Q_{10} values in peat soils are known to be highly variable (i.e. 4.6 – 9.4) (Chapman and Thurlow, 1998; Christensen et al., 1999; Mikan et al., 2002), which indicates that other environmental controls mediate the temperature response of microbial activity. In addition, the Q_{10} of microbial decomposition can vary by up to 40% depending on the recalcitrance of the soil and the complexity of C compounds in the decomposing material (i.e. the type of litter and extent of litter decomposition) (Dalias et al., 2001). Fierer et al. (2005) predicts that the decomposition of lower quality C substrates (i.e. more recalcitrant shrub litter) will be more sensitive to changes in temperature than the decomposition of higher quality C substrates (i.e. graminoid litter), a pattern that was detected later by Conant et al. (2008b) in a soil incubation study. In contrast, (Christensen et al., 1999) observed lower temperature sensitivity to increased OM recalcitrance. Therefore, the temperature sensitivity of labile and more recalcitrant OM is inconclusive, with studies reporting the temperature sensitivity of labile OM decomposition to be more, less than, or equivalent to that of more resistant OM (Briones et al., 2014; Conant et al., 2008b; Craine et al., 2010; Davidson and Janssens, 2006; Jones et al., 2003).

Temperature sensitivity of decomposition is dependent on litter quality, but because the quality of litters in mixture can differ to those in monoculture, the effects of litter mixing on decomposition has increasingly become a subject of research in the last several years (Gartner and Cardon, 2004; Harguindeguy et al., 2008; Hoorens et al., 2010, 2002). In natural ecosystems, litter from different species returns to the ground and forms a mixture, with the effect of litter mixing on decomposition likely controlled by the species involved. Therefore the decomposition of any given litter type may be influenced by the presence of other litter types. Experimental evidence suggests that where several species grow and shed their litter in close proximity, there are interactions between litters of different species decomposing together (Blair, 1990; Gartner and Cardon, 2004; Hoorens, 2003; McTiernan et al., 1997).

Some studies show that when litter species are in mixture, the properties relating to decomposition appear to be additive, such that a mixture behaves as expected based on the average influence of the individual species involved (Ball et al., 2008; Wardle et al., 1997). Alternatively, other studies have found non-additive dynamics that differ from those expected based on the monocultures, either positively or negatively (Ball et al., 2009; Chapman and Newman, 2010; Gartner and Cardon, 2004). For example, while monocultures of labile litter high in nutrients and low in structural compounds tend to provide a better resource for decomposers and support a larger decomposer community biomass, plant litter in mixture may support a more diverse decomposer community than a monoculture (Chapman and Newman, 2010; Wardle et al., 2006). Positive non-additive effects might arise due to rapidly decaying litters releasing nutrients, which can stimulate the decay of nearby recalcitrant litters (Ayres et al., 2009b; Vivanco and Austin, 2008). Negative non-additive effects could be caused by competition and microbial release of inhibitory substances from more recalcitrant litters, such as phenolics and tannins (Gartner and Cardon, 2004; Hector et al., 2000), leading to antagonistic interactions that prevent or reverse any positive mixing effects (Hättenschwiler et al., 2005). However, studies have found that interactions between litter species are often short-lived because chemical interactions are most likely to occur in the initial stages of litter decomposition (Hättenschwiler et al., 2005).

Research on single species litter decomposition dynamics has shown correlations with chemical properties of the soil and litter, especially the N content, C:N and concentration of lignin (Blair, 1990; Hättenschwiler et al., 2005; Hector et al., 2000). Studies have also investigated the response of single species litter decomposition to climate change (Cornelissen et al., 2007; Fierer et al., 2005; Luo et al., 2010), however it has become clear that single species litter decomposition may not adequately represent natural ecosystems (Gartner and Cardon, 2004; Hättenschwiler et al., 2005). Decomposition dynamics in litter mixtures have been observed to deviate from those of single species litters, such that differences of 20-30% between observed and expected mass loss are not uncommon (Ball et al., 2008; Gartner and Cardon, 2004; Hättenschwiler et al., 2005; Hoorens, 2003). In addition, the measured amount of CO_2 production from litter mixtures is often greater, but not always, than the predicted fluxes calculated from single litter CO_2 fluxes (Gartner and Cardon, 2004; Hättenschwiler et al., 2005).

Interactions between litters are usually studied between species, but more information on interactions amongst PFTs is needed in order to improve estimates of decomposition rates, and their temperature sensitivity, at the ecosystem level (Hoorens et al., 2010). Species

level studies indicate that interactions between litters are highly idiosyncratic (i.e. positive, negative, or neutral), which can be attributed to differences in the properties of litters within the mixtures (Ball et al., 2008; Hättenschwiler et al., 2005). At the PFT level, positive and negative interactions can balance each other so that interactions are not significant (Hoorens et al., 2010); therefore an overall additive effect indicates that the decomposition of PFT mixtures would equal the sum of the average decomposition rates of the contributing PFTs (Hoorens et al., 2010).

Depletion of northern peatland C stocks could result from altered litter decomposition and GHG emissions, caused by small-scale changes in temperature arising from land use change and climate change. Litter decomposition and GHG fluxes are strongly regulated by temperature (Bardgett et al., 2008; Carlson et al., 2010), but also by plant and soil properties that determine C cycle responses to climate and land use change (Gallego-Sala and Prentice, 2012; Ward et al., 2013). Some knowledge is available on the potential responses of litter mass loss to climate warming (Cornelissen et al., 2007; Fierer et al., 2005; Luo et al., 2010). To accurately assess the impacts of future climate change on terrestrial C dynamics, the factors that control temperature sensitivity of litter decomposition need to be better understood (Fierer et al., 2005).

In this study the influence of warming on the interactions between plant litter diversity and peat PFT legacy, and their effects on respiration and litter decomposition rates, were examined. It was hypothesised that: (1) temperature will be a stronger driver of litter decomposition and heterotrophic respiration than the PFT of the litter or underlying peat, (2) temperature sensitivity of litter decomposition and heterotrophic respiration will decrease with increasing litter and peat quality, (3) monoculture litters will decompose differently on peat derived from each PFT, with HFA decomposition likely to occur for low quality litter such as that from bryophytes, (4) non-additive effects of litter mixing will occur, with high quality litter promoting the decomposition of low quality litter in litter mixtures. To test these hypotheses a multi-factorial microcosm experiment was designed to investigate the interactive effects of temperature and litter species diversity, on litter decomposition and heterotrophic respiration from peat sampled from under three different PFTs. By investigating litter mixtures, the aim of this study was to improve understanding of the consequences of plant community composition change, i.e. the relative proportion of each PFT within the ecosystem, as a result of global and land use change effects on peatland ecosystems.

5.2 Methods

5.2.1 Determining litter decomposition

Peat cores were taken in October 2012 from a 10 m^2 sampling area of blanket bog at Black Law Wind Farm (Figure 1.1, Chapter 1), using the same method as described in section 2.2 of Chapter 2. Two hundred and eighty eight intact cores (PVC pipe, 5 cm diameter, 15 cm depth) were taken in total, with ninety six from beneath each PFT. Live vegetation was removed and senesced litter from bryophytes, graminoids and shrubs was collected prior to peat coring. Shed *Calluna vulgaris* leaves were collected, and leaves that had not been shed but had lost their green colour were harvested with the brown shoots to which they were attached. *Eriophorum vaginatum* leaves were collected by loosely shaking the plant and separating the senesced leaves by hand. Decomposition of Sphagnum litter is difficult to identify (Hogg, 1993), however in accordance with previous studies (Aerts et al., 2001; Bragazza et al., 2007), the stem section 2-4cm beneath the capitulum (i.e. growing tip) was used to represent freshly deposited *Sphagnum* litter stored in the acrotelm.

In order to ascertain the initial biochemical characteristics of peat and litter, 15 additional peat cores (PVC pipe, 5 cm diameter, 15 cm depth) were taken from the same core collection area. Total C content, total N content and microbial community composition were assessed using methods described in section 2.2 of Chapter 2. Four air-dried plant litter samples of each litter PFT, in monoculture and mixtures (Table 5.1), were also analysed for total C content and total N content.

Table 5.1: Litter bag treatments comprised of no litter, single litters of each PFT and each mixed combination of the three PFTs.

Litter bag treatment		Mixing ratio
N	No litter	-
B	Bryophyte	-
G	Graminoid	-
S	Shrub	-
BG	Bryophyte + Graminoid	1:1
BS	Bryophyte + Shrub	1:1
GS	Graminoid + Shrub	1:1
BGS	Bryophyte + Graminoid + Shrub	1:1:1

A fully factorial experimental design comprising three temperatures, three peat PFTs and eight litter bag treatments was established. Incubation temperatures of 12, 14 and 16 °C were selected in order to simulate small scale temperature changes. At each temperature, thirty two peat cores from each peat PFT were randomly assigned a litter bag treatment, i.e. each core was overlain by a litter bag. At each temperature, there were four replicates of each peat core PFT and litter bag treatment combination.

Field moisture levels in the peat cores were maintained gravimetrically, and litter bags kept moist, with the regular addition of deionised water. Deionised water was used in preference to rainwater collected from Black Law Wind Farm to control for variable nutrient inputs. Peat cores were incubated for 363 days, in order to capture slow decomposition.

Litter decomposition rates were determined using the litter mass loss method (Graças et al., 2005). Litter bags contained a total of 0.5 g of air-dried litter and were assembled using polyethylene mesh (litter bags: 5 cm^2, mesh width: 1 mm) (see section 4.2.1. of Chapter 4). The first set of litter bags contained no litter and the second, third and fourth sets of litter bags contained litter of just one individual species, from each of the three PFTs (Table 5.1). All other litter bags comprised a mixture of the three PFTs, in equal proportions by weight (Table 5.1). Litter bags were removed from the cores after 363 days and the amount of litter mass remaining was calculated as a percentage of the initial dry litter mass (see section 4.2.1. of Chapter 4).

CO_2 emissions were measured six times at 0, 56, 119, 174, 230 and 363 days after the start of the experiment. To measure respiration rates, peat cores (with litter bags still in place) were transferred into an airtight chamber (1567 cm^3), which was attached to an EGM-4 portable infrared gas analyser (IRGA). The enclosure time for respiration measurements was 300 seconds with a measurement taken every four seconds. The records were examined and fluxes calculated from the gradient of the [CO_2] with time $\left(\frac{dCO_2}{dt}\right)$ and converted into a flux using chamber volume in (V, m^3), temperature (T, °K), chamber footprint (A, m^2) and the molar mass of CO_2 in g mol^{-1} (M, 44.01 for CO_2, reporting as CO_2-C) (Holland et al., 1999).

5.2.2 Temperature sensitivity

In order to determine the temperature sensitivity of percentage litter mass loss and CO_2 emissions, an exponential van't Huff function was used to describe the relationship

between litter mass loss and CO_2 emissions with temperature (Eqn. 1) (Yiqi and Zhou, 2010). R refers to the heterotrophic respiration rate (mg CO_2 - C m^{-2} h^{-1}) or mass loss (% initial dry litter mass) at a given temperature, T is temperature (° C), α is R at 0 °C and β is the temperature response co-efficient.

$$R = \alpha e^{\beta T} \quad \text{Eqn. 1}$$

Q_{10} values were calculated using the temperature response co-efficient (β) in the following relationship (Eqn. 2).

$$Q_{10} = exp^{10\beta} \quad \text{Eqn. 2}$$

5.2.3 Home field advantage and disadvantage

The HFA or HFD of percentage litter mass loss and CO_2 emissions was determined using a method proposed by Ayres *et al*. (2009), outlined in section 4.2.2. of Chapter 4. HFA or HFD of each peat PFT was calculated for cores with litter bags containing single species, at each temperature.

5.2.4 Mixed litter interactions

Interactions between PFT litters in mixtures were determined by first calculating the expected mass remaining (Eqn. 3) (Hoorens et al., 2010), based on the remaining mass of single PFT litter bags of the component litters, which were incubated at the same temperature and on the same peat PFT. Interactions can be used to determine whether there was an additive or non-additive effect of litter mixing (Hoorens et al., 2010).

R refers to the remaining mass of PFT litter in the single-PFT litter bag and M refers to the initial dry litter mass of a litter PFT in the mixture. The suffixes indicate which particular PFT is referred to: B = bryophyte, G = graminoid and S = shrub. Interaction strength was calculated as shown in Eqn. 4. When observed mass remaining (O) was lower than expected (E) the interaction was positive and when it was higher the interaction was negative (Hoorens et al., 2010).

Expected mass remaining =

$$\frac{M_B \times R_B}{M_B + M_G + M_S} + \frac{M_G \times R_G}{M_B + M_G + M_S} + \frac{M_S \times R_S}{M_B + M_G + M_S} \quad \text{Eqn. 3}$$

Interaction strength =

$$1 - \frac{O}{E} \quad \text{Eqn. 4}$$

5.2.5 Statistical analysis

All statistical analysis was performed using the statistical package R, version 2.14.0 (The R Project, 2012) and all data were checked for normality before final analysis. Throughout the text, 'significant' is referred to if $p < 0.05$.

To identify differences in peat and litter quality that are hypothesised to influence litter decomposition and CO_2 emissions, the significance of PFT on biological and chemical properties of peat cores, single litters and litter mixtures was tested using one-way ANOVAs followed by Tukey's test *post-hoc* analyses.

A linear mixed effects (LME) model was used to further investigate the role that temperature and PFT-derived differences in peat and litter properties have in determining litter decomposition. A LME model of litter mass remaining was constructed for all peat cores at each temperature. Replicate was included as a random effect and biochemical properties of peat and litter were specified as fixed effects. Chemical properties included C:N, total C content and N content of peat and litter. The measures of microbial community composition used were total PLFAs, bacterial PLFAs, fungal PLFAs, F:B, gram positive (gram +ve) PLFAs, gram negative (gram –ve) PLFAs and gram +ve:gram -ve. The initial model including all fixed effects could not be used due to problems with complexity and the presence of co-linear variables. To determine the source of these problems, each fixed effect variable was removed from the model in turn. The following fixed effect variables were removed permanently from the model: peat C:N total PLFAs, bacterial PLFAs, fungal PLFAs, F:B, gram +ve PLFAs, gram -ve PLFAs, gram +ve:gram -ve. The final model and the relative contribution of each variable in explaining the variance of the final model was achieved by following the procedure outlined in section 4.2.4. of Chapter 4. An LME model was also used to investigate how the relative abundance of microbial functional groups in peat and chemical properties of peat and litter

improved predictions of CO_2 emissions. A LME model of CO_2 emissions was constructed for all peat cores at each temperature. Replicate was included as a random effect and biochemical properties of peat and litter were specified as fixed effects. The parameters included and model refinement is the same as the % litter mass remaining LME model above.

In order to test the hypothesis that temperature would be a stronger driver of litter decomposition (% litter mass remaining) than peat PFT and litter PFT, a three-way ANOVA was performed and followed by Tukey's test *post-hoc* analyses. Linear mixed effects (LME) modelling was performed to examine the interactive effects of temperature, peat PFT and litter PFT on CO_2 emissions over the duration of the experiment, in order to test if the hypothesised effects for litter mass loss were the same for heterotrophic respiration rates. Core ID was used as a random effect to account for the repeated measures made over the course of the 363 day incubation. Tukey's test *post-hoc* analyses were used to allow multiple comparisons to be made between treatments and sampling points.

To test the hypothesis that the temperature sensitivity of litter mass loss would be influenced by peat PFT and litter PFT, a two-way ANOVA was used and followed by Tukey's test *post-hoc* analyses. Two-way ANOVA was also used to test the hypothesis that PFT litters (in monoculture) would decompose differently on peat derived from each PFT. The significance of temperature and litter PFT on additional mass loss at home (HFA) or away (HFD) was tested, and followed by Tukey's test *post-hoc* analyses and t-tests to test if additional mass loss at home was significantly different to zero. LME models and Tukey's test *post-hoc* analyses were also used to examine the interactive effects of temperature and litter PFT on additional CO_2 emissions at home (HFA) and away (HFD) over the duration of the experiment. T-tests were used to test if additional mass loss at home or away was significantly different to zero. In both instances, core ID was used as a random effect to account for the repeated measures.

It was hypothesised that non-additive effects of litter mixing would occur, with high quality litter promoting the decomposition of low quality litter in mixtures. A three-way ANOVA and Tukey's test *post-hoc* analyses were performed to test the significance of temperature, peat PFT and litter PFT on the interactions strengths between litters in each PFT mixture. T-tests were also performed, to test if the interaction strengths were significantly different to zero. LME models were also used to examine the interactive effects of peat PFT and litter PFT on temperature sensitivity of CO_2 emissions over the duration of the experiment, followed by Tukey's test *post-hoc* analyses.

5.3 Results

5.3.1 Biochemical properties of peat and litter

ANOVA analyses showed that all biochemical peat properties varied significantly between PFTs, with the exception of total N content and F:B (Table 5.2). Peat total C content was significantly higher in graminoid peat than in bryophyte and shrub peat, whereas the opposite was found for C:N and the ratio of gram +ve to gram -ve bacterial PLFAs (Tables 5.2 and 5.3). The concentration of total PLFAs, bacterial PLFAs, gram +ve and gram -ve bacterial PLFAs were all significantly lower in bryophyte peat, than in graminoid and shrub peat (Tables 5.2 and 5.3). However, for fungal PLFAs, concentrations were only higher in shrub peat than in bryophyte peat (Tables 5.2 and 5.3).

PFT was found to affect the total C content, total N content and C:N of litter (Table 5.4). The total C content of litters in monoculture increased significantly from bryophyte to graminoid to shrub litter (Tables 5.4 and 5.5). Litter mixtures containing bryophyte litter had significantly lower total C content than shrub litter alone, and in combination with graminoid litter (Tables 5.4 and 5.5). Furthermore, litter mixtures containing shrub had significantly higher total C content than the combination of bryophyte and graminoid litters (Tables 5.4 and 5.5). Litter total N content was also lowest in bryophyte litter, whilst graminoid litter in monoculture and in combination with shrub litter had higher concentrations of N that all other litters (Tables 5.4 and 5.5). In monoculture, C:N was lowest in graminoid litter and highest in bryophyte litter. Litter C:N of shrub, the bryophyte and graminoid mix, and the all litters mix was (1) significantly higher than graminoid litter alone and in combination with shrub and (2) significantly lower than in bryophyte litter and the mixture of bryophyte and shrub litters (Tables 5.4 and 5.5).

Table 5.2: Biochemical properties of peat cores collected from beneath each PFT. S = shrub, G = graminoid, B = bryophyte. Peat properties were analysed with one-way ANOVA with peat PFT as the main factor. S = shrub, G = graminoid, B = bryophyte. Symbols indicate significant differences between peat PFTs for each peat property: *ns* = not significant, * = $p < 0.05$, ** = $p < 0.01$. Data are means ± standard error.

	Property	Peat PFT			
		B	G	S	*p*
Peat	Total C	44.01±1.88	50.19±0.57	44.83±1.09	0.0026
	Total N	2.04±0.09	1.97±0.09	2.03±0.03	0.7220
	C:N	21.59±0.29	25.72±1.71	22.14±0.58	0.0026
	Total PLFAs	78.32±13.48	179.43±13.97	179.60±9.06	0.0001
	Total fungi	7.14±1.40	18.63±6.33	27.94±2.17	0.0170
	Total bacteria	42.47±7.66	91.38±7.26	88.79±4.15	0.0003
	F:B	0.17±0.01	0.21±0.07	0.31±0.01	0.1840
	Total gram +ve	21.90±4.03	43.06±3.35	45.31±2.48	0.0008
	Total gram –ve	19.90±3.58	47.18±4.23	42.04±1.85	0.0008
	Gram +ve:gram-ve	1.10±0.02	0.92±0.05	1.08±0.04	0.0123

Table 5.3: Pair-wise comparisons of peat properties between each peat PFT, analysed by one-way ANOVA and Tukey's HSD test.

Peat property	Peat PFT		
	B	G	S
Total C	b	a	b
Total N	a	a	a
C:N	b	a	b
Total PLFAs	b	a	a
Total fungi	b	ab	a
Total bacteria	b	a	a
F:B	a	a	a
Total gram +ve	b	a	a
Total gram -ve	b	a	a
Gram +ve:gram -ve	b	a	b

Table 5.4: Properties of litter used for the single and mixed PFT litter bag treatments. Litter properties were analysed with one-way ANOVA with litter PFT as the main factor. S = shrub, G = graminoid, B = bryophyte. Data are means ± standard error.

Property	Litter PFT – single and mixed litter bag treatments							
	B	G	S	BG	BS	GS	BGS	*p*
Total C	43.49±0.07	47.64±0.15	51.79±0.14	45.11±0.09	47.73±0.12	49.76±0.11	47.06±0.13	<0.0001
Total N	0.61±0.03	1.61±0.03	1.30±0.02	1.16±0.02	1.05±0.01	1.47±0.02	1.23±0.01	<0.0001
C:N	71.84±3.48	29.64±0.42	39.92±0.80	38.98±0.70	45.33±0.73	33.82±0.59	38.14±0.24	<0.0001

5.3.2 Litter decomposition

Temperature exerted a greater influence on litter decomposition than peat PFT, but the PFT composition of litter had the largest effect overall, contrary to the first hypothesis (Table 5.6). Litter bags at 12°C lost more mass than those at 14°C and 16°C (Figure 5.1). Litter bags containing graminoid litter had less mass remaining, compared to litter bags comprised of bryophyte and shrub litter monocultures, and their litters in combination (Figure 5.1). The PFT legacy in peat was found to affect litter decomposition (Table 5.6), but post-hoc testing did not reveal any differences between the mass loss of litter bags that decomposed on peat derived from bryophyte, graminoid or shrub.

There was a significant interaction between temperature and litter PFT (Table 5.6). Decomposition of graminoid and shrub litters in monoculture, as well as all three PFT litters in combination, did not vary significantly between temperatures (Figure 5.1 and Table 5.7). However, at 14°C and 16°C, the remaining litter mass was significantly higher in litter bags comprising bryophyte litter alone, mixtures of bryophyte with graminoid and shrub, and the combination of graminoid and shrub litters (Figure 5.1 and Table 5.7). There was also an interactive effect of peat PFT with litter PFT, which was weakly significant, but indicates the potential for greater than expected litter mass loss on peat derived from the same PFT (Tables 5.6 and 5.7).

Statistical modelling to examine the relationships between microbial and chemical metrics as determinants of the remaining mass of litter after 363 days of decomposition identified litter total C content, litter C:N and total N content of both peat and litter as the only significant terms retained in the model (Table 5.8). The % remaining litter mass was best predicted using litter C:N, which explained the most attributed variance in the model (Table 5.8), but also indicates that litter chemistry can influence litter decomposition at temperatures relevant to northern peatlands.

Table 5.5: Pair-wise comparisons of litter properties between each litter bag treatment, analysed by one-way ANOVA and Tukey's HSD test.

Litter property	Litter PFT						
	B	G	S	BG	BS	GS	BGS
Total C	f	c	e	a	c	d	b
Total N	e	d	c	ab	c	d	ac
C:N	e	c	a	a	b	d	a

Table 5.6: Three-way ANOVA results showing significant factors and their interactions for litter mass remaining (% initial dry litter mass). T = temperature (°C), PFTP = plant functional type of peat, PFTL = plant functional type of litter. Df = degrees of freedom, F = F value and *p* = *p* value.

Three-way ANOVA	df	F	*p*
T	2	25.67	<0.0001
PFTP	2	3.19	0.0436
PFTL	6	47.77	<0.0001
T*PFTP	4	0.24	0.9139
T*PFTL	12	2.62	0.0030
PFTP*PFTL	12	1.81	0.0494

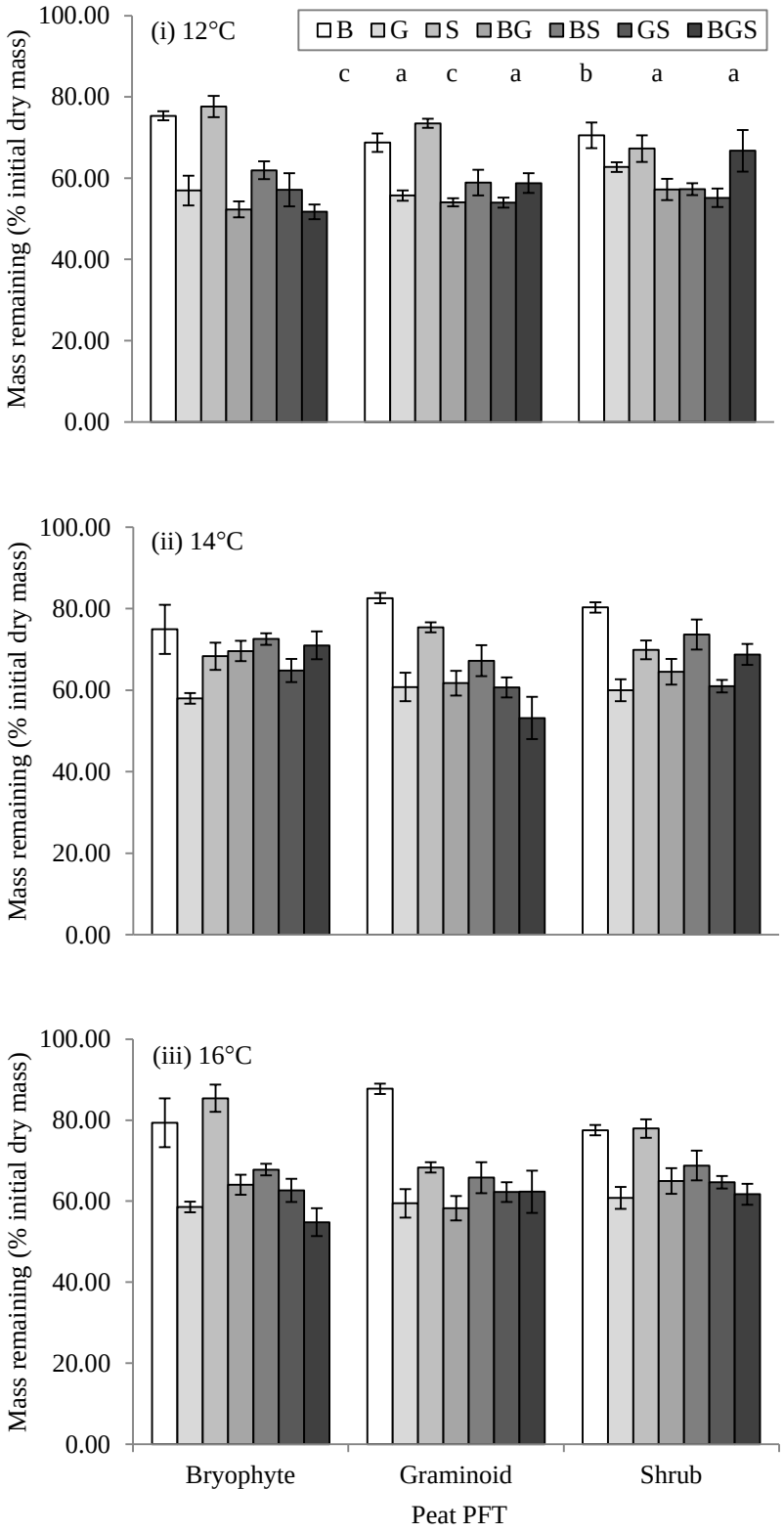

Figure 5.1: Mass remaining of single and mixed PFT litters on each PFT peat core, at 12 °C, 14 °C and 16 °C. Letters indicate pair-wise significant differences between the remaining mass of PFT litter treatments. Pair-wise comparisons of remaining mass for each litter PFT at each temperature, and on each peat PFT, are shown in Table 5.7. Data are means ± standard error.

Table 5.7: Pair wise comparisons between litter PFT and each temperature (T), and each peat PFT (PFTP), for percentage remaining litter mass.

		Litter PFT – single and mixed litter bag treatments						
		B	G	S	BG	BS	GS	BGS
T (°C)	12	aceg	bdf	aeg	b	bdf	bf	bdf
	14	a	bdf	aceg	cde	aceg	bcdf	cdef
	16	a	bdf	ag	bcdf	cdeg	bcdef	bdf
PFTP	B	ab	c	ab	cde	abcde	cd	c
	G	a	c	abe	c	cde	c	c
	S	ab	cd	abde	cde	bcde	c	bcde

Table 5.8: Linear mixed effects model to determine the relationship between litter mass remaining (% initial dry litter mass) and properties of peat and litter. Symbol - = variable not present in refined model. The relative contribution (%) of each variable in explaining model variance was calculated as % difference in adjusted R^2 comparing the full refined model and the model with each variable removed.

Variable	Litter Decomposition	
	%Adj.R^2	*p*
Peat C content	-	-
Peat N content	2.16	0.0489
Peat C:N	-	-
Total PLFA	-	-
Total fungi	-	-
Total bacteria	-	-
F:B	-	-
Total gram +ve	-	-
Total gram –ve	-	-
Gram +ve:gram -ve	-	-
Litter C content	4.16	0.0064
Litter N content	7.19	0.0004
Litter C:N content	8.63	0.0001

5.3.3 Temperature sensitivity of litter decomposition

Temperature sensitivities of litter mass loss determined as Q_{10} values ranged between 0.03-2.71 with a mean of 0.77 and a median of 0.66. Q10 values tended to be higher on graminoid peat, than on bryophyte and shrub peat (Figure 5.2). Trends suggest that mass loss of single graminoid and shrub litters had higher temperature sensitivities than when mixed with other PFTs, and increased the temperature sensitivity of bryophyte litter when combined (Figure 5.2). The effects of peat PFT and litter PFT on the temperature sensitivity of litter decomposition were not significant, however, there was a significant interaction between them (Table 5.9). This interaction was observed as higher Q_{10} values for shrub litter on graminoid peat, than on bryophyte or shrub peat. Hypothesis 2 predicts that the decomposition of more recalcitrant organic material would be more sensitive to changes in temperature than the decomposition of more labile matter. However, findings here do not support this 'quality vs. temperature sensitivity' hypothesis.

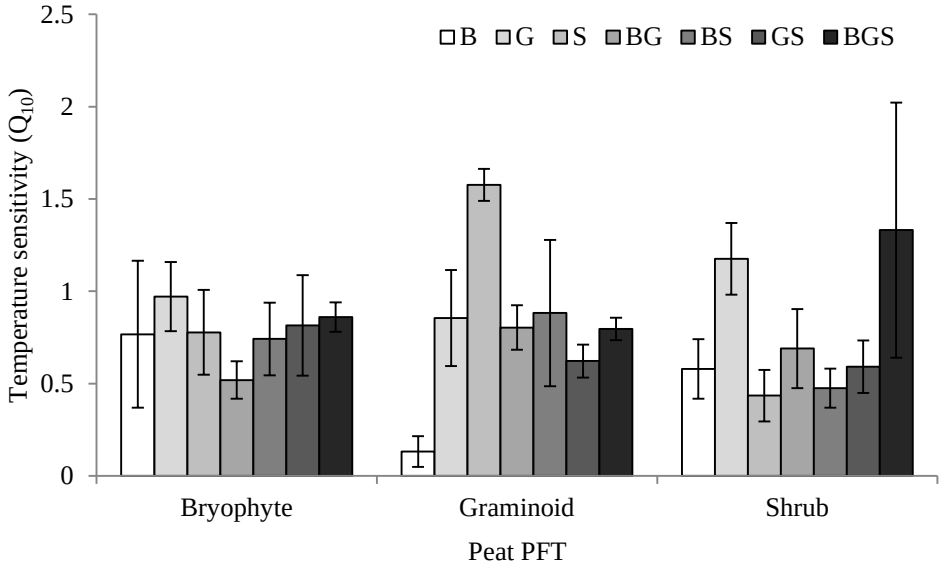

Figure 5.2: Temperature sensitivity of litter mass loss (% initial dry mass), determined by Q_{10} values, for each peat PFT and litter bag PFT treatment combination. Mean values ± standard error.

Table 5.9: Two-way ANOVA results showing significant factors and their interactions for temperature sensitivity of litter mass loss (determined by Q_{10} values). PFTP = plant functional type of peat, PFTL = plant functional type of litter: single and mixed litter bag treatments. Df = degrees of freedom, *F* = *F* value and *p* = *p* value.

Two-way ANOVA:	df	F	*p*
PFTP	2	0.17	0.8417
PFTL	6	2.17	0.0583
PFTP*PFTL	12	2.05	0.0347

5.3.4 Home field advantage of litter decomposition

The amount of additional mass loss of a litter on peat derived from the same PFT (HFA) and from a different PFT (HFD) was significantly affected by litter PFT, and the interaction between litter PFT and temperature (Table 5.10). Hypothesis 3 was partly confirmed as bryophyte and shrub litters both experienced HFA, whereas graminoid litter mass loss did not increase on graminoid peat (i.e. HFD decomposition occurred) (Figure 5.3). The additional mass loss of bryophyte and shrub litters at home were not significantly different to each other, but were both greater than graminoid. At 12°C shrub litter was observed to have HFA, whereas bryophyte litter did not. At 14 °C and °16 C however, significantly more bryophyte mass loss on bryophyte peat was observed (HFA) and not for shrub (Table 5.11). A 2 - 4°C rise in temperature did not significantly affect the respective HFA and HFD decomposition of shrub and graminoid litters, despite the increase in graminoid HFD observed with increasing temperature (Figure 5.3).

Table 5.10: Two-way ANOVA results showing significant factors and their interactions for additional mass loss at home (HFA). T = temperature (°C) and PFTL = plant functional type of litter. Df = degrees of freedom, F = F value and *p* = *p* value.

Two-way ANOVA	df	F	*p*
T	2	0.05	0.9501
PFTL	2	38.36	<0.0001
T*PFTL	4	6.38	0.0010

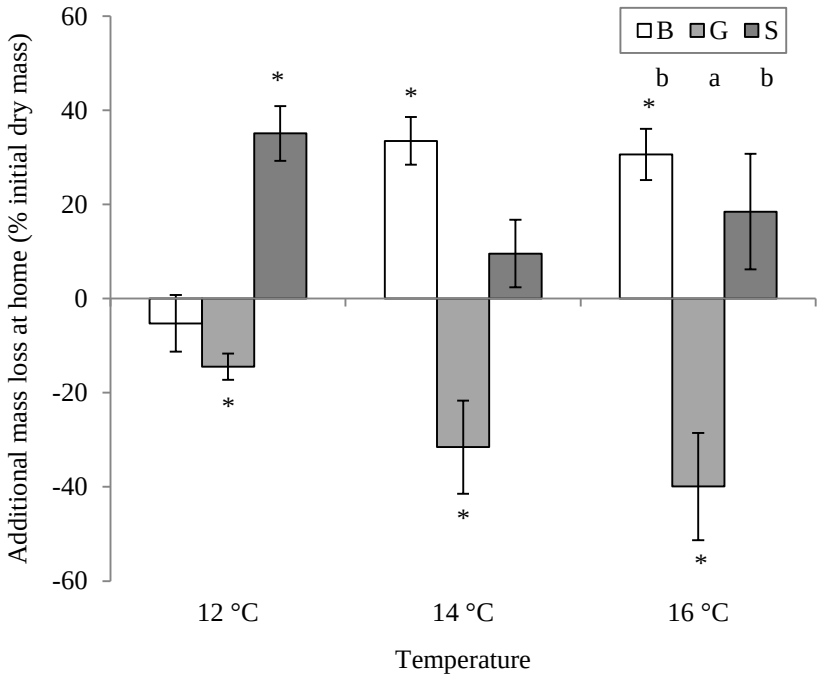

Figure 5.3: Additional litter mass at home for each litter PFT (B = bryophyte litter, G = graminoid litter, S = shrub litter) at each incubation temperature. Asterisks indicate significant differences from zero ($p < 0.05$). Letters indicate pair-wise significant differences between the additional mass loss of each single PFT litter. Pair-wise comparisons between each temperature and peat PFT for additional mass loss at home are shown in Table 5.11. Data are means ± standard error.

Table 5.11: Pair wise comparisons between each temperature and litter PFT, for additional mass loss at home.

		Litter PFT		
		B	G	S
Temperature (°C)	12	abd	ab	c
	14	c	a	bcd
	16	cd	a	bcd

5.3.5 Interactions between litters

Peat PFT influenced the strength of interactions in litter mixtures, but contrary to expectations, litter PFT did not (Table 5.12). Overall, temperature exerted the most control over the interaction strengths (Table 5.12), which were in general relatively low (i.e. close to zero) (Table 5.13). Higher values were observed at 12°C and 16°C than at 14°C, and on graminoid peat compared to shrub peat (Table 5.13). There was a significant interaction between temperature and peat PFT (Tables 5.12 and 5.14), with higher interaction strengths at 12°C and 16°C on bryophyte peat. Positive interactions were observed for all PFT litter mixtures, peat PFTs and temperatures, apart from bryophyte peat at 14°C (Table 5.13). Only 13 significant interactions occurred out of a possible 36, with over half of these occurring at 12°C (Table 5.13). The highest number of interactions occurred on bryophyte peat, and the least on shrub (Table 5.13). More significant interactions were observed for mixtures containing bryophyte and shrub litters than those comprised of graminoid litter (Table 5.13), that is, the presence of shrub and bryophyte litter accelerated the decomposition of other litters in mixture more so than graminoid litter did. The premise that high quality litter would promote the decomposition of low quality litter in mixtures (hypothesis 4) was not found, and instead the opposite occurred.

Table 5.12: Three-way ANOVA results showing significant factors and their interactions for interaction strength of litters in mixture. T = temperature (°C), PFTP = plant functional type of peat and PFTL = plant functional type of litter. Df = degrees of freedom, F = F value and *p* = *p* value.

Three-way ANOVA	df	F	*p*
T	2	12.16	<0.0001
PFTP	2	4.52	0.0130
PFTL	3	1.04	0.3790
T*PFTP	4	8.78	<0.0001
T*PFTL	6	1.15	0.3400
PFTP*PFTL	6	1.26	0.2840

Table 5.13: Mean interaction strength values ±standard error (SE) in the PFT litter mixtures, on bryophyte, graminoid and shrub peat, at 12°C, 14°C and 16°C. Interactions in bold are significantly different from zero (p <0.05). Mixtures contained litters from each PFT: B = bryophyte, G = graminoid, S = shrub.

Peat PFT	PFT litter mixture	Temperature					
		12°C		14°C		16°C	
		Mean	SE	Mean	SE	Mean	SE
Bryophyte	BG	**0.21**	0.03	-0.06	0.08	0.06	0.05
	BS	**0.19**	0.03	-0.02	0.03	**0.18**	0.04
	GS	0.14	0.09	-0.03	0.05	**0.13**	0.02
	BGS	**0.26**	0.01	-0.06	0.04	**0.26**	0.04
Graminoid	BG	**0.13**	0.04	**0.14**	0.02	0.20	0.07
	BS	0.17	0.06	**0.15**	0.04	0.16	0.06
	GS	**0.16**	0.01	0.13	0.06	0.02	0.05
	BGS	0.11	0.04	0.17	0.09	0.14	0.06
Shrub	BG	0.14	0.05	0.08	0.06	0.06	0.06
	BS	**0.17**	0.02	0.02	0.05	**0.12**	0.03
	GS	**0.15**	0.05	0.06	0.01	0.07	0.02
	BGS	0.00	0.08	0.02	0.03	0.14	0.06

Table 5.14: Pair wise comparisons between each temperature and peat PFT, for interaction strength in litter mixtures.

		Peat PFT		
		B	G	S
Temperature (°C)	12	a	ab	ab
	14	c	a	bc
	16	a	ab	ab

5.3.6 Heterotrophic respiration

CO_2 emissions ranged from 5.04 – 198.12 mg CO_2-C m^{-2} h^{-1}, with a mean of 68.17 mg CO_2-C m^{-2} h^{-1} and a median of 63.59 mg CO_2-C m^{-2} h^{-1}. Similarities with litter decomposition were observed, as repeated measures ANOVA analysis showed significant differences in CO_2 emissions with temperature, litter PFT and peat PFT (Table 5.15). CO_2 emissions increased from 12°C to 14°C, and were highest at 16°C (Figure 5.4). CO_2 emissions were higher from cores with litter bags containing a mixture of bryophyte and shrub litters, than from cores i) without litter, ii) with litter bags comprised of graminoid litter alone and iii) in combination with shrub litter (Figure 5.4). Overall, the PFT legacy effect on peat exerted the most influence on CO_2 emissions, with measured fluxes increasing from bryophyte to shrub, to graminoid peat (Figure 5.4). However, there was an interesting interaction between temperature and peat PFT (Table 5.15), which showed CO_2 emissions from graminoid peat to increase with each 2°C rise in temperature, which was not the case with shrub or bryophyte peat (Figure 5.4 and Table 5.16). By subtracting the amount of CO_2 measured from peat cores without litterbags, it allowed the additional CO_2 emitted from the decomposing litter to be observed more clearly (Figure 5.5). Overall, the litterbags were contributing additional CO_2 to the amount already being emitted from the peat cores. In some cases this was not always observed, for instance graminoid peat cores at 12 °C emitted more CO_2 in the absence of litter (Figure 5.5).

Overall, there was a significant decline in CO_2 emissions over time (Figure 5.6 and Table 5.15). CO_2 emissions at the beginning of the experiment and after 56 days were not significantly different, but were significantly higher than CO_2 emissions at day 119, 174, 230 and 363 overall. CO_2 emissions at day 230 were significantly lower than those measured at any other point during the incubation (Figure 5.6). There was a significant

interaction between time and temperature (Tables 5.15 and 5.17). Overall, CO_2 emissions at 16°C remained higher than those at 12°C for the duration of the experiment, but CO_2 emissions at 14°C were not consistently higher or lower than 12°C or 16°C. Effects of peat PFT on CO_2 emissions also varied significantly with time (Tables 5.15 and 5.17), with the reduction in CO_2 emissions from graminoid peat cores larger than that from bryophyte and shrub-derived peat from day 56 to day 230.

The dominant factors driving the differences in observed CO_2 emissions were identified using statistical modelling, which examined the relationships between microbial and chemical metrics as determinants of CO_2 emissions. Total C and N content of litter and peat were the only significant terms remaining in the model (Table 5.18). CO_2 emissions were best predicted using litter terms, with total litter C content explaining the most attributed variance in the model (Table 5.18).

Table 5.15: Linear mixed effects (LME) model of CO_2 emissions (mg CO_2 – C m^{-2} h^{-1}). D = days since start of experiment, T = temperature (°C), PFTP = plant functional type of peat, PFTL = litter plant functional type treatment. Df = degrees of freedom, *F* = *F* value and *p* = *p* value.

LME: Repeated Measures ANOVA	df	F	*p*
D	5	25.39	<0.0001
T	2	44.59	<0.0001
PFTP	2	77.18	<0.0001
PFTL	7	4.12	0.0003
D * T	10	3.27	0.0004
D * PFTP	10	8.01	0.0004
D * PFTL	35	0.94	0.5704
PFTP * PFTL	14	1.58	0.0852
T * PFTP	4	4.10	0.0031
T * PFTL	14	1.60	0.0803

Table 5.16: Pair wise comparisons between each temperature and peat PFT, for CO_2 emissions.

		Peat PFT		
		B	G	S
Temperature (°C)	12	b	c	ac
	14	ab	d	f
	16	ac	e	df

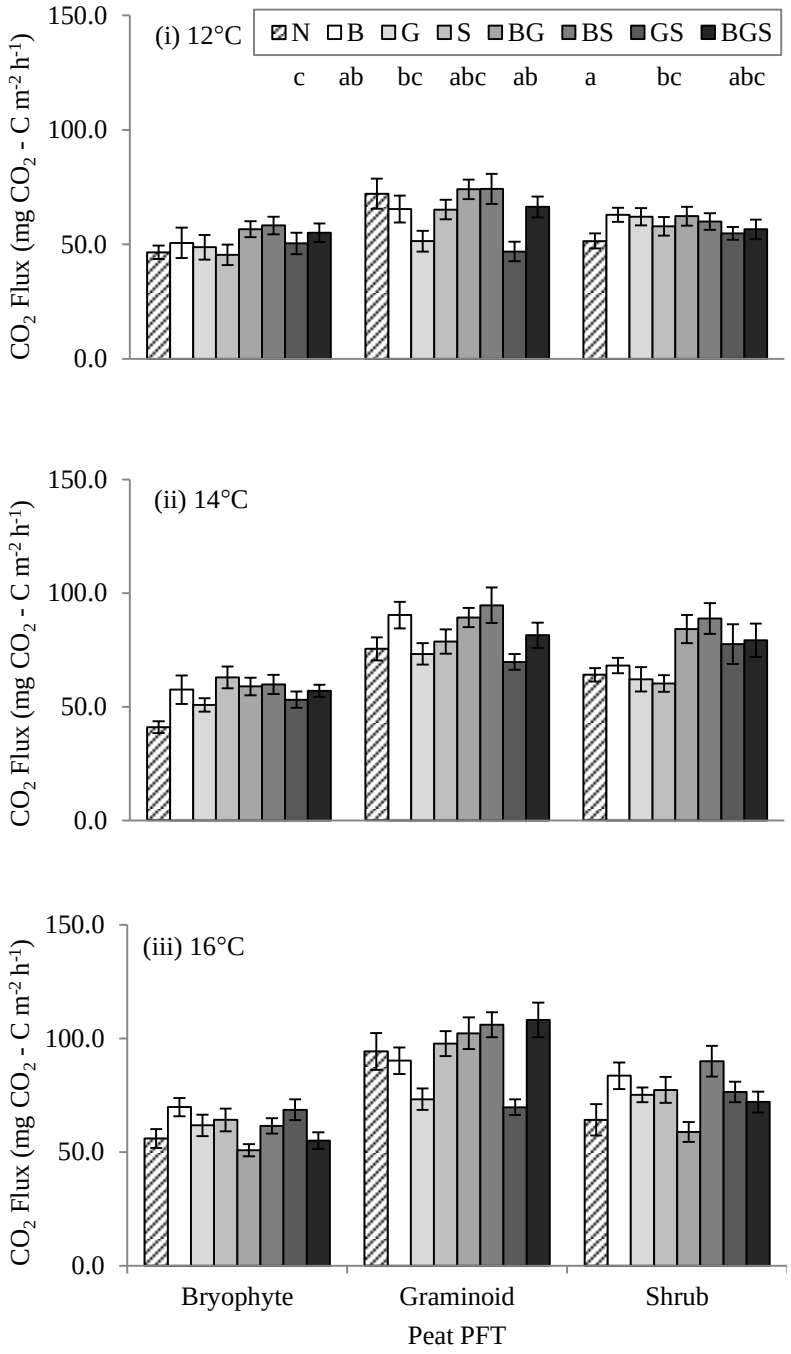

Figure 5.4: CO_2 emissions from cores of each peat PFT with litterbags comprised of no litter (N), bryophyte litter (B), graminoid litter (G) and shrub litter (S), in monoculture and mixtures, incubated at (i) 12°C, (ii) 14°C and (iii) 16°C. Letters indicate pair-wise significant differences between CO_2 emissions from each litter bag treatment. Pair-wise comparisons of CO_2 emissions between each peat PFT and each temperature are shown in Table 5.16. Mean data (averages taken from 6 sampling dates over 1 year) ± standard error.

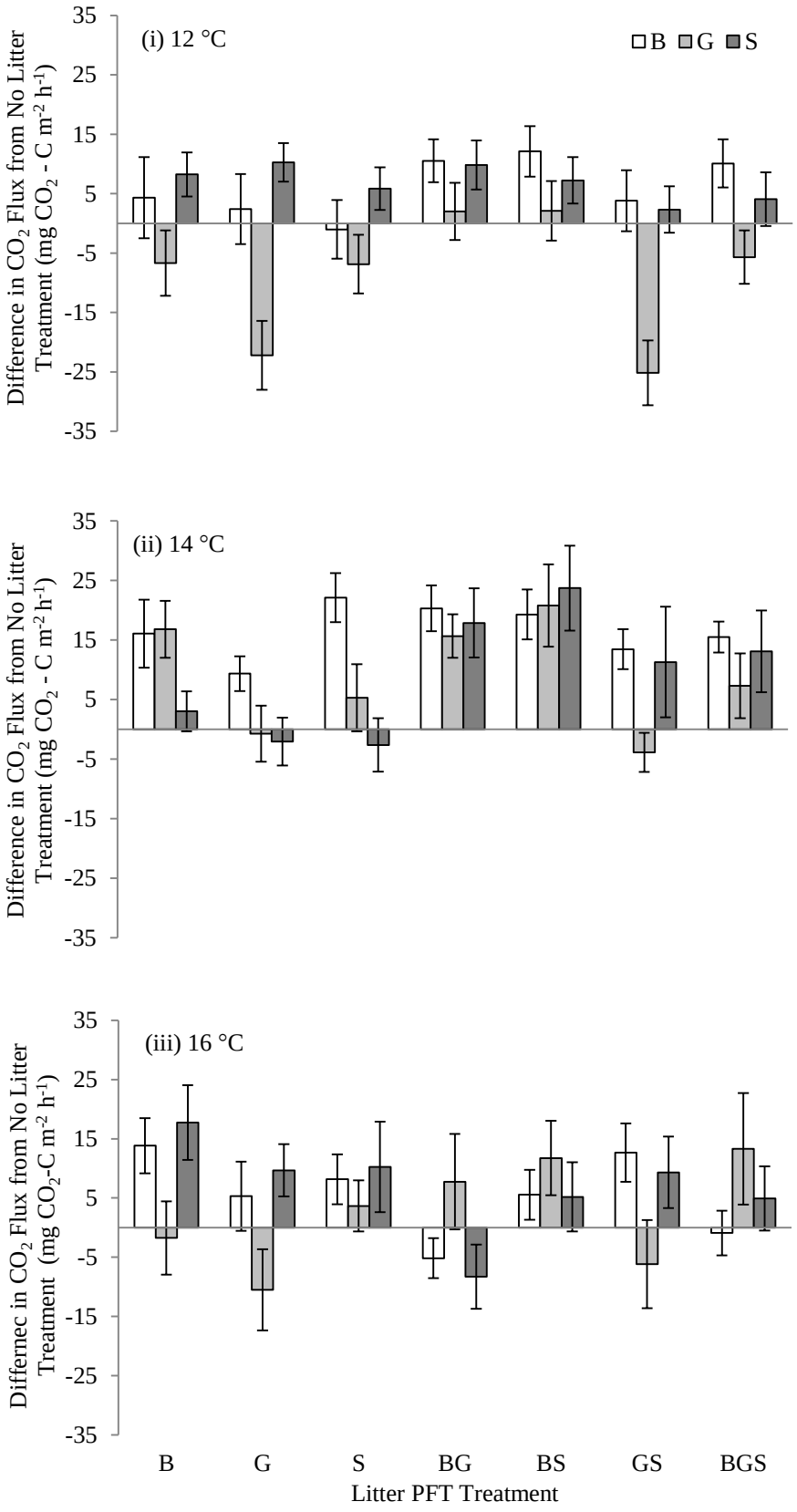

Figure 5.5: Difference in CO_2 emissions from PFT cores without and with litterbags comprising bryophyte (B), graminoid (G) and shrub (S) litter, in monoculture and mixtures, at (i) 12 °C, (ii) 14 °C and (iii) 16 °C. Mean data±standard error (averages over 6 sampling dates in 1 year).

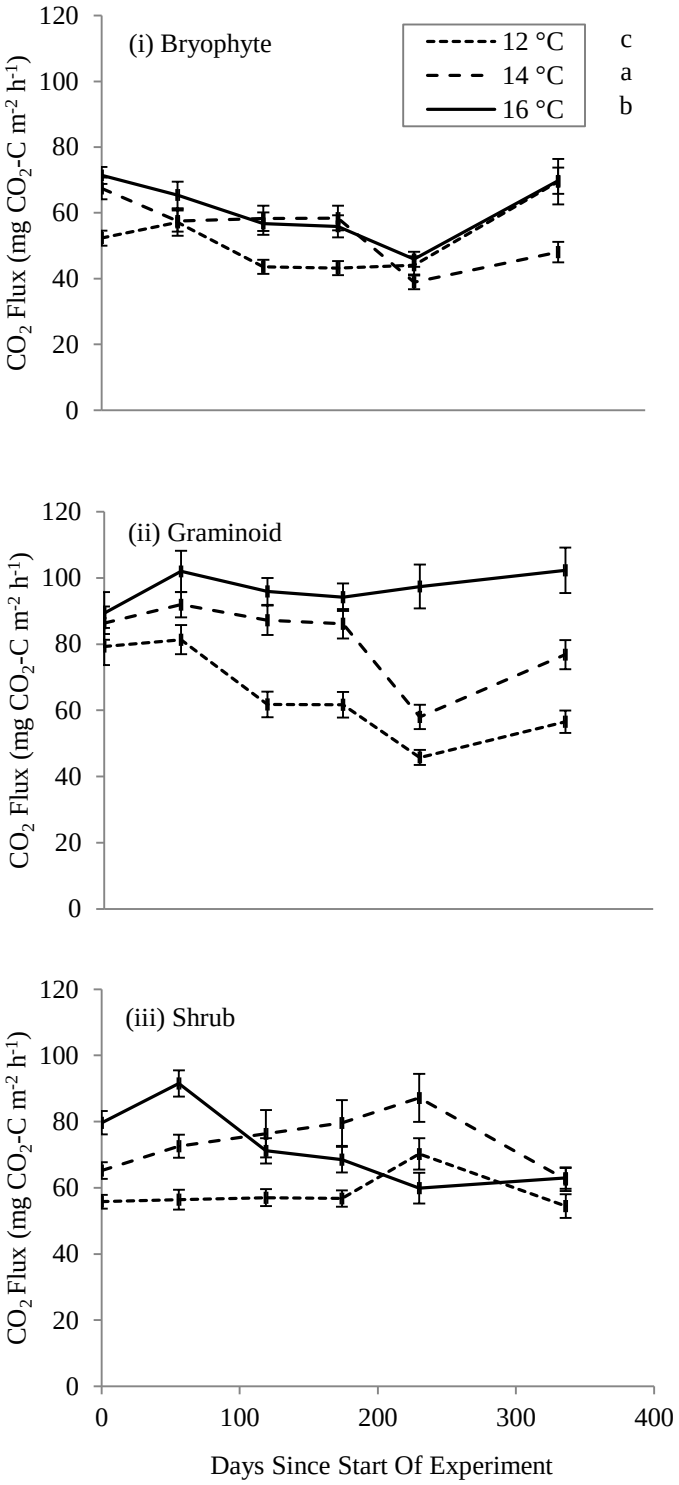

Figure 5.6: CO_2 emissions from (i) bryophyte, (ii) graminoid and (iii) shrub peat cores, incubated for 1 year at 12°C, 14°C and 16°C. Letters indicate pair-wise significant differences between CO_2 emissions at each temperature. Pair-wise comparisons of CO_2 emissions for each sampling day, temperature and peat PFT are shown in Table 5.17. Data is averaged across all litter bag treatments ± standard error.

Table 5.17: Pair wise comparisons between each sampling day and each temperature (T), and each peat PFT (PFTP), for CO_2 emissions.

		Days since start of experiment					
		0	56	119	174	230	363
T (°C)	12	abde	adcd	ae	ae	e	ae
	14	bcf	bcdf	bcdf	bcdf	ae	ade
	16	f	f	bcdf	bcdf	abde	cf
PFTP	B	bgh	ab	a	ac	c	ab
	G	de	d	def	def	abg	efh
	S	bfgh	efgh	bfgh	bfgh	befgh	ab

Table 5.18: Linear mixed effects model to determine the relationship between CO_2 emissions and peat-litter properties. Symbol - = variable not present in refined model. The relative contribution (%) of each variable in explaining model variance was calculated as % difference in adjusted R^2 comparing the full refined model and the model with each variable removed.

Variable	CO_2 fluxes	
	%Adj.R^2	*p*
Peat C content	23.52	<0.0001
Peat N content	23.50	<0.0001
Peat C:N	-	-
Total PLFA	-	-
Total fungi	-	-
Total bacteria	-	-
F:B	-	-
Total gram +ve	-	-
Total gram –ve	-	-
Gram +ve:gram -ve	-	-
Litter C content	96.93	0.0001
Litter N content	95.06	<0.0001
Litter C:N	-	-

5.3.7 Temperature sensitivity of respiration

The Q_{10} values ranged from 0.02-13.98, with a mean of 2.95 and a median of 1.92. Overall, there were no effects of peat and litter PFT, or time, but there were significant interactions between them (Table 5.19). However, post-hoc tests did not reveal any significant differences between the Q_{10} values of CO_2 emissions for litter treatments, over the duration of the experiment. Q10 values tended to increase over time for CO_2 emissions from graminoid peat and decrease for shrub peat (Figure 5.7), but there was no discernible pattern in the temperature sensitivity of bryophyte peat respiration rates over time. Therefore, the anticipated heightened sensitivity of CO_2 emissions from more recalcitrant organic matter to changes in temperature (hypothesis 2) was not found.

Table 5.19: Linear mixed effects (LME) model results showing significant factors and their interactions for temperature sensitivity of CO_2 emissions (Q_{10} values). D = days since start of experiment, T = temperature (°C), PFTP = plant functional type of peat, PFTL = litter plant functional type treatment. Df = degrees of freedom, *F* = *F* value and *p* = *p* value.

LME: Repeated Measures ANOVA	df	F	*p*
D	5	0.18	0.9706
PFTP	7	2.91	0.0612
PFTL	2	1.40	0.2169
D * PFTP	35	3.34	0.0040
D * PFTL	10	1.73	0.0076
PFTP * PFTL	14	0.72	0.7513

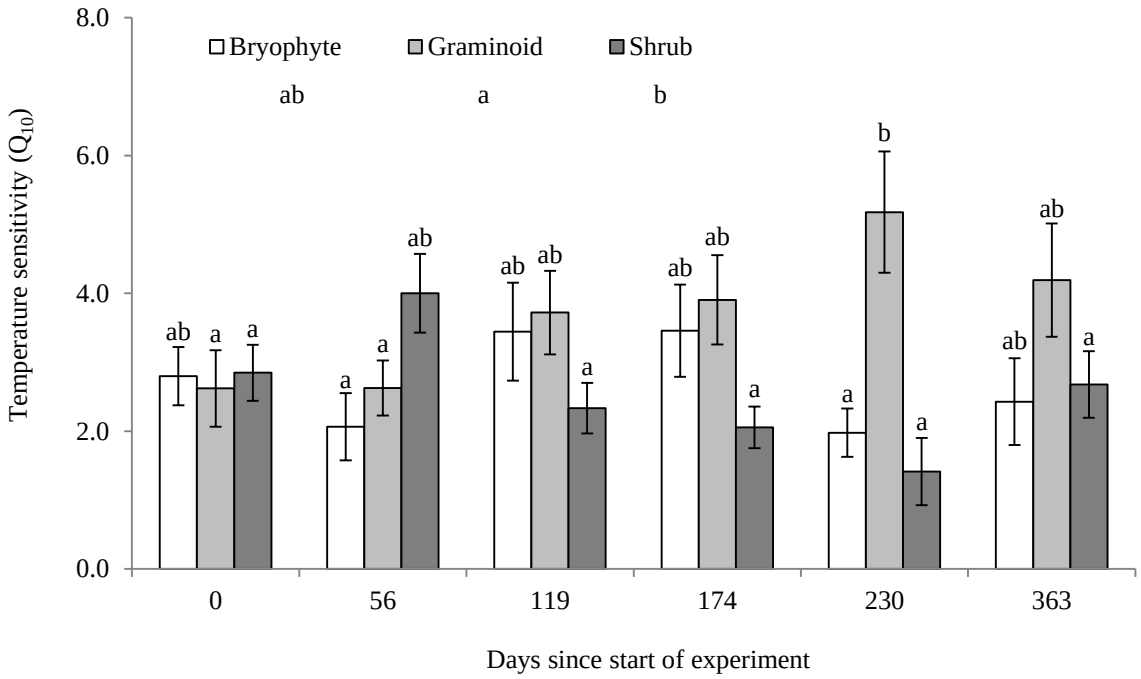

Figure 5.7: Temperature sensitivity of CO_2 emissions, determined by Q_{10} values, for each peat PFT and each sampling day for 1 year. Letters beneath the legend indicate pair-wise significant differences between the Q_{10} values of each peat PFT, whilst letters on the graph denote significant differences between peat PFT and sampling day. Mean values (averaged over litter PFT) ± standard error.

5.3.8 Home field advantage and disadvantage of respiration

The occurrence of HFA and HFD decomposition, measured as the amount of additional CO_2 emissions from litters on peat derived from the same or a different PFT, was controlled predominantly by the composition of the litter bags and the interaction with time (Tables 5.20 and 5.21). There were only a few occasions where additional CO_2 emissions were significantly different from zero (HFA apparent): on day 0, 56 and 363 at 14 °C for shrub and graminoid litter (Figure 5.8). However, three significant cases of HFD also occurred (Figure 5.8). HFD values for graminoid litter at day 0 at 14 °C, and for bryophyte litter at day 56 at 14 °C and 16 °C indicate that CO_2 emissions for these litters near the beginning of the incubation decomposed preferentially on peat derived from a different PFT (i.e. 'away from home').

Table 5.20: Linear mixed effects (LME) model results showing significant factors and their interactions for additional CO_2 emissions at home and away. D = days since start of experiment, T = temperature (°C), PFTL = litter plant functional type treatment. Df = degrees of freedom, *F* = *F* value and *p* = *p* value.

LME: Repeated Measures ANOVA	df	F	*p*
D	5	0.28	0.9244
T	2	0.13	0.8763
PFTL	2	23.74	<0.0001
D * T	7	0.81	0.5829
D * PFTL	10	3.25	0.0010
T * PFTL	4	1.34	0.2602

Table 5.21: Pair wise comparisons between each sampling day and each litter PFT (PFTL), for additional CO_2 emissions at home and away.

		Days since start of experiment					
		0	56	119	174	230	363
PFTP	B	ab	a	ab	ab	abc	ab
	G	abc	c	abc	bc	abc	abc
	S	bc	abc	abc	abc	abc	abc

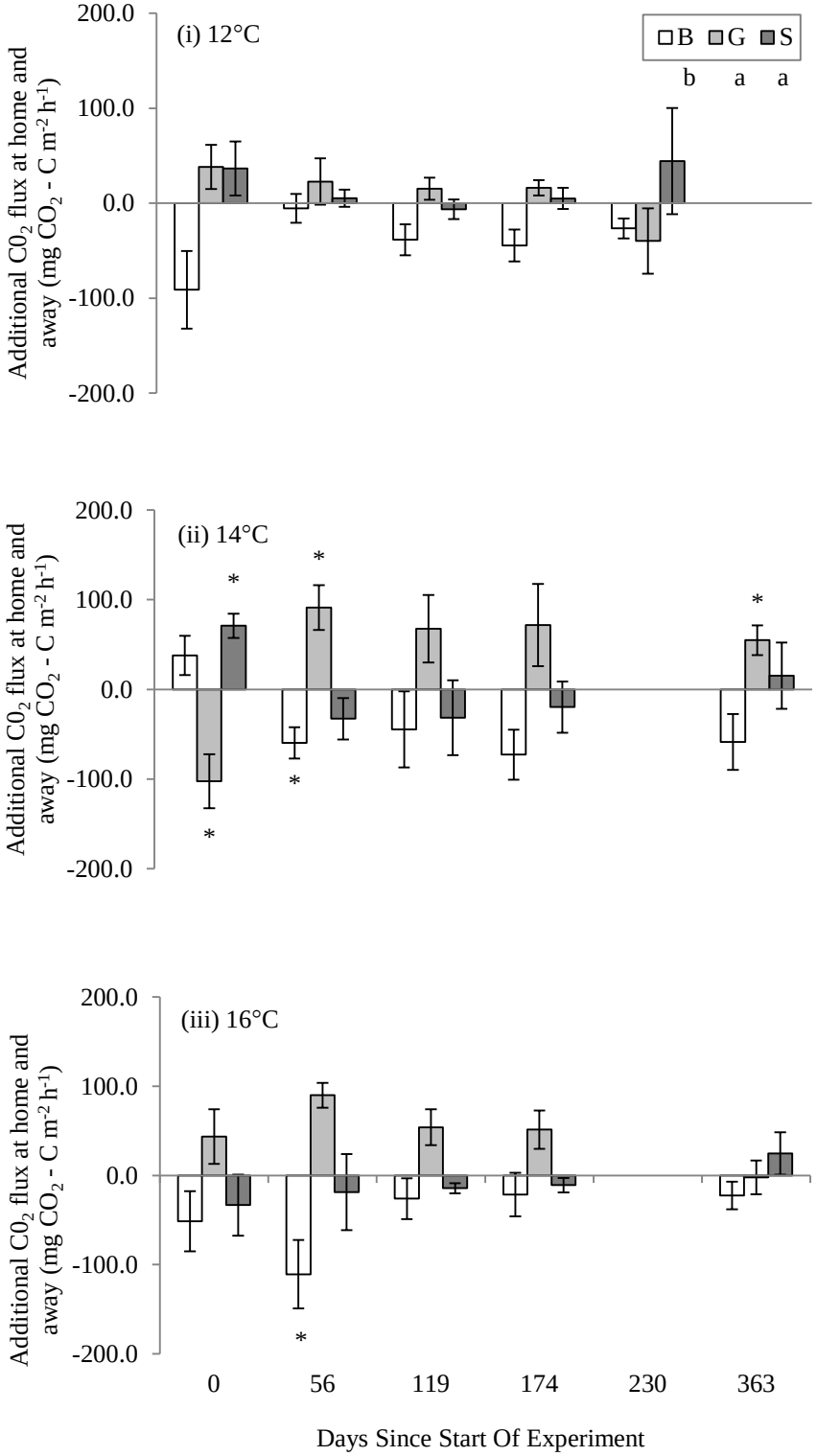

Figure 5.8: Mean additional CO_2 emissions at home (± standard error) for each single litter PFT (B = bryophyte litter, G = graminoid litter, S = shrub litter) at 12°C, 14°C and 16°C, over 363 days. Asterisks indicate significant differences from zero ($p < 0.05$). Letters indicate pair-wise significant differences between PFT litters. Pair-wise comparisons between sampling day and litter PFT are shown in Table 5.21. Mean data is not shown for (i) day 363, (ii) day 230 and (iii) day 230 due to missing replicates.

5.4 Discussion

5.4.1 Drivers of decomposition

It was hypothesised that decomposition would vary with PFT, due to differences in litter chemistry and biochemical peat properties, but that changes in temperature would exert the most control overall (Aerts, 2006). However, as observed in Chapter 4, PFT was found to be the most important control on litter mass loss and heterotrophic respiration rates. Litter bags containing graminoid litter lost more mass than those containing shrub and bryophyte litters, in monocultures and in mixtures (Figure 5.1), whereas respiration rates were greatest from cores with litter bags containing a mixture of bryophyte and shrub litters (Figure 5.4). In a short-term field decomposition study, greater rates of decomposition have previously been observed for shrub litter (Ward et al., 2010), with higher weight loss and rates of respiration for litter mixtures dominated by shrub than graminoid litter. The low decomposability of bryophytes compared to vascular plants is a general phenomenon, and is attributed to the low quality of this litter type (Aerts et al., 1999; Ward et al., 2010). These findings support the growing opinion that differences in litter decomposability often correspond well with the classification of PFTs based on plant traits (Li et al., 2013; Strakova et al., 2011; Ward et al., 2010). However, there can be considerable overlap among PFTs so that decomposition is not always significantly different for a specific litter and its adjacent litter(s), as seen by Pérez-Harguindeguy et al. (2000) and Quested et al. (2003). Furthermore, decomposition may not always be different for litters in contact with peat derived from different PFTs. Despite a weakly significant effect, the PFT legacy in the underlying peat did not produce marked differences in litter bag mass loss, whereas for respiration, PFT composition differences in peat had a stronger effect on CO_2 emissions than the species composition of litter bags. Higher respiration rates were measured from graminoid-derived peat (Figure 5.4), a pattern also observed in section 3.3.2, Chapter 3. This is consistent with an interpretation that more labile substrates are available in the peat beneath this PFT. Without living plants to replenish the labile C pool (Davidson and Janssens, 2006), microbial activity will be limited by the quality and quantity of root exudates that remain in the peat cores. Therefore, differences in the quality and quantity of root exudates entering the soil from different PFTs are likely to affect rates of respiration (De Deyn et al., 2008). Further, CO_2 emissions from shrub-derived peat remained relatively steady over the 363 day incubation period, a time over which graminoid and bryophyte peat CO_2 emissions declined more rapidly (Figure 5.6). This implies that the more recalcitrant shrub-derived peat undergoes slower depletion of C substrates and

supports the idea that peat of different qualities release CO_2 at different rates under increased temperatures (De Deyn et al., 2008).

In addition, the interaction between peat and litter PFT that facilitated increased CO_2 emissions from bryophyte and shrub litter bags on graminoid compared to on bryophyte or shrub peat (Figure 5.4) may arise due to nutrient transfer. A relatively high quality peat (i.e. graminoid-derived peat) could enhance the decomposition rate of poor quality litters (i.e. shrub and bryophyte litters) (Hättenschwiler et al., 2005) as a result of preferential exploitation of the high quality peat by decomposer organisms, and so eventually lead to a nutrient transfer to the low quality litter. In turn, transferred nutrients would hypothetically increase the decomposition of the low quality litter (Hättenschwiler et al., 2005) and therefore increase CO_2 emissions.

The chemistry of the litter inputs and the underlying peat were most important in determining differences in decomposition, with the concentration of C and N in peat and litter explaining the most variation in litter mass loss and resultant CO_2 emissions. While these properties only explained a small proportion of the modelled variation in the amount of remaining mass in litter bags (i.e. between 2 – 9%), they accounted for more of the variability in CO_2 (i.e. between 24 - 97%). In both instances though, chemical characteristics of litter explained up to four times more modelled variation in decomposition and respiration rates than properties of peat. The quality of litter and the surrounding soil has been used often in making predictions of decomposition rates (Gartner and Cardon, 2004; Hobbie, 1996). Recent decomposition studies have found stronger relationships between decomposition rates and initial N content than with C:N (Wang et al., 2014; Ward et al., 2010), which was true of CO_2 emissions in this study, but not litter mass loss. In addition to concentrations of C and N in litter, compounds such as lignins and tannins may also be good indicators of litter decomposition (Jiang et al., 2013). Chemical properties that increase litter decomposability can also select for a microbial community that is suited to the fast decomposition of more labile litters (Myers et al., 2012). For instance, graminoid-derived peat had higher total bacterial PLFAs than shrub or bryophyte-derived peat (Table 5.2). In contrast, slow decomposing litters (i.e. shrub and bryophyte) are associated with a more fungal-dominated (e.g. shrub-derived peat) or small (e.g. bryophyte-derived peat) microbial community (Table 5.2), known for slower turnover rates of C because of the low quality of those litter types (Gartner and Cardon, 2004; Latter et al., 1998; Rousk and Bååth, 2007)

The heterogeneity created by mixing different litter types may also change soil decomposer activities and indirectly affect litter decomposition, by affecting the ratio of fungi to bacteria and thus the ability of the decomposer community to degrade lower or higher quality litter mixtures (Hector et al., 2000), but microbial metrics were not identified as playing an important part in decomposition in this study (Tables 5.8 and 5.18). A more detailed analysis of microbial composition and diversity, and community comparisons made before and after decomposition, could identify important regulators of peat respiration and litter mass loss (Artz et al., 2007).

Although temperature was a significant factor in both cases, litter decomposition and rates of respiration responded differently to incubation at 12°C, 14°C and 16°C. For instance, more litter decomposition occurred in cooler conditions (Figure 5.1), whilst CO_2 emissions increased with warming (Figure 5.4). Respiration rates declined over the course of the experiment, which suggests that litter mass loss may have become increasingly limited by the availability of labile substrates. In view of this, it could be assumed that faster rates of decomposition occurred at 16°C initially. In turn, rapid breakdown of litter could have depleted the pool of available labile substrates in the peat, which then reduced the rate at which decomposition could be sustained under warmer conditions (Kirschbaum, 2013). At lower temperatures (12°C and 14°C), rates of initial decomposition may have been slower than at 16°C, leaving a larger pool of labile substrates to facilitate further decomposition over longer periods of time. Therefore, litter bags at 12°C could be expected to undergo more decomposition than at 14°C and 16°C. However, the response of litter decomposition to temperature seen in this laboratory study was not observed under similar conditions in the field. At a sub-arctic bog, small increases in litter decomposition rates were evident over a 4 year period under rising temperatures relevant to moderate climate change scenarios (i.e. 0.7 – 1.2°C) (Aerts et al., 2012). Other studies that examined the effects of larger increases in temperature (i.e. greater than 4°C) found substantial increases in litter decomposition rates (Cornelissen et al., 2007; Hobbie, 1996). The rise in CO_2 emissions with each 2°C increase was not surprising, given the known relationship between temperature and GHG fluxes (Bond-Lamberty and Thomson, 2010) and the effects of small-scale increases in temperature on peat respiration under controlled conditions in the laboratory (Chapter 3) and in the field (Dorrepaal et al., 2009; Ward et al., 2013).

The effect of temperature change on decomposition may depend on the quality of the decomposing litter and underlying peat (e.g. Conant et al., 2008; Kirschbaum, 2013). In this study, the decomposition of shrub litter was more sensitive to changes in temperature when on graminoid-derived peat (Figure 5.2) but broadly PFT-induced differences in litter

and peat quality did not control differences in Q_{10} values for CO_2 emissions (Table 5.19), and so the temperature sensitivities of labile and more resistant OM are similar.

For example, short-term responses of $^{13}CO_2$ fluxes derived from younger vs. older soil OM (Conen et al., 2006), models of different soils incubated at a range of temperatures (Rey and Jarvis, 2006), laboratory incubation data (Fang et al., 2005) and field experimental data (Luo et al., 2001) all show that there was no significant change in temperature sensitivity with decreasing OM lability. However, in a subarctic peatland, the temperature sensitivity of recalcitrant OM was greater than when OM contained more labile compounds (Dorrepaal et al., 2009). Other investigations using different approaches, such as adding compounds of differing lability to soil or by incubating soil OM components separately, also suggest that resistant soil OM or OM-depleted soils may be more sensitive to temperature than soils that have more labile or are less OM-depleted (Conant et al., 2008a; Fierer et al., 2005; Leifeld and Fuhrer, 2005). In this study, CO_2 emissions from the graminoid-derived peat appeared to become more temperature sensitive over time (Figure 5.7), but not by a significant degree, most probably owing to the exhaustion of the labile OM pool. It is apparent that across a range of environmental conditions and experimental approaches, labile OM decomposition has the potential to be more, less or equally sensitive to changes in temperature than more resistant OM.

5.4.2 Litter and peat interactions

While it is clear that the primary factors that control decomposition rates are litter quality and temperature (Aerts, 1997; Cornwell et al., 2008), home-field advantage has been recognised as a secondary factor controlling decomposition. Few studies have explored the effect of HFA on litter decomposition in peatlands, despite studies of other ecosystems reporting higher decomposition rates when litters decompose in their native environment (Ayres et al., 2009b, 2006; Strickland et al., 2009; Vivanco and Austin, 2008). In this study, findings show that litters from different PFTs in peatlands have the potential to decompose with HFA, and HFD, but changes in temperature do not control this.

There was a weakly significant interaction between litter PFT and peat PFT on litter mass loss, but not for CO_2 emissions. This indicates that the likelihood of HFA or HFD was low. Bryophyte and shrub litters decomposed more rapidly when in contact with bryophyte- and shrub-derived peat, respectively (Figure 5.3); the opposite was observed for graminoid litter and peat. However, these trends were not the same as with CO_2 emissions. Figure 5.8 shows that additional fluxes of CO_2 were measured from shrub litter on shrub peat at the start of the experiment, but never from bryophyte litter on bryophyte peat. Rather,

bryophyte litter respiration rates were greater on peat derived from other PFTs (i.e. at day 56) (Figure 5.8), whereas additional CO_2 emissions from graminoid litter were measured on peat derived from all PFTs (Figure 5.8). The average amount of additional CO_2 emissions at home did not deviate significantly away from zero on more than six occasions, across the temperature range (Figure 5.8). It is therefore likely that the effects of HFD offset HFA, which produced 'no effect' on average. The majority of significant HFA and HFD-influenced CO_2 emissions were observed within the first 56 days of the incubation, which suggests that the effect of HFA or HFD was short-lived and limited by the availability of labile substrates. It was hypothesised that the legacy of a particular PFT in peat would affect the microbial community, with adaptation in the abundance and composition of the microbial community increasing the ability of decomposer organisms to rapidly colonise and start decomposing litters from the same PFT. However, the findings reported in this study do not provide convincing evidence of this occurring.

In another relatively short-term study, plant species did not encourage the development of soil microbial communities that specialised in decomposing their litter rapidly (Ayres et al., 2006). A decomposer community is relatively unlikely to be dominated by both fungi and bacteria (Wardle, 2002). Therefore, the HFA-HFD hypothesis might not account for the range of litter quality and decomposability occurring in ecosystems at small spatial scales (i.e. between PFTs in peatlands) (Freschet et al., 2012). Moreover, changes in litter structure and chemistry during decomposition could result in a litter becoming more similar to another litter, which would allow an 'away' soil microbial community to decompose it rapidly, thus producing no home-field advantage effect. However, in experiments using litters from forest, herbaceous and grassland species, HFA increased with decreasing litter quality (Ayres et al., 2009b; Strickland et al., 2009; Wardle et al., 2003). Therefore, high quality litter might be expected to have little or no HFA, due to the lack of competition within the microbial community for resources. Furthermore, this relationship will become clearer when there is a greater dissimilarity between litter types and possibly larger compositional differences within the soil community (Strickland et al., 2009). Not only that, but a more comprehensive assessment of litter quality, including the abundance and composition of phenolic compounds, might be necessary to accurately predict HFA and HFD for different litter types (Ayres et al., 2006).

The initial litter quality can control the early stages of litter decomposition (i.e. loss of labile litter compounds (Bray et al., 2012; Prescott et al., 2004), but the composition of the microbial community has more influence over decomposition rates in the later stages of decay (i.e. loss of recalcitrant litter compounds) (Bray et al., 2012). Therefore, it is possible

for HFA and HFD effects to become more apparent and consistent with time, as labile substrates are lost and the role of the microbial community becomes more important. Similarly, the effects of changing the decomposition microclimate (i.e. warmer temperatures) might become more pronounced in HFA or HFD with time due to adaptation of microbial communities.

The influence of HFA on decomposition has been reported to be comparable in magnitude to the effect of litter interactions in mixtures (Gartner and Cardon, 2004; McTiernan et al., 1997; Wardle et al., 1997). In this study, there were non-additive effects of litter mixing on litter mass loss, but less than half of the possible interactions between mixed litters were significant (Table 5.13). On average, the interaction strengths did not deviate much from zero (Table 5.13), which indicates that the presence of positive interactions were most likely to be counterbalanced by negative interactions, leading to a more neutral effect overall. Therefore, it can be surmised that the effects of HFA, HFD and interactions between mixed litters on decomposition were similar, in that these factors had relatively limited influence over the amount of litter mass loss. Nevertheless, more significant positive interactions occurred in mixed litter bags containing shrub and bryophyte litters, than with graminoid litter. It is surprising that bryophyte and shrub litters would promote the decomposition of other litters in mixture, owing to their slow decomposition as single litters (Figure 5.1), and because the species associated with these PFTs have traditionally been thought to have a negative effect on decomposition (van Breemen, 1995; Verhoeven and Toth, 1995). Significant interactions in litter mixtures containing *Sphagnum* were also found by Hoorens et al. (2002). An explanation for the positive interaction associated with *Sphagnum* could be that the water retaining properties of *Sphagnum* litter may provide more constant favourable conditions for decomposition (i.e. remaining moist) (Hoorens et al., 2002; Wardle et al., 2003). The differences between observed and expected weight loss of mixed litters at a peatland in the Moor House National Nature Reserve (NNR), in northern England, were greatest for litter mixtures dominated by shrub than by bryophyte or graminoid litters (Ward et al., 2010). The acceleration of decomposition associated with shrub litter in mixtures may arise from increased resource competition within the soil decomposer community, owing to the initial low quality of the litter. Non-additive rates of decomposition for mixed litters in agroforestry systems and Mediterranean maquis shrubland increased when component litters had contrasting N contents (Marco et al., 2011; Wang et al., 2014). However, Wang et al. (2014) also found that litter decomposition was also enhanced when two litters, both with low N, were mixed. There have been few reports of increased mass loss in mixtures comprised of low quality litters (Montané et al.,

2013), but these findings indicate that the synergistic effect of mixing different types of litter together is not limited to mixing litter types with high N, at least in the first year of decomposition (Wang et al., 2014).

A range of litter mixing effects on decomposition processes has been reported in the literature, ranging from negative (Hansen, 2000; Li et al., 2013) to neutral (Blair, 1990) and to positive (Bardgett and Shine, 1999; Hector et al., 2000; Jonsson and Wardle, 2008; McTiernan et al., 1997); indeed both positive and negative effects of litter mixing have sometimes been detected in the same study (Duan et al., 2013; Jiang et al., 2013; Wardle et al., 1997). A limitation of these studies, including this one, is that the litter from the component species of the mixture were not separated from one another at the end of the experiment, so it is impossible to determine how the species present influenced the decomposition of each litter, rather than just the overall decomposition of the mixture.

The decomposition of litter mixtures depends on the balance of stimulatory and inhibitory effects of different species properties. Therefore the relative amount of the component species can affect the magnitude of the non-additive effect in litter mixtures (Marco et al., 2011; Ward et al., 2010). The litter mixing ratio (1:1) used in this study only reflects one of the many possible mixing ratios that could occur in the field. A more complete exploration of litter mixing effects should include multiple harvests and mixing ratios, as different litter decomposition phases may show opposing trends with litter species evenness and diversity (McTiernan et al., 1997; Ward et al., 2010).

Results from this study support the collective opinion that plant functional traits, specifically those of litter, are the principal factors that control litter decomposition rates (Aerts, 1997; Butenschoen et al., 2011; Cornwell et al., 2008; Pérez-Harguindeguy et al., 2000). PFT effects should be acknowledged to be as important as temperature, if not more so, in predicting future changes in litter decomposition and resultant respiration rates. The significant effect of temperature change on litter mass loss and heterotrophic respiration rates reported here is still important, by indicating that decomposition rates are different under microclimatic conditions (i.e. 2 - 4°C warming). Vegetation composition has been shown to be a strong control over CO_2 emissions with approximately 1°C warming (Ward et al., 2013), and highlights how important actively-growing vegetation can be in controlling GHG exchange. In view of this, the interactive effects of PFT with temperature for litter mass loss and CO_2 emissions observed in this study demonstrate that plant functional traits of a species, its litter and the peat upon which it grows and decomposes, are also important in determining decomposition, respiration rates and therefore net CO_2

emissions. However, the limited effects of HFA, HFD and interactions between litters on decomposition at the PFT level has important implications for predicting decomposition in peatlands (Hoorens et al., 2010).

5.5 Conclusions

By using two measures of decomposition, namely litter mass loss and respired CO_2, this study demonstrates the effects of PFT on decomposition processes. Not only that, but evidence shows that these decomposition processes are likely to be sensitive to peatland microclimates, which could result from climate change or land use change (i.e. wind farms) (Armstrong et al., 2014b; Ward et al., 2013).

By showing that graminoid litter decomposed faster, but that non-additive interactions between shrub and bryophyte litter contributed towards higher CO_2 emissions, this study adds to the growing body of evidence that highlights the importance of PFTs in peatland C cycling (Cornwell et al., 2008; De Deyn et al., 2008; Trinder et al., 2009; Ward et al., 2009). PFT litters showed both HFA and HFD decomposition, on account of the quality of the underlying peat and litter inputs, but not microclimatic changes in temperature. This is important as the relative proportions of dominant PFTs in peatland plant communities are expected to shift with climate change, with vascular plant species (i.e. graminoids and shrubs) predicted to dominate over bryophytes (Gallego-Sala and Prentice, 2012). Climate change and land use change effects on plant community composition could therefore have important implications for litter decomposition rates in peatland ecosystems, by altering litter inputs, the decomposition environment and the likelihood of HFA and interactions between adjacent litters.

In this unique study, the interactive effects of PFT and microclimate on early stages of decomposition were examined. Therefore, findings from this work must be carefully considered in projections of long term effects of peatland microclimate change and the relative proportion of each PFT within the plant community. Future studies focusing on peatland decomposition would benefit from exploring the mechanisms of interaction in litter mixtures, by examining nutrient transfer with isotopic labelling, particularly in the field and in the long term, to enable accurate predictions of litter decomposition under climate change and land use-induced microclimate change scenarios.

Chapter 6

General discussion

6.1 Overview

Vast quantities of C are stored in northern peatlands; therefore these ecosystems represent a large proportion of the global terrestrial C budget. Peatlands are particularly sensitive to climate and land use change, and their role in the global C cycle can change from acting as a net sink of C to a net C source when disturbed (Dise, 2009; Dise and Phoenix, 2011). Functionally, the links between aboveground communities, belowground communities and peatland C cycling processes have been well-established (Bardgett et al., 2008; Gorham, 1991; Wardle et al., 2004). However, there are still knowledge gaps regarding the sensitivity of peatland carbon cycling processes and the role that PFTs play in mediating the response of peatland ecosystem functions to climate and land use changes i.e. wind farm developments.

Further, as a result of climate change and the continued developments of onshore wind farms on peatlands, the need to understand the dynamics of peatland C stores is ever-increasing. The impact of operational wind farms on near surface atmospheric conditions has attracted attention from the scientific community (Armstrong et al., 2014a; Baidya Roy and Traiteur, 2010; L. Zhou et al., 2012), however the effects of operational wind farms on the C balance of peatlands are uncertain.

In my doctoral research, I examined the influence of PFTs on environmental, biological, physical and chemical peatland properties, and the role of PFTs in regulating peatland carbon cycling at a wind farm, and under controlled microclimatic conditions. This was to test an overarching hypothesis that peatland PFTs, and their interactions with a wind farm-induced microclimate, explain abiotic and biotic peatland properties and C cycling processes. This hypothesis was generated as it addressed several areas where the scientific community lack knowledge. In this discussion I will draw out the important findings and consider the implications of climate change and land use change on the C balance of peatlands, taking into account changes in PFT abundance within the peatland plant community (Gallego-Sala and Prentice, 2012; Jassey et al., 2013).

6.2 Composition of aboveground and belowground communities

The relationship between the aboveground (plant) and belowground (microbial) communities and physicochemical peatland properties at Black Law Wind Farm was examined in Chapter 2. Results showed that PFT significantly influenced the relative abundance of fungi and bacteria. Of the observed peatland properties, peat bulk density, peat C:N and the total C content of peat, litter and vegetation were found to significantly

explain variance in a spatially changing microbial community, which is consistent with other research that was not from a wind farm peatland (Andersen et al., 2010; Fierer et al., 2009; Mitchell et al., 2010). The C content of litter was significantly different between PFTs and provided a consistent seasonal control on the belowground community. Peat physicochemical properties appeared to be the dominant factor influencing the abundance and composition of the microbial community throughout the year; however this was not the case after accounting for variability in the height of the water table. Once seasonal changes in water table level were considered, physicochemical properties of litter became more influential than peat on the overall abundance and relative proportion of different microbial groups. In this study, microbial communities were more sensitive to changes in the quality and quantity of litter inputs than to changes in the physical or chemical characteristics of the soil environment, a response found in other peatlands (Strakova et al., 2011), but still one we have little information for. However, this study did not take into account inputs of C from roots, or fully consider the effects of nutrients (e.g. phosphorus (P) and potassium (K)) on the microbial community. Inputs of labile C, via rhizodeposition and root turnover, provide significant flows of C belowground from both vascular plants (Crow and Wieder, 2005; Ström et al., 2005) and bryophytes (Fenner et al., 2004). Therefore, the contribution of root-derived inputs of labile C from different plant functional types to peat, could affect the composition of the belowground decomposer community. Similarly, nutrients have an important role in shaping the plant community composition, which in turn affects peat microbial community composition and decomposition processes. Increased nutrient availability would be expected to increase microbial activity and growth (Bragazza et al., 2012a), and has been shown to significantly change the plant community composition by increasing the proportion of vascular plants at sites previously dominated by *Sphagnum* – in turn this could alter microbial community composition (Berendse et al., 2001). As a result, the findings of this study and their interpretation may be different if the effects of roots and nutrients on microbial community composition had been explored.

From the understanding gained from this study, shifts in the spatial distribution of PFTs within the plant community, caused by climate or land use-induced changes in the water table, could affect the composition of the microbial community to a greater extent than the direct effects of altering the position of the water table. For example, a land use- or climate-induced increase in the extent of the acrotelm is likely to promote the growth of vascular plants such as shrubs and graminoids, instead of non-vascular plant types like bryophytes (Gallego-Sala and Prentice, 2012; Jassey et al., 2013). Shrub dominance would

be expected to favour a more fungal-rich, slower C cycling, microbial community (Read et al., 2004), whereas if graminoids became more abundant a more bacterial-dominated, faster C cycling, decomposer community might be more prevalent (Bardgett and Wardle, 2010).

The results presented in Chapter 2 are consistent with findings by Andersen et al. (2013), a study that also demonstrates the importance of vegetation and physicochemical characteristics to soil organisms in disturbed peatlands. In addition, the importance of PFT as a regulator of physical, chemical and biological peatland properties (Chapter 2) supports the view that the composition of the aboveground community can be used to improve predictions of the belowground community composition and activity (Mitchell et al., 2010). If this is so, PFTs could be used as an integrative proxy of climate, land use and physicochemical soil properties. By affecting the quality of litter and also the relative abundance of fungi and bacteria, PFTs therefore have the capacity to affect the decomposition of OM in peatlands.

6.3 Plant functional types and their role in peatland C cycling

Through a survey of peat properties at the field site (Chapter 2), PFTs were shown to create a legacy in the peat formed from these PFTs, producing peat with some distinct, physicochemical and biological properties. To investigate the influence of PFTs and their legacy in peat, together with microclimate change on peatland C cycling processes, laboratory research in Chapters 3 and 5 examined the interactive effects of PFT and controlled microclimatic conditions on GHG emissions. The experiments showed that a PFT legacy influenced GHG emissions from peat. Higher CO_2 and CH_4 fluxes were measured from graminoid-derived peat (Chapter 3), under increases in temperature and water table level that are predicted to arise from climate change or land use change. The results of this research are consistent with the findings from a mesocosm study conducted by Green and Baird (2012) and the PFT effects observed by Greenup et al. (2000) and Marinier (2004) in the field: these studies found GHG emissions to be greatest from graminoids. In a second experiment investigating PFT effects on litter decomposition, heterotrophic respiration rates were also higher from graminoid-derived peat, providing further evidence that this PFT contributes towards the flux of C from the soil to the atmosphere more so than the other two dominant peatland plant types. The importance of graminoids on GHG emissions has been previously attributed to the living plant surface; however this research provides additional support to show that PFTs (i.e. graminoids) can

influence CO_2 and CH_4 fluxes in the absence of live vegetation through legacy effects within the peat.

The role of PFTs and microclimate change in regulating litter mass loss was examined in the field (Chapter 4) and in the laboratory (Chapter 5), to further test the hypothesis that PFT is a significant factor driving the rates of peatland C cycling processes under microclimatic conditions. Specifically, litter PFT had a greater influence on litter mass loss than the PFT legacy in the underlying peat, observed in situ at the wind farm and under laboratory-controlled air temperatures. Decomposition of bryophyte and shrub litters occurs more slowly than graminoid litter (Chapters 4 and 5). In addition, the C content and C:N of litter explains the most variance in litter mass loss.

These findings contribute towards the growing body of evidence that plant functional trait differences are the principal controls on litter decomposition (Cornwell et al., 2008; Freschet et al., 2012). In this research, litter types not only decompose at different rates due to the direct effects of litter quality on decomposition, but as a result of the indirect effects of interactions between litter quality and peat quality. This, in turn, could influence the likelihood of a home-field advantage (HFA) or home-field disadvantage (HFD) decomposition response. Bryophyte litter decomposed more rapidly beneath the bryophyte litter layer (Chapter 4) and on bryophyte-derived peat (Chapter 5): an indication of HFA. In contrast, HFD was observed for graminoid litter mass loss in both the field (Chapter 4) and laboratory (Chapter 5).

In the context of climate and land use change, HFA and HFD decomposition could have important implications for peatland C cycling and storage. The composition of the plant community in peatlands is expected to change with increases in temperature (Gallego-Sala and Prentice, 2012; Jassey et al., 2013), to favour the growth of vascular plants that are more suited to warmer, drier conditions. Shifts in the distribution of PFTs over small spatial scales could lead to plant species growing on peat previously receiving the bulk of its inputs from another species. For shrub litter, this would not lead to significant changes in mass loss (Chapters 4 and 5). For graminoid litter, decomposition would accelerate if this PFT advanced into areas formerly dominated by bryophytes or shrubs (Chapters 4 and 5). The main variables (i.e. light and moisture) that can result in peatland plant community composition change, such as a shift from bryophyte to vascular plants, are expected to play-out over decades. However, Dieleman et al. (2014) and Weltzin et al. (2003) suggest that ecosystem shifts in peatlands due to changes in temperature and water table may occur much more quickly. A rapid shift (i.e. over 1 year) in plant community composition was

observed, as a result of increased temperature (by 4 - 8°C) decreasing *Sphagnum* and increasing graminoid abundance (Dieleman et al., 2014). Over a period of 5 years, increased temperature and decreased water table level increased the cover of shrubs at an area of bog by 50%, and decreased the cover of graminoids by 50% (Weltzin et al., 2003). Therefore, HFA and HFD have the potential to affect peatland C sequestration rates over years to decades, and thus within the lifetime of an operational wind farm (i.e. approximately 25 years).

Bryophyte and shrub litters typically decompose slowly in monocultures (Chapters 4 and 5). Interestingly, synergistic effects of mixing bryophyte and shrub litters on mass loss were reported in Chapter 5. Currently there is limited understanding of litter mixing effects on litter decomposition rates in peatlands. The findings of this research add to those reported by Ward et al. (2010), who observed the greatest differences between observed and expected mass losses were for mixtures containing shrub litter. Within a framework of changes in the plant community, whether climatic and land use change-induced, my research supports the supposition that the decomposition rates of bryophyte and shrub litters would increase if the litter layer consisted of these litter types in combination.

These combined experiments (Chapters 4 and 5) represent an important experimental contribution to the work on plant-soil interactions in peatlands as I demonstrate for the first time that HFA and HFD decomposition can occur in peatland ecosystems. Additionally, my research improves the understanding of PFT effects on the decomposition of litter mixtures and monocultures.

6.4 Peatland ecosystem function: what difference does microclimate change make?

The effects of small-scale changes in climate on GHG emissions from peat were explored explicitly in Chapters 3 and 5. From the mesocosm experiments, we now know that microclimatic changes have the capacity to affect GHG fluxes from peat, with small alterations in air temperature (2-4 °C) affecting CO_2 emissions (Chapters 3 and 5), and modest adjustments in water table level (10-20 cm) influencing CH_4 emissions (Chapter 3). The increase in CO_2 emissions with a 2-4 °C increase in temperature shows that peatland microclimates arising from land use change or climate change could affect C cycling processes. Previous studies have demonstrated that increasing air temperatures by approximately 1 °C can accelerate short-term (plant) and longer-term (peat) respiration in the field (Dorrepaal et al., 2009; Ward et al., 2013). However, as Ward et al., (2013) observed, whilst the rate of respired CO_2 may increase with small-scale increases in

temperature, the effect on CO_2 emissions may not be the same when taking into account plant community composition, plant productivity and water table variability. This research shows that CH_4 emissions and litter mass loss were influenced more by water table level and PFT than microclimatic changes in temperature, respectively (Chapters 3 and 5). Total C content of litter was found to explain more variation in the microbial community (Chapter 2) and litter mass loss (Chapter 4) than microclimatic factors, such as water table level and soil temperature. Therefore, this research indicates that the effects of climate or land use-induced temperature changes on peatland C cycling processes would be mediated by the composition of the plant community. This supports previous research on non-wind farm peatlands where litter type was found to affect the activity of aerobic decomposers more than the water table regime, and warming effects on GHG fluxes were moderated by the plant community (Strakova et al., 2011; Ward et al., 2013).

Considering the results presented and discussed in this thesis, the indirect effects of warming (i.e. as a result of global climate change or wind farm-induced microclimate change) on the dominance and distribution of PFTs would be expected to affect C storage in peatlands more so than the direct effects of rising temperatures on the processes that control decomposition of OM and the subsequent release of GHGs.

6.5 Future work

In the context of land use and climate change, this research improves the understanding of peatlands and the roles that PFT and microclimatic differences in temperature and water table level play in C cycling processes. Changes in plant community structure, as a result of climate change or land use change, have the potential to influence the C balance of peatlands through interactions between the peat matrix and the changing quality of litter inputs.

To further develop this research, it would be valuable to understand how temporal changes in labile substrates and microbial communities influence decomposition in peatlands (Bardgett et al., 2005; Bray et al., 2012; Kirschbaum, 2013), and how these biochemical changes could favour rapid decomposition of litter beneath different plant species (HFA and HFD), and interactions in litter mixtures over the short-term (i.e. days to weeks) and long-term (i.e. over decades). In addition, it would be important to ascertain how interactions between PFT litters respond to different litter mixing ratios and microclimatic differences in both temperature and water table level.

Identifying the sensitivity of GHG flux and decomposition rates to smaller microclimatic changes in temperature (i.e. increases of 0.2 °C) are key to understanding the response of peatland C stocks to wind farm-induced microclimates (Armstrong et al., 2014a). In this study, peatland properties and C cycling processes were measured within the wind farm along a transect oriented with the main axis of the wind farm and dominant wind direction, as the wind turbine-induced microclimate effect was hypothesised to increase along the transect. However, as a result of a concurrent study at Black Law Wind Farm that was completed towards the end of my PhD, we now understand that wind farm effects on ground-level climate are associated with individual wake effects of operational turbines (Armstrong et al., 2014a), rather than a cumulative effect of wind turbine wakes within a wind farm (i.e. the microclimate effect does not increase towards one end of the wind farm). Therefore, future field-based assessments of peatland C cycling sensitivity to wind farm microclimate effects would benefit from establishing sampling transects within individual turbine wake zones.

Future research that incorporates these suggestions would provide the understanding required to improve predictions of future peatland C stock sensitivity, with respect to the direct and indirect effects of land use change and climate change.

Furthermore, many land biosphere and global C cycle models do not currently take into account the effects of asymmetric diurnal warming on ecosystem functioning and terrestrial C cycling (Potter et al., 1993; Sitch et al., 2003). Night-time warming of the land surface is an effect associated with wind farm-induced microclimates (Armstrong et al., 2014a) and climate change (Karl et al., 1991). Night-time warming is expected to affect carbon assimilation by plants, due to enhanced autotrophic respiration and stimulation of photosynthesis through decreased risk of frost (Peng et al., 2013). The effects of land use change and climate change on asymmetric diurnal warming are small; nevertheless small shifts in temperature have the potential to influence plant community composition, and thus the cycling of C. However, the significance of wind farm-induced microclimates on peatland C cycling under changing climate projections remains uncertain (Armstrong et al., 2014b). The effects of night-time warming on plant productivity and C sequestration need to be quantified, particularly in sensitive C stores such as peatlands. This will enable terrestrial ecosystem models to capture the response of vegetation to asymmetric diurnal temperature changes produced by operational wind farms and global climate change.

6.6 Conclusions

Changes in land use and climate are important in determining the C balance of peatlands, by influencing abiotic and biotic factors and their interactions that drive C cycling processes. The effect of wind farm-induced microclimatic conditions on peatland ecosystem functioning represents a significant gap in knowledge. The aim of this research was, therefore, to investigate the sensitivity of peatland C cycling processes, including GHG emissions and decomposition, to hosting a wind farm, notably small-scale changes in temperature and water table level associated with a hypothesised wind farm-induced microclimate.

Findings provide evidence of the role of PFTs in influencing peatland ecosystem processes, such as increased respiration and decomposition of peat and litter derived from graminoids. Small-scale increases in temperature (2-4 °C) and water table (10-20 cm) were identified as the most important drivers of increases in CO_2 and CH_4 emissions, respectively, but were mediated by a PFT legacy in peat (Chapters 3 and 5). However, temperature and water table were secondary to PFT in controlling decomposition, which was primarily driven by differences in litter C content and C:N (Chapters 4 and 5). This thesis provides new information about the interactions between litter quality and peat quality. For example, litter decomposition in peatlands can exhibit a home-field advantage or disadvantage depending on the PFT origin of litter (Chapters 4 and 5). In addition, synergistic non-additive effects on litter mass loss of mixtures, comprised of more than one slow decomposing litter type, can occur (Chapter 5).

Whilst C cycling processes in peatlands are strongly influenced by biotic controls, these controls will interact with microclimatic conditions to regulate decomposition. The implications of this research are that climate and land use change effects on plant community composition could influence C cycling processes by altering: (1) the quality of litter inputs to peat; (2) the abiotic and biotic characteristics of the decomposition environment; (3) the likelihood of home-field advantage and home-field disadvantage decomposition; and (4) interactions between different litter types in litter mixtures. The findings presented in this thesis contribute to the existing knowledge of aboveground and belowground communities in peatlands, and their key controls on C cycling. Particularly important here is that the study site has been subjected to a significant land use change (i.e. wind energy generation) and yet the system functioning is broadly comparable to peatlands either undisturbed or with far less disturbance. The simplest interpretation here is that with time, a response to such disturbance becomes secondary. Despite similar biogeochemical

functioning to other peatlands, there is an undeniable increase in CO_2 emissions with microclimatic increases in air temperature observed in the laboratory. This needs to be further explored in the field and then incorporated into estimates of wind farm impacts on C dynamics of peatlands, contribute to the full life-cycle based calculation of wind farm C payback time (Nayak et al., 2010) and ensure the effects of siting wind farms on sensitive ecosystems are fully considered before development. By identifying the association of PFTs with peat and litter quality, soil microbial community composition, GHG emissions and litter decomposition, this research recognises the significant role that peatland PFTs have in responding to climate and land use change.

References

Aerts, R., 1997. Climate, Leaf Litter Chemistry and Leaf Litter Decomposition in Terrestrial Ecosystems: A Triangular Relationship. Oikos 79, 439–449. doi:10.2307/3546886

Aerts, R., 1999. Interspecific competition in natural plant communities: mechanisms, trade-offs and plant-soil feedbacks. Journal of Experimental Botany 50.

Aerts, R., 2003. Plant community mediated vs. nutritional controls on litter decomposition rates in grasslands. Ecology 84.

Aerts, R., 2006. The freezer defrosting: global warming and litter decomposition rates in cold biomes. Journal of Ecology 94, 713–724. doi:10.1111/j.1365-2745.2006.01142.x

Aerts, R., Callaghan, T.V., Dorrepaal, E., Logtestijn, R.S.P. van, Cornelissen, J.H.C., 2012. Seasonal climate manipulations have only minor effects on litter decomposition rates and N dynamics but strong effects on litter P dynamics of sub-arctic bog species. Oecologia 170, 809–819. doi:10.1007/s00442-012-2330-z

Aerts, R., Ludwig, F., 1997. Water-table changes and nutritional status affect trace gas emissions from laboratory columns of peatland soils. Soil Biology and Biochemistry 29, 1691–1698. doi:Doi: 10.1016/s0038-0717(97)00074-6

Aerts, R., Verhoeven, J.T.A., Whigham, D.F., 1999. Plant-mediated controls on nutrient cycling in temperate fens and bogs. Ecology 80, 2170–2181. doi:10.1890/0012-9658(1999)080[2170:PMCONC]2.0.CO;2

Aerts, R., Wallén, B., Malmer, N., De Caluwe, H., 2001. Nutritional constraints on Sphagnum-growth and potential decay in northern peatlands. Journal of Ecology 89, 292–299. doi:10.1046/j.1365-2745.2001.00539.x

Allison, S.D., Treseder, K.K., 2011. Climate change feedbacks to microbial decomposition in boreal soils. Fungal Ecology 4, 362–374. doi:10.1016/j.funeco.2011.01.003

Allison, S.D., Wallenstein, M.D., Bradford, M.A., 2010. Soil-carbon response to warming dependent on microbial physiology. Nature Geoscience 3, 336–340. doi:10.1038/ngeo846

Allison, S.D., Weintraub, M.N., Gartner, T.B., Waldrop, M.P., 2011. Evolutionary-Economic Principles as Regulators of Soil Enzyme Production and Ecosystem Function, in: Shukla, G., Varma, A. (Eds.), Soil Enzymology, Soil Biology. Springer Berlin Heidelberg, pp. 229–243.

Alm, J., Schulman, L., Walden, J., Nykanen, H., Martikainen, P.J., Silvola, J., 1999. Carbon balance of a boreal bog during a year with an exceptionally dry summer. Ecology 80, 161–174.

Andersen, R., Chapman, S.J., Artz, R.R.E., 2013. Microbial communities in natural and disturbed peatlands: A review. Soil Biology and Biochemistry 57, 979–994. doi:10.1016/j.soilbio.2012.10.003

Andersen, R., Grasset, L., Thormann, M.N., Rochefort, L., Francez, A.-J., 2010. Changes in microbial community structure and function following Sphagnum peatland restoration. Soil Biology and Biochemistry 42, 291–301. doi:10.1016/j.soilbio.2009.11.006

Armstrong, A., Burton, R.R., Lee, S.E., Mobbs, S., Ostle, N., Smith, V., Waldron, S., Whitaker, J., 2014a. Wind farms change the ground-level climate. Proceedings of the National Academy of Sciences (submitted).

Armstrong, A., Waldron, S., Whitaker, J., Ostle, N.J., 2014b. Wind farm and solar park effects on plant–soil carbon cycling: uncertain impacts of changes in ground-level microclimate. Glob Change Biol 20, 1699–1706. doi:10.1111/gcb.12437

Artz, R., 2009. Microbial Community Structure and Carbon Substrate Use in Northern Peatlands, in: Baird, A., Belyea, L.R., Comas, X., Reeve, A.S., Slater, L. (Eds.), Carbon Cycling in Northern Peatlands. American Geophysical Union, Washington DC.

Artz, R., Anderson, I., Chapman, S., Hagn, A., Schloter, M., Potts, J., Campbell, C., 2007. Changes in Fungal Community Composition in Response to Vegetational Succession During the Natural Regeneration of Cutover Peatlands. Microbial Ecology 54, 508–522. doi:10.1007/s00248-007-9220-7

Atlas, R.M., 1988. Microbiology: Fundamentals and Applications, second. ed. Collier Macmillan publishers, London.

Ayres, E., Dromph, K.M., Bardgett, R.D., 2006. Do plant species encourage soil biota that specialise in the rapid decomposition of their litter? Soil Biology and Biochemistry 38, 183–186. doi:DOI: 10.1016/j.soilbio.2005.04.018

Ayres, E., Steltzer, H., Berg, S., Wall, D.H., 2009a. Soil biota accelerate decomposition in high-elevation forests by specializing in the breakdown of litter produced by the plant species above them. Journal of Ecology 97, 901–912. doi:10.1111/j.1365-2745.2009.01539.x

Ayres, E., Steltzer, H., Simmons, B.L., Simpson, R.T., Steinweg, J.M., Wallenstein, M.D., Mellor, N., Parton, W.J., Moore, J.C., Wall, D.H., 2009b. Home-field advantage

accelerates leaf litter decomposition in forests. Soil Biology and Biochemistry 41, 606–610. doi:10.1016/j.soilbio.2008.12.022

Baidya Roy, S., Pacala, S., Walko, R., 2004. Can large wind farms affect local meteorology? Journal of Geophysical Research 109.

Baidya Roy, S., Traiteur, J., 2010. Impacts of wind farms on surface air temperatures. Proceedings of the National Academy of Sciences 107. doi:10.1073/pnas.1000493107

Ball, B.A., Bradford, M.A., Hunter, M.D., 2009. Nitrogen and Phosphorus Release from Mixed Litter Layers is Lower than Predicted from Single Species Decay. Ecosystems 12, 87–100. doi:10.1007/s10021-008-9208-2

Ball, B.A., Carrillo, Y., Molina, M., 2014. The influence of litter composition across the litter–soil interface on mass loss, nitrogen dynamics and the decomposer community. Soil Biology and Biochemistry 69, 71–82. doi:10.1016/j.soilbio.2013.10.048

Ball, B.A., Hunter, M.D., Kominoski, J.S., Swan, C.M., Bradford, M.A., 2008. Consequences of non-random species loss for decomposition dynamics: experimental evidence for additive and non-additive effects. Journal of Ecology 96, 303–313. doi:10.1111/j.1365-2745.2007.01346.x

Bardgett, R., 2005. The Biology of Soil. Oxford University Press.

Bardgett, R.D., Bowman, W.D., Kaufmann, R., Schmidt, S.K., 2005. A temporal approach to linking aboveground and belowground ecology. Trends in Ecology & Evolution 20, 634–641. doi:10.1016/j.tree.2005.08.005

Bardgett, R.D., Freeman, C., Ostle, N.J., 2008. Microbial contributions to climate change through carbon cycle feedbacks. Isme Journal 2, 805–814. doi:10.1038/ismej.2008.58

Bardgett, R.D., Hobbs, P.J., Frostegård, Å., 1996. Changes in soil fungal:bacterial biomass ratios following reductions in the intensity of management of an upland grassland. Biol Fert Soils 22, 261–264. doi:10.1007/BF00382522

Bardgett, R.D., Manning, P., Morriën, E., De Vries, F.T., 2013. Hierarchical responses of plant–soil interactions to climate change: consequences for the global carbon cycle. Journal of Ecology 101, 334–343. doi:10.1111/1365-2745.12043

Bardgett, R.D., Shine, A., 1999. Linkages between plant litter diversity, soil microbial biomass and ecosystem function in temperate grasslands. Soil Biology & Biochemistry 31, 317–321.

Bardgett, R., Wardle, D., 2010. Aboveground-belowground linkages:biotic interactions, ecosystem processes, and global change. Oxford University Press, Oxford.

Bellisario, L.M., Bubier, J.L., Moore, T.R., Chanton, J.P., 1999. Controls on CH4 emissions from a northern peatland. Global Biogeochemical Cycles 13, 81–91.

Belyea, L.R., 1996. Separating the Effects of Litter Quality and Microenvironment on Decomposition Rates in a Patterned Peatland. Oikos 77, 529. doi:10.2307/3545942

Berendse, F., Van Breemen, N., Rydin, H., Buttler, A., Heijmans, M., Hoosbeek, M.R., Lee, J.A., Mitchell, E., Saarinen, T., Vasander, H., Wallen, B., 2001. Raised atmospheric CO2 levels and increased N deposition cause shifts in plant species composition and production in Sphagnum bogs. Global Change Biology 7, 591–598.

Berg, B., Laskowski, R., 2005. Litter Decomposition: A Guide to Carbon and Nutrient Turnover, Advances in ecological research. Elsevier, Amsterdam.

Bezemer, T.M., Lawson, C.S., Hedlund, K., Edwards, A.R., Brook, A.J., Igual, J.M., Mortimer, S.R., Van Der Putten, W.H., 2006. Plant species and functional group effects on abiotic and microbial soil properties and plant–soil feedback responses in two grasslands. Journal of Ecology 94, 893–904. doi:10.1111/j.1365-2745.2006.01158.x

Blair, J.M., 1990. Decay Rates, Nitrogen Fluxes, and Decomposer Communiies of Single- and Mixed-Species Foliar Litter. Ecology 71.

Bligh, E.G., Dyer, W.J., 1959. A rapid method of total lipod extraction and purification. Canadian Journal of Biochemistry and Physiology 37, 911–917. doi:10.1139/o59-099

Blodau, C., 2002. Carbon cycling in peatlands - A review of processes and controls. Environmental Reviews 10, 111–134.

Blodau, C., Basiliko, N., Moore, T.R., 2004. Carbon turnover in peatland mesocosms exposed to different water table levels. Biogeochemistry 67, 331–351. doi:10.1023/B:BIOG.0000015788.30164.e2

Bond-Lamberty, B., Thomson, A., 2010. Temperature-associated increases in the global soil respiration record. Nature 464, 579–582. doi:http://www.nature.com/nature/journal/v464/n7288/suppinfo/nature08930_S1.html

Borcard, D., Legendre, P., Gillet, F., 2011a. Canonical Ordination., in: Numerical Ecology with R. Springer, London, pp. 153–225.

Borcard, D., Legendre, P., Gillet, F., 2011b. Association Measures and Matrices., in: Numerical Ecology with R. Springer, London, pp. 31–51.

Boss, C.B., Fredeen, K.J., 1999. Concepts, instrumentation and techniques in inductively coupled plasma optical emission spectrometry. Norwalk: Perkin Elmer.

Bossio, D.A., Scow, K.M., Gunapala, N., Graham, K.J., 1998. Determinants of Soil Microbial Communities: Effects of Agricultural Management, Season, and Soil Type on Phospholipid Fatty Acid Profiles. Microb Ecol 36, 1–12. doi:10.1007/s002489900087

Bouillon, S., Moens, T., Koedam, N., Dahdouh-Guebas, F., Baeyens, W., Dehairs, F., 2004. Variability in the origin of carbon substrates for bacterial communities in mangrove sediments. FEMS Microbiology Ecology 49, 171–179. doi:10.1016/j.femsec.2004.03.004

Bradford, M.A., Fierer, N., Reynolds, J.F., 2008. Soil carbon stocks in experimental mesocosms are dependent on the rate of labile carbon, nitrogen and phosphorus inputs to soils. Functional Ecology 22, 964–974. doi:10.1111/j.1365-2435.2008.01404.x

Bragazza, L., Buttler, A., Habermacher, J., Brancaleoni, L., Gerdol, R., Fritze, H., Hanajík, P., Laiho, R., Johnson, D., 2012a. High nitrogen deposition alters the decomposition of bog plant litter and reduces carbon accumulation. Glob Change Biol 18, 1163–1172. doi:10.1111/j.1365-2486.2011.02585.x

Bragazza, L., Parisod, J., Buttler, A., Bardgett, R.D., 2012b. Biogeochemical plant-soil microbe feedback in response to climate warming in peatlands. Nature Climate Change. doi:10.1038/nclimate1781

Bragazza, L., Siffi, C., Iacumin, P., Gerdol, R., 2007. Mass loss and nutrient release during litter decay in peatland: The role of microbial adaptability to litter chemistry. Soil Biology & Biochemistry 39, 257–267. doi:10.1016/j.soilbio.2006.07.014

Brake, M., Höper, H., Joergensen, R.G., 1999. Land use-induced changes in activity and biomass of microorganisms in raised bog peats at different depths. Soil Biology and Biochemistry 31, 1489–1497. doi:Doi: 10.1016/s0038-0717(99)00053-x

Bray, S.R., Kitajima, K., Mack, M.C., 2012. Temporal dynamics of microbial communities on decomposing leaf litter of 10 plant species in relation to decomposition rate. Soil Biology and Biochemistry 49, 30–37. doi:10.1016/j.soilbio.2012.02.009

Bridgham, S.D., 1992. Mechanisms controlling soil respiration (CO2 and CH4) in southern peatlands. Soil Biology and Biochemistry 24.

Bridgham, S.D., Richardson, C.J., 2003. Endogenous versus exogenous nutrient control over decomposition and mineralization in North Carolina peatlands. Biogeochemistry 65, 151–178. doi:10.1023/A:1026026212581

Briones, M.J.I., 2009. Uncertainties related to the temperature sensitivity of soil carbon decomposition, in: Baveye, P.C., Laba, M., Mysiak, J. (Eds.), Uncertainties in Environmental Modelling and Consequences for Policy Making, NATO Science for Peace and Security Series C - Environmental Security. pp. 317–335.

Briones, M.J.I., McNamara, N.P., Poskitt, J., Crow, S.E., Ostle, N.J., 2014. Interactive biotic and abiotic regulators of soil carbon cycling: evidence from controlled climate experiments on peatland and boreal soils. Glob Change Biol 20, 2971–2982. doi:10.1111/gcb.12585

Bru, D., Ramette, A., Saby, N.P.A., Dequiedt, S., Ranjard, L., Jolivet, C., Arrouays, D., Philippot, L., 2011. Determinants of the distribution of nitrogen-cycling microbial communities at the landscape scale. ISME J 5, 532–542. doi:10.1038/ismej.2010.130

Bubier, J.L., 1995. The Relationship of Vegetation to Methane Emission and Hydrochemical Gradients in Northern Peatlands. Journal of Ecology 83, 403–420.

Bubier, J.L., Bhatia, G., Moore, T.R., Roulet, N.T., Lafleur, P.M., 2003. Spatial and Temporal Variability in Growing-Season Net Ecosystem Carbon Dioxide Exchange at a Large Peatland in Ontario, Canada. Ecosystems 6, 353–367. doi:10.1007/s10021-003-0125-0

Bubier, J.L., Moore, T.R., 1994. An ecological perspective on methane emissions from northern wetlands. Trends in Ecology & Evolution 9, 460–464. doi:10.1016/0169-5347(94)90309-3

Burke, I.C., Kaye, J.P., Bird, S.P., Hall, S.A., McCulley, R.L., Sommerville, G.L., 2003. Evaluating and Testing Models of Terrestrial Biogeochemistry: The Role of Temperature in Controlling Decomposition, in: Canham, J., Lauenroth, W. (Eds.), Models in Ecosystem Science. Princeton University Press, New Jersey, USA, pp. 225–253.

Butenschoen, O., Scheu, S., Eisenhauer, N., 2011. Interactive effects of warming, soil humidity and plant diversity on litter decomposition and microbial activity. Soil Biology and Biochemistry 43, 1902–1907. doi:10.1016/j.soilbio.2011.05.011

Cadisch, G., Giller, K.E., 1997. Driven by nature: plant litter quality and decomposition. CAB INTERNATIONAL.

Carlson, M., Chen, J., Elgie, S., Henschel, C., Montenegro, A., Roulet, N., Scott, N., Tarnocai, C., Wells, J., 2010. Maintaining the role of Canada's forests and peatlands in climate regulation. Forestry Chronicle 86, 434–443.

Carney, K., Matson, P., 2005. Plant Communities, Soil Microorganisms, and Soil Carbon Cycling: Does Altering the World Belowground Matter to Ecosystem Functioning? Ecosystems 8, 928–940. doi:10.1007/s10021-005-0047-0

Carrillo, Y., Ball, B.A., Strickland, M.S., Bradford, M.A., 2012. Legacies of plant litter on carbon and nitrogen dynamics and the role of the soil community. Pedobiologia 55, 185–192. doi:10.1016/j.pedobi.2012.02.002

Carter, M.R., 1993. Soil sampling and methods of analysis. Canadian Society of Soil Science, Florida.

Case, S.D.C., McNamara, N.P., Reay, D.S., Whitaker, J., 2013. Can biochar reduce soil greenhouse gas emissions from a Miscanthus bioenergy crop? GCB Bioenergy. doi:10.1111/gcbb.12052

Chapin, F.S., Bret-Harte, M.S., Hobbie, S.E., Zhong, H., 1996. Plant functional types as predictors of transient responses of arctic vegetation to global change. Journal of Vegetation Science 7, 347–358. doi:10.2307/3236278

Chapman, S.J., Thurlow, M., 1998. Peat respiration at low temperatures. Soil Biology and Biochemistry 30, 1013–1021. doi:10.1016/S0038-0717(98)00009-1

Chapman, S.K., Newman, G.S., 2010. Biodiversity at the plant–soil interface: microbial abundance and community structure respond to litter mixing. Oecologia 162, 763–769. doi:10.1007/s00442-009-1498-3

Charman, D., 2002. Peatlands and environmental change. Wiley.

Charman, D., Sirin, A., Minayeva, T., 2008. Impacts of future climate chnage on peatlands., in: Parish, F., Sirin, A., Charman, D., Joosten, H., Minayeva, T., Silvius, M., Stringer, L. (Eds.), Assesment on Peatlands, Biodiversity and Climate Change. Wetlands International, Wageningen, pp. 118–138.

Chivers, M.R., Turetsky, M.R., Waddington, J.M., Harden, J.W., McGuire, A.D., 2009. Effects of Experimental Water Table and Temperature Manipulations on Ecosystem CO2 Fluxes in an Alaskan Rich Fen. Ecosystems 12, 1329–1342. doi:10.1007/s10021-009-9292-y

Christensen, T.R., Jonasson, S., Callaghan, T.V., Havström, M., 1999. On the potential CO2 release from tundra soils in a changing climate. Applied Soil Ecology 11, 127–134. doi:10.1016/S0929-1393(98)00146-2

Clarke, S., 2009. Balancing Environmental and Cultural Impact against the Strategic Need for Wind Power. International Journal of Heritage Studies 15, 175–191. doi:10.1080/13527250902890688

Clarke, S.R., Norman, J.M., 1995. Home Ground Advantage of Individual Clubs in English Soccer. Journal of the Royal Statistical Society. Series D (The Statistician) 44, 509–521. doi:10.2307/2348899

Clark, J.M., Ashley, D., Wagner, M., Chapman, P.J., Lane, S.N., Evans, C.D., Heathwaite, A.L., 2009. Increased temperature sensitivity of net DOC production from ombrotrophic peat due to water table draw-down. Global Change Biology 15, 794–807. doi:10.1111/j.1365-2486.2008.01683.x

Clarkson, B.R., Moore, T.R., Fitzgerald, N.B., Thornburrow, D., Watts, C.H., Miller, S., 2014. Water Table Regime Regulates Litter Decomposition in Restiad Peatlands, New Zealand. Ecosystems 17, 317–326. doi:10.1007/s10021-013-9726-4

Clymo, R.S., Turunen, J., Tolonen, K., 1998. Carbon accumulation in peatland. Oikos 81, 368–388.

Conant, R.T., Drijber, R.A., Haddix, M.L., Parton, W.J., Paul, E.A., Plante, A.F., Six, J., Steinweg, J.M., 2008a. Sensitivity of organic matter decomposition to warming varies with its quality. Global Change Biology 14, 868–877. doi:10.1111/j.1365-2486.2008.01541.x

Conant, R.T., Steinweg, J.M., Haddix, M.L., Paul, E.A., Plante, A.F., Six, J., 2008b. EXPERIMENTAL WARMING SHOWS THAT DECOMPOSITION TEMPERATURE SENSITIVITY INCREASES WITH SOIL ORGANIC MATTER RECALCITRANCE. Ecology 89, 2384–2391. doi:10.1890/08-0137.1

Conen, F., Leifeld, J., Seth, B., Alewell, C., 2006. Warming mineralises young and old soil carbon equally. Biogeosciences 3, 515–519. doi:10.5194/bg-3-515-2006

Cornelissen, J.H.C., Van Bodegom, P.M., Aerts, R., Callaghan, T.V., Van Logtestijn, R.S.P., Alatalo, J., Stuart Chapin, F., Gerdol, R., Gudmundsson, J., Gwynn-Jones, D., Hartley, A.E., Hik, D.S., Hofgaard, A., Jónsdóttir, I.S., Karlsson, S., Klein, J.A., Laundre, J., Magnusson, B., Michelsen, A., Molau, U., Onipchenko, V.G., Quested, H.M., Sandvik, S.M., Schmidt, I.K., Shaver, G.R., Solheim, B., Soudzilovskaia, N.A., Stenström, A., Tolvanen, A., Totland, Ø., Wada, N., Welker, J.M., Zhao, X., Team, M.O.L., 2007. Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. Ecology Letters 10, 619–627. doi:10.1111/j.1461-0248.2007.01051.x

Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., Hobbie, S.E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H.M., Santiago, L.S., Wardle, D.A., Wright, I.J., Aerts, R., Allison, S.D., Van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T.V., Díaz, S., Garnier, E., Gurvich, D.E., Kazakou, E., Klein, J.A., Read, J., Reich, P.B., Soudzilovskaia, N.A., Vaieretti, M.V., Westoby, M., 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecology Letters 11, 1065–1071. doi:10.1111/j.1461-0248.2008.01219.x

Couteaux, M., Bottner, P., Berg, B., 1995. Litter decomposition, climate and litter quality. Trends in Ecology & Evolution 10, 63–66. doi:10.1016/S0169-5347(00)88978-8

Couwenberg, J., Thiele, A., Tanneberger, F., Augustin, J., Bärisch, S., Dubovik, D., Liashchynskaya, N., Michaelis, D., Minke, M., Skuratovich, A., Joosten, H., 2011. Assessing greenhouse gas emissions from peatlands using vegetation as a proxy. Hydrobiologia 674, 67–89. doi:10.1007/s10750-011-0729-x

Cox, P.M., Betts, R.A., Jones, C.D., Spall, S.A., Totterdell, I.J., 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature 408, 184–187.

Craine, J.M., Fierer, N., McLauchlan, K.K., 2010. Widespread coupling between the rate and temperature sensitivity of organic matter decay. Nature Geosci 3, 854–857. doi:10.1038/ngeo1009

Crow, S.E., Wieder, R.K., 2005. Sources of Co-2 emission from a northern peatland: Root respiration, exudation, and decomposition. Ecology 86, 1825–1834.

Dalias, P., Anderson, J.M., Bottner, P., Coûteaux, M.-M., 2001. Long-term effects of temperature on carbon mineralisation processes. Soil Biology and Biochemistry 33, 1049–1057. doi:10.1016/S0038-0717(01)00009-8

Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440, 165–173. doi:10.1038/nature04514

Dawson, J.J.C., Smith, P., 2007. Carbon losses from soil and its consequences for land-use management. Science of the Total Environment 382, 165–190. doi:DOI: 10.1016/j.scitotenv.2007.03.023

De Boer, W., Folman, L.B., Summerbell, R.C., Boddy, L., 2005. Living in a fungal world: impact of fungi on soil bacterial niche development⋆. FEMS Microbiology Reviews 29, 795–811. doi:10.1016/j.femsre.2004.11.005

DECC, 2013. UK Renewable Energy Roadmap Update 2013.

De Deyn, G.B., 2011. Plant species richness, identity and productivity differentially influence key groups of microbes in grassland soils of contrasting fertility. Biology Letters 7.

De Deyn, G.B., Cornelissen, J.H.C., Bardgett, R.D., 2008. Plant functional traits and soil carbon sequestration in contrasting biomes. Ecology Letters 11, 516–531. doi:10.1111/j.1461-0248.2008.01164.x

DeLuca, T.H., Zackrisson, O., Nilsson, M.-C., Sellstedt, A., 2002. Quantifying nitrogen-fixation in feather moss carpets of boreal forests. Nature 419, 917–920. doi:10.1038/nature01051

De Toledo Castanho, C., de Oliveira, A.A., 2008. Relative effect of litter quality, forest type and their interaction on leaf decomposition in south-east Brazilian forests. Journal of Tropical Ecology 24, 149–156. doi:10.1017/S0266467407004749

Dieleman, C.M., Branfireun, B.A., McLaughlin, J.W., Lindo, Z., 2014. Climate change drives a shift in peatland ecosystem plant community: Implications for ecosystem function and stability. Glob Change Biol n/a–n/a. doi:10.1111/gcb.12643

Dijkstra, F., Prior, S., Runion, G., Torbert, H., Tian, H., Lu, C., Venterea, R., 2012. Effects of elevated carbon dioxide and increased temperature on methane and nitrous oxide fluxes: evidence from field experiments. Frontiers in Ecology and the Environment 10, 520–527.

Dinsmore, K., Skiba, U., Billett, M., Rees, R., 2009. Effect of water table on greenhouse gas emissions from peatland mesocosms. Plant and Soil 318, 229–242. doi:10.1007/s11104-008-9832-9

Dinsmore, K., Skiba, U.M., Billett, M.F., Rees, R.M., Drewer, J., 2009. Spatial and temporal variability in CH4 and N2O fluxes from a Scottish ombrotrophic peatland: Implications for modelling and up-scaling. Soil Biology and Biochemistry 41, 1315–1323. doi:10.1016/j.soilbio.2009.03.022

Dise, N.B., 2009. Peatland Response to Global Change. Science 326, 810–811. doi:10.1126/science.1174268

Dise, N.B., Phoenix, G.K., 2011. Peatlands in a changing world. New Phytologist 191, 309–311. doi:10.1111/j.1469-8137.2011.03801.x

Dorrepaal, E., Cornelissen, J.H. c., Aerts, R., Wallén, B., Van Logtestijn, R.S. p., 2005. Are growth forms consistent predictors of leaf litter quality and decomposability across peatlands along a latitudinal gradient? Journal of Ecology 93, 817–828. doi:10.1111/j.1365-2745.2005.01024.x

Dorrepaal, E., Toet, S., van Logtestijn, R.S.P., Swart, E., van de Weg, M.J., Callaghan, T.V., Aerts, R., 2009. Carbon respiration from subsurface peat accelerated by climate warming in the subarctic. Nature 460, 616–619. doi:10.1038/nature08216

Dray, S., Legendre, P., Blanchet, G., 2009. packfor: Forward Selection with permutation.

Duan, J., Wang, S., Zhang, Z., Xu, G., Luo, C., Chang, X., Zhu, X., Cui, S., Zhao, X., Wang, W., Du, M., 2013. Non-additive effect of species diversity and temperature sensitivity of mixed litter decomposition in the alpine meadow on Tibetan Plateau. Soil Biology and Biochemistry 57, 841–847. doi:10.1016/j.soilbio.2012.08.009

Dunfield, P., knowles, R., Dumont, R., Moore, T.R., 1993. Methane production and consumption in temperate and subarctic peat soils: Response to temperature and pH. Soil Biology and Biochemistry 25, 321–326. doi:10.1016/0038-0717(93)90130-4

Emmett, B., Frogbrook, Z., Chamberlain, P., Griffiths, R., Pickup, R., Poskitt, J., Reynolds, B., Spurgeon, D., Wilson, D., Wood, C., 2008. Countryside Survey Techincal Report No.03/07: Soils Manual.

Estop-Aragonés, C., 2012. Effects of experimental drying intensity and duration on respiration and methane production recovery in fen peat incubations. Soil Biology and Biochemistry 47.

Fang, C., Smith, P., Moncrieff, J.B., Smith, J.U., 2005. Similar response of labile and resistant soil organic matter pools to changes in temperature. Nature 433, 57–59. doi:10.1038/nature03138

Fenner, N., Freeman, C., Reynolds, B., 2005. Observations of a seasonally shifting thermal optimum in peatland carbon-cycling processes; implications for the global carbon cycle and soil enzyme methodologies. Soil Biology & Biochemistry 37, 1814–1821. doi:10.1016/j.soilbio.2005.02.032

Fenner, N., Ostle, N., Freeman, C., Sleep, D., Reynolds, B., 2004. Peatland carbon efflux partitioning reveals that Sphagnum photosynthate contributes to the DOC pool. Plant and Soil 259, 345–354. doi:10.1023/B:PLSO.0000020981.90823.c1

Fierer, N., 2003. Variations in microbial community composition through two soil depth profiles. Soil Biology and Biochemistry 35.

Fierer, N., Craine, J.M., McLauchlan, K., Schimel, J.P., 2005. Litter quality and the temperature sensitivity of decomposition. Ecology 86, 320–326. doi:10.1890/04-1254

Fierer, N., Strickland, M.S., Liptzin, D., Bradford, M.A., Cleveland, C.C., 2009. Global patterns in belowground communities. Ecology Letters 12, 1238–1249. doi:10.1111/j.1461-0248.2009.01360.x

Fisk, M.C., Ruether, K.F., Yavitt, J.B., 2003. Microbial activity and functional composition among northern peatland ecosystems. Soil Biology & Biochemistry 35, 591–602. doi:10.1016/s0038-0717(03)00053-1

Freeman, C., Fenner, N., Ostle, N.J., Kang, H., Dowrick, D.J., Reynolds, B., Lock, M.A., Sleep, D., Hughes, S., Hudson, J., 2004. Export of dissolved organic carbon from peatlands under elevated carbon dioxide levels. Nature 430, 195–198.

Freeman, C., Ostle, N., Kang, H., 2001. An enzymic "latch" on a global carbon store. Nature 409, 149–149.

Frenzel, P., Karofeld, E., 2000. CH4 emission from a hollow-ridge complex in a raised bog: The role of CH4 production and oxidation. Biogeochemistry 51, 91–112. doi:10.1023/A:1006351118347

Freschet, G.T., Aerts, R., Cornelissen, J.H.C., 2012. Multiple mechanisms for trait effects on litter decomposition: moving beyond home-field advantage with a new hypothesis. Journal of Ecology 100, 619–630. doi:10.1111/j.1365-2745.2011.01943.x

Frolking, S., Roulet, N.T., 2007. Holocene radiative forcing impact of northern peatland carbon accumulation and methane emissions. Global Change Biology 13, 1079–1088. doi:10.1111/j.1365-2486.2007.01339.x

Frostegard, A., 1993. Shifts in the structure of soil microbial communities in limed forests as revealed by phospholipid fatty acid analysis. Soil Biology and Biochemistry 25.

Frostegård, A., Bååth, E., 1996. The use of phospholipid fatty acid analysis to estimate bacterial and fungal biomass in soil. Biology and Fertility of Soils 22, 59–65. doi:10.1007/bf00384433

Frostegård, Å., Tunlid, A., Bååth, E., 1991. Microbial biomass measured as total lipid phosphate in soils of different organic content. Journal of Microbiological Methods 14, 151–163. doi:10.1016/0167-7012(91)90018-L

Galand, P.E., Fritze, H., Yrjälä, K., 2003. Microsite-dependent changes in methanogenic populations in a boreal oligotrophic fen. Environmental Microbiology 5, 1133–1143. doi:10.1046/j.1462-2920.2003.00520.x

Gallego-Sala, A.V., Prentice, I.., 2012. Blanket peat biome endangered by climate change. Nature Climate Change 3, 152–155. doi:10.1038/nclimate1672

Garnett, M.H., Ineson, P., Stevenson, A.C., 2000. Effects of burning and grazing on carbon sequestration in a Pennine blanket bog, UK. The Holocene 10, 729–736. doi:10.1191/09596830094971

Gartner, T.B., Cardon, Z.G., 2004. Decomposition dynamics in mixed-species leaf litter. Oikos 104, 230–246. doi:10.1111/j.0030-1299.2004.12738.x

Gavazov, K.S., 2010. Dynamics of alpine plant litter decomposition in a changing climate. Plant Soil 337, 19–32. doi:10.1007/s11104-010-0477-0

Gholz, H.L., Wedin, D.A., Smitherman, S.M., Harmon, M.E., Parton, W.J., 2000. Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. Global Change Biology 6, 751–765. doi:10.1046/j.1365-2486.2000.00349.x

Gießelmann, U.C., Martins, K.G., Brändle, M., Schädler, M., Marques, R., Brandl, R., 2011. Lack of home-field advantage in the decomposition of leaf litter in the Atlantic Rainforest of Brazil. Applied Soil Ecology 49, 5–10. doi:10.1016/j.apsoil.2011.07.010

Glatzel, S., Basiliko, N., Moore, T., 2004. Carbon dioxide and methane production potentials of peats from natural, harvested and restored sites, eastern Québec, Canada. Wetlands 24, 261–267. doi:10.1672/0277-5212(2004)024[0261:CDAMPP]2.0.CO;2

Gorham, E., 1991. Northern peatlands - role in the carbon-cycle and probable responses to climatic warming. Ecological Applications 1, 182–195.

Graças, M.A.S., Bärlocher, F., Gessner, M.O., 2005. Methods to Study Litter Decomposition: A Practical Guide. Springer.

Grace, J., Marks, T.C., 1978. Physiological aspects of bog production at Moor House, Production ecology of British moors and montane grasslands. Springer-Verlag, New York.

Grayston, S.J., 1998. Selective influence of plant species on microbial diversity in the rhizosphere. Soil Biology and Biochemistry 30.

Green, S., Boardman, C., Baird, A., Gauci, V., 2011. Investigation of peatland restoration (grip blocking) techniques to achieve best outcomes for methane and greenhouse gas emissions/balance. Controlled Environment (Mesocosm) Experiment. Final Report to Defra. (No. Project code SP1202). Defra.

Green, S.M., Baird, A.J., 2012. A mesocosm study of the role of the sedge Eriophorum angustifolium in the efflux of methane—including that due to episodic ebullition—from peatlands. Plant Soil 351, 207–218. doi:10.1007/s11104-011-0945-1

Greenup, A., Bradford, M., McNamara, N., Ineson, P., Lee, J., 2000. The role of Eriophorum vaginatum in CH4 flux from an ombrotrophic peatland. Plant and Soil 227, 265–272. doi:10.1023/a:1026573727311

Grieve, I., Gilvear, D., 2009. Effects of wind farm construction on concentrations and fluxes of dissolved organic carbon and suspended sediment from peat catchments at Braes of Doune, central Scotland. Presented at the Mires and Peat, International Peat Society, p. Article 03.

Guggenberger, G., Frey, S., Six, J., Paustian, K., Elliott, E., 1999. Bacterial and Fungal Cell-Wall Residues in Conventional and No-Tillage Agroecosystems. Soil Sci Soc Am J 63, 1188–1198.

Hamdi, S., Moyano, F., Sall, S., Bernoux, M., Chevallier, T., 2013. Synthesis analysis of the temperature sensitivity of soil respiration from laboratory studies in relation to incubation methods and soil conditions. Soil Biology and Biochemistry 58, 115–126. doi:10.1016/j.soilbio.2012.11.012

Hansen, R.A., 2000. Effects of habitat complexity and composition on a diverse litter microarthropod assemblage. Ecology 81, 1120–1132. doi:10.1890/0012-9658(2000)081[1120:EOHCAC]2.0.CO;2

Harguindeguy, N.P., Blundo, C.M., Gurvich, D.E., Díaz, S., Cuevas, E., 2008. More than the sum of its parts? Assessing litter heterogeneity effects on the decomposition of litter mixtures through leaf chemistry. Plant Soil 303, 151–159. doi:10.1007/s11104-007-9495-y

Hartman, W.H., Richardson, C.J., Vilgalys, R., Bruland, G.L., 2008. Environmental and anthropogenic controls over bacterial communities in wetland soils. PNAS 105, 17842–17847. doi:10.1073/pnas.0808254105

Hättenschwiler, S., Tiunov, A.V., Scheu, S., 2005. Biodiversity and litter decomposition in terrestrial ecosystems. Annual Review of Ecology, Evolution, and Systematics 36, 191–218. doi:10.1146/annurev.ecolsys.36.112904.151932

Hättenschwiler, S., Vitousek, P.M., 2000. The role of polyphenols in terrestrial ecosystem nutrient cycling. Trends in Ecology & Evolution 15, 238–243. doi:10.1016/S0169-5347(00)01861-9

Hector, A., Beale, A.J., Minns, A., Otway, S.J., Lawton, J.H., 2000. Consequences of the Reduction of Plant Diversity for Litter Decomposition: Effects through Litter Quality and Microenvironment. Oikos 90, 357–371.

Hilasvuori, E., Akujärvi, A., Fritze, H., Karhu, K., Laiho, R., Mäkiranta, P., Oinonen, M., Palonen, V., Vanhala, P., Liski, J., 2013. Temperature sensitivity of decomposition

in a peat profile. Soil Biology and Biochemistry 67, 47–54. doi:10.1016/j.soilbio.2013.08.009

Hobbie, S.E., 1996. Temperature and Plant Species Control Over Litter Decomposition in Alaskan Tundra. Ecological Monographs 66, 503–522. doi:10.2307/2963492

Hogg, E.H., 1993. Decay potential of hummock and hollow Sphagnum peats at different depths in a Swedish raised bog. Oikos 66, 269–278.

Høj, L., Rusten, M., Haugen, L.E., Olsen, R.A., Torsvik, V.L., 2006. Effects of water regime on archaeal community composition in Arctic soils. Environmental Microbiology 8, 984–996. doi:10.1111/j.1462-2920.2006.00982.x

Holden, J., Burt, T.P., 2003. Hydrological studies on blanket peat: the significance of the acrotelm-catotelm model. Journal of Ecology 91, 86–102. doi:10.1046/j.1365-2745.2003.00748.x

Holden, J., Evans, M.G., Burt, T.P., Horton, M., 2006. Impact of Land Drainage on Peatland Hydrology. J. Environ. Qual. 35, 1764–1778. doi:10.2134/jeq2005.0477

Holland, E.A., Robertson, G.P., Greenberg, J., Groffman, P., Boone, R., Gosz, J., 1999. Soil CO2, N2O, and CH4 exchange, in: Standard Soil Methods for Long-Term Ecological Research. Oxford University Press, New York, pp. 185–201.

Hooper, D.U., Bignell, D.E., Brown, V.K., Brussard, L., Dangerfield, J.M., Wall, D.H., Wardle, D.A., Coleman, D.C., Giller, K.E., Lavelle, P., Van de Putten, W.H., DE Ruiter, P.C., Rusek, J., Silver, W.L., Tiedje, J.M., Wolters, V., 2000. Interactions between Aboveground and Belowground Biodiversity in Terrestrial Ecosystems: Patterns, Mechanisms, and Feedbacks. Bioscience 50, 1049–1061. doi:10.1641/0006-3568(2000)050[1049:IBAABB]2.0.CO;2

Hoorens, B., 2003. Does initial litter chemistry explain litter mixture effects on decomposition? Oecologia 137.

Hoorens, B., Aerts, R., Stroetenga, M., 2002. Litter quality and interactive effects in litter mixtures: more negative interactions under elevated CO2? Journal of Ecology 90, 1009–1016. doi:10.1046/j.1365-2745.2002.00732.x

Hoorens, B., Stroetenga, M., Aerts, R., 2010. Litter Mixture Interactions at the Level of Plant Functional Types are Additive. Ecosystems 13, 90–98. doi:10.1007/s10021-009-9301-1

Hothorn, T., Bretz, F., Westfall, P., Heiberger, R., 2008. Multcomp: simultaneous inference for general linear hypotheses. R Package Version 1.0-3.

Hunt, H.W., Ingham, E.R., Coleman, D.C., Elliott, E.T., Reid, C.P.P., 1988. Nitrogen Limitation of Production and Decomposition in Prairie, Mountain Meadow, and Pine Forest. Ecology 1009–1016.

Ingram, H. a. P., 1978. Soil Layers in Mires: Function and Terminology. Journal of Soil Science 29, 224–227. doi:10.1111/j.1365-2389.1978.tb02053.x

IPCC, (Intergovernmental Panel on Climate Change, 2013. Climate Change 2013-the physical science basis.

Ise, T., Dunn, A.L., Wofsy, S.C., Moorcroft, P.R., 2008. High sensitivity of peat decomposition to climate change through water-table feedback. Nature Geoscience 1, 763–766. doi:10.1038/ngeo331

Jaatinen, K., Fritze, H., Laine, J., Laiho, R., 2007. Effects of short- and long-term water-level drawdown on the populations and activity of aerobic decomposers in a boreal peatland. Global Change Biology 13, 491–510. doi:10.1111/j.1365-2486.2006.01312.x

Jassey, V.E., Chiapusio, G., Binet, P., Buttler, A., Laggoun-Défarge, F., Delarue, F., Bernard, N., Mitchell, E.A., Toussaint, M.-L., Francez, A.-J., Gilbert, D., 2013. Above- and belowground linkages in Sphagnum peatland: climate warming affects plant-microbial interactions. Glob Change Biol 19, 811–823. doi:10.1111/gcb.12075

Jiang, J., Li, Y., Wang, M., Zhou, C., Cao, G., Shi, P., Song, M., 2013. Litter species traits, but not richness, contribute to carbon and nitrogen dynamics in an alpine meadow on the Tibetan Plateau. Plant Soil 373, 931–941. doi:10.1007/s11104-013-1859-x

Jobbágy, E.G., Jackson, R.B., 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecological Applications 10, 423–436. doi:10.1890/1051-0761(2000)010[0423:TVDOSO]2.0.CO;2

Joergensen, R.G., Wichern, F., 2008. Quantitative assessment of the fungal contribution to microbial tissue in soil. Soil biology & biochemistry 40, 2977–2991.

Johnson, L.C., Damman, A.W.H., 1991. Species-Controlled Sphagnum Decay on a South Swedish Raised Bog. Oikos 61, 234–242. doi:10.2307/3545341

Jones, C.D., Cox, P., Huntingford, C., 2003. Uncertainty in climate-carbon-cycle projections associated with the sensitivity of soil respiration to temperature. Tellus Series B-Chemical and Physical Meteorology 55, 642–648.

Jonsson, M., Wardle, D.A., 2008. Context dependency of litter-mixing effects on decomposition and nutrient release across a long-term chronosequence. Oikos 117, 1674–1682. doi:10.1111/j.1600-0706.2008.16810.x

Kardol, P., Cregger, M.A., Campany, C.E., Classen, A.T., 2010. Soil ecosystem functioning under climate change: plant species and community effects. Ecology 91, 767–781. doi:10.1890/09-0135.1

Karl, T.R., Kukla, G., Razuvayev, V.N., Changery, M.J., Quayle, R.G., Heim, R.R., Easterling, D.R., Fu, C.B., 1991. Global warming: Evidence for asymmetric diurnal temperature change. Geophys. Res. Lett. 18, 2253–2256. doi:10.1029/91GL02900

Keinänen, M.M., Korhonen, L.K., Lehtola, M.J., Miettinen, I.T., Martikainen, P.J., Vartiainen, T., Suutari, M.H., 2002. The Microbial Community Structure of Drinking Water Biofilms Can Be Affected by Phosphorus Availability. Appl. Environ. Microbiol. 68, 434–439. doi:10.1128/AEM.68.1.434-439.2002

Keller, J.K., White, J.R., Bridgham, S.D., Pastor, J., 2004. Climate change effects on carbon and nitrogen mineralization in peatlands through changes in soil quality. Global Change Biology 10, 1053–1064. doi:10.1111/j.1529-8817.2003.00785.x

Kip, N., van Winden, J.F., Pan, Y., Bodrossy, L., Reichart, G.-J., Smolders, A.J.P., Jetten, M.S.M., Damsté, J.S.S., Op den Camp, H.J.M., 2010. Global prevalence of methane oxidation by symbiotic bacteria in peat-moss ecosystems. Nature Geosci 3, 617–621. doi:10.1038/ngeo939

Kirschbaum, M.U.F., 1995. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. Soil Biology and Biochemistry 27, 753–760. doi:10.1016/0038-0717(94)00242-S

Kirschbaum, M.U.F., 2004. Soil respiration under prolonged soil warming: are rate reductions caused by acclimation or substrate loss? Global Change Biology 10, 1870–1877. doi:10.1111/j.1365-2486.2004.00852.x

Kirschbaum, M.U.F., 2013. Seasonal variations in the availability of labile substrate confound the temperature dependence of organic matter decomposition. Soil Biology and Biochemistry 57, 568–576. doi:10.1016/j.soilbio.2012.10.012

Kirwan, M.L., Blum, L.K., 2011. Enhanced decomposition offsets enhanced productivity and soil carbon accumulation in coastal wetlands responding to climate change. Biogeosciences 8, 987–993. doi:10.5194/bg-8-987-2011

Klamer, M., Bååth, E., 2004. Estimation of conversion factors for fungal biomass determination in compost using ergosterol and PLFA 18:2ω6,9. Soil Biology and Biochemistry 36, 57–65. doi:10.1016/j.soilbio.2003.08.019

Lafleur, P.M., Hember, R.A., Admiral, S.W., Roulet, N.T., 2005. Annual and seasonal variability in evapotranspiration and water table at a shrub-covered bog in southern Ontario, Canada. Hydrological Processes 19, 3533–3550. doi:10.1002/hyp.5842

Laiho, R., 2006. Decomposition in peatlands: Reconciling seemingly contrasting results on the impacts of lowered water levels. Soil Biology & Biochemistry 38, 2011–2024. doi:10.1016/j.soilbio.2006.02.017

Laiho, R., Laine, J., Trettin, C.C., Finér, L., 2004. Scots pine litter decomposition along drainage succession and soil nutrient gradients in peatland forests, and the effects of inter-annual weather variation. Soil Biology and Biochemistry 36, 1095–1109. doi:10.1016/j.soilbio.2004.02.020

Laiho, R., Vasander, H., Penttilä, T., Laine, J., 2003. Dynamics of plant-mediated organic matter and nutrient cycling following water-level drawdown in boreal peatlands. Global Biogeochem. Cycles 17, 1053. doi:10.1029/2002gb002015

Laine, A., Byrne, K.A., Kiely, G., Tuittila, E.-S., 2007. Patterns in Vegetation and CO2 Dynamics along a Water Level Gradient in a Lowland Blanket Bog. Ecosystems 10, 890–905. doi:10.1007/s10021-007-9067-2

Latter, P.M., Howson, G., Howard, D.M., Scott, W.A., 1998. Long-term study of litter decomposition on a Pennine peat bog: which regression? Oecologia 113, 94–103. doi:10.1007/s004420050357

Lauber, C.L., Strickland, M.S., Bradford, M.A., Fierer, N., 2008. The influence of soil properties on the structure of bacterial and fungal communities across land-use types. Soil Biology and Biochemistry 40, 2407–2415. doi:10.1016/j.soilbio.2008.05.021

Leifeld, J., Fuhrer, J., 2005. The Temperature Response of CO2 Production from Bulk Soils and Soil Fractions is Related to Soil Organic Matter Quality. Biogeochemistry 75, 433–453. doi:10.1007/s10533-005-2237-4

Li, D., Peng, S., Chen, B., 2013. The effects of leaf litter evenness on decomposition depend on which plant functional group is dominant. Plant Soil 365, 255–266. doi:10.1007/s11104-012-1337-x

Lieffers, V.J., 1988. Sphagnum and cellulose decomposition drained and natural areas of an Alberta peatland. Canadian Journal of Soil Science 68, 755–761. doi:10.4141/cjss88-073

Limpens, J., Berendse, F., Blodau, C., Canadell, J.G., Freeman, C., Holden, J., Roulet, N., Rydin, H., Schaepman-Strub, G., 2008. Peatlands and the carbon cycle: from local processes to global implications a synthesis (vol 5, pg 1475, 2008). Biogeosciences 5, 1739–1739.

Lipson, D.A., Schadt, C.W., Schmidt, S.K., 2002. Changes in Soil Microbial Community Structure and Function in an Alpine Dry Meadow Following Spring Snow Melt. Microbial Ecology 43, 307–314. doi:10.1007/s00248-001-1057-x

Lloyd, J., Taylor, J.A., 1994. On the Temperature Dependence of Soil Respiration. Functional Ecology 8, 315–323. doi:citeulike-article-id:1572631

Luo, C., Xu, G., Chao, Z., Wang, S., Lin, X., Hu, Y., Zhang, Z., Duan, J., Chang, X., Su, A., Li, Y., Zhao, X., Du, M., Tang, Y., Kimball, B., 2010. Effect of warming and grazing on litter mass loss and temperature sensitivity of litter and dung mass loss on the Tibetan plateau. Global Change Biology 16, 1606–1617. doi:10.1111/j.1365-2486.2009.02026.x

Luo, Y., Wan, S., Hui, D., Wallace, L.L., 2001. Acclimatization of soil respiration to warming in a tall grass prairie. Nature 413, 622–625. doi:10.1038/35098065

Mäkiranta, P., Laiho, R., Fritze, H., Hytönen, J., Laine, J., Minkkinen, K., 2009. Indirect regulation of heterotrophic peat soil respiration by water level via microbial community structure and temperature sensitivity. Soil Biology and Biochemistry 41, 695–703. doi:10.1016/j.soilbio.2009.01.004

Maljanen, M., Liikanen, A., Silvola, J., Martikainen, P.J., 2003. Nitrous oxide emissions from boreal organic soil under different land-use. Soil Biology and Biochemistry 35, 689–700. doi:Doi: 10.1016/s0038-0717(03)00085-3

Marco, A.D., Meola, A., Maisto, G., Giordano, M., Santo, A.V.D., 2011. Non-additive effects of litter mixtures on decomposition of leaf litters in a Mediterranean maquis. Plant Soil 344, 305–317. doi:10.1007/s11104-011-0748-4

Marinier, M., 2004. The role of cotton-grass (Eriophorum vaginatum) in the exchange of CO2 and CH4 at two restored peatlands, eastern Canada. Ecoscience 11, 141.

McGuire, K.L., Bent, E., Borneman, J., Majumder, A., Allison, S.D., Treseder, K.K., 2010. Functional diversity in resource use by fungi. Ecology 91, 2324–2332. doi:10.1890/09-0654.1

McKenzie, C., Schiff, S., Aravena, R., Kelly, C., Louis, V.S., 1998. Effect of temperature on production of CH4 and CO2 from Peat in a Natural and Flooded Boreal Forest Wetland. Climatic Change 40, 247–266. doi:10.1023/A:1005416903368

McNamara, N.P., Plant, T., Oakley, S., Ward, S., Wood, C., Ostle, N., 2008. Gully hotspot contribution to landscape methane (CH4) and carbon dioxide (CO2) fluxes in a northern peatland. Science of the Total Environment 404, 354–360. doi:10.1016/j.scitotenv.2008.03.015

McTiernan, K.B., Ineson, P., Coward, P.A., 1997. Respiration and Nutrient Release from Tree Leaf Litter Mixtures. Oikos 78, 527. doi:10.2307/3545614

Mikan, C.J., Schimel, J.P., Doyle, A.P., 2002. Temperature controls of microbial respiration in arctic tundra soils above and below freezing. Soil Biology and Biochemistry 34, 1785–1795. doi:10.1016/S0038-0717(02)00168-2

Millenium Ecosystem Assessment, 2005. Ecosystems and Human Well-being: Synthesis. Washington, DC.

Mitchell, R.J., Hester, A.J., Campbell, C.D., Chapman, S.J., Cameron, C.M., Hewison, R.L., Potts, J.M., 2010. Is vegetation composition or soil chemistry the best predictor of the soil microbial community? Plant Soil 333, 417–430. doi:10.1007/s11104-010-0357-7

Montané, F., Romanyà, J., Rovira, P., Casals, P., 2013. Mixtures with grass litter may hasten shrub litter decomposition after shrub encroachment into mountain grasslands. Plant Soil 368, 459–469. doi:10.1007/s11104-012-1533-8

Moore, T., Basiliko, N., Wieder, R.K., Vitt, D.H., 2006. Decomposition in Boreal Peatlands Boreal Peatland Ecosystems, in: Caldwell, M.M., Heldmaier, G., Jackson, R.B., Lange, O.L., Mooney, H.A., Schulze, E.D., Sommer, U. (Eds.), Ecological Studies. Springer Berlin Heidelberg, pp. 125–143.

Moore, T., Bubier, J., Bledzki, L., 2007. Litter Decomposition in Temperate Peatland Ecosystems: The Effect of Substrate and Site. Ecosystems 10, 949–963. doi:10.1007/s10021-007-9064-5

Moore, T.R., 2007. Litter decomposition in temperate peatland ecosystems: the effect of substrate and site. Ecosystems 10.

Moore, T.R., Bubier, J.L., Bledzki, L., 2007. Litter Decomposition in Temperate Peatland Ecosystems: The Effect of Substrate and Site. Ecosystems 10, 949–963. doi:10.1007/s10021-007-9064-5

Moore, T.R., Dalva, M., 1993. The influence of temperature and water table position on carbon dioxide and methane emissions from laboratory columns of peatland soils. European Journal of Soil Science 44, 651–664. doi:10.1111/j.1365-2389.1993.tb02330.x

Moore, T.R., Dalva, M., 1997. Methane and carbon dioxide exchange potentials of peat soils in aerobic and anaerobic laboratory incubations. Soil Biology and Biochemistry 29, 1157–1164. doi:Doi: 10.1016/s0038-0717(97)00037-0

Moore, T.R., Dalva, M., 2001. Some controls on the release of dissolved organic carbon by plant tissues and soils. Soil science 166, 38–47.

Moore, T.R., Knowles, R., 1989. The influence of water table levels on methane and carbon dioxide emissions from peatland soils. Canadian Journal of Soil Science 69, 33–38. doi:10.4141/cjss89-004

Myers, B., Webster, K., McLaughlin, J., Basiliko, N., 2012. Microbial activity across a boreal peatland nutrient gradient: the role of fungi and bacteria. Wetlands Ecology and Management 20, 77–88. doi:10.1007/s11273-011-9242-2

Nayak, D., Miller, D., Nolan, A., Smith, P., Smith, J., 2010. Calculating carbon budgets of wind farms on Scottish peatlands. Mires and Peat 4.

Nieminen, M., 2004. Export of dissolved organic carbon, nitrogen and phosphorus following clear-cutting of three Norway spruce forest growing on drained peatlands in southern Finland.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, H., 2006. Vegan: community ecology package.

Opelt, K., Berg, C., Schönmann, S., Eberl, L., Berg, G., 2007. High specificity but contrasting biodiversity of Sphagnum-associated bacterial and plant communities in bog ecosystems independent of the geographical region. ISME J 1, 502–516. doi:10.1038/ismej.2007.58

Orwin, K.H., Wardle, D.A., Greenfield, L.G., 2006. Ecological consequences of carbon substrate identity and diversity in a laboratory study. Ecology 87, 580–593. doi:10.1890/05-0383

Osanai, Y., Flittner, A., Janes, J.K., Theobald, P., Pendall, E., Newton, P.C.D., Hovenden, M.J., 2012. Decomposition and nitrogen transformation rates in a temperate grassland vary among co-occurring plant species. Plant Soil 350, 365–378. doi:10.1007/s11104-011-0920-x

Osono, T., Hagiwara, Y., Masuya, H., 2011. Effects of temperature and litter type on fungal growth and decomposition of leaf litter. Mycoscience 52, 327–332. doi:10.1007/s10267-011-0112-9

Ostle, N.J., Levy, P.E., Evans, C.D., Smith, P., 2009. UK land use and soil carbon sequestration. Land Use Policy 26, S274–S283. doi:10.1016/j.landusepol.2009.08.006

Pastor, J., Peckham, B., Bridgham, S., Weltzin, J., Chen, J., 2002. Plant Community Dynamics, Nutrient Cycling, and Alternative Stable Equilibria in Peatlands. The American Naturalist 160, 553–568.

Pendall, E., Rustad, L., Schimel, J., 2008. Towards a predictive understanding of belowground process responses to climate change: have we moved any closer? Functional Ecology 22, 937–940. doi:10.1111/j.1365-2435.2008.01506.x

Peng, S., Piao, S., Ciais, P., Myneni, R.B., Chen, A., Chevallier, F., Dolman, A.J., Janssens, I.A., Peñuelas, J., Zhang, G., Vicca, S., Wan, S., Wang, S., Zeng, H., 2013. Asymmetric effects of daytime and night-time warming on Northern Hemisphere vegetation. Nature 501, 88–92. doi:10.1038/nature12434

Perez, G., Aubert, M., Decaëns, T., Trap, J., Chauvat, M., 2013. Home-Field Advantage: A matter of interaction between litter biochemistry and decomposer biota. Soil Biology and Biochemistry 67, 245–254. doi:10.1016/j.soilbio.2013.09.004

Pérez-Harguindeguy, N., Díaz, S., Cornelissen, J.H.C., Vendramini, F., Cabido, M., Castellanos, A., 2000. Chemistry and toughness predict leaf litter decomposition rates over a wide spectrum of functional types and taxa in central Argentina. Plant and Soil 218, 21–30. doi:10.1023/A:1014981715532

Pietikåinen, J., Pettersson, M., Bååth, E., 2005. Comparison of temperature effects on soil respiration and bacterial and fungal growth rates. FEMS Microbiology Ecology 52, 49–58. doi:10.1016/j.femsec.2004.10.002

Pinheiro, J., Bates, D., DebRoy, S., Sarker, D., 2011. R Development Core Team (2011) nlme: linear and nonlinear mixed effects models. R package version 3.1–98., in: R Foundation for Statistical Computing. Vienna.

Potter, C.., Randerson, J.R., Field, C.., Matson, P.., Vitousek, P.., Mooney, H.., Klooster, S.., 1993. Terrestrial ecosystem production-aprocess model based on global satellite and surfce data. Global Biogeochemical Cycles 7, 811–841.

Pregitzer, K.S., Zak, D.R., Zogg, G.P., Ringelberg, D.B., MacDonald, N.W., White, D.C., 1997. Compositional and Functional Shifts in Microbial Communities Due to Soil Warming. Soil Science Society of America Journal 61, 475–481. doi:10.2136/sssaj1997.03615995006100020015x

Prescott, C.E., 2005. Do rates of litter decomposition tell us anything we really need to know? Forest Ecology and Management 220, 66–74. doi:10.1016/j.foreco.2005.08.005

Prescott, C.E., Vesterdal, L., Preston, C.M., Simard, S.W., 2004. Influence of initial chemistry on decomposition of foliar litter in contrasting forest types in British Columbia. Can. J. For. Res. 34, 1714–1729. doi:10.1139/x04-040

Price, J.S., Heathwaite, A.L., Baird, A.J., 2003. Hydrological processes in abandoned and restored peatlands: An overview of management approaches. Wetlands Ecology and Management 11, 65–83. doi:10.1023/A:1022046409485

Quested, H.M., Cornelissen, J.H.C., Press, M.C., Callaghan, T.V., Aerts, R., Trosien, F., Riemann, P., Gwynn-Jones, D., Kondratchuk, A., Jonasson, S.E., 2003. Decomposition of sub-arctic plants with differing nitrogen economies: a functional role for hemiparasites. Ecology 84, 3209–3221. doi:10.1890/02-0426

Ranneklev, S.B., Bååth, E., 2001. Temperature-Driven Adaptation of the Bacterial Community in Peat Measured by Using Thymidine and Leucine Incorporation. Appl. Environ. Microbiol. 67, 1116–1122. doi:10.1128/AEM.67.3.1116-1122.2001

Read, D.J., Leake, J.R., Perez-Moreno, J., 2004. Mycorrhizal fungi as drivers of ecosystem processes in heathland and boreal forest biomes. Canadian Journal of Botany 82.

REN21, 2012. Renewables 2012 Global Status Report. REN21 Secretariat, Paris, France.

Rey, A., Jarvis, P., 2006. Modelling the effect of temperature on carbon mineralization rates across a network of European forest sites (FORCAST). Global Change Biology 12, 1894–1908. doi:10.1111/j.1365-2486.2006.01230.x

Riutta, T., Laine, J., Aurela, M., Rinne, J., Vesala, T., Laurila, T., Haapanala, S., Pihlatie, M., Tuittila, E.-S., 2007. Spatial variation in plant community functions regulates carbon gas dynamics in a boreal fen ecosystem. Tellus B 59, 838–852. doi:10.1111/j.1600-0889.2007.00302.x

Riutta, T., Laine, J., Tuittila, E.S., 2007. Sensitivity of CO2 Exchange of Fen Ecosystem Components to Water Level Variation. Ecosystems 10, 718–733. doi:10.1007/s10021-007-9046-7

Robroek, B.J.M., Smart, R.P., Holden, J., 2010. Sensitivity of blanket peat vegetation and hydrochemistry to local disturbances. Science of The Total Environment 408, 5028–5034. doi:10.1016/j.scitotenv.2010.07.027

Rodwell, J.S., 1998. British Plant Communities: Mires and heaths. Cambridge University Press, Cambridge.

Rousk, J., Bååth, E., 2007. Fungal biomass production and turnover in soil estimated using the acetate-in-ergosterol technique. Soil Biology and Biochemistry 39, 2173–2177. doi:10.1016/j.soilbio.2007.03.023

Rydin, H., Jeglum, J., Hooijer, A., 2006. The biology of peatlands. Oxford University Press.

Scanlon, D., Moore, T., 2000. Carbon Dioxide Production From Peatland Soil Profiles: the Influence of Temperature, Oxic/Anoxic Conditions and Substrate. Soil Science 165, 153–160.

Schadt, C.W., Martin, A.P., Lipson, D.A., Schmidt, S.K., 2003. Seasonal Dynamics of Previously Unknown Fungal Lineages in Tundra Soils. Science 301, 1359–1361. doi:10.1126/science.1086940

Scheffer, R.A., Van Logtestijn, R.S.P., Verhoeven, J.T.A., 2001. Decomposition of Carex and Sphagnum litter in two mesotrophic fens differing in dominant plant species. Oikos 92, 44–54. doi:10.1034/j.1600-0706.2001.920106.x

Schmidt, S.K., Costello, E.K., Nemergut, D.R., Cleveland, C.C., Reed, S.C., Weintraub, M.N., Meyer, A.F., Martin, A.M., 2007. Biogeochemical Consequences of Rapid Microbial Turnover and Seasonal Succession in Soil. Ecology 88, 1379–1385. doi:10.2307/27651245

Shaw, A., Goffinet, B., 2000. Bryophyte Biology. Cambridge University Press.

Silvola, J., Alm, J., Ahlholm, U., Nykanen, H., Martikainen, P.J., 1996. CO2 fluxes from peat in boreal mires under varying temperature and moisture conditions. Journal of Ecology 84, 219–228.

Sirin, A., Laine, J., 2008. Peatlands and greenhouse gases., in: Assesment on Peatlands, Biodiversity and Climate Change. pp. 118–138.

Sitch, S., Smith, B., Prentice, I.., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J.., 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. Global Change Biology 9, 161–185.

Six, J., Frey, S.D., Thiet, R.K., Batten, K.M., 2006. Bacterial and Fungal Contributions to Carbon Sequestration in Agroecosystems. Soil Science Society of America Journal 70, 555. doi:10.2136/sssaj2004.0347

Smith, J., Nayak, D.R., Smith, P., 2012. Renewable energy: Avoid constructing wind farms on peat. Nature 489, 33–33. doi:10.1038/489033d

Smith, J., Nayak, D.R., Smith, P., 2014. Wind farms on undegraded peatlands are unlikely to reduce future carbon emissions. Energy Policy 66, 585–591. doi:10.1016/j.enpol.2013.10.066

Smith, S.E., Read, D.J., 2010. Mycorrhizal Symbiosis. Academic Press.

St. John, M.G., Orwin, K.H., Dickie, I.A., 2011. No “home” versus “away” effects of decomposition found in a grassland–forest reciprocal litter transplant study. Soil Biology and Biochemistry 43, 1482–1489. doi:10.1016/j.soilbio.2011.03.022

Strack, M., Waddington, J.M., Tuittila, E.-S., 2004. Effect of water table drawdown on northern peatland methane dynamics : Implications for climate change. Global biogeochemical cycles 18, GB4003.1–GB4003.7.

Strack, M., Waddington, J.M., Turetsky, M., Roulet, N.T., Byrne, K.A., 2008. Northern peatlands, greenhouse gas exchnage and climate change, in: Peatlands and Climate Change. p. 44.

Strakova, P., Niemi, R.M., Freeman, C., Peltoniemi, K., Toberman, H., Heiskanen, I., Fritze, H., Laiho, R., 2011. Litter type affects the activity of aerobic decomposers in a boreal peatland more than site nutrient and water table regimes. Biogeosciences 8, 2741–2755. doi:10.5194/bg-8-2741-2011

Strickland, M.S., Osburn, E., Lauber, C., Fierer, N., Bradford, M.A., 2009. Litter quality is in the eye of the beholder: initial decomposition rates as a function of inoculum characteristics. Functional Ecology 23, 627–636. doi:10.1111/j.1365-2435.2008.01515.x

Ström, L., Mastepanov, M., Christensen, T.R., 2005. Species-specific Effects of Vascular Plants on Carbon Turnover and Methane Emissions from Wetlands. Biogeochemistry 75, 65–82. doi:10.1007/s10533-004-6124-1

Ström, L., Tagesson, T., Mastepanov, M., Christensen, T.R., 2012. Presence of Eriophorum scheuchzeri enhances substrate availability and methane emission in an Arctic wetland. Soil Biology and Biochemistry 45, 61–70. doi:10.1016/j.soilbio.2011.09.005

Sulman, B.N., Desai, A.R., Mladenoff, D.J., 2013. Modeling Soil and Biomass Carbon Responses to Declining Water Table in a Wetland-Rich Landscape. Ecosystems 16, 491–507. doi:10.1007/s10021-012-9624-1

Sundh, I., Nilsson, M., Borga, P., 1997. Variation in microbial community structure in two boreal peatlands as determined by analysis of phospholipid fatty acid profiles. Applied and Environmental Microbiology 63, 1476–1482.

Swift, M.J., Heal, O.W., Anderson, J.M., 1979. Decomp Terres Ecosystems -. University of California Press.

Szumigalski, A.R., Bayley, S.E., 1996. Decomposition along a bog to rich fen gradient in central Alberta, Canada. Can. J. Bot. 74, 573–581. doi:10.1139/b96-073

Talbot, J.M., Allison, S.D., Treseder, K.K., 2008. Decomposers in disguise: mycorrhizal fungi as regulators of soil C dynamics in ecosystems under global change. Functional Ecology 22, 955–963. doi:10.1111/j.1365-2435.2008.01402.x

Thormann, M.N., 2006. Diversity and function of fungi in peatlands: A carbon cycling perspective. Canadian Journal of Soil Science 86, 281–293.

Treseder, K.K., Kivlin, S.N., Hawkes, C.V., 2011. Evolutionary trade-offs among decomposers determine responses to nitrogen enrichment. Ecology Letters 14, 933–938. doi:10.1111/j.1461-0248.2011.01650.x

Trinder, C., Johnson, D., Artz, R., 2009. Litter type, but not plant cover, regulates initial litter decomposition and fungal community structure in a recolonising cutover peatland. Soil Biology & Biochemistry 41, 651–655.

Turetsky, M.R., 2003. The role of bryophytes in carbon and nitrogen cycling. Bryologist 106, 395–409.

Turetsky, M.R., Treat, C.C., Waldrop, M.P., Waddington, J.M., Harden, J.W., McGuire, A.D., 2008. Short-term response of methane fluxes and methanogen activity to water table and soil warming manipulations in an Alaskan peatland. J. Geophys. Res. 113, G00A10. doi:10.1029/2007jg000496

Turetsky, M., Wieder, K., Halsey, L., Vitt, D., 2002. Current disturbance and the diminishing peatland carbon sink. Geophysical Research Letters 29. doi:1526 10.1029/2001gl014000

Vaieretti, M.V., Harguindeguy, N.P., Gurvich, D.E., Cingolani, A.M., Cabido, M., 2005. Decomposition Dynamics and Physico-chemical Leaf Quality of Abundant Species in a Montane Woodland in Central Argentina. Plant Soil 278, 223–234. doi:10.1007/s11104-005-8432-1

Van Breemen, N., 1995. How Sphagnum bogs down other plants. Trends in Ecology & Evolution 10, 270–275. doi:10.1016/0169-5347(95)90007-1

Van Der Heijden, M.G.A., 1988. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Geological Society of America Bulletin 100.

Van Meeteren, M.J.M., Tietema, A., van Loon, E.E., Verstraten, J.M., 2008. Microbial dynamics and litter decomposition under a changed climate in a Dutch heathland. Applied Soil Ecology 38, 119–127. doi:10.1016/j.apsoil.2007.09.006

Van Soest, P.J., 1994. Nutritional Ecology of the Ruminant. Cornell University Press.

Van Soest, P.J., Wine, R.H., 1967. Use of detergents in the analysis of fibrous feeds. IV. Determination of plant cell-wall constituents. JAOAC 50, 50–55.

Verhoeven, J.T.A., Toth, E., 1995. Decomposition of Carex and Sphagnum litter in fens: Effect of litter quality and inhibition by living tissue homogenates. Soil Biology and Biochemistry 27, 271–275. doi:10.1016/0038-0717(94)00183-2

Vivanco, L., Austin, A.T., 2008. Tree species identity alters forest litter decomposition through long-term plant and soil interactions in Patagonia, Argentina. Journal of Ecology 96, 727–736. doi:10.1111/j.1365-2745.2008.01393.x

Vivanco, L., Austin, A.T., 2011. Nitrogen addition stimulates forest litter decomposition and disrupts species interactions in Patagonia, Argentina. Global Change Biology 17, 1963–1974. doi:10.1111/j.1365-2486.2010.02344.x

Waddington, J.M., Rotenberg, P.A., Warren, F.J., 2001. Peat CO2 production in a natural and cutover peatland: Implications for restoration. Biogeochemistry 54, 115–130. doi:10.1023/A:1010617207537

Waddington, J.M., Roulet, N.T., 2000. Carbon balance of a boreal patterned peatland. Global Change Biology 6, 87–97. doi:10.1046/j.1365-2486.2000.00283.x

Waddington, J.M., Roulet, N.T., Swanson, R.V., 1996. Water table control of CH4 emission enhancement by vascular plants in boreal peatlands. Journal of Geophysical Research: Atmospheres 101, 22775–22785. doi:10.1029/96JD02014

Waldron, S., Flowers, H., Arlaud, C., Bryant, C., Mcfarlane, S., 2009. The significance of organic carbon and nutrient export from peatland-dominated landscapes subject to disturbance, a stoichiometric perspective. Biogeosciences 6, 363–374. doi:10.5194/bg-6-363-2009

Walker, M.D., Wahren, C.H., Hollister, R.D., Henry, G.H.R., Ahlquist, L.E., Alatalo, J.M., Bret-Harte, M.S., Calef, M.P., Callaghan, T.V., Carroll, A.B., Epstein, H.E., Jónsdóttir, I.S., Klein, J.A., Magnússon, B., Molau, U., Oberbauer, S.F., Rewa, S.P., Robinson, C.H., Shaver, G.R., Suding, K.N., Thompson, C.C., Tolvanen, A., Totland, Ø., Turner, P.L., Tweedie, C.E., Webber, P.J., Wookey, P.A., 2006. Plant community responses to experimental warming across the tundra biome. PNAS 103, 1342–1346. doi:10.1073/pnas.0503198103

Wallenstein, M.D., McMahon, S., Schimel, J., 2007. Bacterial and fungal community structure in Arctic tundra tussock and shrub soils. FEMS Microbiology Ecology 59, 428–435. doi:10.1111/j.1574-6941.2006.00260.x

Wang, Y., Chang, S.X., Fang, S., Tian, Y., 2014. Contrasting decomposition rates and nutrient release patterns in mixed vs singular species litter in agroforestry systems. J Soils Sediments 1–11. doi:10.1007/s11368-014-0853-0

Wardle, D.A., 2002. Communities and Ecosystems: Linking the Aboveground and Belowground Components. Princeton University Press, Princeton NJ.

Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setala, H., van der Putten, W.H., Wall, D.H., 2004. Ecological Linkages Between Aboveground and Belowground Biota. Science 304, 1629–1633. doi:10.1126/science.1094875

Wardle, D.A., Bonner, K.I., Nicholson, K.S., 1997. Biodiversity and Plant Litter: Experimental Evidence Which Does Not Support the View That Enhanced Species Richness Improves Ecosystem Function. Oikos 79, 247. doi:10.2307/3546010

Wardle, D.A., Nilsson, M.-C., Zackrisson, O., Gallet, C., 2003. Determinants of litter mixing effects in a Swedish boreal forest. Soil Biology and Biochemistry 35, 827–835. doi:10.1016/S0038-0717(03)00118-4

Wardle, D.A., Yeates, G.W., Barker, G.M., Bonner, K.I., 2006. The influence of plant litter diversity on decomposer abundance and diversity. Soil Biology and Biochemistry 38, 1052–1062. doi:10.1016/j.soilbio.2005.09.003

Wardle, D.A., Zackrisson, O., 2005. Effects of species and functional group loss on island ecosystem properties. Nature 435, 806–810. doi:10.1038/nature03611

Ward, S., Bardgett, R., McNamara, N., Adamson, J., Ostle, N., 2007. Long-Term Consequences of Grazing and Burning on Northern Peatland Carbon Dynamics. Ecosystems 10, 1069–1083. doi:10.1007/s10021-007-9080-5

Ward, S.E., Bardgett, R.D., McNamara, N.P., Ostle, N.J., 2009. Plant functional group identity influences short-term peatland ecosystem carbon flux: evidence from a plant removal experiment. Functional Ecology 23, 454–462. doi:10.1111/j.1365-2435.2008.01521.x

Ward, S.E., Ostle, N.J., Oakley, S., Quirk, H., Henrys, P.A., Bardgett, R.D., 2013. Warming effects on greenhouse gas fluxes in peatlands are modulated by vegetation composition. Ecology Letters n/a–n/a. doi:10.1111/ele.12167

Ward, S.E., Ostle, N.J., Oakley, S., Quirk, H., Stott, A., Henrys, P.A., Scott, W.A., Bardgett, R.D., 2012. Fire Accelerates Assimilation and Transfer of Photosynthetic Carbon from Plants to Soil Microbes in a Northern Peatland. Ecosystems 15, 1245–1257. doi:10.1007/s10021-012-9581-8

Ward, S., Ostle, N., McNamara, N., Bardgett, R., 2010. Litter evenness influences short-term peatland decomposition processes. Oecologia 164, 511–520. doi:10.1007/s00442-010-1636-y

Waring, B.G., Averill, C., Hawkes, C.V., 2013. Differences in fungal and bacterial physiology alter soil carbon and nitrogen cycling: insights from meta-analysis and theoretical models. Ecology Letters 16, 887–894. doi:10.1111/ele.12125

Weltzin, J.F., Bridgham, S.D., Pastor, J., Chen, J., Harth, C., 2003. Potential effects of warming and drying on peatland plant community composition. Global Change Biology 9, 141–151. doi:10.1046/j.1365-2486.2003.00571.x

Weltzin, J.F., Harth, C., Bridgham, S.D., Pastor, J., Vonderharr, M., 2001. Production and microtopography of bog bryophytes: response to warming and water-table manipulations. Oecologia 128, 557–565. doi:10.1007/s004420100691

Weltzin, J.F., Pastor, J., Harth, C., Bridgham, S.D., Updegraff, K., Chapin, C.T., 2000. Response of bog and fen plant communities to warming and water-table manipulations. Ecology 81, 3464–3478.

White, D.C., Davis, W.M., Nickels, J.S., King, J.D., Bobbie, R.J., 1979. Determination of the sedimentary microbial biomass by extractible lipid phosphate. Oecologia 40, 51–62. doi:10.1007/BF00388810

White, J.R., Shannon, R.D., Weltzin, J.F., Pastor, J., Bridgham, S.D., 2008. Effects of soil warming and drying on methane cycling in a northern peatland mesocosm study. Journal of Geophysical Research: Biogeosciences 113, n/a–n/a. doi:10.1029/2007JG000609

Whiting, G.J., Chanton, J.P., 1993. Primary production control of methane emission from wetlands. Nature 364, 794–795. doi:10.1038/364794a0

Wieder, R., Vitt, D., 2006. Boreal peatland ecosystems. Springer.

Williams, R.T., Crawford, R.L., 1984. Methane Production in Minnesota Peatlands. Appl. Environ. Microbiol. 47, 1266–1271.

Winsborough, C., Basiliko, N., 2010. Fungal and Bacterial Activity in Northern Peatlands. Geomicrobiology Journal 27, 315–320. doi:10.1080/01490450903424432

Worrall, F., Burt, T., Adamson, J., 2004. Can climate change explain increases in DOC flux from upland peat catchments? Science of the Total Environment 326, 95–112. doi:10.1016/j.scitotenv.2003.11.022

Wynn-Williams, D.D., 1982. Simulation of seasonal changes in microbial activity of maritime antarctic peat. Soil Biology and Biochemistry 14, 1–12. doi:10.1016/0038-0717(82)90069-4

Yiqi, L., Zhou, X., 2010. Soil Respiration and the Environment. Academic Press.

Yuste, J.C., Baldocchi, D.D., Gershenson, A., Goldstein, A., Misson, L., Wong, S., 2007. Microbial soil respiration and its dependency on carbon inputs, soil temperature and moisture. Global Change Biology 13, 2018–2035. doi:10.1111/j.1365-2486.2007.01415.x

Yu, Z., Beilman, D.W., Frolking, S., MacDonald, G.M., Roulet, N.T., Camill, P., Charman, D.J., 2011. Peatlands and Their Role in the Global Carbon Cycle. Eos Trans. AGU 92, 97–98. doi:10.1029/2011EO120001

Zhou, J., Xue, K., Xie, J., Deng, Y., Wu, L., Cheng, X., Fei, S., Deng, S., He, Z., Van Nostrand, J.D., Luo, Y., 2012. Microbial mediation of carbon-cycle feedbacks to climate warming. Nature Clim. Change 2, 106–110. doi:10.1038/nclimate1331

Zhou, L., Tian, Y., Baidya Roy, S., Thorncroft, C., Bosart, L.F., Hu, Y., 2012. Impacts of wind farms on land surface temperature. Nature Clim. Change 2, 539–543.