Drought and fuel structure controls on fire severity. Effects on post-fire vegetation and soil carbon dynamics

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Abstract

Calluna-dominated habitats, including dry heaths and peat bogs, provide important ecosystem services such as biodiversity, soil carbon stores and water supply. Climate change projections estimate drier conditions throughout their range, which could lead to increased wildfire activity. Such altered fire regime could induce a fundamental change to the ecology of *Calluna* moorlands and increase carbon emissions from their carbon-rich soils. The aim of this research was to understand how ecosystem response varies in relation to increased fire severity in *Calluna* heathlands and peat bogs. I completed experimental fires at two sites in Scotland, a dry heath and a raised bog, where I manipulated pre-fire fuel structure and fuel moisture content to achieve a gradient of fire severity and investigated the subsequent effect on post-fire vegetation regeneration and soil carbon dynamics.

I found that drought increased fire severity in terms of ground fuel consumption and soil heating through increased flammability of the moss and litter layer. Substantially higher fire-induced ground heating was recorded when this layer ignited. When consumption of the moss and litter layer was extensive, post-fire soil thermal dynamics were altered and diurnal and seasonal thermal variation was higher, resulting in warmer soils that may lead to higher soil carbon emissions. Fire effects (ground fuel consumption, ground heating, changes in post-fire soil thermal dynamics) were much stronger at the dry heath than at the raised bog, likely due to ecohydrological differences between sites, i.e. thicker moss layer and deeper, wetter soil at the raised bog. For example, average fire-induced maximum temperatures at the soil surface

at the dry heath increased from 31 °C to 189 °C due to drought, but at the raised bog they increased from 10 °C to 15 °C.

Post-fire vegetation community composition varied in relation to the gradient of fire severity at the dry heath. Higher fire severity increased abundance of dominant ericoid species (*Calluna vulgaris*, *Erica cinerea* and *Erica tetralix*) through improved substrate conditions (consumption of the moss and litter layer leading to bare soil), despite the fact that higher fire-induced soil heating hindered their regeneration.

Short-term soil carbon emissions increased after burning due to a greater reduction in photosynthesis than in ecosystem respiration. Methane fluxes were negligible at the dry heath, but increased after burning at the raised bog, especially in warmer conditions. Generally, higher fire severity had little effect on soil carbon dynamics (ecosystem respiration, net ecosystem exhange, methane flux and dissolved organic carbon concentration), but higher autumn emission after higher fire severity at the dry heath and the important control of plant functional type cover suggest differences may become apparent in the longer term.

This research advances our understanding of how an altered fire regime with higher fire severity could alter ecosystem functioning in *Calluna* moorlands and impact on its conservation value and belowground carbon stores. The work presented here can be useful to managers using burning as a land management tool, or who need to plan for wildfire occurrence in these fire-prone habitats, to inform strategies to accomplish a range of objectives, including conservation, protection of carbon stores and recreation, and to researchers interested in environmental change in *Calluna* moorlands.

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Author's declaration

I declare that the work outlined and described in this thesis has been carried out by myself unless otherwise acknowledged. This thesis is completely my own composition and has not, in whole or part, been submitted for any other degree at this or any other university.

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Acknowledgements

I want to thank the University of Glasgow for the fantastic support I have received during these four years. I remember the moment I was told that I had been awarded the Lord Kelvin and Adam Smith Scholarship for doctoral study as one of the most joyful moments of my adult life. The cynical reader may jump to the wrong conclusion about my joy standards, but the truth is that I rightly recognised then the great opportunity for professional development that such a scholarship meant. It is easy to forget, as things get busy and we get into our little PhD bubble, how fortunate we are to have the opportunity to be doing exciting research, and I want to thank the University of Glasgow for making this possible.

I am very grateful to my supervisors Dr. Matt Davies, Prof. Susan Waldron, Dr. Alan Gray and Prof. Marian Scott for their help throughout this PhD. They have given me excellent guidance and support and, despite their busy schedules, have always been available and have made me feel like my work was a priority for them. I recognise this is not always the case for all PhD students and I think I have been extremely lucky with my supervisory team. Special thanks to Matt, whose experience in fire research was instrumental, particularly during the critical first half of the project when everything was to be decided and carried out. Matt provided great guidance on valuable research directions, and actively participated in most of the experimental fires that are the basis for this research, including igniting those at Braehead Moss. I want to thank Susan for her advice on the carbon work and for her great feedback on all my research output. She made me feel very welcome when

I moved to the School of Geographical and Earth Sciences, and has since then continued to do so by supporting my work in every possible way. Alan's expertise on carbon flux and vegetation survey allowed great progress on those difficult areas. Marian helped me navigate the confusing yet fascinating world of statistics. It is difficult to overstate how much I have learnt from all of them. Thank you very much.

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Figure 1: Alan and Julie during their fire-controlling duties at Brahead Moss.

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Chapter 1

Introduction

Under a changing climate, it is projected that changes in the seasonality of rainfall and warmer conditions in terrestrial ecosystems north of 45°N will result in increased frequency and/or severity of summer drought (Sheffield and Wood, 2008; IPCC, 2013; Dai, 2013; Cook et al., 2014) and greater wildfire activity (Krawchuk et al., 2009; de Groot et al., 2013). For example, mean summer temperature in the United Kingdom (UK) is estimated to increase by 2.5 °C, and rainfall to decrease by 16 % by 2050 (Murphy et al., 2009), which could lead to higher frequency of wildfires (Albertson et al., 2010). Changes to fire regimes (the frequency, seasonality, size and severity of fires; Pyne et al., 1996) could impact on ecosystem services such as water supply (Yallop and Clutterbuck, 2009; Holden et al., 2012), biodiversity (Davies and Legg, 2008; Sutherland et al., 2008; Pausas, 2015) and soil carbon stores (Kasischke and Turetsky, 2006; Ward et al., 2007; Davies et al., 2013), whilst putting increased strain on emergency services (Flannigan et al., 2009).

1.1 Carbon stores and conservation value of *Calluna* moorlands

There is particular concern over the potential effect of altered fire regimes on the carbon dynamics of northern (> 45°N) peatlands, which contain globally significant carbon stores (ca. 500 Pg C; Yu, 2012). Peatlands are defined as peat-covered terrain with a minimum peat depth, arbitrarily set by different authorities at 0.3 m (Joosten and Clarke, 2002) or 0.5 m (Jackson, 2000). Wildfires are one of the most important disturbances in northern peatlands (Turetsky et al., 2004), and higher wildfire activity could increase net carbon emissions through greater combustion of organic soil layers (Turetsky et al., 2002; Davies et al., 2013), increased post-fire peat erosion (Clay et al., 2015) and warmer soil leading to higher respiration (Freeman et al., 2001a; Zhuang et al., 2002). Furthermore, altered fire regimes may change the vegetation community composition, which has been shown to have a key role in regulating carbon exchange between the soil and the atmosphere (De Deyn et al., 2008). Plant traits characterising different plant functional types determine respiration and photosynthesis rates (Ward et al., 2013; Armstrong et al., 2015), methane production and transport (Gray et al., 2013), carbon inputs into the soil from root exudates (Artz, 2013), decomposability of litter (Bragazza et al., 2015) and soil microbial community (Bragazza et al., 2013). An altered fire regime resulting in higher net carbon emissions from peatlands could potentially contribute to a positive feedback mechanism with climate change, as higher atmospheric greenhouse gas concentrations could lead to warmer and drier conditions that further increase wildfire activity (Heimann and Reichstein, 2008; de Groot et al., 2013).

In the UK, almost half (ca. 2 Pg) of the belowground carbon stored up to 1 m deep is found in semi-natural habitats such as dry heathlands, peat bogs and semi-natural grasslands (Bradley et al., 2005; Ostle et al., 2009). These are habitats that have been strongly influenced by human disturbance, principally in the form of sheep grazing and managed burning for livestock and game, and drainage for increasing productivity and afforestation, but also due to acid and nutrient deposition from atmospheric pollution (Dodgshon and Olsson, 2006; Holden et al., 2007; Allen et al., 2016).

Among such semi-natural habitats *Calluna vulgaris* (L.) Hull (hereafter *Calluna*) moorlands are of particular interest given their internationally significant conservation importance (Thompson et al., 1995; Carboni et al., 2015). Typically found in north-west Europe, including Sweden, Norway, Denmark, the Netherlands, Italy and Spain, *Calluna* moorlands are perhaps best represented in the UK and Ireland (Gimingham, 1972; Thompson et al., 1995) (Figure 1.1). *Calluna* moorlands encompass a range of UK habitats, most importantly dry and wet heathlands on well-drained soils and *Calluna*-dominated blanket bogs in wetter conditions, when peat depth is > 0.5 m (Jackson, 2000). *Calluna* can also become dominant on raised bogs when these have been degraded by drainage. *Calluna* moorlands resulted from extensive human land-use since the Mesolithic (Simmons and Innes, 1987). Management activities have included forest clearances (from ca. 5000 BP; Innes et al., 2010) and, more recently, intensified grazing from cattle and sheep and burning to promote nutritious new growth for livestock and game (extensive from ca. 1750; Ratcliffe and Thompson, 1988; Dodgshon and Olsson, 2006).

1.2 Managed burning in *Calluna* moorlands

Anthropogenic fire played a significant role in the expansion and maintenance of *Calluna* moorlands (Dodgshon and Olsson, 2006). In the UK, burning was used to improve grazing for sheep and cattle, and remains a common practice increasingly associated with deer (*Cervus elaphus* L.) and especially red grouse (*Lagopus lagopus scoticus* Latham) management on sporting estates. *Calluna* productivity is increased, and a range of habitat structures provided, where burning is done using narrow (ca. 30 m) strips that create a mosaic of different stand-ages (Allen et al., 2016). Managed burning is regulated by Heather and Grass Burning Codes in England (DEFRA, 2007) and Wales (WAG, 2008) and by the Muirburn Code in Scotland (SEERAD, 2011a). These regulations generally allow burning between the 1st of October and the 15th of April (exact dates vary by country and elevation) to avoid dry conditions that make fire control difficult and increase wilfire risk, greater during spring

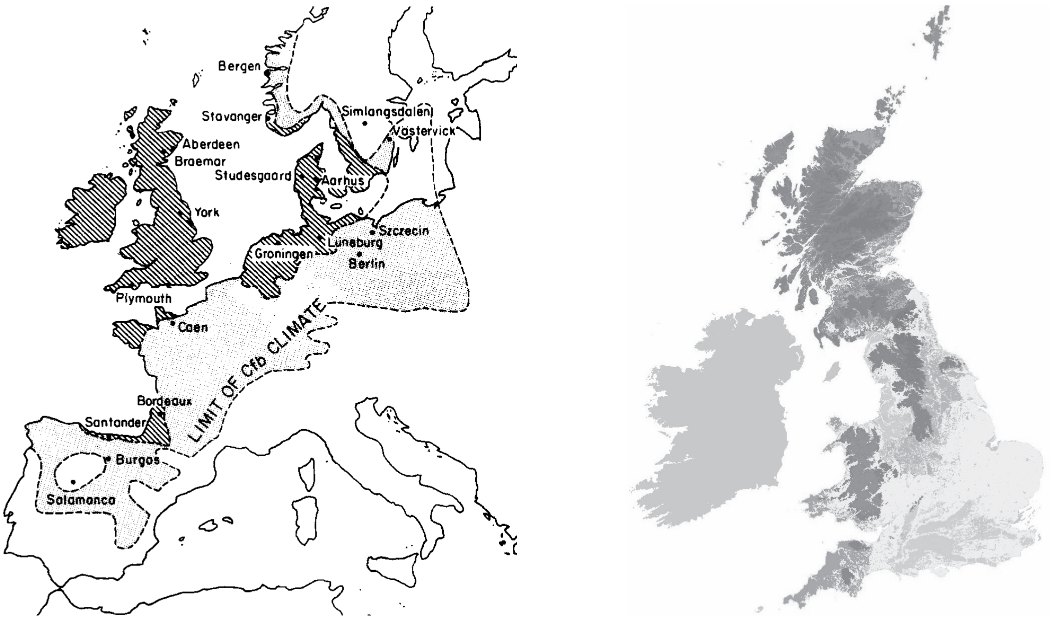

Figure 1.1: (left) Distribution of *Calluna* moorlands in Europe. Dotted line indicates limit of the oceanic type climatic zone. Figure from Gimingham (1972). (right) Distribution of dry heathlands in the UK estimated from the 1998 Countryside Survey by the Centre for Ecology and Hydrology. Darker colours represent increased heathland cover. Figure from Davies et al. (2008a).

and summer (Legg et al., 2007; Davies and Legg, 2016), and impacts on ground-nesting birds. Recommendations include burning using head fires to achieve lower flame residence thus limiting soil heating and damage to vegetation regeneration, avoid burning when weather conditions may lead to extreme fire behaviour (high wind speed, dry moss and litter) and when there is risk of soil erosion because of thin soils or steep hillsides (SEERAD, 2011b). Suggested rotation lengths vary between 8–25 years, depending on growth in specific environmental conditions. Research based on 2001–2010 aerial photographs reported occurrence of moorland managed fire scars up to 25 years old in 8551 1-km squares across mainland UK, with an average burn cover of 16.7 % (Douglas et al., 2015), resulting in 1428 km^2 burnt in the previous 25 years. This equals to 57.1 km^2 burnt each year, 0.42 % of total UK dwarf shrub cover (13600 km^2; Carey et al., 2008).

Positive effects of managed burning have been documented on heather moorland biodiversity (Thompson et al., 1995; Davies and Legg, 2008; Harris et al., 2011; Velle et al., 2014), *Sphagnum* abundance (Lee et al., 2013), and carbon stores through production of refractory forms of carbon (Worrall et al., 2013a) and reduced post-fire ecosystem respiration (Clay et al., 2015). However, managed burning has also been found to increase dissolved organic carbon production and alteration of aquatic ecosystems (Ramchunder et al., 2013), decrease carbon sequestration at low frequency (10-year) managed burning rotations (Garnett et al., 2000) and to induce loss of nutrients (Rosenburgh et al., 2013). Managed burning in peatlands is particularly controversial due to concerns over negative effects on peatland ecology, belowground carbon stores, hydrology and water quality (Bain et al., 2011; Brown et al., 2014). Misunderstanding of the complex effects of fire on peatlands (e.g. failing to recognise the lower severity of managed fires compared to wildfires), as well as negative attitudes towards the ethics of driven grouse shooting and land ownership associated with managed burning have also been pointed out as important contributors to such controversy (Davies et al., 2016b).

1.3 *Calluna* fuel structure in relation to fire behaviour

Calluna often forms dense, continuous stands with distinct fuel layers that affect fire behaviour differently (Gimingham, 1960). These fuel layers are comprised of an upper canopy with a high proportion of live vegetation, a lower canopy with a higher proportion of dead foliage, a lower layer of dead and live stems without foliage and finally a moss and litter (M/L) layer on top of a carbon-rich soil (Davies and Legg, 2011) (Figure 1.2). Where the M/L layer is particularly deep, a layer of partly decomposed moss, litter and fine roots (duff) may overlie the more well-humified soil.

The developmental stage of *Calluna* determines the structure and relative importance of the different fuel layers. A fine fuel canopy develops through the pioneer (nearly all live foliage) and building (when dead canopy begins to accumulate) phases, up to 15–20 years old. Below the canopy, a low density layer of stems and thin branches is created during the Mature phase (up to ca. 25 years; Gimingham, 1989; Davies et al., 2008b), when flammability increases due to improved aeration (Davies et al., 2009). Short-term variation in flammability in *Calluna* heathlands is largely controlled by the moisture content of the different fuel layers: dry dead fine fuels are key in facilitating initial prescribed fire establishment, while low moisture content of the live canopy, which represent most of the available fuel, leads to higher fire rate of spread (Davies et al., 2009; Davies and Legg, 2011). The moisture of the M/L layer is thought to have a minor importance on fire behaviour in established fires in dense *Calluna* heathlands as fire spreads through the canopy, resembling a crown fire (Fernandes et al., 2000; Davies et al., 2009). However, flammability of the M/L layer may facilitate fire establishment (Legg et al., 2007; Davies and Legg, 2016) and lead to increased ground heating (Davies et al., 2010b).

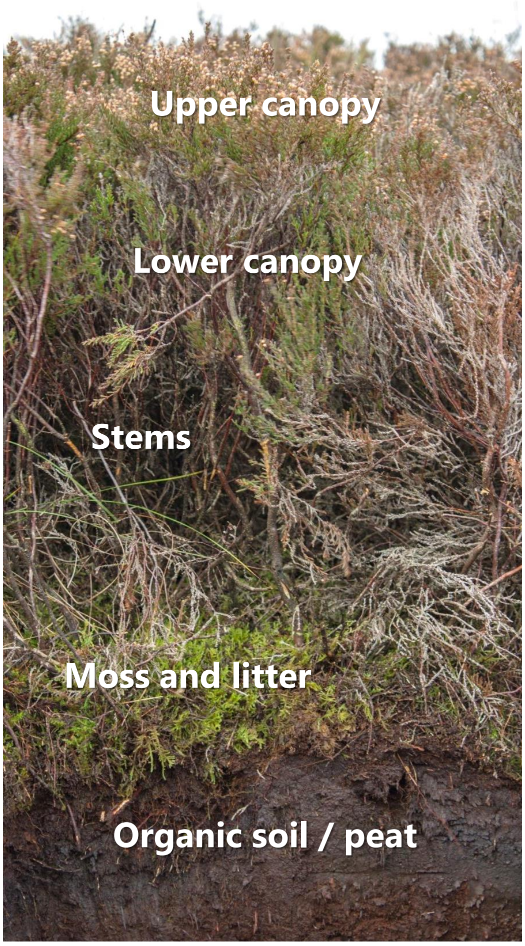

Figure 1.2: Fuel structure in a *Calluna*-dominated raised bog (Braehead Moss). This structure is more accentuated in mature vegetation but it is also representative of younger stands (Davies and Legg, 2011).

1.4 Drivers of change in *Calluna* moorlands

Currently, dwarf shrub heathlands cover 5.5 % of the UK (13600 km^2; 8940 km^2 in Scotland) and bogs, 9.7 % (23930 km^2; 20440 km^2 in Scotland) (Carey et al., 2008). Land use changes, mainly afforestation and increased grazing, as well as nutrient deposition and climatic change have resulted in an approximate 20 % decline in heather moorland cover during the 20th century (Thompson et al., 1995; Holden et al., 2007; van der Wal et al., 2011). Climate, pollution and grazing have also been linked to biotic homogenisation and decreases in the biodiversity value of *Calluna* moorlands (van der Wal et al., 2011; Britton et al., 2016). Prescribed burning can help maintain these cultural landscapes and have a positive effect on biodiversity (Vandvik et al., 2005; Harris et al., 2011) although outcomes depend on how management priorities are traded-off (Marshall et al., 2007; Kelemen et al., 2013; Gallo and Pejchar, 2016).

Superimposed on these drivers, an altered fire regime, caused by climatic and environmental change, could potentially impact on the ecology of *Calluna*-dominated heathlands and bogs by changing post-fire vegetation regeneration through mechanisms occurring during the fire itself and subsequently through altered post-fire environmental conditions. Fire mechanisms include thermal damage to plant structures (Schimmel and Granström, 1996; Neary et al., 1999) and germination cues related to temperature pulses (Whittaker and Gimingham, 1962) and chemicals from smoke and ash (Bargmann et al., 2014). Altered environmental conditions include substrate change due to consumption of the M/L layer during higher severity fires (Davies et al., 2010b, 2016a) and altered post-fire soil microclimate resulting from loss of vegetation (Mallik, 1986; Brown et al., 2015). Soil microclimate is also an important control on soil respiration and is essential in understanding soil carbon dynamics (Lloyd and Taylor, 1994; Kettridge et al., 2012; Walker et al., 2016). The effects of fire on soils range from release of nutrients at low fire severities (Haase and Sackett, 1998) to loss of nutrients and organic matter at higher fire severities (Neary et al., 1999), and the consumption of the peat layer in extreme cases (Rein et al., 2008; Davies et al., 2013).

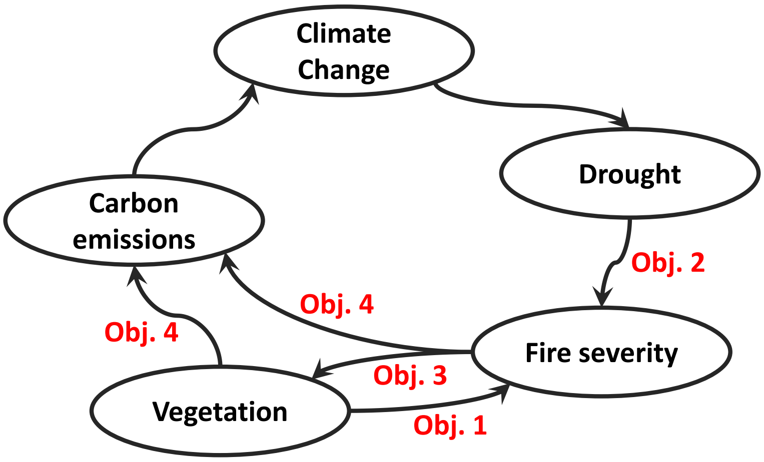

Figure 1.3: Climate change may increase drought occurrence and alter fire regimes in *Calluna* moorlands, possibly leading to higher severity fires (Objective 2 of this research). Such conditions could increase soil carbon emissions through higher combustion of below-ground carbon and higher net post-fire carbon emission (Objective 4). Higher fire severity could also alter post-fire vegetation community composition (Objective 3), thus resulting in further changes in carbon dynamics. Vegetation structure may in turn have an effect on fire severity (Objective 1). Potentially, larger belowground carbon loss from higher severity could contribute to a positive feedback with climate change.

1.5 Aims and objectives

The general aim of this research is to understand how fuel structure and moisture content control fire severity in UK *Calluna* moorlands and bogs, and to assess the ecological significance of these observed effects in terms of vegetation regeneration and soil carbon dynamics (Figure 1.3). The main objectives are:

1. **Quantify the role of fuel structure in driving variation in indicators of fire severity (e.g. soil heating)**. Fire severity may be a key control of post-fire vegetation regeneration and soil carbon dynamics. In particular, the importance of the M/L layer remains poorly understood despite previous research on fire-induced ground heating in relation to fuel characteristics in *Calluna* moorlands (Hobbs and Gimingham, 1984a; Hamilton, 2000; Davies et al., 2010b).

2. **Assess the effect of drought on altering flammability of *Calluna* fuels and on subsequent variation in fire severity**. No work to date has explicitly investigated fire behaviour in *Calluna* moorlands under drought conditions, important given the projected increase in summer drought occurrence in many regions, including the UK.

3. **Determine differences in post-fire vegetation community composition in response to variation in disturbance severity**. Higher severity wildfires in *Calluna* moorlands are likely under current climate projections, and so a better understanding of how vegetation might regenerate is important to assess potential ecological and carbon cycling changes. Research investigating heathland vegetation response to managed and wildfires (Hobbs and Legg, 1984; Legg et al., 1992; Davies et al., 2010b; Harris et al., 2011; Velle et al., 2012) has not been able to clearly separate the relative importance of direct fire effects (plant mortality, seed germination due to heating, smoke and ash) and indirect fire effects (changes in microclimate, removal of the M/L layer as seedbed) and so I aim to address this research gap.

4. **Quantify the effect of variation in fire severity on post-fire soil carbon dynamics**. Direct carbon losses due to fire have received considerable attention, particularly in peatlands given their substantial belowground carbon store (Turetsky et al., 2004; Davies et al., 2013; Turetsky et al., 2015). However, comparatively few studies have focused on altered post-fire soil carbon dynamics in *Calluna* moorlands (Ward et al., 2007; Clay et al., 2010, 2015) and none have studied post-fire carbon dynamics in relation to variation in fire severity.

Thesis structure

Chapters 3 to 6 are self-contained studies each with their own introduction, methods, results, discussion and conclusions sections. To avoid repetition, methods that were common to two or more studies are detailed in a general methods chapter (Chapter 2). There is no separate literature review chapter; instead, relevant research is presented and discussed in the introduction and discussion sections within each data chapter. Primary data generated throughout this project will be made publicly available following the policy for management of research data of the University of Glasgow. Table 1.1 describes the thesis structure.

This research advances our knowledge on the potential impacts of an altered fire regime in *Calluna*-dominated heathlands and peatlands. I identify and provide quantitative information on controlling mechanisms of fire behaviour, and analyse its effect on vegetation regeneration and soil carbon dynamics. The research may be of particular interest to managers using burning as a land management tool, or working on habitats prone to wildfire, and can inform strategies to accomplish a range of objectives, including conservation, protection of carbon stores and recreation.

Table 1.1: Structure of the thesis, detailing a description of each chapter, whether it was carried out in the dry heath site or both in the dry heath and raised bog sites, and the main objective it addresses.

Ch.	Chapter description	Sites	Obj.
2	This chapter provides detailed information on materials and methods relevant to more than one chapter, including experimental sites and data analysis techniques.		
3	I quantify the role of the moss and litter (M/L) layer in controlling fire-induced soil heating and post-fire soil thermal dynamics in a dry heath. Simulated variation in fire severity (i.e. regular managed fires where the M/L layer does not ignite and higher severity fires where the M/L layer is completely combusted) is accomplished by manually removing the M/L layer in some small-scale plots, either before or after the fire.	Dry heath	1
4	I examine the effect of higher severity fire (as simulated in the previous chapter) on vegetation regeneration. Here, I use a series of treatments combining manual removal of vegetation (cutting) and/or burning to identify the dominant mechanisms controlling regeneration across a range of disturbance severities. I investigate the relative importance of direct fire effects and altered post-fire environment in controlling community composition, as well as resprouting and seed germination in ericoid species, along a disturbance severity gradient.	Dry heath	3
5	This chapter studies the effect of simulated drought on fire intensity and fire severity, and subsequent changes in post-fire soil thermal dynamics. Work on a dry heath and a raised bog allows comparison of the effect of drought on fire effects in both ecosystems.	Dry heath & raised bog	2
6	I study the effect of a gradient of fire severity, as achieved in the previous chapter, on soil carbon dynamics (ecosystem respiration, net ecosystem exchange, methane flux and concentration of soil water dissolved organic carbon).	Dry heath & raised bog	4
7	Finally, Chapter 7 provides a synthesis of the work accomplished and considers management applications and future research directions.		

Chapter 2

Materials and methods

2.1 Sites

Calluna moorlands vary across a north-south latitudinal and altitudinal gradient, and an east-west oceanic gradient (Thompson et al., 1995). The most abundant communities are the *Calluna–Vaccinium myrtillus* heaths, on peaty podzols, typical of drier conditions, and the *Calluna–Eriophorum vaginatum* blanket bogs, on deep peat (> 0.5 m; Jackson, 2000). Research was completed on two different sites to capture the variation in *Calluna* moorland habitats. Both sites have a similar above-ground fuel structure, with a high cover (> 85 %) of generally mature *Calluna* and a bryophyte layer dominated by pleurocaropous mosses, but have contrasting edaphic characteristics: Glen Tanar is an upland dry heath with thin peaty podzols and Braehead Moss is a lowland raised bog with deep, saturated peat.

2.1.1 Glen Tanar

Two experiments (one described in Chapters 3 and 4 and the other in Chapters 5 and 6) were completed at Glen Tanar Estate, Aberdeenshire, Scotland (Figure 2.1). Both locations are dry heaths actively managed for red grouse with similar edaphic and vegetation characteristics. Soils are peaty podzols with a mean organic horizon depth of 9 cm. Weather records for 1994–2007 available from Aboyne weather station, 13 km east of the site, elevation 130 m, show a total annual rainfall of 837 mm, mean summer temperature of 13.8 °C and mean winter temperature of 3.1 °C (Met Office, 2012).

The experiment involving M/L layer manipulation (Chapters 3 and 4) was completed in a valley limited by the Red Craig, Black Craig and Cairn Nairvie mountains, north of the Water of Glen Tanar river (latitude 57.013°N, longitude 2.957°W, elevation of 330 m a.s.l., south location in Figure 2.2). The site where the drought experiment was completed was approximately 1 km north-west, at an elevation of 460 m (latitude 57.016°N, longitude 2.974°W, north location in Figure 2.2). The steeper slope at this site compared to Breahead Moss could have implications for soil moisture content in drought plots (Chapter 5) due to the topographic influence on overland and subsurface flow (Holden and Burt, 2003).

Vegetation is dominated by a dense and homogenous canopy of mature (*sensu* Gimingham, 1989) *Calluna*, with *Erica cinerea* L., *Vaccinium myrtillus* L., *Trichophorum cespitosum* (L.) Hartm. and *Carex* spp. also common. Beneath the *Calluna* canopy I found a discontinuous layer of pleurocarpous mosses (dominant species: *Hypnum jutlandicum* Holmen and Warncke, and *Pleurozium schreberi* (Brid.) Mitt.) which were replaced by layers of *Calluna* litter where stand canopies were particularly dense. The south location had frequent wet flushes dominated by *Molinia caerulea* (L.) Moench, *Eriophorum vaginatum* L. and *Sphagnum* spp. More recently-burnt areas included patches of building phase *Calluna* and areas dominated by *Nardus stricta* L. and *M. caerulea*.

2.1.2 Braehead Moss

Braehead Moss is a raised bog located to the north and east of the village of Braehead, in central Scotland (latitude 55.740°N, longitude 3.658°W), at an elevation of 270 m above sea level (Figure 2.3). 87 hectares of Braehead Moss were declared National Nature Reserve in 1981, and the whole bog was designated Site of Special Scientific Interest in 1997 and Special Area

Figure 2.1: Location of Glen Tanar (dry heath; Chapters 3 to 6) and Braehead Moss (raised bog; Chapters 5 and 6).

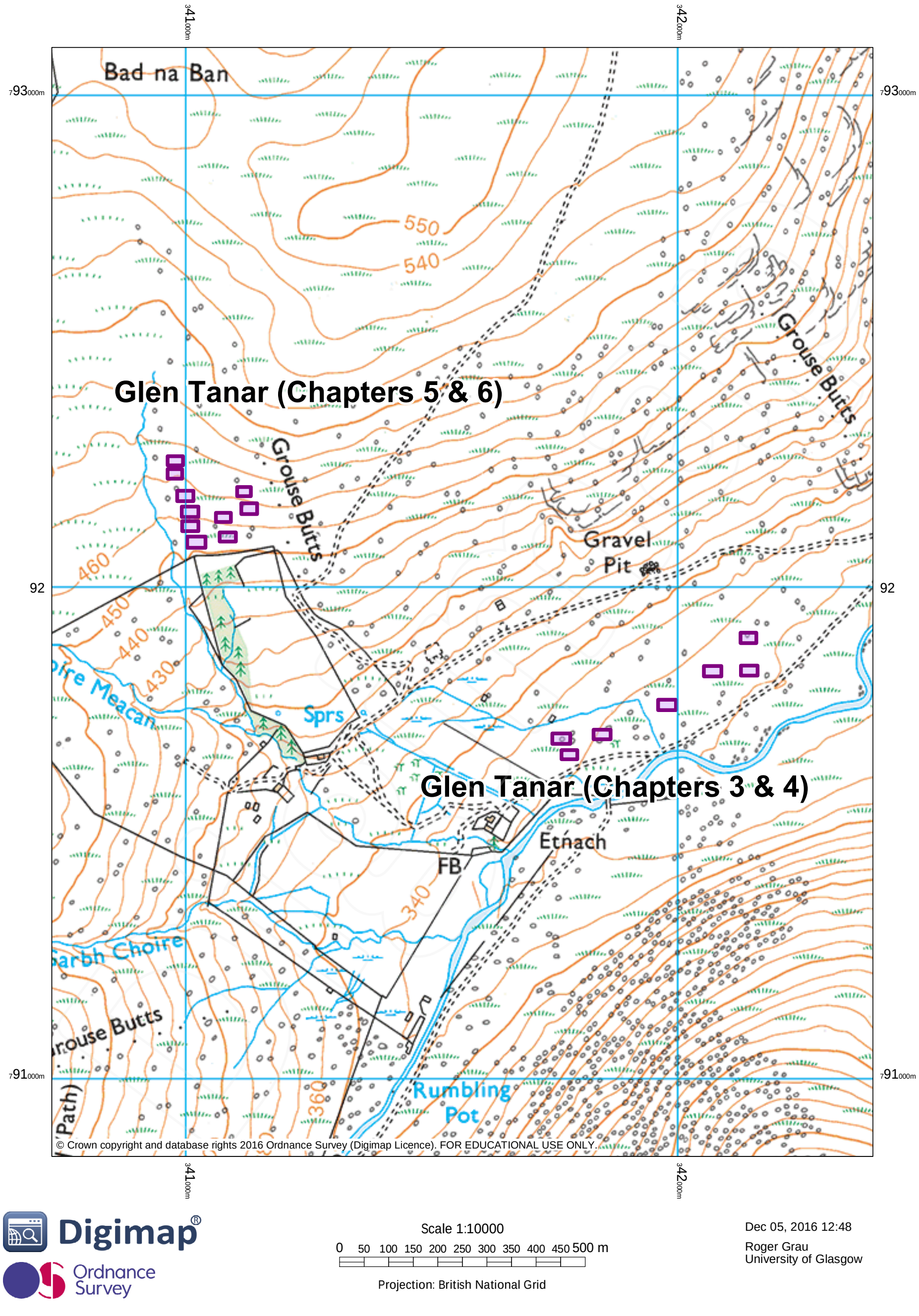

Figure 2.2: Locations of experimental fires in Glen Tanar. Polygons indicate approximate location and area of fires.

of Conservation in 2005 (SNH, 2012). Although a detailed management history of the bog prior to conservation was not available, it is known to have been subjected to low levels of livestock grazing, managed burning, as well as limited drainage and peat cutting. Recent management have included removal of birch scrub in 2001, fencing to prevent overgrazing in 2003 and managed burning to remove rank heather and encourage bog plants in 2010. 1981–2010 weather records from Drumalbin weather station, elevation 200 m, 13 km south of the site, show a total annual rainfall of 900 mm, a mean summer temperature of 13.2 °C and a mean winter temperature of 2.8 °C (Met Office, 2012).

I completed the experiments described in Chapters 5 and 6 in the southern section of the bog, where drier conditions allow a continuous *Calluna* cover. The vegetation community is characterised by a continuous stand of mature *Calluna* (*sensu* Gimingham, 1989) with frequent *Eriophorum vaginatum* L. and *Erica tetralix* L. The bryophyte layer is dominated by *Hypnum jutlandicum* Holmen & Warncke. *Sphagnum* mosses are frequent, especially *Sphagnum capillifolium* (Ehrh.) Hedw. Detailed peat depth information is not available but depth at the centre of the bog is > 9 m (Scottish Natural Heritage, personal communication, September 2016).

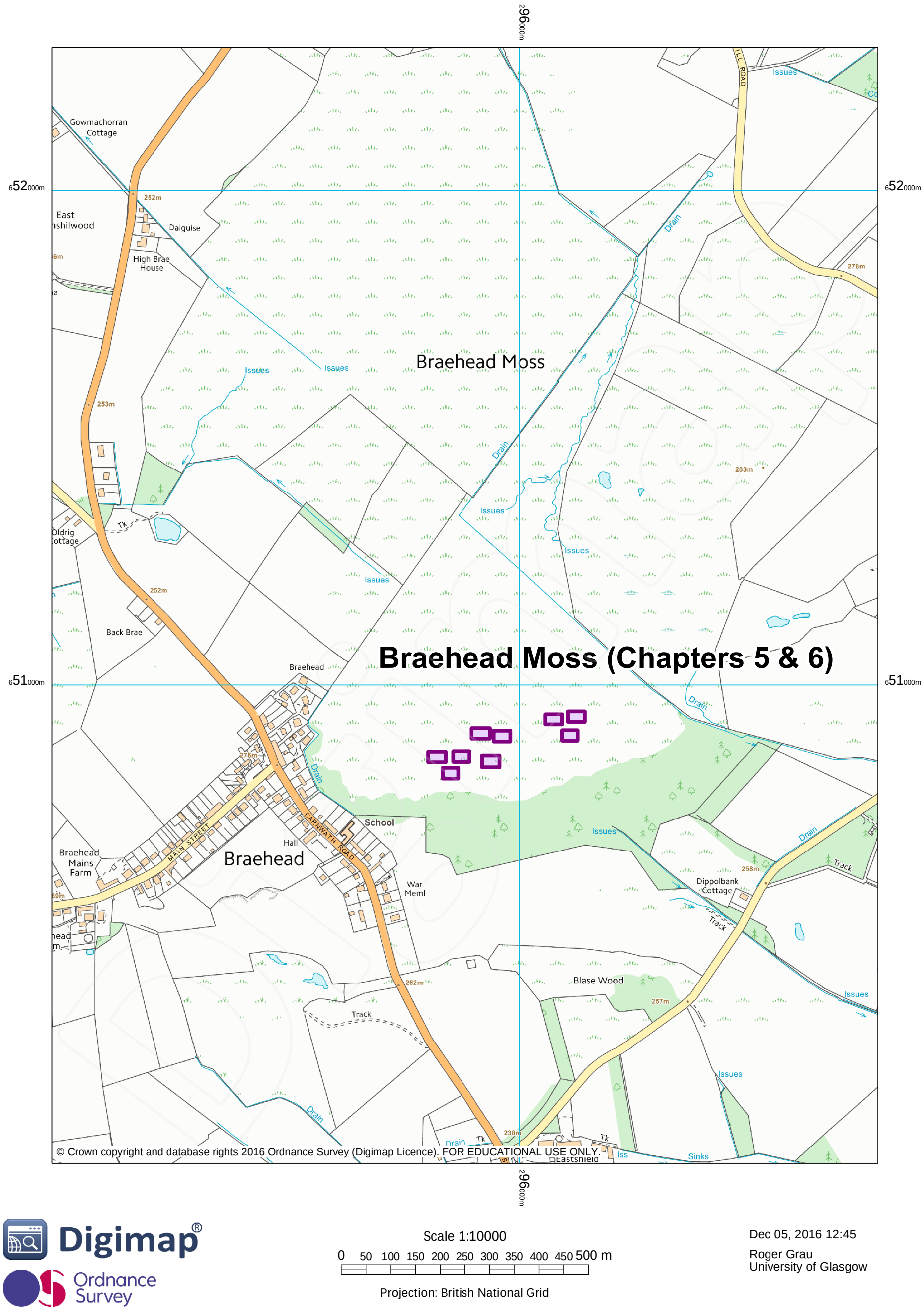

Figure 2.3: Polygons indicate the approximate location and area of experimental fires in Braehead Moss.

2.2 Fuel load and moisture content

I used the non-destructive FuelRule method (Davies et al., 2008b) to estimate plot fuel load and structure with five measurements taken in each plot. The method is based on observed visual obstruction (function of height and density of the vegetation) of a banded measurement stick. Davies et al.'s calibration of visual obstruction in *Calluna* allows estimation of a series of fuel load mesurements such as total biomass above moss, fine fuel biomass (live and dead stems < 2 mm in diameter and all foliage) and moss biomass. Biomass is expressed in dry weight per unit of area. I calibrated the method by comparing the FuelRule-estimated fuel load of 14 different 1 m^2 plots with the fuel loads estimated by destructive sampling (Table 2.1, Figure 2.4). The testing was carried out in Kirkconnell Flow (southern Scotland, latitude 55.0156°N, longitude 3.618°W), a raised bog with areas around the margins showing similar fuel structure as that found in Glen Tanar and Braehead Moss, i.e. mature *Calluna* cover above 85 % and a bryophyte layer dominated by pleurocarpous mosses. 9 FuelRule measurements were averaged in each plot. Fuel was separated by type in the laboratory, and dried at 80 °C until constant weight using a fan-assisten oven.

Immediately before each fire I sampled the top 2 cm of the M/L layer, live *Calluna* shoots (defined *sensu* Davies et al. (2010a), as live shoots bearing predominantly green shoots, discarding the top 5 cm as moisture is unrepresentative due to wind damage to leaf cuticules) and dead *Calluna* shoots (elevated dead foliage and fine branches) to estimate fuel moisture content (FMC). Samples were dried in a fan-assisted oven at 80 °C for 48 h, and FMC expressed as percentage of dry weight.

I used a FieldScout TDR 100 soil (Spectrum Technologies) and a Campbell Hydrosense (Campbell Scientific) moisture meters to estimate the moisture content of the top 3.6 cm and 6 cm, respectively, of the soil (here I use soil to refer to both the peaty podzols of Glen Tanar and the peat of Braehead Moss). Usage of a single meter was not possible due to availability constraints. The meters were calibrated by taking measurements of soil samples

Table 2.1: Details of the linear regression models relating fuel load (kg m^{-2}) estimated with the FuelRule methodology and fuel load calculated using destructive sampling.

	Estimate	Std. Error	t value	p value	DF	R^2
Total fuel above moss						
Intercept	0.16	0.43	0.38	0.71	12	0.64
Slope	1.35	0.29	4.61	<0.001		
Fine fuel above moss						
Intercept	0.18	0.42	0.43	0.68	12	0.41
Slope	1.31	0.45	2.91	0.01		
Moss						
Intercept	0.67	0.09	7.08	<0.001	12	0.5
Slope	0.43	0.12	3.5	<0.001		
Moss and buried stems						
Intercept	0.94	0.14	6.81	<0.001	12	0.45
Slope	0.48	0.15	3.15	0.01		

of known moisture contents. Both instruments measure the travel time of an electromagnetic impulse through a medium (soil), which varies with soil permittivity, in turn related to its moisture content. To calibrate the travel time measurement to the moisture content of the soil I took a sample from Braehead Moss, placed it on a tray in stable laboratory conditions and added distilled water until saturation. 24 h later, I applied a uniform weight of 20 kg for 3 h on the sample to compact it and then averaged five moisture meter measurements. I collected a soil sub-sample and calculated its moisture content gravimetrically, drying the sample at 80 °C until constant weight (approximately 48 h) in a fan-assisted oven. I spread the soil over a large surface to aid air drying overnight, and then mixed it and compressed it again for 3 h before taking the following measurement with the moisture meter, and another soil sub-sample for gravimetrical analysis of moisture. I repeated the process for two weeks, collecting a total of 12 datapoints. The relationship between soil moisture content and the moisture meter measurements was estimated using simple linear regression (Table 2.2 and Figure 2.5).

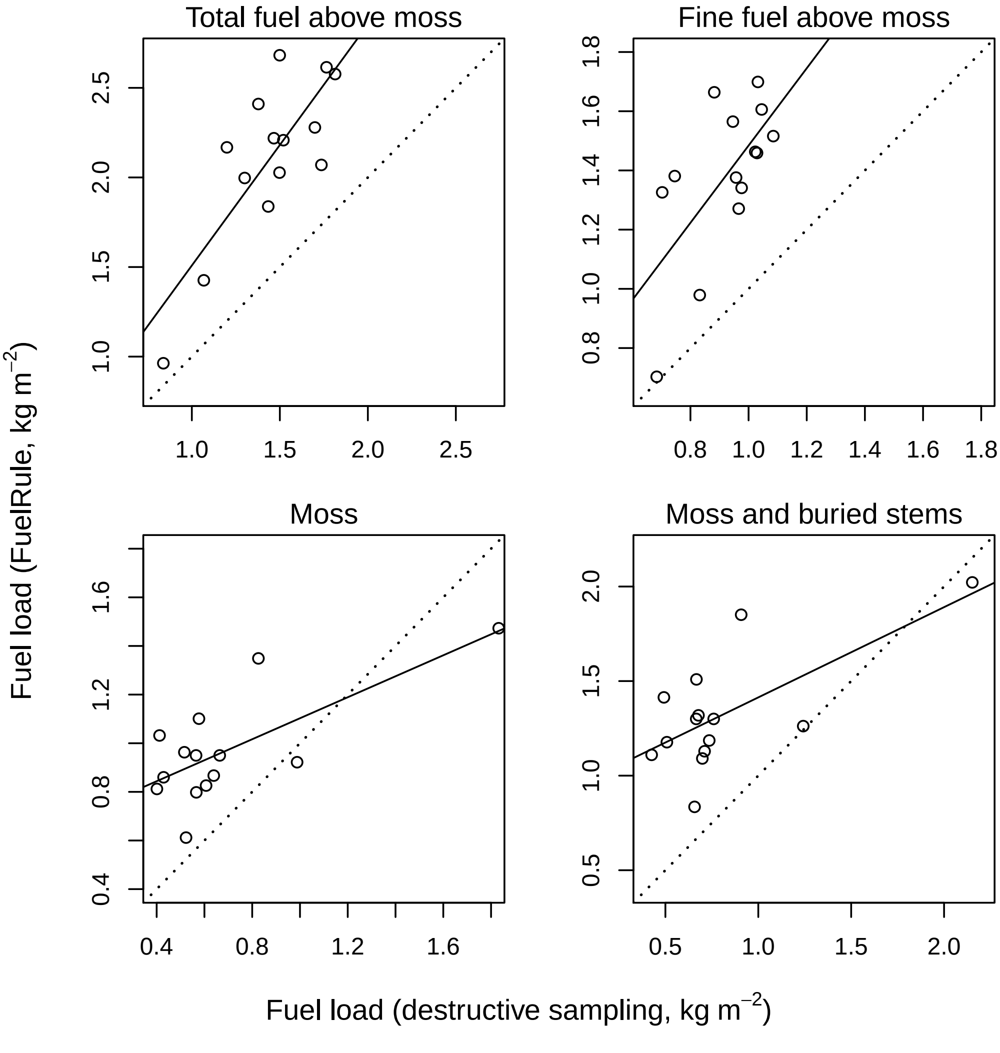

Figure 2.4: Relationship between fuel load of different fuel layers estimated using the FuelRule method and using destructive sampling. Dotted lines indicate perfect agreement and solid lines show fitted values following the models described in Table 2.1.

Table 2.2: Details of the linear regression models relating soil moisture content in dry weight and the permittance measurements from the soil moisture meters.

	Estimate	Std. Error	t value	p value	DF	R^2
Spectrum FieldScout moisture meter						
Intercept	-329.2	53.08	-6.2	<0.001	10	0.92
Slope	0.21	0.02	10.41	<0.001		
Campbell Hydrosense moisture meter						
Intercept	-254.81	61.05	-4.17	<0.001	10	0.86
Slope	456.8	58.31	7.83	<0.001		

2.3 Metrics of fire-induced soil heating

I used Hobo^{TM} loggers (Onset Computer Corporation) connected to K-type twisted pair thermocouples (multi-stranded leads of 0.2 mm of diameter) to measure soil heating during the fires and up to 50 min after. Two loggers were buried in a central location in each experimental plot, and the thermocouples were located at the soil surface (i.e. below overlying layers of moss and litter in plots where these layers were not removed) and 2 cm below the top of the O-layer (Glen Tanar) or peat (Braehead Moss). Following traditional managed burning guidelines, fires were ignited with drip torches and burnt as head fires with the predominant wind direction to limit flame residence and damage to vegetation regeneration and soil.

I measured the extent of soil heating during the fire as total heat by summing the differences between the measured temperatures and the temperature just before ignition, from the start of the fire until up to 50 min following the burn:

$$Total\ heat\ (^{\circ}C.s) = \sum_{i=1}^{t_f}(t_i - t_0) \times t_{interval} \tag{2.1}$$

where t_i is the soil temperature at i seconds after the start of the fire and t_0 is the temperature before the start of the fire. i ranges from 1 s (start of the fire) to t_f = 2100 s (35 min after the start of the fire, in fires

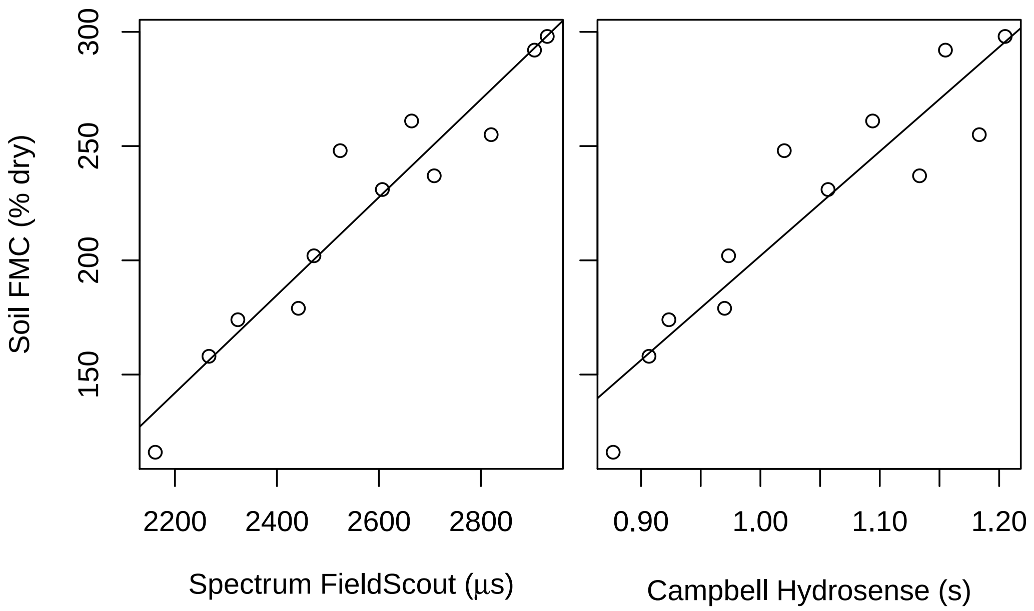

Figure 2.5: Relationship between soil moisture content in dry weight and the signal time travel measurements given by the soil moisture meters. The lines indicate fitted values following the models described in Table 2.2.

detailed in Chapter 3) or $t_f = 3000$ s (50 min after the start of the fire, in fires detailed in Chapter 5) at $t_{interval}$ intervals (measurement interval of the thermocouple logger, 1 s in fires in Chapter 3 and 5 s in fires in Chapter 5). Total heat is a sensitive indicator of fire-induced heating (i.e. area under a temperature-time curve) and, together with maximum temperature and the rate of heating and cooling, also calculated for each thermocouple, provide a good description of soil heating characteristics during the fire. This could help infer fire behaviour such as temperature residence and combustion of ground fuels. Additionally, the duration of temperatures above 50 °C, an ecologically important threshold, was also calculated. Temperatures above 50 °C are associated with damage to, and mortality of, plant tissues (Granström and Schimmel, 1993; Massman et al., 2010) and have also been observed to stimulate *Calluna* seed germination (Whittaker and Gimingham, 1962). I estimated the rates of soil heating and cooling as the exponential growth (heating) and exponential decay (cooling) constants associated with non-linear models fitted to the rising and falling limbs of the temperature-time curves:

$$Temperature\,(°C) = t_a + e^{\,(\lambda\,\cdot\,time)} \tag{2.2}$$

where t_a is the soil temperature at the horizontal asymptote, λ the exponential growth/decay constant and time is expressed in minutes since the start of the fire. Large values of λ indicate high rates of soil temperature change. I fitted separate models to the rising and falling limbs using the "gnm" function from the package *gnm* (Turner and Firth, 2015) in R 3.2.2 (R Core Team, 2015).

2.4 Weather and fire rate of spread

During the burns I recorded ambient temperature, relative humidity and wind speed using a Kestrel 4000 Wind Tracker weather station mounted on a wind vane and 1.25 m tripod (i.e. at approximately mid-flame height). Smoke and changing wind direction made observed fire rate of spread unreliable, and was estimated instead using a model presented in Davies et al. (2009):

$$R = 8.304 + 7.286\,h^2\,U - 0.097\,M_l \tag{2.3}$$

where R is the rate of spread of the fire (m min^{-1}), h is the mean *Calluna* height in m, U is the wind speed (m min^{-1}) and M_l is the live *Calluna* moisture content (% dry weight).

When live *Calluna* FMC data was not available, I used an alternative model also from Davies et al. (2009) (Equation 2.4):

$$R = 0.791 + 7.917\,h^2\,U \tag{2.4}$$

2.5 Linear mixed effects modelling tools and model selection

Linear regression is defined as:

$$Y_i = \alpha + \beta X_i \ + \epsilon_i \tag{2.5}$$

where Y is the response variable, α is the intercept, X is the explanatory variable, β its coefficient and ϵ is the error term or variance not explained by the explanatory variable. Important assumptions of linear regression are (i) Y is normally distributed at each value of X (a consquence of this is that the error term is normally distributed); (ii) variance of Y is homogeneous across different values of X; and (iii) observations are independent, i.e. the value of Y at X_i is not influenced by Y_i at X_{i-1} (Zuur et al., 2009). Violation of the independence assumption happens when there is a dependence structure in the data, either temporal or spatial. For example, fire-induced soil heating in a plot will likely be more similar to another plot in the same fire than to a plot in a separate fire (spatial dependence). Likewise, soil temperature at a certain location will be related to temperature measured 2 h before (temporal dependence). Also, fire-induced temperatures may be more variable at the soil surface than at certain depth in the soil profile (homogeneity of variance). Linear mixed effects models allow to overcome these issues by incorporating information on the hierarchical or spatial structure of the data, temporal autocorrelation and differences in variance across levels of a factor explanatory variable.

I often needed to perform statistical tests to compare different levels of one or more factor variables within a linear mixed effects model. I generally approached this by using multiple comparison procedures. These adjust statistical inferences for multiplicity, thus neutralizing the increased probability of finding a significant effect by chance when increasing the number of tests.

Environmental variables are often correlated, e.g. high air temperature is likely to be associated with low fuel moisture contents. In a multiple regression setting, high correlation among covariates (multicollinearity) is problematic as this leads to artificially inflated p-values. The variance inflation factor (VIF) of each covariate was used to detect multicollinearity (VIF > 3; Zuur et al., 2010) and covariates causing it were dropped from further analysis.

Selection of an optimal set of predictors in each model was based on the Akaike information criterion (AIC), a measure of goodness of fit that penalises number of parameters in the model. I used the "drop1" function in *R* to calculate the AIC of a model after sequentially dropping every possible parameter. I dropped the predictor that resulted in the lowest model AIC until dropping any remaining variable increased the AIC by more than 2 points (Symonds and Moussalli, 2010).

While in linear regression the coefficient of determination (R^2) provides a unique measure of model goodness of fit as variance explained, in linear mixed effects models the variation is partitioned into fixed and random effects. Therefore two measures of variance explained are provided: the marginal R^2 (variance explained by fixed effects) and the conditional R^2 (variance explained by both fixed and random effects) (Nakagawa and Schielzeth, 2013; Johnson, 2014). All data analysis was preformed using R 3.2.2. Functions "random", "correlation" and "weights" in *nlme* (Pinheiro et al., 2015), respectively, were used to account for spatial and temporal dependence structures, and with heterogeneity of variance. Multiple comparisons were implemented using the function "glht" in the package *multcomp* (Hothorn et al., 2008). VIF was calculated using the function "vif" in *usdm* (Naimi, 2015). R^2 marginal and conditional were calculated using "g.squaredGLMM" in *MuMIn* (Barton, 2015).

2.6 Harmonic regression

Harmonic regression is a modelling approach recommended for data with periodic patterns such as seasonal temperature variation (Piegorsch and Bailer, 2005). A simple harmonic regression model has a sine and a cosine

Table 2.3: Details of harmonic regression terms (Equation 2.6) in the two experiments described in Chapter 3 and Chapter 5.

Term	Chapter 3	Chapter 5
Y	Soil temperature metric (mean daily T and daily T range) within treatment (unburnt; burnt; burnt, M/L layer removed; M/L layer removed, then burnt) at Glen Tanar.	Soil temperature metric (mean daily T and daily T range) within treatment (unburnt; no-drought; drought) and site (Glen Tanar and Braehead Moss).
t_i	Sampling day: 1, 25th April 2013, to 350, 10th April 2014.	Sampling day: 1, 27th November 2014, to 302, 24th September 2015.

component:

$$Y_i = \beta_0 + \beta_{cos}\, cos(2\pi t_i/p) + \beta_{sin}\, sin(2\pi t_i/p) \tag{2.6}$$

where Y_i is the estimated temperature metric (mean daily temperature or daily temperature range) at time i, β_0 is the intercept, β_{cos} is the coefficient of the cosine term, t_i is the sampling day at time i, p is the period of the wave (time of one cycle: 365 days) and β_{sin} is the coefficient of the sine term. I fitted separate harmonic models for different soil microclimate metrics, treatments and sites (Table 2.3). The harmonic expressions were used as fixed effects in linear mixed effects models that included fire as a random effect and an autocorrelation structure of first order to account for the temporal dependence of the measurements (function "corAR1" in *nlme*).

2.6.1 Amplitude and phase

I followed Piegorsch and Bailer (2005) to calculate amplitude and phase associated with the sinusoidal waves from modelling seasonal variation of soil thermal dynamics. Amplitude was calculated as:

$$\gamma = \sqrt{\beta_{sin}^2 + \beta_{cos}^2} \tag{2.7}$$

where γ is the amplitude of the sinusoidal wave or vertical distance from the centreline to the wave maximum, in °C, and β_{sin} and β_{cos} are the sine and cosine term coefficients from the harmonic regression (Equation 2.6).

Phase was calcualted following:

$$\phi = (2\pi)^{-1} p \cos^{-1} (\beta_{sin}/\gamma) \tag{2.8}$$

where ϕ is phase or the horizontal distance to a wave starting at sampling day 1, in days, and p is the period of the sinusoid, 365 days.

2.6.2 Variance of amplitude and phase

The standard errors of the estimated coefficients of the sine and cosine terms of the harmonic expressions were used to calculate the variance of amplitude and phase. Amplitude and phase are functions of random variables the variance of which can be approximated using a Taylor expansion (Meyer, 1970).

$$\begin{aligned} V\ (Amplitude) &= f\ (sin,\ cos) \\ z &= f\ (x,\ y) \end{aligned}$$

x, y are random variables with $Var(x) = \sigma_x^2$, $Var(y) = \sigma_y^2$.

$$Var\ (Z) \approx (\frac{\partial\, f\ (x, y)}{\partial x})^2 | \sigma_y^2 + (\frac{\partial\, f\ (x, y)}{\partial y})^2 | \sigma_x^2 \tag{2.9}$$

From Equation 2.7:

$$\gamma = \sqrt{\beta_{sin}^2 + \beta_{cos}^2}$$

$$\frac{\partial \sqrt{\beta_{sin}^2 + \beta_{cos}^2}}{\partial \beta_{sin}} = \frac{1}{2} \left(\beta_{sin}^2 + \beta_{cos}^2\right)^{\frac{-1}{2}} \cdot 2\, \beta_{sin} = \beta_{sin} \left(\beta_{sin}^2 + \beta_{cos}^2\right)^{-1/2}$$

$$\frac{\partial \sqrt{\beta_{sin}^2 + \beta_{cos}^2}}{\partial \beta_{cos}} = \beta_{cos} \left(\beta_{sin}^2 + \beta_{cos}^2\right)^{-1/2}$$

$$Var\,(\gamma) \approx [\beta_{sin}\,(\beta_{sin}^2 + \beta_{cos}^2)^{-1/2}]^2 \cdot \sigma^2_{\beta_{cos}} + [\beta_{cos}\,(\beta_{sin}^2 + \beta_{cos}^2)^{-1/2}]^2 \cdot \sigma^2_{\beta_{sin}} \quad (2.10)$$

For calculating the variance associated with phase, I followed the same approach as described for calculating the variance associated with amplitude.

From Equation 2.8:

$$\phi = (2\pi)^{-1} p \cos^{-1}\,(\beta_{sin}/\gamma)$$

$$\frac{\partial\,(2\pi)^{-1} p \cos^{-1}\,(\beta_{sin}/\gamma)}{\partial \beta_{cos}} = -\frac{p}{2\,\pi\,\gamma\sqrt{1-\frac{\beta_{cos}^2}{\gamma^2}}} \quad (2.11)$$

$$\frac{\partial\,(2\pi)^{-1} p \cos^{-1}\,(\beta_{sin}/\gamma)}{\partial \gamma} = -\frac{p\,\beta_{cos}}{2\,\pi\,\sqrt{1-\frac{\beta_{cos}^2}{\gamma^2}}\gamma^2} \quad (2.12)$$

$$Var\,(\hat{\phi}) \approx [-\frac{p}{2\,\pi\,\gamma\sqrt{1-\frac{\beta_{cos}^2}{\gamma^2}}}]^2 \cdot \sigma^2_\gamma + [-\frac{p\,\beta_{cos}}{2\,\pi\,\sqrt{1-\frac{\beta_{cos}^2}{\gamma^2}}\gamma^2}]^2 \cdot \sigma^2_{\beta_{cos}} \quad (2.13)$$

Chapter 3

Leaving moss and litter layers undisturbed reduces the short-term environmental consequences of heathland managed burns

Abstract

High severity fires involving large soil heating and the consumption of the moss and litter (M/L) layer may have important ecological consequences for vegetation regeneration and soil carbon dynamics. I completed experimental fires in a *Calluna vulgaris* dominated heathland to study the role of the M/L layer in determining (i) fire-induced temperature pulses into the soil and (ii) post-fire soil thermal dynamics. Higher fire severity was simulated by removing the M/L layer in 1×1 m plots prior to the fires, which resulted in increased soil heating. I quantified temperature residence, maximum temperature, heating rate, cooling rate and time above 50 °C at the soil surface and 2 cm below ground, and monitored soil thermal dynamics for a year after the experimental fires. Post-fire soil thermal dynamics were greatly

affected by the M/L layer; where it had been removed: (i) mean soil temperatures were higher in warm months and lower in cold months, (ii) diurnal range was always higher, especially in warmer months and (iii) soil temperature patterns were similar to those observed after wildfires. Quantification of the role of the M/L layer in controlling fire-induced soil heating and post-fire soils thermal dynamics can inform management strategies to promote *Calluna* moorlands vegetation regeneration and protect soil carbon stocks.

3.1 Introduction

European *Calluna* heathlands developed as a result of human disturbance to forests from tree harvesting and the use of fire to increase grazing and browsing productivity (Prøsch-Danielsen and Simonsen, 2000; Innes and Blackford, 2003), and were maintained by the introduction of a disturbance regime (chiefly managed burning and increased grazing by livestock and game) that prevented recolonization by trees (Dodgshon and Olsson, 2006). In the last two centuries, managed burning of UK *Calluna* heathlands has been strongly associated with management for red grouse shooting (Figure 3.1). Such traditional burning can have benefits for habitat maintenance, biodiversity (Allen et al., 2016; Glaves et al., 2013) and fire risk reduction (Davies et al., 2008a). However, negative consequences have been noted for peatland carbon sequestration (Garnett et al., 2000) and stream water chemistry and ecology (Ramchunder et al., 2013).

During managed burns the M/L layer typically has a high fuel moisture content (FMC) (> 250 %) and thus plays an important role in insulating soil from substantial temperature pulses, and possibly ignition, during the passage of a flaming fire-front (Davies and Legg, 2011). This often means that fire severity (*sensu* Keeley, 2009 as the direct, immediate effect of the fire on the ecosystem) is low despite high fireline intensities (Davies et al., 2009). However, during high severity fires where the M/L layer is dry enough to be consumed, fuel available for combustion increases considerably, influencing

Figure 3.1: Managed burning ("muirburn") at Glen Tanar.

fire intensity, ease of control (Davies et al., 2010b) and soil temperatures (Bradstock and Auld, 1995).

Climate change may lead to increased wildfire activity and to high severity wildfires that consume a larger proportion of the M/L layer (Davies et al., 2016a). With many *Calluna* moorlands overlying peat deposits or organic soils that store substantial amounts of carbon (Bradley et al., 2005; Clay et al., 2010) there is concern that higher severity fires could increase carbon emissions both from direct combustion (Davies et al., 2013) and from greater soil respiration resulting from an altered soil microclimate (Brown et al., 2015).

Currently we have little quantitative evidence of how fuel structure, especially the presence of the M/L layer, controls fire-induced soil heating and post-fire soil thermal dynamics. I investigated this, and particularly the role of the M/L layer in these processes, by manually removing the M/L layer in small plots in order to safely simulate the higher severity conditions that occur where there is extensive consumption of the M/L layer and direct contact between the fire and the soil surface. The simulated approach is useful as when ground fuels become flammable (low moisture content), fuel available for combustion increases substantially (Davies et al., 2010b), normal fire control methods have limited effectiveness and managed burning becomes too hazardous. The simulated higher severity treatment is probably a conservative estimate of high severity fires as the combustion of the M/L layer may substantially contribute to soil heating. Additionally, I monitored post-fire soil thermal dynamics in three wildfires. My objectives were to (i) quantify the role of the M/L layer in insulating soils from raised temperatures during managed burning, (ii) examine the effect of environmental variables (e.g. thickness and moisture content of the M/L layer, canopy density) in controlling fire-induced soil heating, (iii) model post-fire soil thermal dynamics in relation to simulated variation in fire severity, (iv) compare post-fire soil thermal dynamics in managed fires and wildfires, and (v) estimate the potential effect of altered soil thermal dynamics on soil respiration.

3.2 Material and methods

3.2.1 Experimental design and measurements

Seven experimental fires on four separate days, between the 12th and the 26th of April 2013, were completed at Glen Tanar (see site information in Section 2.1). All fires were ignited with a drip torch as head fires (i.e. main fire spread direction was the same as wind direction) and covered an area of around 25 × 30 m. Within each fire I established six 1 × 1 m plots assigned to one of three treatments (each treatment replicated twice per fire): (i) plots where the M/L layer was not altered, (ii) the M/L layer was removed after the fire, (iii) the M/L layer was removed before the fire. I manually removed the M/L layer down to the top of the O-horizon in the latter two fuel treatments. The treatments established a disturbance severity gradient, from low severity (low fire-induced soil heating, low alteration to the M/L layer) in plots where the M/L layer was not removed, to high severity (increased soil heating, M/L layer removed) in plots where the M/L layer was removed before the fire. Comparisons between treatments allowed elucidating the role of the M/L layer on controlling fire severity and the subsequent effect on post-fire soil thermal dynamics.

Fire behaviour within a single fire varies widely due to changes in microtopography, heterogeneity in fuel density, fuel gaps and variation in wind speed (Bradstock and Auld, 1995; Bova and Dickinson, 2008; Davies et al., 2010b). I therefore followed the microplot approach for fire behaviour measurements (Fernandes et al., 2000) and considered plots within fires as independent observations with regards to data analysis. The validity of the approach was assessed by examining variation in fuel characteristics (e.g. fuel load, bulk density, M/L layer depth) within and between fires using a random effects model to partition the variance in each of these metrics across the different levels of the experimental design (function "lmer" in package *lme4*; Bates et al., 2015 in R 3.2.2 R Core Team, 2015).

The non-destructive FuelRule method (Davies et al., 2008b) was used to estimate plot fuel load and structure with five measurements taken in each plot. The method is based on visual obstruction of a banded measurement stick. I used Davies et al.'s calibration of visual obstruction (function of height and density of the vegetation) in *Calluna* to obtain an estimate of total fuel load above moss (dry weight per area). See Section 2.2 for details. Immediately before each fire, to estimate fuel moisture content (FMC), I sampled the top 2 cm of the M/L layer, dead *Calluna* shoots and live *Calluna* shoots (defined *sensu* Davies and Legg (2011), as live shoots bearing predominantly live leaves and discarding the top 5 cm of the shoot). M/L layer moisture content samples were taken from three randomly-selected locations in each plot where the M/L layer had not been removed. For live and dead *Calluna* FMC, a single, integrated sample was taken from all the plots within each fire. I extracted a single soil core from a random location in each plot and calculated the FMC and dry bulk density of the top 2 cm of soil.

Table 3.1: Fire-induced soil heating metrics calculated from temperature measurements at the soil surface and 2 cm below ground, see Section 2.3 for details.

Variable	Details
Total heat (°C.s)	Soil heating measurement that integrates both the extent of temperature increase and its duration.
Maximum T (°C)	Maximum soil temperature.
Heating slope (λ)	Rate of temperature increase of the rising limb a temperature-time curve, as approximated by an exponential growth constant.
Cooling slope (λ)	Rate of temperature decrease of the falling limb a temperature-time curve, as approximated by an exponential decay constant.
t above 50 °C (s)	Time that soil temperature was above the 50 °C threshold.

Fire temperatures were recorded using thermocouple loggers at the soil surface and 2 cm below, at 1 s intervals. Where it was present, I measured the thickness of the M/L layer above the top thermocouple to the nearest 0.5 cm. Fire-induced soil heating was estimated with five soil temperature metrics (Table 3.1). I used four duff spikes (metal spkies with a notch levelled with the M/L surface) per plot to assess consumption of the M/L layer during the fires to the nearest 1 cm.

Following each fire, I buried iButton$^{\text{TM}}$ temperature loggers (0.5 °C accuracy, 2 h logging interval) 2 cm below the top of the soil for long-term recording of soil thermal dynamics. In each of the seven fires, I buried a single iButton in a randomly-selected plot of each treatment. Next to each fire I also located an iButton in a single unburnt (control) plot. Temperatures were recorded from April 26th 2013 to April 10th 2014.

In addition, post-fire soil thermal dynamics data from three wildfires was analysed to assess whether the experimental manipulation of fire severity approximated the effects seen in moderately-severe to severe wildfires. The three wildfires burnt *Calluna*-dominated heaths and/or bogs in northern England (Anglezarke, 53.658°N, 2.569°W; Wainstalls, 53.777°N, 1.928°W) and north-east Scotland (Finzean, 57.025°N, 2.702°W) between April 2011 and March 2012 (Davies et al., 2016a). The wildfires captured a range of variability in fire severity and alteration to ground fuel. In each wildfire two paired plots were monitored, each with an unburnt and a burnt subplot located either side of the perimeter of the fire. Davies et al. used iButtons to record 2 h frequency temperature measurements 2 cm below the top of the soil for approximately a month between August and September 2012. Soil types included rocky organic soils at Finzean and deep peat soils at the other sites. The potential effect of site, habitat type and fire behaviour were confounded in this experimental design but it still provides us with useful comparative data where information is otherwise lacking.

3.2.2 Data analysis

Fire-induced soil heating

Due to thermocouple logger malfunction, temperature data was not collected from a surface location and four 2 cm depth locations. I tested for differences in fire-induced soil heating between burnt plots where the M/L layer was not altered and plots where it was removed after the fire, at both temperature measurement depths, to assess whether the two treatments could be grouped together in subsequent analyses. Differences were not statistically significant (see Appendix A.2) and both treatments were combined into a "M/L layer present" group in further analyses of fire-induced soil heating. These focused on addressing two questions:

i *What role did the M/L layer play in insulating the soil from fire-induced temperature pulses?* I investigated the effect of the presence or absence of the M/L layer on the different metrics of fire-induced soil heating (Table 3.1) using used linear mixed effects models that included an interaction between M/L layer (levels: present and removed) and the depth of measurement (soil surface and 2 cm below) as fixed effects and fire as a random effect (function "lme" in the package *nlme*; Pinheiro et al., 2015). Response variables were logarithmically transformed, except for total heat, for which a square root transformation was used.

A constant variance function ("varIdent" in *nlme*) was used to account for the heterogeneity of variance between temperature measurements at the soil surface and 2 cm below (Appendix A.3). With these models I tested for differences in fire-induced soil heating between normal burn conditions and simulated high severity (those where the M/L layer was removed).

ii *What role did environmental variables play in controlling fire-induced soil heating in plots where the M/L layer was present?* I aimed to identify and quantify the most important environmental variables controlling fire-induced soil heating during normal managed burns, i.e. in those plots where the M/L layer was not removed. Among the covariates available (Table 3.2) for modelling fire-induced soil heating metrics (Table 3.1), those measured at the plot level were prioritised. In order to avoid multicollinearity, and since scatterplots of response variables against covariates suggested weak relationships, only covariates with a variance inflation factor (function "vif" in package *usdm*; Naimi, 2015) smaller than 2 were retained (Zuur et al., 2010). As in the previous analysis, a square root transformation was used for total heat, whilst a logarithmic transformation was used for the other metrics. I used separate linear mixed effects models for each measuring depth (soil surface and 2 cm below), with the selected covariates as fixed effects and fire as a random effect. Model selection was based on the Akaike information criterion (see Section 2.5).

Table 3.2: Variables measured at the fire and plot level. *n*, number of observations; FMC, fuel moisture content. M/L layer thickness and FMC refer to no-removed treatment only. M/L layer and soil FMC, as well as soil bulk density, refer to the upper 2 cm. See Section 2.4 for details on fire rate of spread and fuel load estimates.

Variable	Level	n	Mean	Range
Fire rate of spread (m min^{-1})	Fire	7	1.4	0.8–2.4
Wind speed (m s^{-1})	Fire	7	3.3	1.9–6.3
Air temperature (°C)	Fire	7	8.6	5.1–11.1
Relative humidity (%)	Fire	7	58	41–73
Live *Calluna* FMC (%)	Fire	7	81	74–92
Dead *Calluna* FMC (%)	Fire	7	15	13–23
Calluna height (cm)	Plot	42	51.3	31–65
Fuel load above moss (kg m^{-2})	Plot	42	1.5	1–1.9
M/L layer thickness (cm)	Plot	28	4	1–8
M/L layer FMC (%)	Plot	28	251	103–398
Soil FMC (%)	Plot	42	422	192–630
Soil bulk density (g cm^{-3})	Plot	42	0.1	0.02–0.4

Longer-term implications of variation in fire severity

Analysis of post-fire soil thermal dynamics aimed to address three questions:

iii *What effect did burning and removal of the M/L layer have on post-fire soil thermal dynamics?* I examined changes in soil thermal dynamics associated with low and high fire severities (as simulated by removing the M/L layer). Post-fire mean daily temperature (00:00 to 22:00) and daily temperature range, defined as the difference between maximum and minimum daily temperatures, were calculated in four plots per fire (treatments: burnt, burnt where the M/L layer was removed after the fire, burnt where the M/L layer was removed before the fire, and unburnt). Harmonic regression was used to model variation in mean daily temperature and daily temperature range during the measuring period (25th April 2013 to 10th April 2014) as a function of treatment. I averaged the amplitude (vertical distance from the centreline to the wave maximum, in °C) and phase (horizontal distance to a wave starting at sampling day 1, in days) defining the sinusoidal waves of mean daily temperature and daily temperature range in each treatment, and then computed 95 % confidence intervals of differences between all pairs of treatment levels. Detailed information on harmonic regression and amplitude and phase calculation is provided in Section 2.6.

iv *Did post-fire soil thermal dynamics differ between managed and wildfires?* I tested whether soil temperatures following the experimental fires responded differently to changing weather conditions compared to soils burnt-over by wildfires. To allow comparison of data from the experimental fires with the paired plot data from the wildfires (which burnt different sites in different years) I treated burnt plots and unburnt plots in the same experimental fire as if they were paired plots. Two paired plots were defined in each experimental fire: one included the unburnt plot and the plot where the M/L layer was not removed, and the other included the same unburnt plot and an average of the plots where the M/L layer was removed. To examine changes in post-fire soil thermal dynamics relative to unburnt, I calculated the difference between temperatures in the unburnt subplot and the burnt subplot in each paired plot, both in the wildfires and the experimental burns. I only used data from the experimental fires where mean daily temperature in the unburnt plot was within the range of mean daily temperatures recorded in the unburnt wildfire subplots (6.6–15.4 °C). Post-fire changes in mean daily temperature were modelled as a function of mean daily temperature in the unburnt plot and the fire type associated with the paired plot (wildfire, low severity experimental fire and simulated high severity experimental fire). Mean daily temperature in the unburnt plot was considered a proxy for weather conditions, and was included in the model to account for the effect of weather on post-fire thermal dynamics. I fitted a random slopes and intercept model with an interaction between mean daily temperature in the unburnt plot and fire type as fixed effects, paired plot as random effect, an autocorrelation structure of order 1 and a constant variance structure for the three levels of the factor "fire type".

v *Could observed changes in soil thermal dynamics have an effect on soil respiration?* Given the key role of temperature in controlling metabolic rates, temperature-driven models are often used to estimate soil respiration (Del Grosso et al., 2005). I used Equation 3.1 (Lloyd and Taylor, 1994) to estimate the effect of observed changes in soil thermal dynamics on soil respiration.

$$R = R_{10}\, e^{308.56\,(\frac{1}{56.02} - \frac{1}{T-227.13})} \tag{3.1}$$

where R_{10} is the estimated respiration at 10 °C and T is the soil temperature in K. As R_{10} was unknown for the site, I used a unitless value of 1 and thus expressed estimates of respiration as the proportional change in respiration relative to that at 10 °C. I estimated relative respiration during the first year after the fire in each plot using the bi-hourly temperature measurements. This approach assumes that changes in other sources of variation of soil respiration such as moisture content and substrate dynamics (Curiel-Yuste et al., 2007) were similar across treatments. Therefore, the estimates should be treated with care, and taken as a means of generating hypotheses regarding the potential impact of fire severity on soil respiration. Further research needs to investigate these and clarify whether temperature remains a dominant control after different fire severities. Average relative respiration estimates were calculated for each plot in each season (spring: March–May, summer: June–August, autumn: September–November, winter: December–February), providing seven averages (one per fire) for each treatment and season. The data was analysed using a linear mixed effects model including an interaction between treatment and season as fixed effects and fire as a random effect. I performed multiple comparisons tests using the function "glht" in the package *multcomp* (Hothorn et al., 2008).

3.3 Results

Variance of fuel load and structure (total fuel, fine fuel, bulk density, height and M/L layer thickness) had a similar magnitude within and between fires, thus justifying the microplot approach (Appendix A.1).

3.3.1 Fire-induced soil heating

The form of the temperature-time curves consistently showed a steep rising limb associated with the arrival of the fire front followed by a shallow falling limb related to residual flaming and smouldering combustion and the slow cool down of the heated soil mass (Figure 3.2). Soil heating, as measured by total heat, maximum temperature and time above 50 °C, was higher in plots where the M/L layer had been removed prior to the fire than in those where it was present during the burn (Table 3.3). Temperatures were also considerably higher at the soil surface compared to 2 cm below ground: e.g. average maximum temperature during the fires was 21 versus 7 °C in plots where the M/L layer was present, and 73 versus 9 °C where it was removed. For total heat, maximum temperature, rate of heating and rate of cooling, the interaction between M/L layer treatment factors and depth of measurement was statistically significant (Table 3.4), indicating that treatment had a larger effect at the top of the soil compared to 2 cm below the soil surface.

After dropping multicollinear covariates, total fuel load above the M/L layer, M/L layer thickness, M/L layer moisture content and soil moisture content were used to model the different metrics of fire-induced soil heating in unaltered burnt plots (M/L layer present) (Table 3.5). Model performance was generally low at both depths of measurement, and only the moisture content of the M/L layer had a substantial effect on fire-induced heating rates 2 cm below the soil surface (p-value = 0.008, marginal R^2 = 0.30).

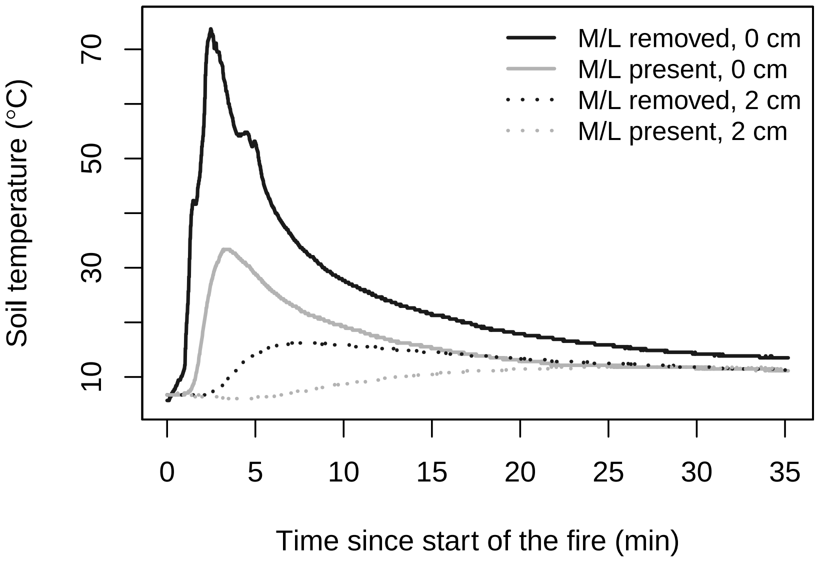

Figure 3.2: A representative example of the fire-induced soil heating curves associated with each of the treatments (plots where the M/L layer was present and plots where it was removed at the time of the fire) and measurement depths (soil surface and 2 cm below). Curves with the same colour belong to the same plot/treatment.

Table 3.3: Mean values and standard deviations (in parentheses) of fire-induced soil heating metrics by depth of measurement and presence or absence of the M/L layer.

	Soil surface		2 cm below	
Variable	M/L present	M/L removed	M/L present	M/L removed
Total heat (°C.s)	7791 (7012)	20469 (10170)	1895 (2256)	4322 (3874)
Maximum T (°C)	21 (22)	73 (34)	7 (3)	9 (4)
Heating slope (λ)	0.8 (2)	5 (4)	0.02 (0.04)	0.03 (0.04)
Cooling slope (λ)	0.08 (0.1)	0.5 (0.3)	3e-05 (4e-05)	0.003 (0.01)
t above 50 °C (s)	11.1 (34.2)	57.8 (57.7)	0 (0)	0 (0)

Table 3.4: Results of linear mixed effects models examining variation in fire-induced soil heating metrics as a function of the interaction between treatment (M/L layer present or removed) and depth of measurement (soil surface or 2 cm below). R^2 marginal is the variance explained by fixed effects, and R^2 conditional, by both fixed and random effects.

Response	DF	R^2m	R^2c	Fixed effect	t-value	p-value
Total heat (°C.s)	69	0.43	0.55	treatment:depth	3.21	0.002
				treatment	2.21	0.030
				depth	4.97	<0.001
Maximum T (°C)	69	0.51	0.62	treatment:depth	5.24	<0.001
				treatment	2.64	0.010
				depth	5.40	<0.001
Heating slope (λ)	69	0.39	0.53	treatment:depth	3.09	0.003
				treatment	2.11	0.038
				depth	3.60	<0.001
Cooling slope (λ)	69	0.48	0.50	treatment:depth	3.21	0.002
				treatment	2.21	0.030
				depth	4.97	<0.001

Table 3.5: Final models (after selection) of soil heating metrics in unaltered burnt plots as a function of environmental covariates (total fuel load above moss, M/L layer thickness, M/L layer moisture content and soil moisture content) per thermocouple depth (soil surface or 2 cm below). Due to high frequency of zeros, time above 50 °C (at both measurement depths) and cooling slope (at 2 cm depth) could not be adequately modelled.

Response	Depth	DF	R^2m	R^2c	Fixed effect	t-value	p-value
Total heat (°C.s)	Surface	20	0.06	0.12	Fuel load	-1.24	0.230
	2 cm	18	0.16	0.58	Soil FMC	2.47	0.024
Maximum T (°C)	Surface	20	0.09	0.17	Fuel load	-1.53	0.142
	2 cm	18	0.04	0.84	Soil FMC	1.97	0.065
Heating slope (λ)	Surface	20	0.13	0.13	Fuel load	-1.96	0.064
	2 cm	18	0.30	0.53	M/L FMC	-2.97	0.008
Cooling slope (λ)	Surface	20	0.06	0.13	Fuel load	-1.21	0.240

3.3.2 Post-fire soil thermal dynamics

The harmonic expressions used to model mean daily temperature and daily temperature range had a significant effect (Table 3.6). Marginal R^2 (variance explained by fixed effects) ranged between 0.88 and 0.90 in mean daily temperature models and between 0.27 and 0.61 in daily temperature range models. Low marginal R^2 in daily temperature range models was associated with weak seasonal patterns in unburnt plots. Burnt plots where the M/L layer was removed had the highest daily temperature range, whilst diurnal variation was lowest in the unburnt plots (Figure 3.3). This pattern continued throughout the year: daily temperature range was highest in plots where the M/L layer had been removed, lowest in unburnt plots, whilst burnt only plots showed intermediate values (e.g. maximum range was 8.4, 5.0 and 2.3 °C, respectively; Figure 3.4). Differences in daily temperature range between treatments were highest in summer and lowest in winter. Burnt plots showed higher mean daily temperature than unburnt plots in summer (13.3 °C versus 11.9 °C) and lower in winter (1.4 °C versus 2.3 °C). The removal of the M/L layer had an additive effect on this altered temperature pattern, with higher temperatures in summer (14.4 °C) and lower temperatures in winter (0.8 °C) compared to burnt plots.

Mean daily temperature and daily temperature range were similar in burnt plots where the M/L layer was removed after the fire and in plots where it was removed before the fire. Comparisons between treatments suggest that the contribution of *Calluna* canopy and M/L layer to soil thermal dynamics were of similar magnitude. For example, mean daily temperature in burnt plots was 1.6 °C higher than in unburnt in July, while it was approximately 2.6 °C higher in burnt plots where the M/L layer was removed. The relative contribution of the absence of the *Calluna* canopy and the M/L layer was also similar for daily temperature range (2.6 °C and 5.9 °C for the above comparison).

Comparison of the 95 % confidence intervals of the difference in amplitude and phase between treatments revealed that seasonal patterns in mean daily temperature and daily range were generally significantly different between all treatments except between plots where the M/L layer was removed before the fire and plots where it was removed afterwards (Table 3.7). Larger mean daily temperature amplitude in burnt plots where the M/L layer was removed (7.7 °C) indicated more extreme seasonal soil thermal dynamics than in burnt (6.8 °C) and unburnt plots (5.6 °C). The larger amplitude of the daily temperature range in the same plots (3.7 °C versus 2.2 °C in burnt and 0.9 °C in unburnt plots) indicated greater diurnal extremes. The negative phase for mean daily temperature and daily temperature range in burnt plots indicated that annual patterns of soil thermal dynamics in these plots led those of unburnt plots, i.e. maximum (summer) and minimum (winter) temperatures occurred earlier in the year (6–10 days) in burnt compared to unburnt plots.

Post-fire change in soil mean daily temperature in plots where the M/L layer was not altered in experimental fires and in plots in wildfires showed different responses to weather conditions (p-value of the interaction between mean daily temperature in unburnt plots and fire type was 0.03) (Figure 3.5). However, post-fire change in soil mean daily temperature in plots where the M/L layer was removed in experimental fires was not statistically different to plots in wildfires (p-value = 0.8). Thus, post-fire soil mean daily temperature increase with warmer weather conditions (as estimated by soil temperature in the unburnt plot) was higher in wildfires than in experimental fire plots where the M/L layer was not altered, but similar to experimental fire plots where the M/L layer was removed. Details of the models are provided in Appendix A.4.

3.3.3 Soil respiration estimates

The higher temperatures recorded in burnt plots where the M/L layer was removed led to significantly higher estimated relative respiration, particularly in the warmer summer months (Figure 3.6).

Table 3.6: Details of mean daily temperature and daily temperature range models for each treatment (unburnt; B: burnt; BR: burnt, then M/L layer removed; RB: M/L layer removed, then burnt).

Response	Treatment	DF	R^2m	R^2c	Fixed effects	t-value	p-value
MDT	Unburnt	2412	0.88	0.88	Intercept	23.29	<0.001
					sday	6.62	<0.001
					cos	-5.05	<0.001
					sin	30.02	<0.001
	B	2758	0.90	0.90	Intercept	23.61	<0.001
					sday	7.61	<0.001
					cos	0.14	0.885
					sin	37.36	<0.001
	BR	2412	0.89	0.89	Intercept	21.57	<0.001
					sday	7.00	<0.001
					cos	3.91	<0.001
					sin	36.60	<0.001
	RB	2067	0.89	0.89	Intercept	19.19	<0.001
					sday	6.43	<0.001
					cos	4.20	<0.001
					sin	34.92	<0.001
DTR	Unburnt	2412	0.27	0.48	Intercept	6.77	<0.001
					sday	1.39	0.165
					cos	6.99	<0.001
					sin	14.76	<0.001
	B	2758	0.38	0.57	Intercept	6.54	<0.001
					sday	3.44	0.001
					cos	12.20	<0.001
					sin	20.35	<0.001
	BR	2412	0.53	0.61	Intercept	10.40	<0.001
					sday	0.42	0.674
					cos	16.73	<0.001
					sin	21.45	<0.001
	RB	2067	0.61	0.65	Intercept	14.99	<0.001
					sday	1.06	0.289
					cos	20.94	<0.001
					sin	26.34	<0.001

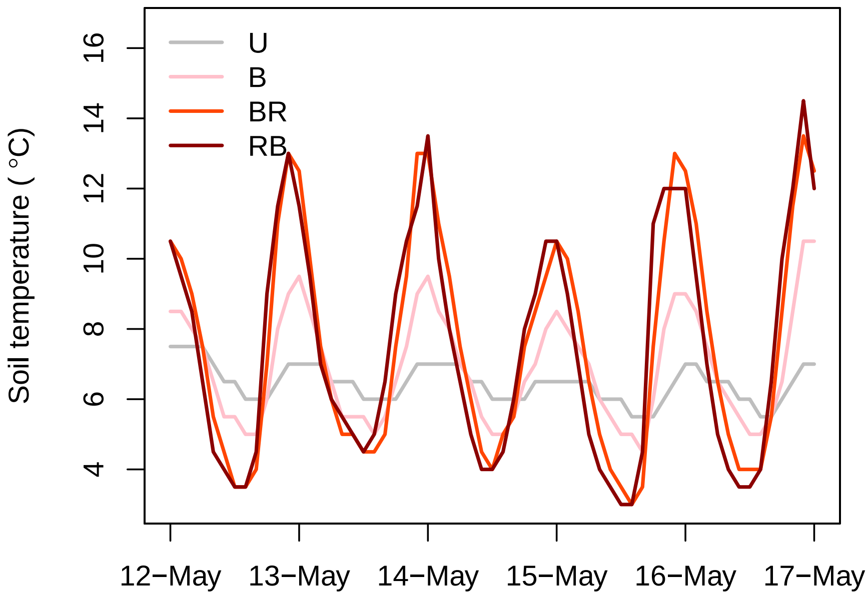

Figure 3.3: Representative examples of recorded bi-hourly soil temperatures in unburnt (U), burnt (B), and burnt plots where the M/L layer was removed after (BR) and before (RB) the fire, from 11th July 2013 at 00:00 to 16th July 2013 at 22:00.

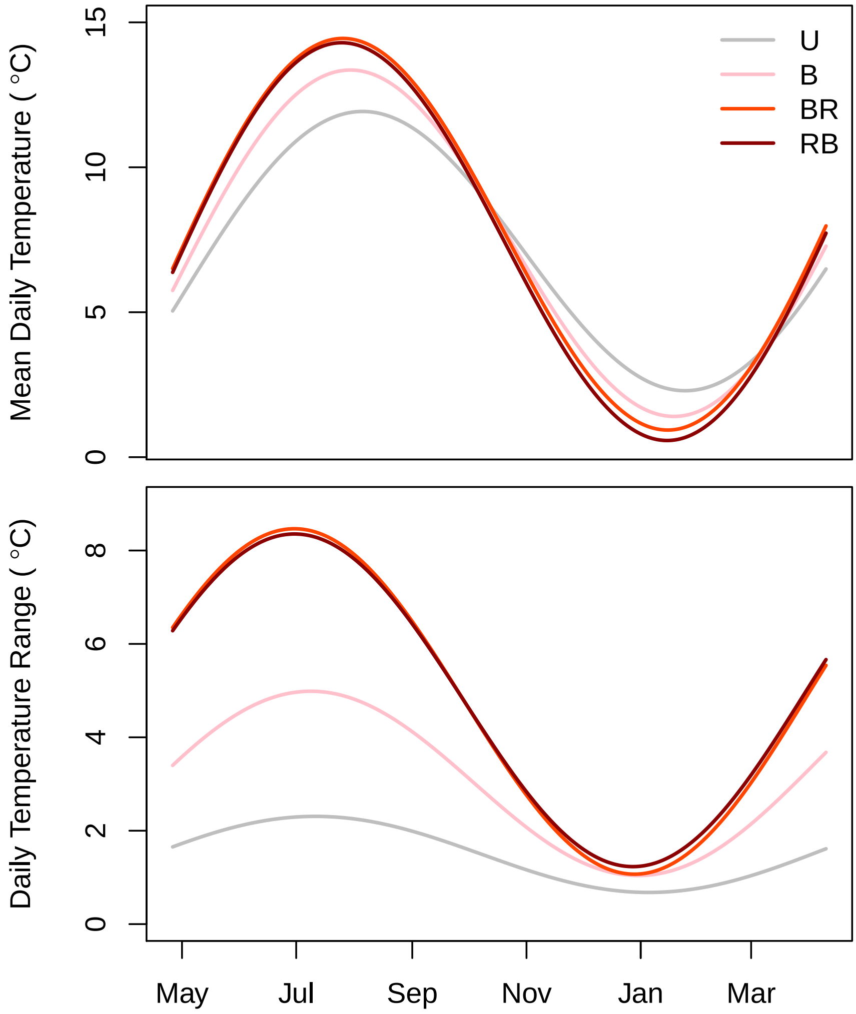

Figure 3.4: Modelled mean daily temperature and daily temperature range (26th April 2013 to 10th April 2014) for the four fuel treatments (codes follow Figure 3.3). See Section 2.6 for harmonic regression details.

Table 3.7: Amplitude and phase of the mean daily temperature and daily temperature range models (Table 3.6), for each fuel treatment (unburnt; B: burnt; BR: burnt, M/L layer removed; RB: M/L layer removed, then burnt). Variance in parenthesis. Different letters within columns indicate significant differences between fuel treatments ($\alpha = 0.05$). Phase is expressed as the difference with phase in unburnt plots. Negative values indicate the sinusoidal wave is to the left (leading) the unburnt.

	Mean Daily Temperature		Daily Temperature Range	
Treatment	Amplitude (°C)	Phase (days)	Amplitude (°C)	Phase (days)
Unburnt	5.6 (0.01) a	0.0 (0.04) a	0.9 (0.001) a	0.0 (0.4) a
B	6.8 (0.01) b	-6.0 (0.01) b	2.2 (0.005) b	-4.0 (0.4) b
BR	7.7 (0.02) c	-9.9 (0.02) c	3.7 (0.012) c	-9.4 (0.5) c
RB	7.7 (0.02) c	-10.4 (0.03) d	3.6 (0.008) c	-9.8 (0.4) c

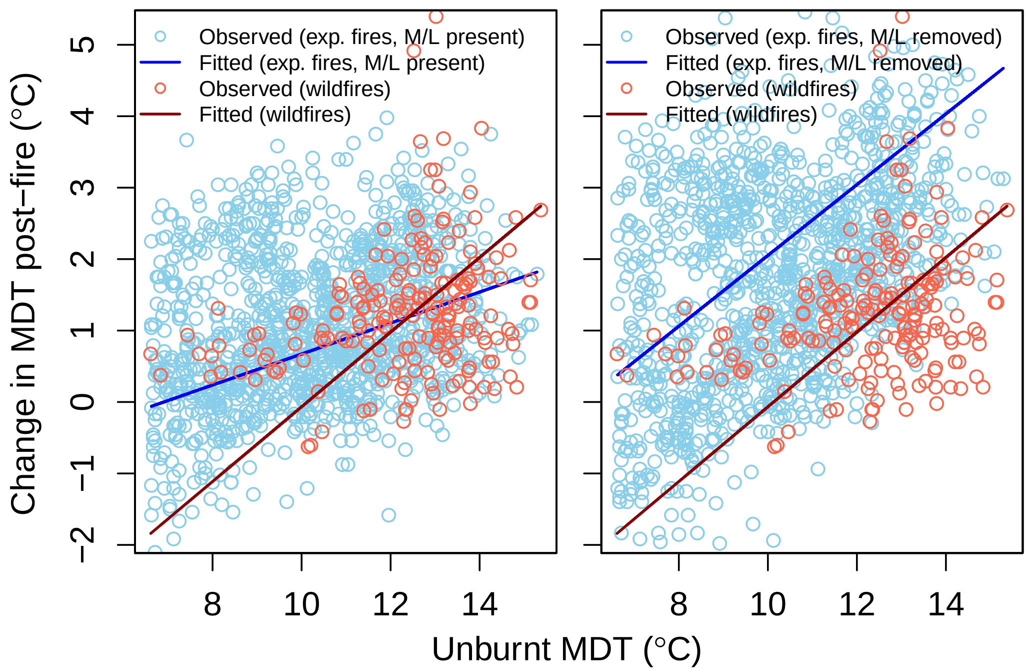

Figure 3.5: Difference in post-fire mean daily temperature (MDT) between burnt and unburnt plots in experimental fires (blue) and wildfires (red). (left) The M/L layer was unaltered in burnt plots in experimental fires; (right) the M/L layer was removed in burnt plots in experimental fires. Fitted values from linear mixed models, that included an interaction between unburnt MDT and fire type (wildfire, low severity experimental fire and high severity experimental fire, i.e. where the M/L layer was removed) and paired plot as a random effect, are also shown. Models are detailed in Appendix A.4.

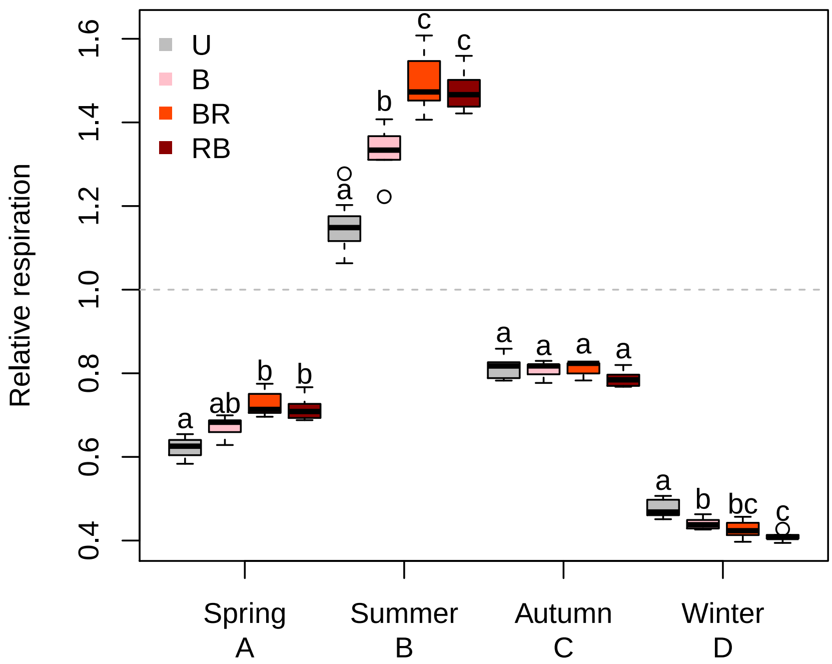

Figure 3.6: Estimates of soil respiration relative to soil respiration at 10 °C, per season and treatment (codes follow Figure 3.3). Soil respiration estimates are based on measured soil temperature using Equation 3.1 (Lloyd and Taylor, 1994). The height of the boxes indicate approximate first and third percentiles; the bar across is the median; the whiskers extend to most extreme datapoint within 1.5 times the interquartile range; circles are data outwith this range. Within each season, treatments with different lower-case letters are significantly different. Capital letters refer to overall differences between seasons ($\alpha = 0.05$).

3.4 Discussion

3.4.1 Fire-induced soil heating

The effect of removing the M/L layer was similar across all measures of fire-induced soil heating: a small increase in the response variable at 2 cm depth and a substantial increase at the top of the soil (Table 3.3). Average maximum temperatures at the top of the soil went from ca. 20 °C in burnt plots where the M/L layer was present to ca. 75 °C where it had been removed. The insulating effect of the M/L layer was also apparent from the increased heating and cooling rates in plots where the M/L layer had been removed prior to the fire. Where the M/L layer was present, soil and M/L layer moisture contents explained some of the variation in the response variables, although overall model performance was low (Table 3.5). This is possibly due to a combination of the limited range of environmental and weather conditions under which I was able to safely complete the burns and the stochastic nature of fire behaviour and fuel structures at small temporal and/or spatial scales.

Although average maximum temperatures in plots where the M/L layer was removed were above the critical threshold for damage to rhizomes (55–59 °C) and seeds (65–75 °C) for common heathland species (Granström and Schimmel, 1993), the relatively short average time above 50 °C (around a minute) suggests fire severity was unlikely to be sufficient to damage *Calluna* rhizomes and seeds (Mallik and Gimingham, 1985; Schimmel and Granström, 1996). Nevertheless, considering 90 % of viable *Calluna* seeds in shallow organic soils are located in the moss layer and first four centimeters of the soil profile (Legg et al., 1992), the increased fire-induced soil heating observed in simulated high severity plots suggests it could be an important control on post-fire vegetation response (Maltby et al., 1990; Schimmel and Granström, 1996). Furthermore, the simulated high severity plots were probably conservative estimates of high severity managed burning conditions as total fuel consumed, and the associated energy release, could be substantially higher due to consumption of the M/L layer (Davies et al., 2010b).

The severity of the fire determines not only fire-induced temperature pulses into the soil but also the post-fire substrate available for vegetation regeneration. The establishment of *Calluna* seeds may be improved when the substrate is soil rather than moss or litter (Davies et al., 2010b). Thus under high fire severity conditions that consume the M/L layer, the potentially detrimental effect on *Calluna* post-fire regeneration of greater exposure to temperature pulses could be compensated for by enhanced substrate conditions. Fire-induced seed germination cues such as temperature pulses (Whittaker and Gimingham, 1962), ash and smoke (Bargmann et al., 2014) may also be favoured under high fire severities, although regeneration would decline sharply past a certain fire severity threshold (Schimmel and Granström, 1996).

3.4.2 Post-fire soil thermal dynamics

Differences in longer-term post-fire soil thermal dynamics between treatments can be explained by three main mechanisms: (i) the removal of insulating layers (*Calluna* canopy and M/L layer) above the soil, increasing solar radiation and air movement and facilitating heat exchange between soil and atmosphere (Barclay-Estrup, 1971); (ii) decreased albedo in burnt plots, especially in burnt plots where the M/L layer was removed, due to the dark exposed soil (Chambers and Chapin, 2002); (iii) the alteration of soil moisture content, likely dependent on complex interactions between habitat, fire behaviour and weather. For example, depending on the extent of fire-induced heating and soil characteristics, fire can create a water repellent layer that reduces infiltration (Certini, 2005). A decrease in evapotranspiration and an increase in water-holding capacity of the surface soil can increase post-fire soil moisture content in heathlands, but the increased exposure of the ground surface to solar radiation and air flow can result in decreased soil moisture in the top 2 cm during dry weather (Mallik et al., 1984a; Mallik, 1986). Low post-fire soil moisture near the peatland surface (5 cm depth) can reduce the latent heat flux post-fire, resulting in large diurnal temperature variations at the soil surface (up to 1.5 cm depth) that are not substantially transmitted down into the soil profile (Kettridge et al., 2012).

Comparison of soil thermal dynamics in unburnt plots, burnt plots and burnt plots where the M/L layer was removed suggests the contribution of the combustion of the *Calluna* canopy and the removal of the M/L layer to alteration of post-fire thermal dynamics were of similar magnitude: in summer, burning increased mean daily temperature by 1.4 °C, and burning and M/L layer removal by 2.5 °C, compared to unburnt (Figure 3.4). The results indicate that soil temperature after high severity fires in which the M/L layer is consumed have both wider seasonal and diurnal ranges than after low serverity fires (Table 3.7). The similarity in soil thermal dynamics between burnt plots where the M/L layer was removed after and before the fires can be explained by the high soil moisture content (mean 417 %, max 469 %, min 336 %), which was likely to have minimised the potential for soil scorching and the formation of hydrophobic surface layers. The change in soil thermal dynamics in burnt plots resulted in warmer soil temperatures during the growing season. This effect was even greater in burnt plots where the M/L was removed.

Higher mean and maximum daily temperatures and lower minimum daily temperatures in recently burnt plots have been observed previously in peatland soils (Brown et al., 2015). The wildfires studied, although short in duration and occurring within limited range of weather conditions, show similar change in mean daily soil temperature to weather conditions than experimental fires where the M/L layer was removed (Figure 3.5). This may indicate that the combustion of the M/L layer in wildfires (Davies et al., 2016a) could be an important driver of increased alteration to post-fire soil thermal dynamics. However, further research will need to confirm this as differences in habitat and soil characteristics between the experimental and wildfires sites (e.g. soils were generally deeper in the wildfires sites), as well as differences in weather not accounted for by the model (solar radiation and precipitation), may also have contributed to differences in post-fire soil thermal dynamics.

3.4.3 Soil respiration estimates

The observed changes in soil thermal dynamics after fire may have significant implications for soil carbon dynamics (Figure 3.6). Differences between treatments were statistically significant during the summer, when soil respiration is at its greatest (Falge et al., 2002). During the summer, modelled relative soil respiration in burnt plots where the M/L layer was removed was higher than in burnt plots where the M/L layer remained. Therefore, a temperature-driven increase in soil respiration (Blodau et al., 2007; Dorrepaal et al., 2009) could result from high severity fires where the M/L layer is consumed. However, the soil respiration estimates provided here should be treated with care, as the effect of fire severity on altering soil temperature is superimposed on the effects of changes in moisture content and vegetation community composition, important in controlling soil carbon dynamics (Curiel-Yuste et al., 2007). The sometimes conflicting results on the effect of vegetation on soil respiration indicate mechanisms are complex and not fully understood. For example, vascular plants can increase peatland soil respiration under warm conditions (Ward et al., 2013; Walker et al., 2016), whilst the inhibitory action of phenolics associated with shrubs has been reported to lower soil respiration (Wang et al., 2015). Community response to fire severity is therefore likely to be an important driver of carbon dynamics in *Calluna* heathlands, and could be key in determining the fate of large quantities of carbon stored in northern soils where higher severity fires are projected.

3.5 Conclusions

I found that the M/L layer plays a critical role in controlling fire severity in *Calluna* heathland fires. Fire-induced soil heating increased significantly in the absence of the M/L layer overlaying the soil, although, due to high soil moisture content, temperatures remained at the lower end of those that could damage plant tissue. Post-fire soil thermal dynamics differed between levels of simulated fire severity. Thus with higher severity fires, where the M/L layer is consumed, soils may be warmer during summer with greater seasonal and diurnal temperature variation. Burning under higher fire severity conditions that leads to the consumption of the M/L layer could be associated with trade-offs in relation to vegetation regeneration: while higher temperature pulses could damage plant tissue and seedlings, improved substrate conditions, warmer soils during the vegetative growing season and stronger fire-induced germination cues could facilitate the reestablishment of *Calluna* and other heathland species. The altered soil microclimate may increase soil respiration in the first years following burning. However, further information on effects of the severity of fires on below and above ground processes, including vegetation community response, is required to understand long-term consequences of a changing fire regime on the overall carbon balance. Managed burning aiming to rejuvenate *Calluna* heathlands whilst minimising soil carbon losses should keep fire severity low to avoid consumption of the M/L layer by burning when the moisture content of the soil and the M/L layer are high.

Chapter 4

Consumption of the moss and litter layer during high severity fires controls community response in *Calluna* heathlands

Abstract

Climate change may lead to higher severity fires in northern regions. Such altered fire regime could result in changes to the vegetation community composition of *Calluna* heathlands, with potential implications for ecosystem services such as conservation value, water supply and soil carbon storage. Mechanisms influencing post-fire vegetation regeneration are not fully understood. In particular, our understanding of the relative importance of direct fire effects (seed and plant tissue mortality and stimulation of seed germination due to heating, smoke and ash effects) and altered post-fire environment (changes in microclimate and in the seedbed structure) in controlling post-fire regeneration is incomplete. I completed a field experiment in which I achieved a range of severity disturbances in 1 × 1 m plots by a combination of fuel manipulation (cutting the *Calluna* canopy, removing the moss and litter layer) and burning. I recorded frequency and cover of vegetation species three growing seasons after the experimental fires, and found that changes in the seedbed and microclimate associated with higher severity fires in which the moss and litter (M/L) layer is consumed were of primary importance in controlling community response by promoting vascular plants, including dominant ericoids. In low severity burnt plots abundance of vascular plants and acrocarpous mosses was higher than in cut plots, where pleurocarpous mosses were dominant. Higher fire severity plots showed decreased abundance of vascular plants and increased abundance of bryophytes. My results highlight the crucial role of the seedbed in controlling post-fire vegetation regeneration and suggest that community composition after higher severity fires is a result of contrasting mechanisms: replacement of the M/L layer by bare soil as seedbed can promote vascular plants, but high temperature pulses into the ground can damage vegetative and seedling regeneration and favour bryophytes.

4.1 Introduction

Managed burns in *Calluna* heathlands usually involve low to moderate severity conditions. These include fast-spreading fires that move through the *Calluna* canopy whilst the high moisture content of the moss and litter (M/L) layer prevents it from igniting, minimising below-ground soil heating (Davies et al., 2009, 2010b). Under such conditions post-fire *Calluna* regeneration is predominantly via vegetative growth from accessory buds on stem bases (Mallik and Gimingham, 1983; Clarke et al., 2013) in stands young enough to resprout (approximately < 20 years), and from seeds in older stands (Hobbs and Gimingham, 1984b). Seeds and stem bases are often protected from lethal temperatures during a fire by the M/L layer (Chapter 3; Mallik and Gimingham, 1983; Schimmel and Granström, 1996). However, *Calluna* heathlands are also subjected to wildfires. While management fires are limited to the colder and wetter months and cover small areas, wildfires tend to occur in spring and summer, are usually greater in extent (Legg et al., 2007) and can have higher fire severities (Davies et al., 2016a). Such fires can damage the stem bases of heathland species and then regeneration from seed becomes dominant (Legg et al., 1992; Schimmel and Granström, 1996).

Fire effects can promote seedling germination and establishment of key heathland species. Mechanisms include the breaking of dormancy by fire-induced temperature pulses (Whittaker and Gimingham, 1962), chemicals in ash and smoke (Bargmann et al., 2014), changes in soil diurnal temperature fluctuations (Thompson and Grime, 1983) and the fertilization effect of ash (Evans and Allen, 1971; Strømgaard, 1992). In higher severity fires where the M/L layer is consumed, seedling establishment may also increase due to the exposure of bare soil, which provides an improved seedbed compared to the M/L layer (Mallik et al., 1984a; Hullu and Gimingham, 1984; Schimmel and Granström, 1996; Davies et al., 2010b). However, seed germination decreases past a certain fire severity threshold (Maltby et al., 1990; Legg et al., 1992). For example, *Calluna* germination has been observed to decrease when seeds are exposed to 120 °C for 1 minute, 160 °C for 30 seconds (Whittaker and Gimingham, 1962) and 60 °C for 10 minutes (Granström and Schimmel, 1993).

Projected climate change in northern Europe could alter fire regimes and potentially lead to a change in community composition in *Calluna* heathlands that may affect ecosystem services (*sensu* Millenium Ecosystem Assessment, 2005, including water provision, climate regulation and recreation). In particular, high severity wildfires can fundamentally alter the vegetation community composition of *Calluna* heathlands (Maltby et al., 1990; Legg et al., 1992). Increased fire severity could have an important effect on conservation value and, given the importance of vegetation on controlling soil carbon dynamics (Gray et al., 2013; Ward et al., 2013; Armstrong et al., 2015; Wang et al., 2015; Walker et al., 2016), altered post-fire successional trajectories could also result in long-term changes to the substantial amount of carbon stored in heathland soils (Bradley et al., 2005; Ostle et al., 2009).

Despite the fact that there have been a number of studies on post-fire vegetation response of *Calluna* heathlands, our understanding of the relative importance of the controlling mechanisms involved is incomplete. In particular, the extent to which the direct effects of fire (fire-induced temperature pulses, germination effects of ash and smoke, and fertilization effects) and the indirect change to environmental conditions (altered seedbed and microclimate) are responsible for post-fire vegetation regeneration is unclear. To study this I completed a field experiment in which I generated different disturbance severities through combinations of burning, cutting the *Calluna* canopy and removing the M/L layer. My specific objectives were to: (i) investigate the relative importance of direct fire effects and altered post-fire environment in controlling community composition following low and higher severity fires; and (ii) study the relative importance of the regeneration strategies of resprouting and seed germination in ericoid species along a fire severity gradient.

4.2 Materials and methods

4.2.1 Experimental design and measurements

I used the non-destructive FuelRule technique (Davies et al., 2008b) to assess pre-fire vegetation structure in plots inside the burn area, taking three to five measurements in each plot. Before the fires I performed fuel treatments in 1 × 1 m plots within the burn area and, immediately following each fire, in an area adjacent that remained unburnt (Figure 4.1). Inside the designated burn area I established the following treatments: (i) burnt plots, (ii) burnt plots where the M/L layer was removed after the fire and (iii) burnt plots where the M/L layer was removed before the fire. In unburnt areas (opposite the prevailing wind direction during the fire to avoid smoke effects) the following treatments were set up: (iv) untreated controls, (v) plots where the *Calluna* canopy was cut and removed (vi) plots where the *Calluna* canopy was cut and the M/L layer removed. M/L layer removal was performed manually down to the top of the O-horizon, and the *Calluna* canopy was cut with secateurs aiming to mimic canopy removal by burning, i.e. leaving the plants'

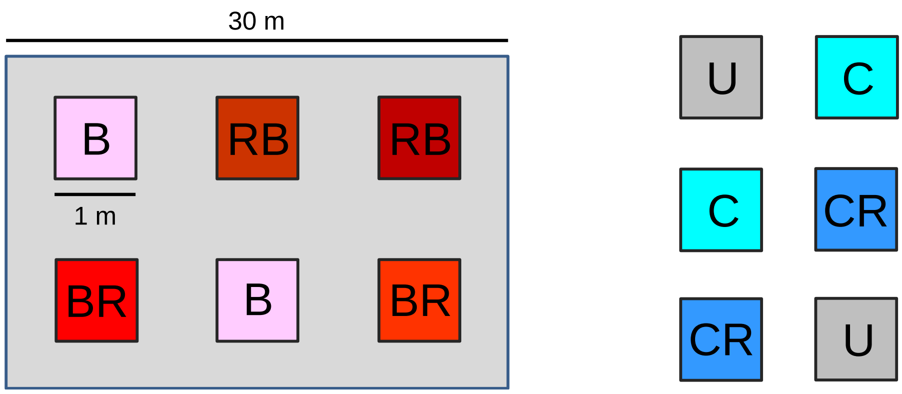

Figure 4.1: Diagram of the experimental design, showing the distribution of the plots in one of seven fires. The different treatments are represented by codes: unburnt controls (U), plots where the *Calluna* canopy was cut (C), plots where the *Calluna* canopy was cut and the M/L layer removed (CR), burnt plots (B) and burnt plots where the M/L layer was removed after (BR) or before the fire (RB).

woody stems (Figure 4.2). Two plots of each treatment were set up per fire. I tested the relative importance of direct fire effects and altered environment on community response in *Calluna* heathlands by comparing different plot-scale treatments (Table 4.1).

Seven experimental fires were burnt as head fires (i.e. with the prevailing wind direction) between the 12th and 26th of April 2013, each covering an area of approximately 30 × 25 m. Thermocouple loggers recorded fire-induced soil heating at the soil surface (i.e. below the M/L layer in plots where it was not removed) and 2 cm below the soil surface. Soil heating was significantly higher where the M/L layer was removed, at both depths of measurement (see Section 3.3.1 for details).

I surveyed vegetation using a 0.25 m^2 quadrat with 25 0.01 m^2 sub-quadrats placed centrally in each plot. I recorded presence/absence of all species in each sub-quadrat and visually estimated species cover for the whole quadrat. Dominant dwarf shrub species *Calluna*, *E. cinerea* and *E. tetralix* were recorded by plant form (seedling, resprout or mature plant). Presence/absence and cover data were also recorded for terricolous lichens (as a group), dead moss, litter and duff. I surveyed all plots in six of the

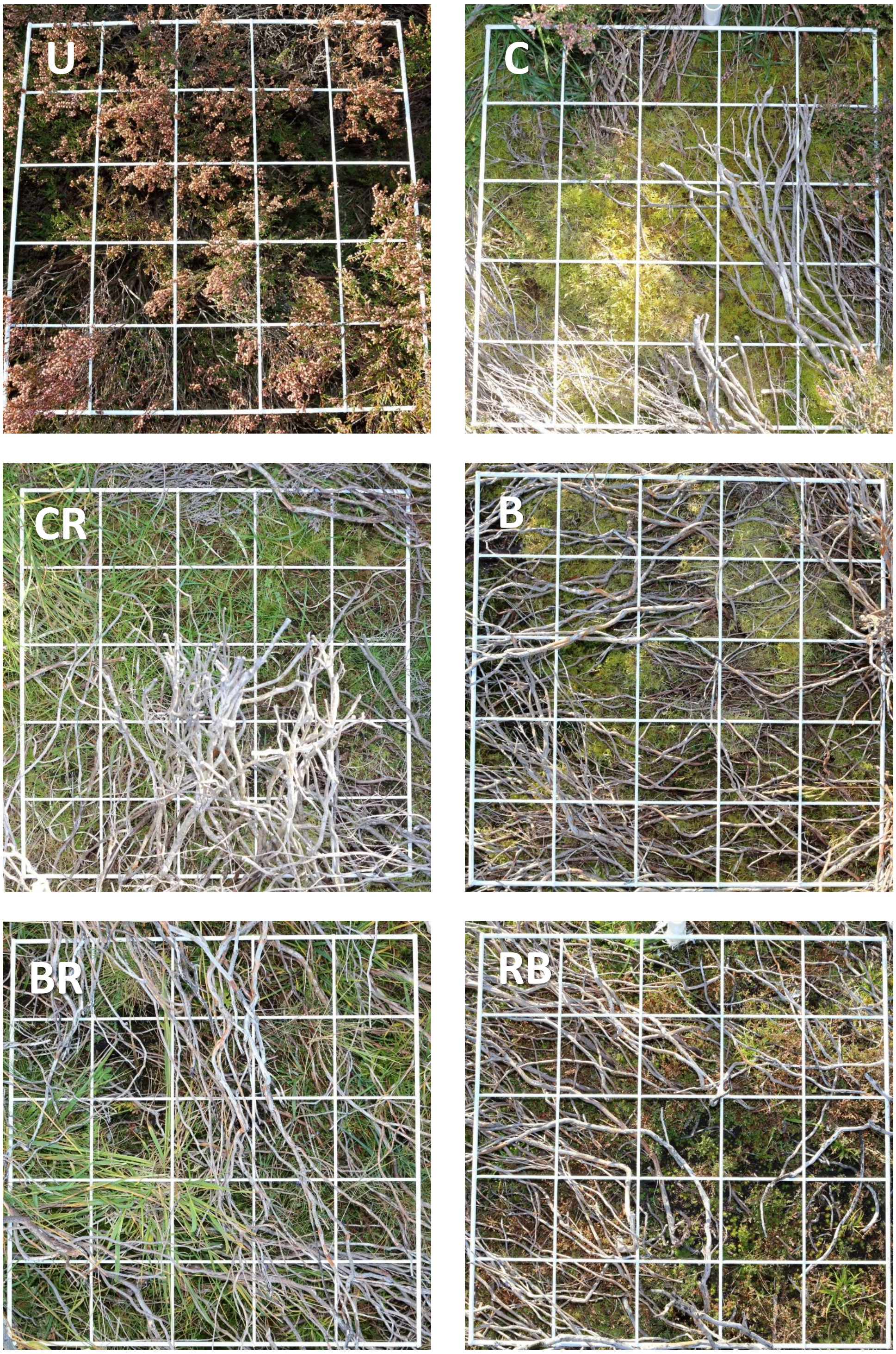

Figure 4.2: Examples of different treatment plots in a single fire. The 0.5 × 0.5 m quadrat was placed centrally in each 1 × 1 m plot. Treatment codes follow Figure 4.1.

Table 4.1: Treatment comparisons that helped investigate each general objective of the study. Treatments were unburnt controls, plots where the *Calluna* canopy was cut, plots where the *Calluna* canopy was cut and the moss and litter (M/L) layer removed, burnt plots and burnt plots where the M/L layer was removed after or before the fire.

Question	Unburnt	Cut	Cut, M/L removed	Burnt	Burnt, M/L removed	M/L removed, Burnt
1.) What is the relative importance of direct fire effects and altered environment on vegetation regeneration following low severity fires?	×	×		×		
2.) What is the relative importance of direct fire effects and altered environment on vegetation regeneration in higher severity fires?			×		×	×
3.) What factors control the mechanisms of regeneration of *Calluna* heathland shrubs?	×	×	×	×	×	×

seven fires ($n = 72$) in October 2015, at the end of the third growing season following the treatments. It was not possible to survey the remaining fire due to standing water covering approximately two thirds of the plots.

4.2.2 Data analysis

Community composition

Comparison of vegetation community composition between treatments was based on three non-metric multidimensional scaling (NMDS) analyses with different subsets of the abundance data. These included: (i) all treatments, (ii) only low severity disturbance treatments (unburnt, cut and burnt plots) and (iii) only high severity disturbance treatments (cut plots where the M/L layer was removed and burnt plots where the M/L layer was removed after or before the fire). With the complete dataset I aimed to understand overall changes in community composition caused by the different treatments. However, given some treatments involved removal of the M/L layer, differences in the bryophyte community composition were likely to dominate the ordination and potentially mask the effect of the variation in disturbance severity on vascular plants. Moreover, in these cases statistical testing of differences in community composition between the different treatments was not possible since the abundance of bryophytes was included both as a response variable and as an explanatory variable (treatment). Therefore I used the restricted analyses to separately examine variation in community composition in low and in high severity disturbance treatments.

R 3.2.2 (R Core Team, 2015) was used for all data analysis and plotting. I summed sub-quadrat species presences/absences in each quadrat to obtain a measure of frequency at the plot level. In order to aid interpretation, and since my interest was in general trends of community response to treatments, I excluded seven rare species, defined as those occurring in less than 5 % of plots, from analysis (see Appendix B.1). I standardized both the frequency and the cover data by first dividing by species maxima and then by site totals (Wisconsin double standardization, Bray and Curtis, 1957). Analysis of standardized data allowed to focus on relative changes in species by neutralizing the influence of overall species abundace (Jackson, 1997). I calculated a matrix of compositional dissimilarities between samples following Bray and Curtis (1957), a robust dissimilarity index (Faith et al., 1987), using the "vegdist" function in the package *vegan* (Oksanen et al., 2015). NMDS ("metaMDS" and related plotting functions in *vegan*) was used to visualize the effect of treatment on post-disturbance vegetation composition. NMDS represents high-dimensional relationships between species and plots in a reduced number of dimensions, producing ordination diagrams that arrange species and plots along axes of variation. NMDS makes no assumptions about the underlying model of species distribution, unlike other indirect gradient analysis techniques such as Principal Components Analysis (linear) and Detrended Correspondence Analysis (unimodal) (Lepš and Šmilauer, 2003) and so it is considered a robust method that can perform particularly well in graphical analysis (Ruokolainen and Salo, 2006). I constructed the ordination diagrams with plots grouped by treatment level and fitted environmental variables onto the species ordination using "envfit" in *vegan*. Environmental variables included the factor treatment and the following covariates describing pre-disturbance vegetation: height (and its standard deviation), density and bulk density of the *Calluna* canopy. Given I only measured pre-disturbance vegetation covariates in plots within the burnt area, I used a fire-level average for both plots within and outside the burnt area in each fire.

I used permutational multivariate analysis of variance (PERMANOVA) to test for differences in community composition, both in terms of frequency and cover, among treatment levels. PERMANOVA was performed on (i) dissimilarity matrices including only low severity disturbance treatments; and (ii) dissimilarity matrices including only high severity disturbance treatments. I used the function "adonis" in *vegan* to perform the four separate PERMANOVA on the frequency and cover dissimilarity matrices, specifying that permutations be constrained within the levels of the "fire" factor variable (including both plots within the burnt area and associated plots outside it) to account for the nested structure of the data. In order to investigate differences in community composition between pairs of treatment levels, I subsetted the dissimilarity matrices and performed PERMANOVA for all pairwise comparisons within each analysis, adjusting the significance level following a Bonferroni correction. PERMANOVA has been shown to be sensitive to heterogeneity of group dispersions (variance), i.e. statistically significant differences between two groups can be due both to differences in dispersion in composition and to different community compositions (Anderson and Walsh, 2013). Differences in within-group heterogeneity, an indicator of beta diversity (extent of change in community composition in an environment; Jost, 2007), were investigated using the function "betadisper" in *vegan* and the Tukey HSD method.

Mechanisms of regeneration

Plant form (seedling, resprout or mature plant) was recorded for *Calluna*, *E. cinerea* and *E. tetralix* in order to examine the effects of fire on mechanisms of regeneration of dominant heathland shrubs. Generalised linear mixed effects models (function "glmer" in *lme4*, Bates et al., 2015) with a poisson distribution and a square root link function were used to analyse *Calluna* frequency. The models included an interaction between treatment and plant form as fixed effects and fire as a random effect. I tested for statistical differences between pairs of treatments following multiple comparisons procedures (Hothorn et al., 2008). Cover data, as well as frequency data for *E. cinerea* and *E. tetralix*, had a large amount of zeros and could not be adequately modelled. Analysis was restricted to qualitative description of patterns seen in boxplots.

4.3 Results

I identified 23 different species. Some plants could not be identified and were recorded as distinct taxonomic units. These included one *Carex* species, a lichen species and a sedge (Cyperaceae) (Table 4.3).

For all NMDS ordinations, a three-dimension solution was selected as optimal given the substantial reduction in stress compared to two dimensions and the subsequent relatively small reduction with higher dimensions (Appendix B.2). Final NMDS stress values ranged between 0.11 and 0.14, which are considered to indicate an adequate representation of the community composition (McCune et al., 2002). Since both frequency and cover ordinations showed similar patterns, I focused on ordination diagrams of the frequency data because of the higher accuracy of its sampling methodology. Three-dimension ordination diagrams of frequency and cover data can be found in Appendices B.3 to B.5.

The ordination including all treatments showed overall changes in community composition in response to a range of disturbance severity (Figure 4.3). The first axis of the ordination was related to the disturbance severity gradient imposed by the different treatments. Low severity disturbance treatments included unburnt controls and cut plots, and were associated with high frequencies of pleurocarpous mosses. The low group dispersion (variance) of control plots indicate that pre-disturbance community composition was relatively homogenous. High severity disturbance treatments included plots where the M/L layer was removed, either in combination with cutting or with burning. These treatments were associated with higher frequencies of acrocarpous mosses, such as *Dicranum scoparium* Hewd. and *Polytrichum juniperinum* Hewd., and vascular plants, including ericoids e.g. *Vaccinium myrtillus* L., graminoids e.g. *F. ovina* and forbs e.g. *Potentilla erecta* Raeuschel. Where the M/L layer was removed, cutting and burning, irrespective of whether the M/L layer was removed after or before the fire, produced similar community response. Burnt plots where the M/L layer was not removed occupied an intermediate position in the disturbance gradient. The second ordination axis

Table 4.2: List of species, plant groups and substrate types identified. Life form follows Hill et al. (2007) for bryophytes and Hill et al. (2004) for vascular plants; "hc" are hemicriptophytes; "Ch" are chamaephytes. Average frequency, based on the presence/absence data, and average cover across all treatments and fires is also shown.

Group	Species	Code	Life form	% Frequency	% Cover
Ericoids	*Calluna vulgaris*	Ca.vu	Ch	49.3	20.0
	Erica cinerea	Er.ci	Ch	7.6	1.3
	Erica tetralix	Er.te	Ch	6.7	0.8
	Vaccinium vitis-idaea	Va.vi	Ch	3.5	0.4
	Vaccinium myrtillus	Va.my	Ch	2.6	0.2
Graminoids	*Carex spp.*	Carex	hc	34.1	8.6
	Festuca ovina	Fe.ov	hc	23.4	8.8
	Cyperaceae unidentified	gram1	hc	0.8	0.2
Forbs	*Potentilla erecta*	Po.er	hc	8.3	0.7
	Galium saxatile	Ga.sa	hc	4.1	0.3
Pleurocarps	*Hypnum jutlandicum*	Hy.ju	Mat	70.3	29.3
	Plagiothecium undulatum	Pl.un	Mat	15.2	0.7
	Hylocomium splendens	Hy.sp	Weft	10.8	0.4
	Pleurozium schreberi	Pl.sh	Weft	9.6	2.4
	Brachythecium rutabulum	Br.ru	Mat	3.2	1.1
	Rhytidiadelphus squarrosus	Ry.sq	Weft	1.9	0.2
Acrocarps	*Campylopus introflexus*	Ca.in	Tuft	21.6	0.5
	Polytrichum juniperinum	Po.ju	Turf	15.4	1.6
	Dicranum scoparium	Di.sc	Tuft	14.8	0.7
	Ceratodon purpureus	Ce.pu	Turf	7.8	0.3
	Campylopus flexuosus	Ca.fl	Tuft	2.7	0.3
Liverworts	*Calypogeia muelleriana*	Ca.mu	Mat	2.8	0.2
	Cephalozia bicuspidata	Ce.bi	Mat	1.5	0.2
	Scapania gracilis	Sc.gr	Weft	1.2	0.08
	Lophocolea bidentata	Lo.bi	Weft	0.5	0.06
Lichen	Lichen	lichen		1.3	0.1
Litter	Litter	litter		27.7	15.2
	Pleurocarp dead	dead.pl		2.7	0.5
Duff	Duff/soil	duff		37.3	17.4

was related to pre-disturbance vegetation structure. Pleurocarpous mosses, liverworts, graminoids and forbs were more abundant in plots where the pre-disturbance vegetation height had been higher, while the opposite was true for acrocarpous mosses and ericoids.

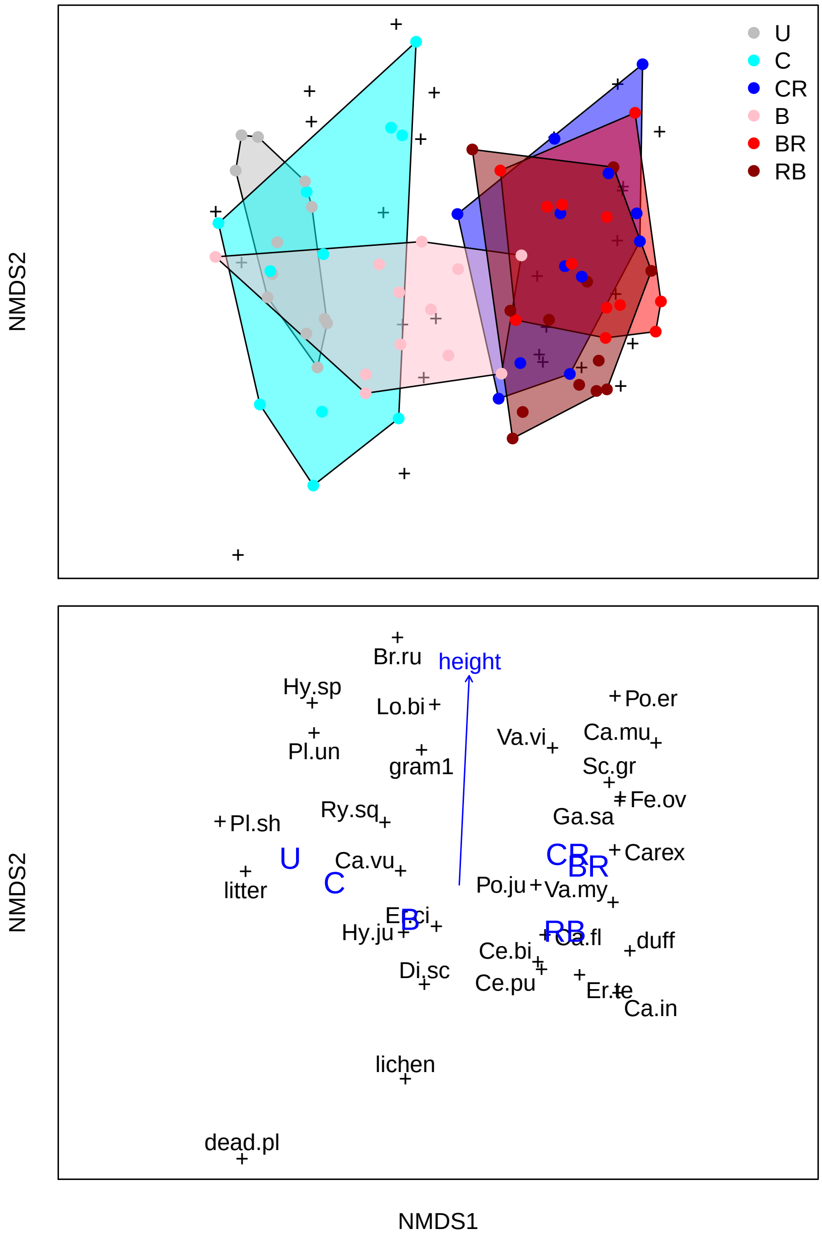

Figure 4.3: NMDS ordination diagrams of the frequency data displaying all treatments in axes 1 and 2. (top) ordination of plots grouped by treatment (U: unburnt; C: cut; CR: cut, M/L layer removed; B: burnt; BR: burnt, M/L layer removed after the fire; RB: burnt, M/L layer removed before the fire); species indicated by "+". (bottom) species ordination (codes follow Table 4.3) with centroid (averages) of treatment levels and direction of correlation with *Calluna* height. Ordination stress was 0.13. 3-D diagrams can be found in Appendix B.3.

4.3.1 Community response to low disturbance severity treatments

The ordination of unburnt, cut and burnt plots showed a first axis related to severity of disturbance and a second axis related to pre-disturbance vegetation structure (Figure 4.4). Graminoids (*Carex sp.*, *F. ovina*), forbs (*V. myrtillus*, *V. vitis-idaea*) and regenerating *Calluna* were more frequent in burnt plots, while cut plots were predominantly associated with pleurocarpous mosses (*H. jutlandicum*, *R. squarrosus*). Taller pre-disturbance vegetation seemed to promote forbs and grasses.

PERMANOVA indicated significant differences in community composition between treatments, both for frequency (pseudo-F = 1.58, p-value = 0.001) and cover (pseudo-F = 1.57, p-value = 0.013). Pairwise comparisons revealed differences between all pairs of treatment levels were statistically significant, both in terms of frequency and cover (Table 4.3). Analysis of group dispersion showed weak evidence of differences in frequency between treatments (pseudo-F = 3.15, p-value = 0.056). Cut plots had the highest dispersion, which was statistically different from that of unburnt plots. Dispersion in cut plots was associated with the second ordination axis (pre-disturbance vegetation structure) rather than the first (disturbance gradient), as were burnt plots. Details of PERMANOVA and of tests of homogeneity of group dispersion are provided in full in Appendix B.6.

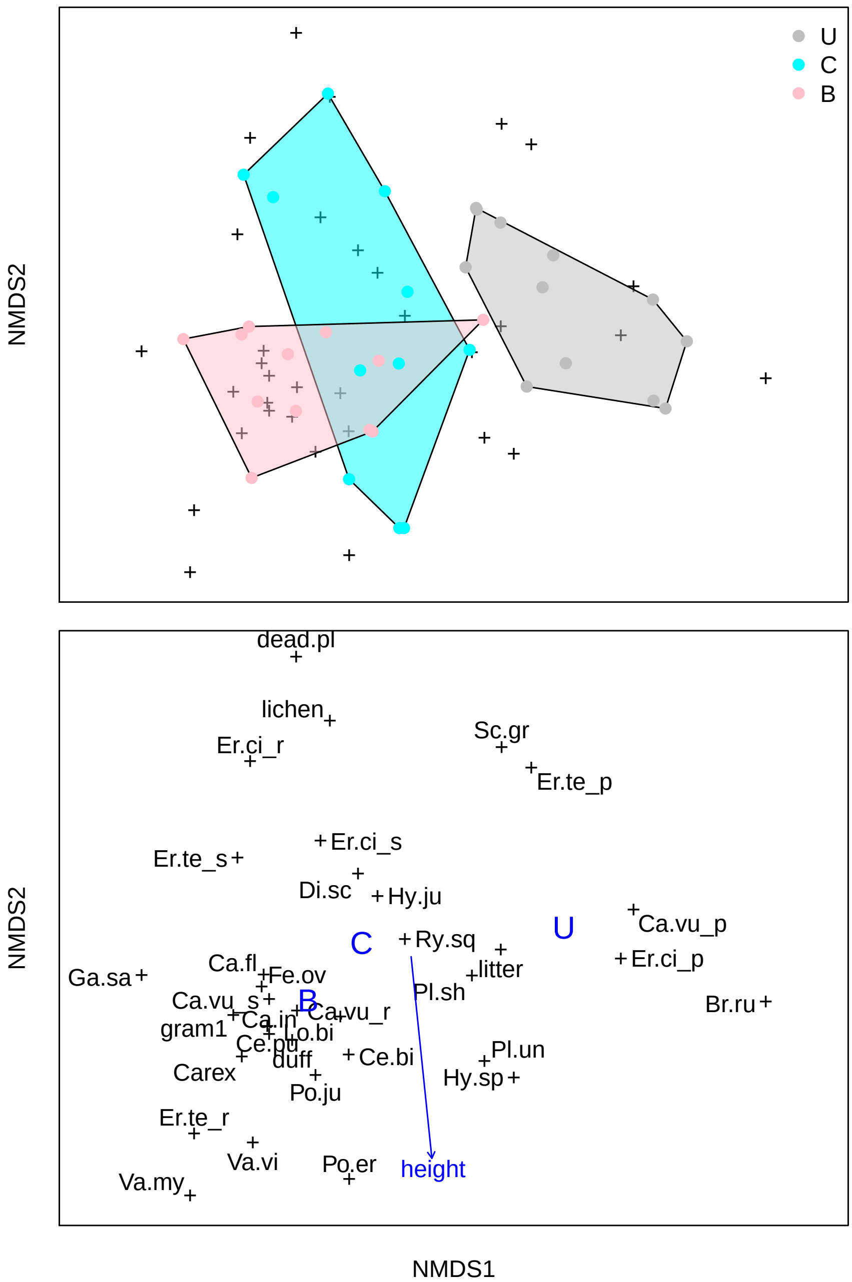

Figure 4.4: NMDS ordination diagrams of the frequency data displaying plots and plant species in axes 1 and 2. (top) ordination of plots grouped by treatment (U: unburnt; C: cut; B: burnt); species indicated by "+". (bottom) species ordination (codes follow Table 4.3) with centroid (averages) of treatment levels and direction of correlation with *Calluna* height. Ordination stress was 0.13. 3-D diagrams can be found in Appendix B.4.

Table 4.3: Differences in dissimilarity in community composition and in group (treatment) dispersion between unburnt (U), cut (C) and burnt (B) plots, and between cut where the M/L layer was removed (CR) and burnt plots where the M/L layer was removed after (BR) or before the fire (RB). Within each column and severity disturbance level, treatments not sharing letters indicate significant differences ($\alpha = 0.05$).

	Frequency		Cover	
	Dissimilarity	Dispersion	Dissimilarity	Dispersion
Low severity disturbance (M/L layer present)				
U	a	a	a	a
C	b	b	b	a
B	c	ab	c	a
High severity disturbance (M/L layer removed)				
CR	a	a	a	a
BR	ab	a	b	a
RB	b	a	b	a

4.3.2 Community response to high disturbance severity treatments

The ordination of cut and burnt plots where the M/L layer was removed showed a first axis related to pre-disturbance vegetation structure and a second axis related to severity of disturbance (Figure 4.5). The ordination indicated a large similarity in the community response to cutting and to burning before the removal of the M/L layer. Cut plots where the M/L layer was removed and burnt plots where the M/L layer was removed after the fire presented higher frequency of vascular plants. Burnt plots where the M/L layer was removed before the fire had high frequencies of pleurocarpous and acrocarpous mosses. In contrast, ordination of the cover data showed high cover values of regenerating ericoids in burnt plots where the M/L layer was removed before the fire (Appendix B.5). Higher pre-disturbance vegetation height was associated with high frequency of forbs and graminoids. Ericoids and pleurocarpous and acrocarpous mosses were more frequent where pre-disturbance vegetation height was lower.

Differences in community composition between treatments were statistically significant, both for frequency (pseudo-F = 1.58, p-value = 0.001) and cover (pseudo-F = 1.57, p-value = 0.013). Pairwise comparisons showed significant differences in community composition between cut and burnt plots (cover), and between cut and burnt plots where the M/L layer was removed before the fire (frequency) (Table 4.3). Differences in group dispersion were not statistically significant. Full details of PERMANOVA and of tests of homogeneity of group dispersion are provided in Appendix B.6.

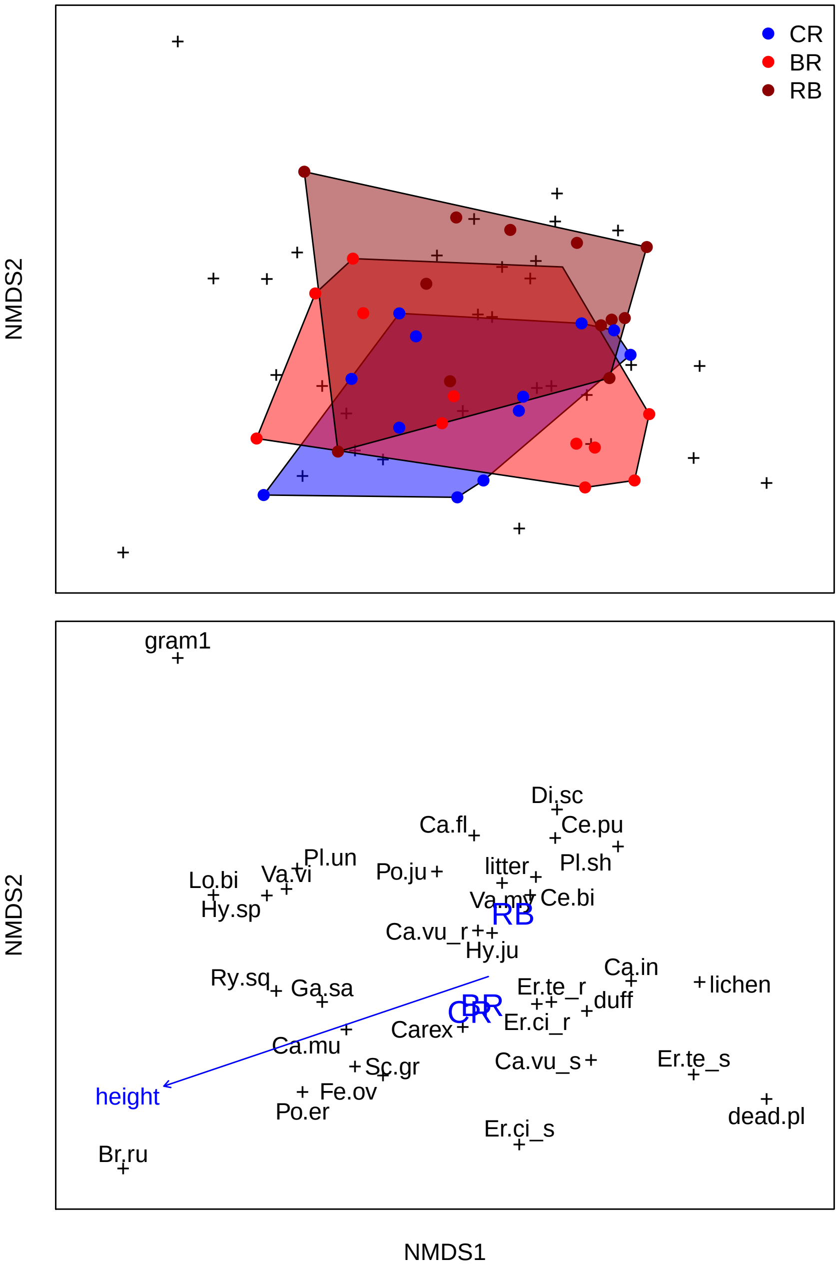

Figure 4.5: NMDS ordination diagrams of the frequency data displaying plots and plant species in axes 1 and 2. (top) ordination of plots grouped by treatment: cut plots where the M/L layer was removed (CR) and burnt plots where the M/L layer was removed before (BR) or after (RB) the fire; species indicated by "+". (bottom) species ordination (codes follow Table 4.3) with centroid (averages) of treatment levels and direction of correlation with *Calluna* height. Ordination stress was 0.13. 3-D diagrams can be found in Appendix B.5.

4.3.3 Mechanisms of regeneration in dominant dwarf shrubs

Calluna resprouts were most frequent in plots where the M/L layer was removed, with no significant differences between plots where the vegetation was also burnt or cut (Figure 4.6). Moreover, there was no significant difference between burnt plots where the M/L layer was removed after or before the fire (tests of pairwise differences in frequency of *Calluna* resprouts between treatments are provided in Appendix B.7). In contrast, *E. cinerea* resprouts were most frequent in cut plots, while *E. tetralix* resprouts were highest in burnt plots where the M/L layer was removed, with no difference between burnt plots where the M/L layer was removed after or before the fire.

The highest cover of *Calluna* resprouts was observed in burnt plots where the M/L was removed, with no apparent difference between plots where the M/L layer was removed before or after the fire. Cover of *E. cinerea* and *E. tetralix* resprouts and seedlings was negligible across all treatments.

Calluna seedlings were most frequent in cut plots where the M/L layer was removed (z-value = 4.74, p-value < 0.001 for the difference with burnt plots where the M/L layer was removed before the fire, the treatment where frequency was second highest). *E. cinerea* seedlings were also most frequent in cut plots where the M/L layer was removed, while frequency of *E. tetralix* seedlings were only important in the two burnt treatments, especially where the M/L layer was removed before the fire.

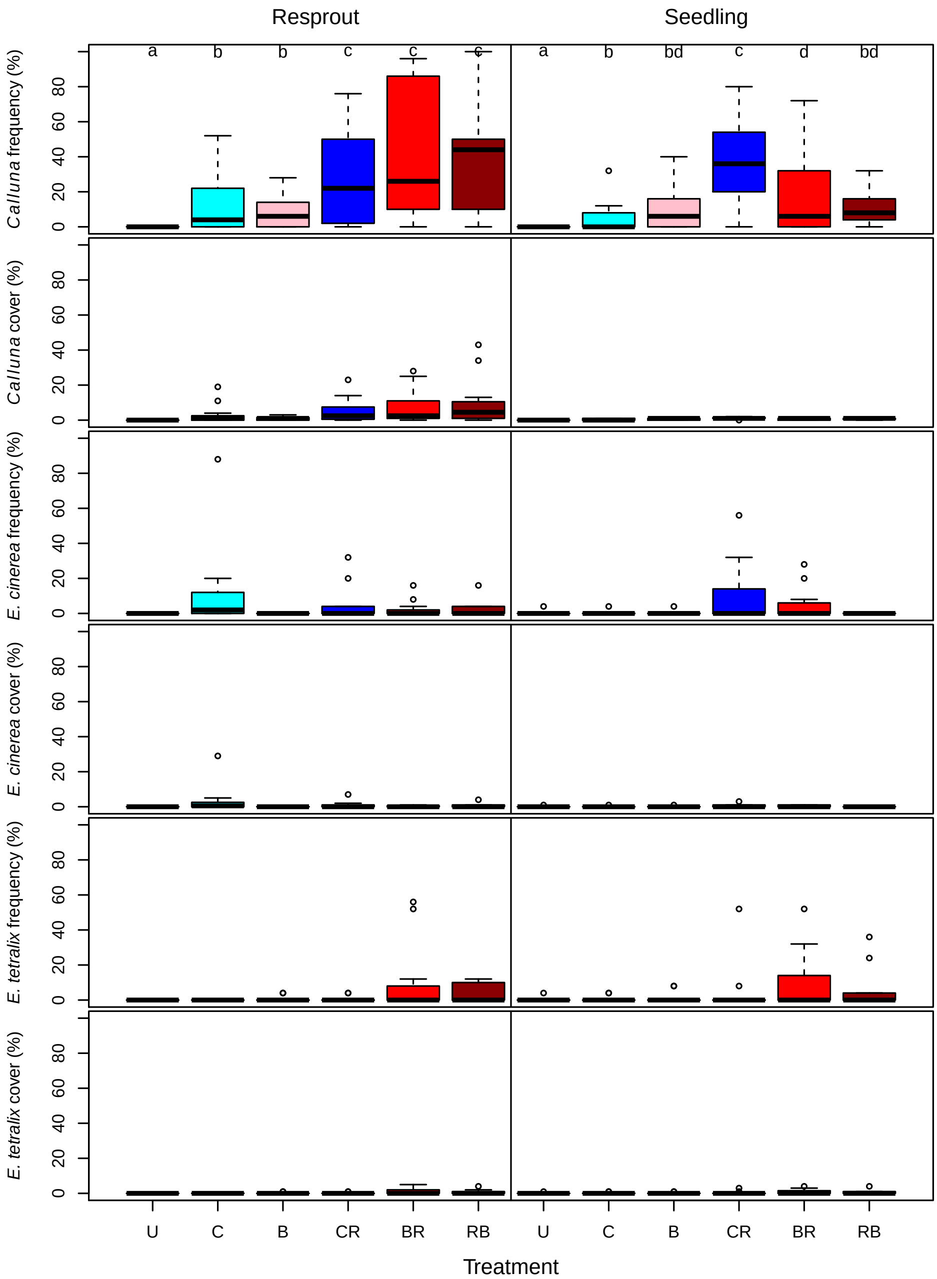

Figure 4.6: Distribution of the percentage frequency and cover data of *Calluna*, *E. tetralix* and *E.cinerea* resprouts and seedlings for each treatment (unburnt, U; cut, C; burnt, B; cut where the M/L layer was removed, CR; burnt where the M/L layer was removed after the fire, BR; burnt where the M/L layer was removed before the fire, RB). Same letters within life form in *Calluna* frequency indicate differences in frequency between treatments are not statistically significant ($\alpha = 0.05$). Test details are provided in Appendix B.7.

4.4 Discussion

4.4.1 Community response to low disturbance severity treatments

Ordination of unburnt, cut and burnt plots was related to a gradient of disturbance severity, with unburnt plots at one end of the NMDS axis 1 and burnt plots at the other (Figure 4.4). Most species had higher frequencies at higher disturbance severities. Besides mature ericoids, only two bryophytes, *Scapania gracilis* Lindb. and *Brachythecium rutabulum* (Hedw.) Schimp., were strongly associated with unburnt plots. In comparison, a high number of pleurocarpous mosses were associated with cut plots, and burnt plots presented high frequencies of forbs, graminoids and regenerating ericoids. The removal of the *Calluna* canopy, both in burnt and in cut plots, may have improved availability of resources (e.g. more light, lower competition for nutrients) and allowed a variety of species to establish. The large number of species with high frequency values in burnt plots may have arisen from small-scale changes to substrate structure and microclimate resulting from the large stochasticity of fire behaviour at small spatial scales (Fernandes et al., 2000; Bova and Dickinson, 2008; Davies et al., 2010b), thus creating adequate habitat for a large number of species. This is supported by the fact that burnt plots were dispersed along the first axis of the ordination (related to a disturbance severity gradient) rather than the second axis (pre-disturbance vegetation structure) as were cut plots.

The high abundance of pleurocarpous mosses in cut plots was merely a function of their pre-disturbance cover. Conversely, burnt plots had higher abundance of acrocarpous mosses. Many acrocarpous mosses follow a “colonist” strategy characterised by short life spans, a high reproductive effort and a short age of first reproduction (During, 1979). Life strategies characteristic of pleurocarpous mosses favour constant environments and result in dominance in the later stages of *Calluna* heathlands development (Hobbs et al., 1984; Hobbs and Legg, 1984; Burch, 2013). Therefore, the higher abundance of acrocarpous mosses in burnt plots when compared to cut plots could be a result of the more severe disturbance associated with burning and subsequent mortality of pleurocarps. The difference in community composition between cut and burnt plots suggests that direct fire effects of the fire (temperature pulses into the ground, germination cues from smoke and ash) in burnt plots had an additional effect over and above the altered microclimate from the removal of the *Calluna* canopy (Table 4.3).

Together with the disturbance severity gradient, pre-disturbance *Calluna* height was an important factor explaining variation in community composition. Pre-disturbance *Calluna* height relates to its developmental phase (Kayll and Gimingham, 1965), which has important implications for post-fire vegetation regeneration, first because it determines species composition (Hobbs and Legg, 1984; Harris et al., 2011), and second because the capacity of *Calluna* to regenerate vegetatively declines at the mature phase (ca. 15 years) (Miller and Miles, 1970; Hobbs and Gimingham, 1984b; Davies et al., 2010b). I found higher frequencies of forbs and graminoids in plots where the pre-disturbance *Calluna* canopy was taller. This was also observed by Hobbs and Gimingham (1984b), who attributed it to reduced competition from slower regeneration of dominant ericoids. Velle et al. (2012) also observed that rhizomatous species such as *Carex pilulifera* L. and *V. vitis-idaea* had strong post-fire regeneration. Frequency of lichens was negatively correlated with *Calluna* height and abundance of pleurocarpous mosses, as also observed by Davies and Legg (2008). It is important to note that pre-disturbance vegetation structure in my study was relatively homogenous (see Appendix B.8) and therefore its effect on regeneration may have had a limited importance compared to other studies.

4.4.2 Community response to high severity disturbance treatments

The ordination of high disturbance plots (cut plots where the M/L layer was removed and burnt plots where the M/L layer was removed after or before the fire) included, as in the previous ordinations, two main axes that were related to pre-disturbance vegetation structure and to a gradient of disturbance severity (Figure 4.5). The frequency ordination showed similar community response between cut plots where the M/L layer was removed and burnt plots where the M/L layer was removed after the fire (Table 4.3), indicating that low severity heating and smoke effects had a negligible ecological effect compared to high severity alteration to seedbed and microclimate. Both treatments were associated with high frequencies of ericoids, forbs and graminoids. Conversely, community composition in burnt plots where the M/L layer was removed before the fire was characterised by high frequencies of bryophytes, suggesting that exposure to higher fire-induced temperatures had a negative effect on regeneration of vascular plants. Higher below-ground temperatures may have damaged vegetative regenerating structures and seeds of vascular plants (Schimmel and Granström, 1996) and favoured the establishment of bryophytes which, particularly in the case of acrocarpous mosses, are among the first colonisers after a severe fire (Clement and Touffet, 1990; Schimmel and Granström, 1996; Esposito et al., 1999; Vandvik et al., 2005).

Contrary to the frequency ordination, the ordination of the cover data showed a clear difference in community composition between cut plots where the M/L layer was removed and burnt plots where the M/L layer was removed after the fire (Table 4.3, Figure 4.5, Appendix B.5). This indicates that the low heating, smoke and ash effects that the latter plots were exposed to had a significant effect on species cover despite not having an effect on frequency. A possible explanation is that, whilst potential low severity fire effects on community composition were neutralized by removing the M/L layer (e.g. seeds in the M/L layer exposed to fire-induced temperature pulses), the longer-lasting fertilization effect of ash promoted growth of vascular plants (Evans and Allen, 1971).

As in the previous ordination, forbs and graminoids were predominantly associated with higher (older) pre-disturbance *Calluna* canopies, likely a result of slow regeneration of the dominant ericoids. Bryophytes and ericoids were more frequent in younger pre-disturbance communities.

4.4.3 Mechanisms of regeneration in dominant dwarf shrubs

The effects of low severity disturbance (cutting or burning alone) on vegetative regeneration varied for different ericoid species: whilst the frequency of *Calluna* resprouts was not significantly different between cut and burnt plots (also observed by Miller and Miles, 1970), frequency of *E. cinerea* resprouts was substantially lower in burnt than in cut plots (Figure 4.6). The negative effect of burning on *E. cinerea* vegetative regeneration when compared to cutting is surprising given the low severity of the fires, the small amount of soil heating (average maximum temperature at the ground surface, below the M/L layer, was 21 °C, see Section 3.3.1) and the lack of consumption of the M/L layer. The negative response of vegetative regeneration to burning in *E. cinerea* when compared to *Calluna* could be due to its thinner stems (Gimingham, 1960; Bannister, 1965), making it less able to withstand fire-induced heating or a result of the shallower depth of its resprouting centres (Mallik and Gimingham, 1983).

Calluna and *E. tetralix* resprouts were more frequent in burnt plots where the M/L layer was removed than in normally burnt plots. Since many vegetative regeneration originates on stem bases usually covered by the M/L layer (Hobbs et al., 1984), this could be due to faster growth resulting from the altered soil microclimate, e.g. more light (Barclay-Estrup, 1971) and warmer soil (Section 3.3.2). Neither low soil heating and smoke effects (as simulated in burnt plots where the M/L layer was removed after the fire) nor higher soil heating and smoke effects (M/L layer removed before the fire) had an observable additional effect on the capacity of *Calluna* or *E. cinerea* to resprout when compared to plots with no fire effects (cut plots where the M/L layer was removed).

Seedling regeneration in low severity disturbance plots did not differ between cutting and burning treatments, suggesting direct fire effects (germination stimulation or death from temperature pulses, smoke and ash effects) were not important when the seedbed was the M/L layer. The extent of heating to which seeds near the ground surface were exposed to during the fires can be approximated by considering fire-induced surface soil heating in plots where the M/L layer was removed as an estimate of heating of the surface of the M/L layer (Section 3.3.1). This is probably a conservative estimate as heating at the surface of the M/L layer would have likely been higher given the faster energy transfer in a medium with lower moisture content and bulk density. Average fire-induced maximum ground surface temperature was 73 °C (standard deviation = 34 °C), and time above 50 °C (threshold associated with damage to plant tissues and *Calluna* seeds germination; Whittaker and Gimingham, 1962; Granström and Schimmel, 1993; Massman et al., 2010), 58 s (SD = 58 s). My results are in apparent conflict with Whittaker and Gimingham (1962), who reported increased *Calluna* germination when heating to 80 °C for 60 s. Also, the results do not support a stimulation effect of ash and smoke on seed germination (Måren et al., 2009; Bargmann et al., 2014). However, these germination studies were completed in laboratory conditions with suitable seedbeds. It is possible that in my study the effects of fire on germination were not apparent due to the unfavourable M/L layer seedbed, which may have made seedling establishment difficult as a result of increased drought in moss carpets (Equihua and Usher, 1993) and allelopathic effects of *Calluna* litter (Bonanomi et al., 2005). This suggests seedbed quality may be a more important control on seedling establishment than fire effects.

Despite the large proportion of seeds in the M/L layer (e.g. 25 % of viable *Calluna* seeds; Legg et al., 1992), the simulated consumption of the M/L layer leading to a bare soil/duff substrate had a positive effect on the establishment of ericoid seedlings, both in cut and in burnt treatments. Increased ericoid seedling establishment on bare ground has been observed before (Mallik et al., 1984a; Hullu and Gimingham, 1984; Schimmel and Granström, 1996; Davies et al., 2010b) and has been attributed to drought induced by large moisture fluctuations in moss carpets (Equihua and Usher, 1993) and to allelopathic effects of *Calluna* litter (Bonanomi et al., 2005).

Seedling establishment of *Calluna* and *E. cinerea* was higher in cut plots where the M/L layer was removed than in both burnt plots where the M/L layer was removed, suggesting a negative effect of burning on the size of the remaining viable *Calluna* seedbank. This is in contrast to the observed similarity in seedling germination between cut and burnt plots where the M/L layer was present, and shows that, when germinating on a favourable seedbed (i.e. on soil rather than on the M/L layer), fire-induced heating had a negative effect on *Calluna* and *E. cinerea* seedling germination. In contrast, *E. tetralix* had higher seedling frequencies in burnt plots. This observation cannot be explained by differences in seed morphology (Gimingham, 1960; Bannister, 1965, 1966), survival (Thompson and Band, 1997) and depth distribution (Putwain and Gillham, 1990) so further research is needed to clarify this.

Implications for ecosystem services

The simulated gradient of severity disturbance was an important control on vegetation regeneration. Managed burning promoted high abundance of vascular plants and acrocarpous mosses when compared to the lower severity cutting treatment, which was dominated by pleurocarpous mosses. In low severity fires where the M/L layer was not consumed, burning had a similar effect on *Calluna* regeneration than cutting, while burning had a negative effect on *E. cinerea* regeneration. Abundance of *Calluna* and *E. tetralix* resprouts, and of *Calluna*, *E. cinerea* and *E. tetralix* seedlings was higher when the seedbed was soil rather than M/L layer. Although my study is limited to short-term community response (survey was completed at the end of the third growing season), these results suggest that the dominance of ericoids in *Calluna* heathlands may increase as a consequence of higher severity fires that consume the M/L layer, compared to low severity fires where the M/L layer remains.

Differences in initial post-fire floristic composition have been found to be important in determining vegetation development (Hobbs and Legg, 1984) and to lead to medium-term (7–8 years) differences in heathland community composition (Hobbs and Gimingham, 1984b; Velle et al., 2012). Thus the observed altered community composition resulting from increased disturbance severity could have long-term implications for ecosystem function in *Calluna* heathlands. Furthermore, many studies have pointed out the key role of vegetation in controlling soil carbon dynamics. In particular, dwarf-shrubs have been associated with increased ecosystem respiration in peatlands (Ward et al., 2013; Armstrong et al., 2015; Walker et al., 2016) although compensatory mechanisms have also been identified in the form of increased photosynthetic carbon assimilation (Ward et al., 2013) or substances that inhibit soil microbiological respiration (Wang et al., 2015). Such changes in community composition, together with increased soil temperatures after high severity fires (see Section 3.3.2), could potentially increase post-fire soil respiration in *Calluna* heathlands.

4.5 Conclusions

Direct fire effects (plant tissue or seed mortality due to high temperature, germination cues from ash, smoke or temperature pulses, fertilisation) were important in shaping post-fire vegetation regeneration over and above the microclimate alteration due to removal of the shrub canopy. The higher disturbance severity in burnt plots resulted in high frequencies of regenerating ericoids, forbs, graminoids and acrocaropous mosses, while cut plots had a more similar community composition to unburnt plots and were dominated by pleurocarpous mosses.

High severity disturbance treatments promoted regeneration of vascular plants mainly due to the replacement of the M/L layer by bare soil as seedbed. Whilst low severity direct fire effects did not alter community composition, high severity fire-induced temperature pulses (where the M/L layer had been removed before the fire) had a negative effect on abundance of vascular plants and increased abundance of bryophytes.

Seedbed was also key in understanding regeneration of dominant ericoids: abundance of regenerating *Calluna*, *E. cinerea* and *E. tetralix* increased when the seedbed was bare ground compared to M/L layer. Regenerating *Calluna* and *E. tetralix* were little affected by low severity fire effects where the substrate was the M/L layer, but fire decreased *Calluna* and *E. cinerea* seedling establishment where the substrate was bare ground.

This study provides useful information on the relative importance of the different mechanisms involved in controlling post-fire vegetation regeneration in *Calluna* heathlands for a range of severity disturbances, and demonstrates the central role of the M/L layer. In a context of changing fire regimes where higher severity fires involving higher consumption of the M/L layer and higher soil heating are expected, these results may help understand future changes to the community composition of *Calluna* heathlands, and inform land managers on strategies to protect ecosystem services.

Chapter 5

Fire severity on heathland is more sensitive to drought than on bog

Abstract

Calluna-dominated habitats, including heathlands and peat bogs, provide important ecosystem services in terms of biodiversity, carbon stores or water supply. Drought is projected to intensify throughout their range, potentially leading to a change in fire regimes. I studied the effect of drought on fire intensity and fire severity in two contrasting Scottish habitats: a dry heath with thin organic soils and a raised bog with deep, saturated peat, both dominated by continuous *Calluna* stands. Simulated drought in 2 × 2 m plots lowered the moisture content of the moss and litter (M/L) layer at both sites, but only lowered the moisture content of the soil at the dry heath.

I completed 19 experimental fires and measured (i) fire intensity as estimated by the burnt branch tip diameter method, (ii) fire severity as estimated by the consumption of the M/L layer and by fire-induced soil heating, and (iii) post-fire soil thermal dynamics. The higher fire intensity and fire severity measured in drought plots was primarily driven by the lower moisture content of the M/L layer. The dry heath was more sensitive to drought, and subsequent fire effects, than the bog: drought significantly increased fire-induced soil heating at the dry heath (e.g. average maximum temperatures at the soil surface increased from 31 °C to 189 °C), but increase at the raised bog was negligible (e.g. 10 °C to 15 °C). Substantial M/L layer consumption was observed when moisture content was below 150 %. At the dry heath, this led to larger post-fire soil daily temperature range, especially in warm months. These results can help us better understand how predicted changes in climate may alter fire regimes and its impact on vegetation composition and soil carbon stores in *Calluna*-dominated habitats.

5.1 Introduction

Moisture content can have long and short-term implications for wildfire occurrence and fire behaviour. In the long term, water availability regulates the composition of the vegetation community, which determines fuel load and structure (e.g. fuel continuity) (Pausas and Ribeiro, 2013; Keeley and Syphard, 2016). In the short term, moisture content can affect inter-annual variation in vegetation productivity, thus influencing fuel load, and fuel flammability (Balzter et al., 2007; Davies et al., 2009; Davies and Legg, 2011; Prat-Guitart et al., 2016). By regulating fuel available for combustion, moisture content can impact on various components of fire regime (*sensu* Pyne et al., 1996 as the frequency, seasonality, size and severity of fires) (Littell et al., 2016).

Although estimates of future global precipitation patterns show large variability across regions, the predicted generalised warming during the 21st century is projected to increase water deficit in most regions, including northern Europe (Dai, 2013; Cook et al., 2014). For example, mean summer temperature in the UK is projected to increase by 2.5 °C, and rainfall to decrease by 16 % by 2050 (Murphy et al., 2009). Drought has been linked to changes to different aspects of wildfire activity such as fire frequency (Legg et al., 2007), seasonality (Westerling et al., 2006), size (Turetsky et al., 2004; Legg et al., 2007; Fernandes et al., 2016) and severity (Turetsky et al., 2011b;

Davies et al., 2013).

In the UK, heathlands and peatlands provide a range of ecosystem services and overlay a substantial amount of belowground carbon (Thompson et al., 1995; Bradley et al., 2005; Ostle et al., 2009). Dwarf shrub-dominated vegetation, in particular, includes a variety of habitats, from dry heaths to drainage-degraded raised bogs (Gimingham, 2003), many of which are prone to wildfires (Legg et al., 2007). Although peatlands contain the largest amount of belowground carbon ($>$ 550 Tg up to 1 m deep), shallow organic soils also store a substantial amount (ca. 125 Tg C; Ostle et al., 2009) and, due to their lower water holding capacity, may be more susceptible to disturbances such as burning during drought periods (Turetsky et al., 2015; Davies et al., 2016a).

Drought has been found to increase wildfire occurrence and area burnt in *Calluna* moorlands (Legg et al., 2007; Albertson et al., 2010). Variation in moisture content in the various *Calluna* fuel layers (Figure 1.2) results in different changes to fire behaviour: low moisture content of dead elevated fuels in the *Calluna* canopy increases fire ignition; low moisture content of the live *Calluna* canopy increases rate of fire spread and fire intensity (Davies et al., 2009); and low moisture content of ground fuels (the moss and litter, M/L, layer) leads to their combustion and high fire severity (Davies et al., 2010b). All these studies highlight the non-linear nature of the relationship between moisture content and fire behaviour in *Calluna* moorlands, with fire intensity and fire severity varying little for a range of moisture content and greatly increasing when moisture content lowers beyond a certain thershold (Fernandes et al., 2016). Important moisture content thresholds have been identified at 60–70 % (dry base) for dead elevated fuels, above which field ignitions in small plots were difficult, and 140 % for the M/L layer, above which no consumption was measured (Davies and Legg, 2011).

Research examining the relationship between moisture content and fire on peatlands has focused on belowground carbon stores. Burning in drought conditions has been associated with higher fire severity, with deeper depth of burn and thus higher carbon losses (Turetsky et al., 2011a; Davies et al., 2013). Peat ignition and self-sustained combustion can occur when peat moisture content is below 125–150 % (Rein et al., 2008; Prat-Guitart et al., 2016).

High severity fires where the soil surface is consumed can have substantial ecological consequences in *Calluna* moorlands. Ignition of the organic soil layer is likely to kill belowground *Calluna* vegetative regenerating structures and viable seedbank (Clement and Touffet, 1990; Legg et al., 1992; Schimmel and Granström, 1996), while physical changes to the soil structure can lead to erosion and further slowing of vegetation regeneration (Maltby et al., 1990). Furthermore, burning after drainage can alter carbon cycling and increase carbon loss by inducing permanent changes to the vegetation composition (Kettridge et al., 2015).

Despite the crucial role of the moisture content of the different fuel layers of *Calluna* moorlands and peatlands in controlling fire behaviour, its response to changing weather, including drought, is not well understood (Legg et al., 2007). I studied the role of drought in controlling fire intensity and fire severity in two *Calluna*-dominated ecosystems with contrasting edaphic characteristics: an upland dry heath with thin organic soils, and a lowland raised bog with deep, saturated peat. Drought was simulated using rain-out shelters in 2 $\times$ 2 m plots prior to experimental fires. Specifically, I examined: (i) the extent to which drought lowers the moisture content of different fuel layers in *Calluna*-dominated habitats; (ii) how drought affects fire intensity and fire severity; (iii) the importance of drought in controlling fire intensity and fire severity relative to other environmental variables; (iv) the effect of an altered fire intensity and fire severity on post-fire soil thermal dynamics; and (v) differences in the response to drought and subsequent alteration to fire intensity and fire severity between a dry heath and a raised bog. Quantifying the relationship between drought, moisture content and fire behaviour is important for forecasting periods of potentially severe wildfires, predicting long-term changes in fire regimes due to climate change and advising on adequate conditions for managed burning.

5.2 Materials and methods

5.2.1 Experimental design and measurements

I completed ten experimental fires at Glen Tanar and nine at Braehead Moss on twelve separate days between September 2013 and November 2014 (see site details in Section 2.1). 2 × 2 m rain-out shelters (Yahdjian and Sala, 2002) were used to simulate drought and reduce soil and vegetation moisture content (Figure 5.1). The rain-out shelters were made of a steel frame (height of the high side was 1.2 m, the low side was 0.5 m) and a clear polythene cover (thickness 250 μm, light transmittance 86 %). A gutter collected the rainfall, which was drained to a minimum of 5 m away through a hose. The rain-out shelters were oriented with the slope facing the direction of the prevailing wind to minimise the drift of precipitation. No ground structures were installed to regulate overland flow or lateral movement of water within the soil profile, thus limiting hydrological alteration in drought-treated plots. I deployed the shelters in the field two to four months before the experimental fires, and removed them immediately before ignition. Two plots under rain-out shelters ("drought" plots) and two untreated ("no-drought") plots were delimited in each fire.

Fuel load and structure were estimated using the FuelRule method (Section 2.2), taking five measurements per plot. Immediately before each fire I took an integrated sample, comprised of three subsamples, of the top 2 cm of the M/L layer from each plot in order to estimate fuel moisture content (FMC). For both live and dead *Calluna* I took an integrated FMC sample for each treatment within a fire, i.e. the samples were bulked across the two plots of each treatment within each fire. Three soil moisture meter measurements in each plot were averaged to estimate the moisture content of the top 3.6 cm of the soil (here I use "soil" to refer both to the organic layer at Glen Tanar and peat at Braehead Moss). Moisture content measurements were taken with a FieldScout TDR 100 soil moisture meter (see Section 2.2 for detais). A portable weather station recorded air temperature, relative humidity and

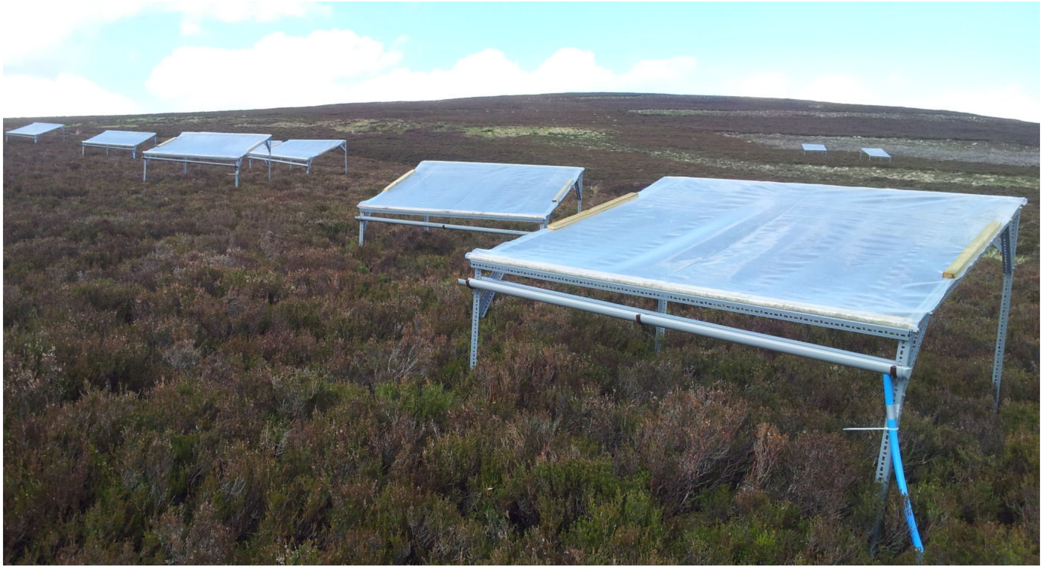

Figure 5.1: Rain-out shelters at Glen Tanar.

wind speed during the fires (Section 2.4).

Thermocouple loggers recorded soil temperatures from the start of the fire to 50 min after in each plot, both at the soil surface and 2 cm below. I measured the depth of the M/L layer above the top thermocouple to the nearest 0.5 cm. The temperature-time curves recorded in each plot and measurement depth were characterized using five temperature metrics: total heat (area under the temperature-time curve), maximum temperature, time above 50 °C, heating rate (slope of the heating limb of the curve) and cooling rate (slope of the cooling limb of the curve) (Table 3.1). Section 2.3 provides detailed information on thermocouple deployment and calculation of temperature metrics.

I used five metal "duff spikes" to mark the pre-fire position of the M/L layer surface in each plot, and assessed the extent of combustion of the M/L layer during the fire by measuring its change in depth to the nearest 1 cm. Fire intensity was estimated using the average minimum burnt branch tip diameter technique (Moreno and Oechel, 1989; Whight and Bradstock, 2000). The technique is based on the principle that higher energy output from the fire front is correlated with greater consumption of the shrub canopy and therefore with larger post-fire burnt branch tip diameters, since remaining branch tips will be closer to the ground where branches are wider. In each plot I sampled an average of 35 plants (SD = 2.7) along four equidistant transects (variation was due to low density of stems in some transects), excluding young plants (less than 15 cm tall), and measured the tip diameter of the highest branch of each plant using callipers.

Temperature loggers (iButtons^{TM}, 2 h recording interval) installed 2 cm below the top of the soil recorded post-fire soil temperatures in five fires at Glen Tanar and in seven fires at Braehead Moss, from November 2014 to September 2015. For each fire I deployed an iButton logger in a randomly selected plot of each treatment (no-drought and drought) and in an unburnt control, and measured the thickness of the M/L layer above the logger to the nearest 0.5 cm. The exact location of the logger was chosen to reflect average M/L layer thickness within each plot. I assessed post-fire soil accumulated heat by calculating the daily growing degree hours (sum of °C above 4 °C, the minimum temperature for plant growth, in each hour during a day; Schenker et al., 2014) for each plot.

5.2.2 Data analysis

I followed the microplot approach where plots within fires are treated as independent observations, and assessed the validity of the approach by partitioning the variance of the fuel load and structure data between and within fires (see Section 3.2.1). All statistical analyses were performed with R 3.2.2 (R Core Team, 2015).

Effect of drought on fuel moisture content

I examined the effect of the rain-out shelters on the FMC of the different *Calluna* fuel layers (live and dead canopy, M/L layer and soil) using separate linear mixed effects models (Pinheiro et al., 2015) with an interaction between site (Glen Tanar, a dry heath, and Braehead Moss, a raised bog) and treatment (no-drought and drought) as fixed effects and fire as a random effect. The interaction models allowed testing, for each fuel layer, (i) differences in moisture content between treatments, within the same site, (ii) differences in moisture content between sites, within the same treatment, and (iii) differences in the extent to which drought altered moisture content in both sites, i.e. the treatment × site interaction. Multiple comparisons were addressed with simultaneous tests for general linear hypothesis (Hothorn et al., 2008).

Effect of drought on fire intensity and fire severity

I tested differences in fire intensity (as estimated by burnt branch tip diameter) and fire severity (as estimated by M/L layer consumption and soil heating metrics, see Table 3.1) between no-drought and drought plots using linear mixed effects models that included an interaction between site (Glen Tanar and Braehead Moss) and treatment (no-drought and drought) as fixed effects and fire as a random effect. Soil heating metrics were log-transformed and a small constant, 1 % of the minimum non-zero value, was added when there were zero values. For soil heating metrics, separate models were fitted for each depth of measurement (soil surface or 2 cm below ground). I performed multiple comparisons to test whether there were (i) differences in fire intensity and fire severity metrics between treatments, within the same site (and depth of measurement in the case of soil heating metrics), (ii) differences between sites, within the same treatment (and depth of measurement for soil heating), and (iii) differences in the extent to which drought altered the fire intensity and fire severity metrics in both sites (within the same depth of measurement for soil heating), i.e. the treatment × site interaction.

Environmental controls on fire intensity and fire severity

I assessed the relative importance of moisture content in controlling fire intensity and fire severity relative to other environmental variables by modelling fire intensity and fire severity metrics as a function of weather and pre-fire fuel structure and moisture content variables. I used average burnt branch tip diameter as an indicator of fire intensity, and two different metrics of fire severity: consumption of the M/L layer and fire-induced soil heating as estimated by total heat (Table 3.1). The available environmental covariates were wind speed, fuel load (biomass above ground), thickness of the M/L layer and FMC of live and dead *Calluna*, the M/L layer and soil. Available factor variables included site and depth of soil temperature measurement (only used for analysing soil heating). I log-transformed the total heat and moss consumption response variables, adding a small constant (1 % of the minimum non-zero value) to zero values. The variance inflation factor was calculated to detect multicollinearity problems among covariates, and the Akaike information criterion was used for model selection (see Section 2.5 for more details).

Effect of drought on post-fire soil thermal dynamics

Differences in thickness of the M/L layer above the long-term soil temperature loggers between treatments and sites were analysed using a linear mixed effects model with an interaction between site (Glen Tanar and Braehead Moss) and treatment (unburnt, no-drought and drought) as fixed effects and fire as random effects. For each plot and day of measurement I calculated the daily mean temperature and the range. The effect of drought on post-fire changes in soil thermal dynamics was investigated using harmonic regression (Section 2.6). Separate models were fitted for each temperature metric (mean daily temperature and daily temperature range), treatment and site.

For both amplitude (vertical distance from the centreline to the wave maximum, in °C) and phase (horizontal distance to a wave starting at sampling day 1, in days) of the sinusoidal waves, I calculated (i) the 95 % confidence intervals of the difference between means for all pairs of treatments, within the same site, and (ii) the 95 % confidence intervals of the difference between means of Glen Tanar versus Braehead Moss, within the same treatment. Detailed information on how amplitude, phase and their variance were calculated can be found in Section 2.6.

Daily growing degree hour values in each plot were averaged per season (winter: December–February; spring: March–May; summer: June–August; autumn: September–November). I used linear mixed effects models, with an interaction between treatment and season as fixed effects, and fire as a random effect, to analyse the effect of treatment on growing degree hours within each season. Separate models were fitted for Glen Tanar and Braehead Moss.

5.3 Results

The experimental fires covered a range of weather conditions (e.g. average wind speed: 2.2–7.5 m s^{-1}; moisture content of the M/L layer: 28–646 %; Table 5.1). The variance partitioning of total fuel load, fine fuel load, fuel bulk density, maximum fuel height and M/L layer depth all indicated that variance within fires was of similar magnitude, if not larger, than between fires, thus supporting the microplot approach for data analysis (Appendix C.1).

5.3.1 Effect of drought on fuel moisture content

The drought treatment significantly lowered the FMC of the M/L layer, both at Glen Tanar (271 to 117 %) and at Braehead Moss (365 to 112 %), and the soil FMC at Glen Tanar (221 to 190 %) (Figure 5.2). Differences in vegetation FMC between sites were generally not statistically significant, except for the higher FMC of live *Calluna* at Glen Tanar (117 % versus 84 % at Braehead Moss). However, soil FMC was significantly higher at Braehead Moss (349 % versus 205 % at Glen Tanar). Drought decreased the FMC of the M/L layer more strongly at Braehead Moss than at Glen Tanar (the interaction site × treatment was only statistically significant in the M/L layer model, p-value = 0.04). Summary statistics and model details can be found in Appendix C.2.

Table 5.1: Summary of fuel and weather conditions during the fires: date of burning, *Calluna* fuel load, fuel moisture content of live and dead *Calluna* and the M/L layer (drought plots in brackets), wind speed and estimated rate of spread of the fire. See Section 2.2 for details on fuel load estimates and Section 2.4 for RoS details. Appendix C.1 provides further information on fuel structure and on rainfall before the fires.

Fire	Date (d/m/y)	Fuel Load (kg m^{-2})	*Calluna* (l) FMC (%)	*Calluna* (d) FMC (%)	M/L FMC (%)	Wind (m s^{-1})	RoS (m min^{-1})
			Glen Tanar				
1	10/09/13	1.7	148 (138)	67 (64)	418 (81)	4.6	1.9
2	10/09/13	1.7	150 (164)	97 (71)	394 (84)	4.3	0.1
3	24/09/13	1.7			234 (90)	2.8	5.5
4	24/09/13	1.6			134 (106)	2.9	5.4
5	30/10/13	1.8	78 (93)	32 (31)	592 (229)	7.5	12.9
6	11/03/14	1.6	84 (75)	16 (13)	380 (152)	3.7	6.8
7	11/03/14	1.5	76 (71)	18 (15)	262 (267)	2.9	5.0
8	11/04/14	1.6	79 (81)	24 (21)	28 (23)	5.2	9.2
9	03/09/14	1.7	140 (152)	22 (21)	148 (49)	4.4	2.1
10	03/09/14	1.7	121 (121)	28 (28)	163 (85)	3.9	2.7
			Braehead Moss				
1	10/10/13	1.2	87 (89)		646 (246)	4.3	8.1
2	10/10/13	1.3	87 (102)	34 (29)	626 (266)	4.1	6.2
3	11/10/13	1.3	93 (86)	32 (31)	541 (200)	3.2	5.8
4	16/04/14	1.4	84 (81)	15 (14)	86 (26)	3.1	5.2
5	16/04/14	1.4	77 (78)	15 (16)	106 (36)	2.3	5.1
6	25/04/14	1.2	86 (88)	24 (28)	71 (30)	2.2	3.3
7	16/10/14	1.6	81 (74)	28 (22)	300 (83)	2.7	5.9
8	16/10/14	1.7	83 (74)	28 (21)	343 (60)	3.1	5.7
9	13/11/14	1.4	74 (64)	25 (25)	628 (60)	4.1	8.0

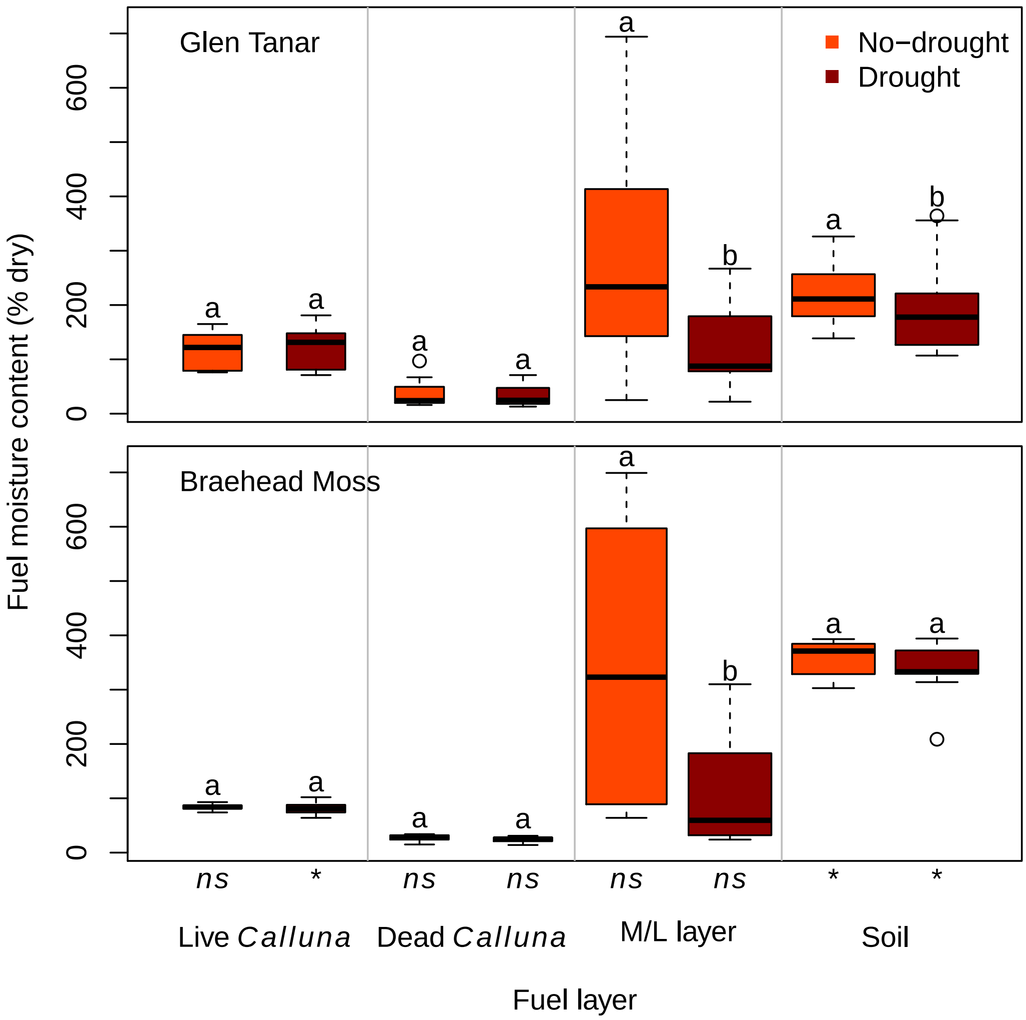

Figure 5.2: Pre-fire fuel moisture content of different fuel layers at Glen Tanar and Braehead Moss, in no-drought and drought plots. The box is the interquartile range and the thick horizontal line the median; whiskers extend to last datapoint within 1.5 times the interquartile range; circles are outliers beyond this range; width of the box is proportional to number of observations (max = 20, min = 7). Different letters above boxplots within the same site and fuel type indicate statistically significant differences. *ns* and * indicate significance of the FMC difference between sites, within the same fuel layer and treatment (*ns* = non-significant, * = statistically significant at $\alpha = 0.05$). See Appendix C.2 for summary statistics and model details.

5.3.2 Effect of drought on fire intensity and fire severity

At Glen Tanar, drought significantly increased fire intensity, as estimated by average burnt branch tip diameter: 3.0 mm (SD = 0.5 mm) in no-drought plots and 3.5 mm (0.7 mm) in drought plots (Figure 5.3). Conversely, at Braehead Moss average burnt branch tip diameter in drought plots (2.2 $\pm$ 0.7 mm) was not significantly different than in no-drought (2.0 $\pm$ 0.5 mm). Drought significantly increased fire severity as measured by M/L layer consumption, both at Glen Tanar (0.7 $\pm$ 1.1 cm in no-drought, 2.3 $\pm$ 1.7 cm in drought plots) and Braehead Moss (0.1 $\pm$ 0.3 cm in no-drought, 1.4 $\pm$ 1.1 cm in drought plots).

The higher fire-induced soil heating in drought compared to no-drought burnt plots was apparent from the temperature-time curves, at both measurement depths and both at Glen Tanar and Braehead Moss (Figure 5.4). Drought significantly increased total heat, at both depths of measurement, and at both sites (Table 5.2). Drought significantly increased average maximum temperatures at Glen Tanar (e.g. 31 to 189 °C at the soil surface), but not at Braehead Moss (e.g. 10 to 15 °C). Most fire-induced soil heating metrics were significantly higher at Glen Tanar than at Braehead Moss (Table 5.3). Generally, temperature metrics showed a stronger increase in fire-induced soil heating due to drought at Glen Tanar compared to Braehead Moss.

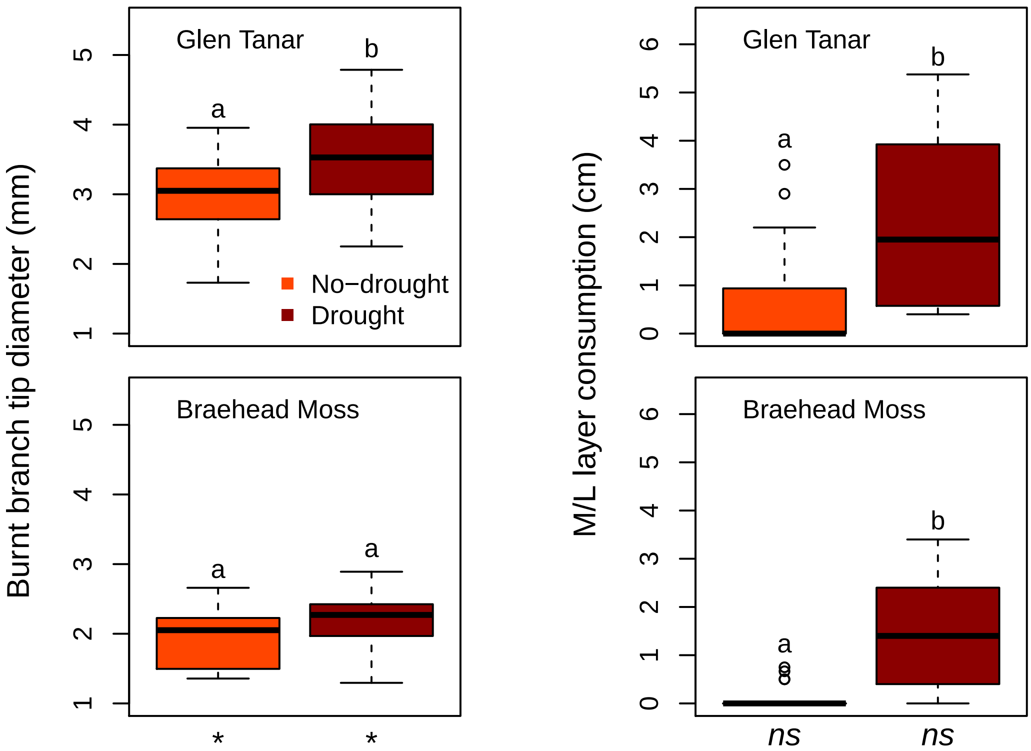

Figure 5.3: Plot level-average burnt branch tip diameter and M/L layer consumption in drought and no-drought plots, at both sites. Different letters above the boxplots indicate significant differences between treatments ($\alpha = 0.05$), and * (significant) and *ns* (not significant) below indicate differences between sites, for the same treatment. Model details are provided in Appendix C.3.

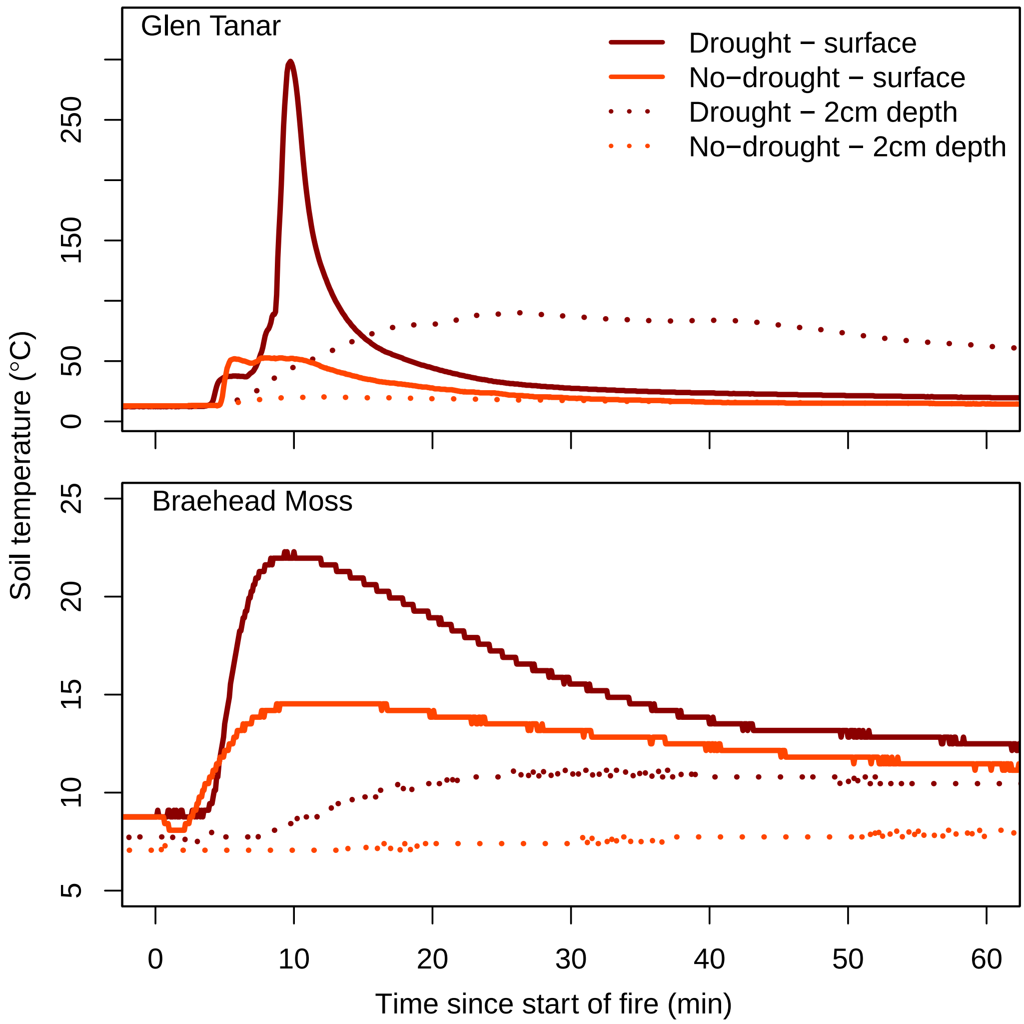

Figure 5.4: Examples of temperature-time curves from thermocouples located at the surface of the soil and 2 cm below, in no-drought and drought plots, both at Glen Tanar and Braehead Moss fires.

Table 5.2: Average values and standard deviation, in parentheses, of metrics of fire-induced soil heating (see Section 2.3) per depth of measurement (top of the soil and 2 cm below), treatment (no-drought and drought plots), and site (Glen Tanar and Braehead Moss). Different letters within temperature metric, depth of measurement and site indicate statistically significant differences between treatments ($\alpha = 0.05$). Models are detailed in full in Appendix C.3.

Measurement depth	2 cm		0 cm	
Treatment	No-drought	Drought	No-drought	Drought
Site	Glen Tanar			
Total heat (°C.s)	7125 (6256) a	40459 (51536) b	18438 (14459) a	102125 (149349) b
Max T (°C)	13 (6) a	40 (58) b	31 (24) a	189 (230) b
t above 50°C (s)	0 (0) a	250 (610) b	34 (88) a	590 (919) b
Heating slope (λ)	0.05 (0.08) a	0.16 (0.23) a	0.8 (1.4) a	0.7 (0.8) a
Cooling slope (λ)	-0.008 (0.02) a	-0.03 (0.06) b	-0.07 (0.09) a	-0.2 (0.2) a
Site	Braehead Moss			
Total heat (°C.s)	867 (991) a	2780 (2458) b	2516 (3792) a	8759 (8735) b
Max T (°C)	9 (1) a	10 (1) a	10 (3) a	15 (10) a
t above 50°C (s)	0 (0) a	0 (0) a	0 (0) a	0 (0) a
Heating slope (λ)	0 (0) a	0.01 (0.02) b	0 (0.1) a	0.2 (0.7) b
Cooling slope (λ)	0 (0) a	0 (0) a	-0.01 (0.01) a	0 (0.1) a

Table 5.3: P-values associated with differences in temperature metrics between sites within the same treatment, and with the interaction site × treatment, for the same depth of measurement (soil surface or 2 cm below). Full model results are provided in Appendix C.3.

	No-drought		Drought		Site × treatment	
Depth of measurement	2 cm	0 cm	2 cm	0 cm	2 cm	0 cm
Total heat (°C.s)	<0.001	<0.001	<0.001	<0.001	0.88	0.13
Maximum T (°C)	0.27	<0.001	0.02	<0.001	0.04	0.04
t above 50 °C (s)	1	0.63	0.02	<0.001	0.02	0.01
Heating slope (λ)	<0.001	<0.001	0.08	0.03	0.06	<0.001
Cooling slope (λ)	0.07	<0.001	<0.001	<0.001	0.03	0.87

5.3.3 Environmental controls on fire intensity and fire severity

The measured environmental variables had different average values at both sites (Figure 5.2, Table 5.4) . For example, the M/L layer above the thermocouple was thinner at Glen Tanar than at Braehead Moss (3.9 versus 7.0 cm). VIF showed a high degree of multicollinearity between the FMC of soil, live *Calluna* and dead *Calluna*. Therefore I kept only the most relevant FMC for each dependent variable: live *Calluna* FMC for the fire intensity model (Davies et al., 2009) and soil moisture for the fire severity models (Busse et al., 2010).

Table 5.4: Mean, standard deviation and number of observations of total biomass above ground, thickness of the M/L layer above the thermocouple measuring point, and wind speed during the fire in both sites.

	Glen Tanar		Braehead Moss	
	Mean (SD)	n	Mean (SD)	n
Fuel load (kg m^{-2})	1.7 (0.1)	40	1.4 (0.2)	35
M/L layer thickness (cm)	3.9 (1.5)	40	7.0 (3.5)	35
Wind speed (m s^{-1})	4.2 (4.2)	10	3.2 (3.2)	9

The best predictors for fire intensity as estimated by burnt branch tip diameter were the moisture content of the M/L layer, pre-fire fuel load and site (Table 5.5). Burnt branch tip diameter had a positive relationship with fuel load and a negative relationship with the moisture content on the M/L layer (Figure 5.5). The combustion of the M/L layer increased when its pre-fire moisture content was low and when wind speed was high. Most M/L layer consumption was observed when the moisture content of the M/L layer was below approximately 150 % (Figure 5.6), although consumption > 1 cm was observed up to 300 %. The main drivers determining fire-induced soil heating in terms of total heat were the thinness of the M/L layer, the FMC of the M/L layer, the FMC of the soil and the depth of measurement (soil surface or 2 cm below) (Table 5.5). Modelled total heat increased substantially when soil moisture content decreased from ca. 300 to 200 %, and when the moisture content of the M/L layer was below 150 % (Figure 5.7).

Table 5.5: Details of the selected models for describing the fire intensity indicator average burnt branch tip diameter and the fire severity indicators combustion of the M/L layer and soil heating. R^2 marginal is the variance explained by fixed effects, R^2 conditional is the variance explained by both fixed and random effects.

Response	R^2_m	R^2_c	Variable	Coefficient	DF	t-value	p-value
Branch tip diameter (mm)	0.8	0.86	Intercept	2.17	40	4.56	<0.001
			M/L FMC (%)	-0.0013	40	-5.01	<0.001
			Fuel load (g m^{-2})	5e-04	40	2.81	0.01
			Site(BM)	-0.74	14	-4.19	<0.001
log(M/L consumed (cm))	0.58	0.74	Intercept	-0.64	53	-0.66	0.51
			M/L FMC (%)	-0.012	53	-10.33	<0.001
			Wind speed (m s^{-1})	0.46	17	1.86	0.08
log(Total heat (°C))	0.67	0.67	Intercept	14.04	117	38.02	<0.001
			TC depth (cm)	-1.11	117	-5.19	<0.001
			Soil FMC (%)	-0.011	117	-8.73	<0.001
			M/L FMC (%)	-0.004	117	-6.82	<0.001
			M/L thickness (cm)	-0.26	117	-5.92	<0.001

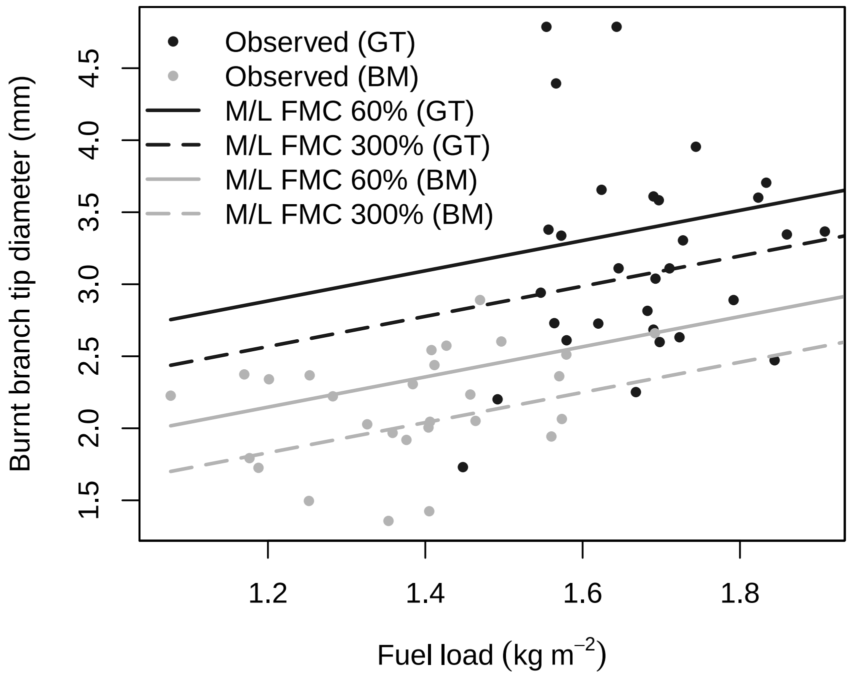

Figure 5.5: Plot-level average burnt branch tip diameter as a function of pre-fire total fuel load at Glen Tanar and Braehead Moss. Lines are predicted values for fuel moisture contents of the M/L layer of 60 % and 300 % (first and third quartiles of the observed data). See Table 5.5 for model details.

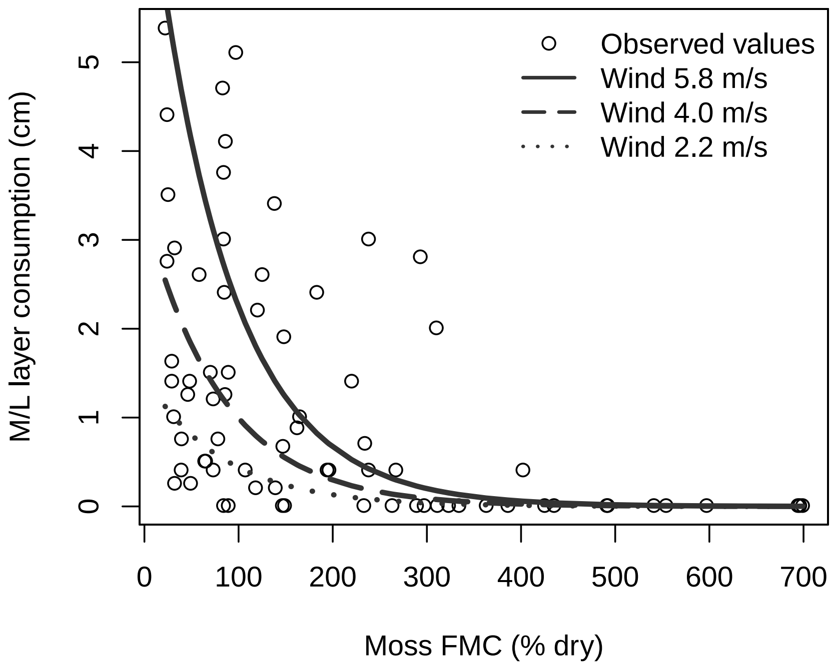

Figure 5.6: Observed consumption of the M/L layer during the fire plotted against the fuel moisture content of the M/L layer. Lines are predicted values for minimum, mean and maximum average recorded wind speed during the fires. See Table 5.5 for model details.

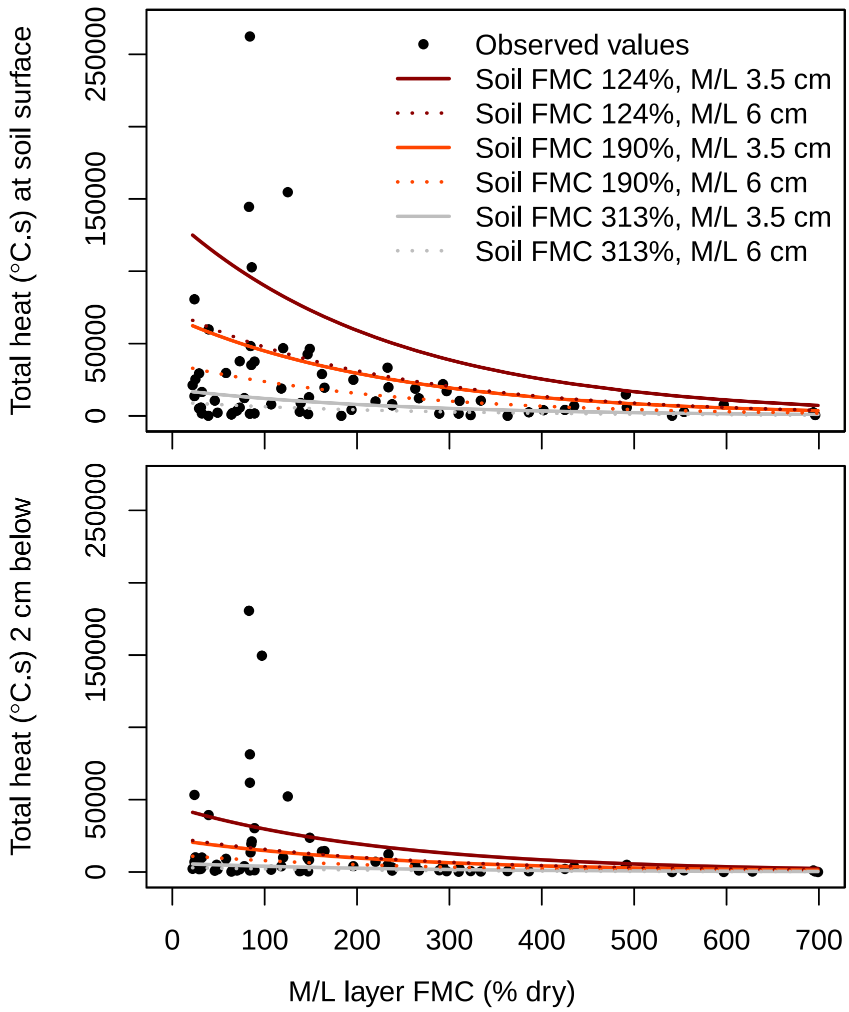

Figure 5.7: Total heat, measured at the soil surface (top) and 2 cm below (bottom) in relation to the fuel moisture content of the M/L layer. Round symbols are observed values; lines are predicted values for 0.05, 0.25 and 0.5 quantiles of soil FMC recorded (wetter soil led to very low soil heating) and for two M/L layer thicknesses (0.25 and 0.75 quantiles of observed). See Table 5.5 for model details. An extreme observation at the soil surface was not plotted (but was included in the model). For reference, maximum temperatures at the soil surface $>$ 50 °C occurred at total heat values $>$ 27000 °C.s.

5.3.4 Effect of drought on post-fire soil thermal dynamics

The thickness of the M/L layer above the post-fire soil temperature loggers was lower in drought (average 1.0 cm, SD 1.4 cm) than in no-drought (3.4 ± 2.0 cm) and unburnt (4.9 ± 1.2 cm) plots at Glen Tanar, but not at Braehead Moss (6.6 ± 3.9, 4.7 ± 1.4 and 5.6 ± 2.0 cm, respectively) (Figure 5.8). Post-fire daily soil temperature range was lowest in unburnt plots and highest in drought plots (Figure 5.9). Modelled long-term daily temperature range patterns at Glen Tanar revealed a strong dependence on season, with drought plots having the largest daily temperature range, especially during the summer (8.8 °C in drought, 5.7 °C in no-drought and 2.3 °C in unburnt plots; Figure 5.10). Differences in daily temperature range amplitude between treatments were all statistically significant at Glen Tanar (Table 5.6). At Braehead Moss, daily temperature range was also larger in burnt plots than in unburnt but, unlike at Glen Tanar, seasonal variation was small (2.6–3.8 °C). Amplitude of daily temperature range was significantly larger in drought plots than in unburnt plots at Braehead Moss. In contrast, phase of the daily temperature range was similar across treatments, at both sites. The amplitude of the daily temperature range sinusoid was significantly larger at Glen Tanar than at Braehead Moss for both burnt plots.

Mean daily temperature patterns were similar in both burnt treatments (no-drought and drought plots): mean daily temperature was higher in summer and lower in winter (i.e. annual extremes were higher) than in unburnt plots at both Glen Tanar and Braehead Moss (Figure 5.10). The amplitude of the mean daily temperature sinusoidal wave was significantly larger in burnt plots than in unburnt plots both at Glen Tanar (5.7 versus 4.5 °C) and at Braehead Moss (5.7 versus 5.1 °C) (Table 5.6). Amplitude of mean daily temperature was significantly larger at Braehead Moss than at Glen Tanar in unburnt plots, but not statistically different in burnt plots (results of tests of differences between sites can be found in Appendix C.5). Phase of mean daily temperature was significantly smaller in burnt plots compared to unburnt plots at Glen Tanar: unburnt plots lagged burnt plots by approximately 10

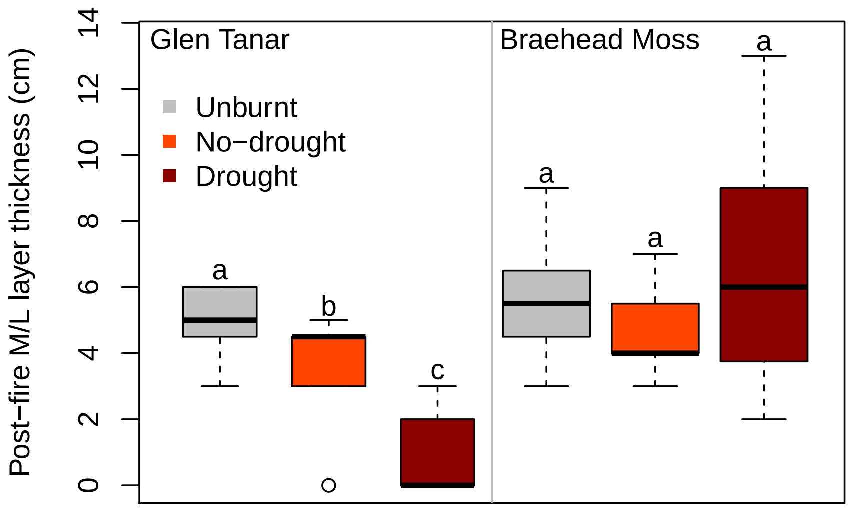

Figure 5.8: Post-fire thickness of the M/L layer above the long-term soil temperature loggers in different treatments (unburnt, no-drought burnt and drought burnt plots) at Glen Tanar and Braehead Moss. Width of the box is proportional to number of observations (5 at Glen Tanar, 7 at Braehead Moss). Different letters indicate significant differences between treatments within the same site ($\alpha = 0.05$). Model details are provided in Appendix C.4.

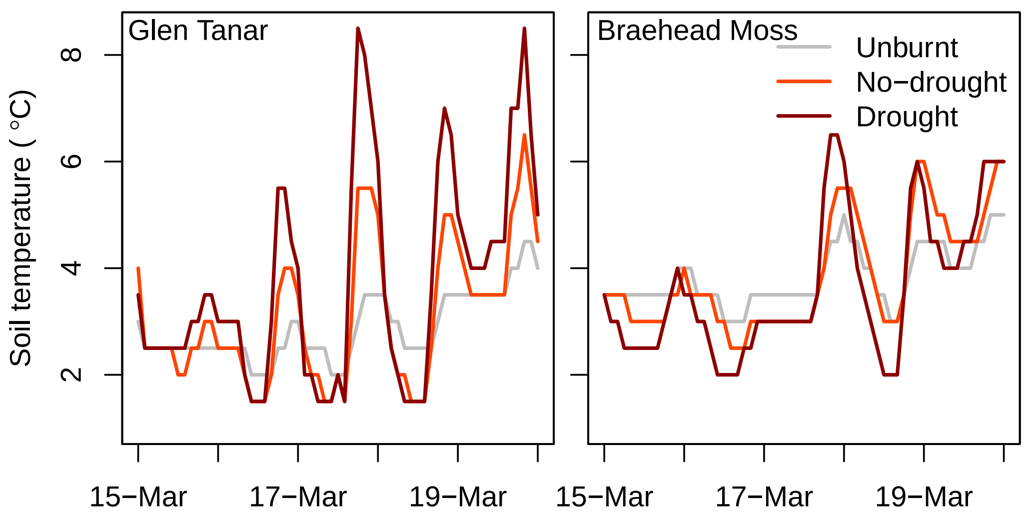

Figure 5.9: Examples of post-fire soil temperatures in three plots of different treatments (unburnt, no-drought and drought) at Glen Tanar and Braehead Moss. 2 h frequency temperature measurements are shown for five days (a length of time that allowed clearly illustrating mean and range differences) in March 2015.

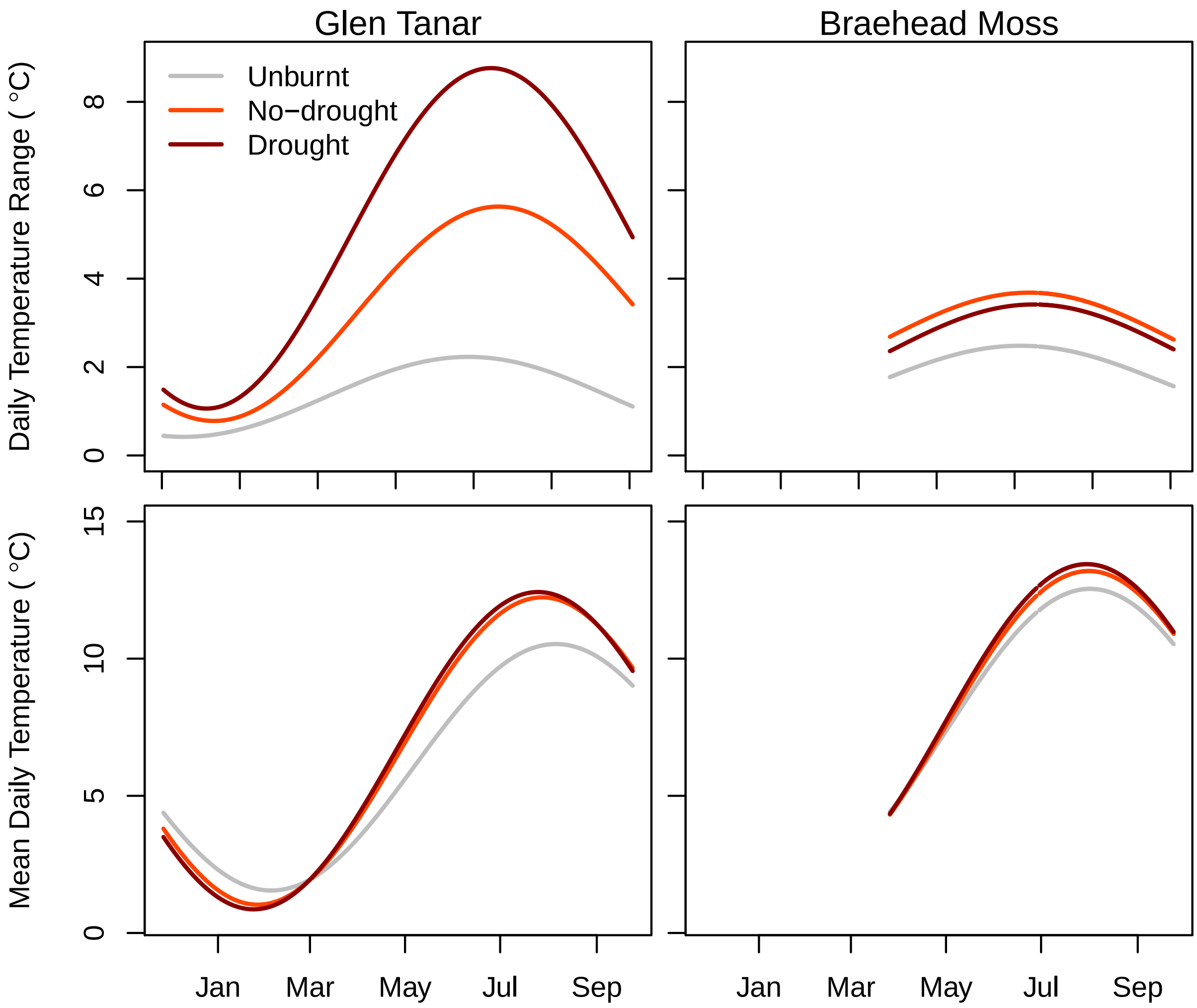

Figure 5.10: Modelled mean daily soil temperature and daily soil temperature range at 2 cm below the soil surface for unburnt, no-drought and drought plots at Glen Tanar and Braehead Moss. Model details are provided in full in the Appendix C.5.

Table 5.6: Average amplitude and phase of modelled sinusoidal post-fire soil thermal dynamics. Variance in parentheses. Different letters within site and column indicate statistically significant differences between treatments ($\alpha = 0.05$). Details of analysis of pairwise comparisons, as well as tests of differences between sites, are provided in Appendix C.5.

	Mean Daily Temperature		Daily Temperature Range	
	Amplitude	Phase	Amplitude	Phase
		Glen Tanar		
Unburnt	4.5 (0.02) a	162 (0.5) a	0.9 (0.002) a	105 (170) a
No-drought	5.6 (0.03) b	153 (1.0) b	2.4 (0.01) b	125 (17) a
Drought	5.8 (0.02) b	150 (1.0) b	3.9 (0.02) c	120 (16) a
		Braehead Moss		
Unburnt	5.1 (0.01) a	157 (0.4) a	0.82 (0.004) a	112 (117) a
No-drought	5.6 (0.02) b	156 (0.4) a	1.03 (0.008) ab	118 (89) a
Drought	5.8 (0.02) b	155 (0.6) a	1.04 (0.005) b	121 (51) a

days.

At Glen Tanar, accumulated soil heat as estimated by daily growing degree hours was higher in burnt than in unburnt plots (e.g. 86 versus 58 GDH in spring, 236 versus 191 in summer) (Figure 5.11). Conversely, burning did not have an effect on soil accumulated heat at Braehead Moss.

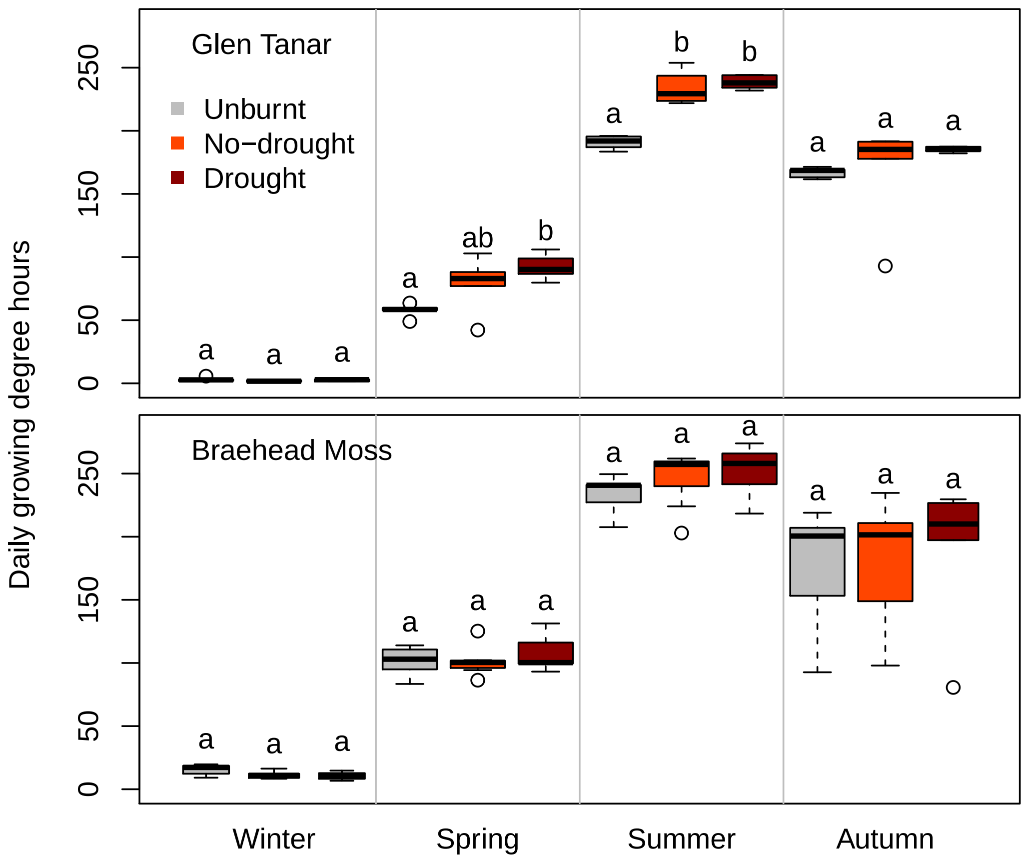

Figure 5.11: Post-fire soil accumulated heat as average daily growing degree hours for each site, season and treatment (unburnt, no-drought and drought plots). Width of the box is proportional to the number of observations (min = 4, max = 7). Different letters within site and season indicate significant differences between treatments ($\alpha = 0.05$). Full model results are provided in Appendix C.6.

5.4 Discussion

5.4.1 Effect of drought on fuel moisture content

The higher M/L layer moisture content and variability in no-drought plots at Braehead Moss compared to Glen Tanar (Figure 5.2) may have been due to the higher abundance of *Sphagnum* moss, which has great water holding capacity (Hayward and Clymo, 1982; Shetler et al., 2008). In contrast, the water repellency exhibited by many pleurocarpous mosses (Proctor, 1979) may have contributed to a lower moisture content at Glen Tanar. Simulated drought had the strongest effect on the FMC of the M/L layer. Bryophytes lack a well-developed root system and their moisture content is greatly affected by drought (Proctor, 2000). The thicker bryophyte layer in Braehead Moss relative to Glen Tanar may explain why the effect of drought on the moisture content of the superficial M/L layer (I sampled the top 2 cm) was stronger at Braehead Moss than at Glen Tanar: surface bryophytes may be more capable of accessing soil moisture in thinner M/L layers while, in thick M/L layers, bryophytes at the surface are more disconnected from the generally stable soil water store.

The lower density of the *Calluna* canopy at Braehead Moss compared to Glen Tanar (Table 5.4) could have enhanced the drought effect on the Braehead Moss M/L layer: in closed canopies *Calluna* can create a near-surface microclimate of lower maximum temperatures, reduced solar radiation and air movement, and higher air relative humidity than open *Calluna* canopies (Barclay-Estrup, 1971) and could result in lower evapotranspiration. Conversely, dead elevated *Calluna* is more exposed to the drying effect of wind and solar radiation which, together with its high surface to volume ratio (thickness < 2 mm, Davies et al., 2008b), result in a fast drying rate (38–77 min for gorse; Anderson and Anderson, 2009). This explains the similarity in dead *Calluna* moisture content between no-drought and drought plots: days suitable for burning when I sampled were dry, and the moisture content of elevated dead *Calluna* would be determined by its equilibrium with air relative humidity and not by rainfall.

The simulated drought did not significantly alter surface (upper 3.6 cm) soil moisture content at Braehead Moss (Figure 5.2), probably because raised bogs have a large capacity to store water, and this could have moved laterally (Waddington et al., 2015). The area covered by the rain-out shelters was relatively small and overland flow, movement of water within the soil profile and indirect rainfall in the frequent wet and windy weather was likely to partially compensate for the lack of direct precipitation in drought plots. Therefore the results should not be taken as representative of effects of large-scale drought on peatland hydrology. In contrast, the thin podzols of Glen Tanar probably had a low water storage capacity and thus were not able to recharge the soil surface when dry, resulting in lower superficial soil moisture content in drought plots.

The moisture content of live *Calluna* was similar in no-drought and drought plots, indicating that *Calluna* was able to access sufficient water that high hydric stress did not occur, even at Glen Tanar where soil moisture was lower. It is possible that the lower soil moisture in drought plots was sufficient for normal physiological functioning of *Calluna*, which has been observed to be tolerant to drought (Bannister, 1964). However, it is also possible that the well-developed root system of *Calluna* (Gimingham, 1960) facilitated access to soil water unaffected by the drought treatment, i.e. deeper soil layers or soil outwidth the area covered by the rain-shelter.

5.4.2 Effect of drought on fire intensity and fire severity

Drought increased fire intensity (as estimated by burnt branch tip diameter averages) at Glen Tanar (Figure 5.3). Considering there were no differences in moisture content in above-ground fuels between both treatments (Figure 5.2), this suggests that the lower moisture content of the M/L layer increased fire intensity. The contribution of the M/L layer to fuel load in *Calluna* moorlands can be important (18–61 % of total fuel load; see fuel load data in Appendix C.1) and so M/L layer consumption can substantially alter fire

Figure 5.12: Smouldering in a drought plot at Glen Tanar after the passage of a flaming fire-front.

behaviour (Davies et al., 2010b, 2016a). The lower moisture content of the M/L layer in drought plots may have increased available fuel (i.e. lowered heat losses; Alexander, 1982) therefore increasing energy output and allowing further consumption of woody fuels (Figure 5.12). However, despite higher M/L layer consumption in drought plots also at Braehead Moss, burnt branch tip diameter was similar in drought and no-drought plots. It is possible that the lower fuel load at Braehead Moss (Table 5.4) resulted in lower energy output and lower drying of the M/L layer, thus leading to lower M/L layer consumption in drought plots (1.4 cm) compared to Glen Tanar (2.3 cm), and this may have been insufficient to significantly increase consumption of woody stems.

Drought led to a general increase in fire-induced soil heating, at both depths of measurement and at both sites (Table 5.2). The increase in fire-induced soil heating due to drought was especially great at Glen Tanar. For example, average time above 50 °C, a temperature threshold of damage to plant tissue, seeds and soil microorganisms (Granström and Schimmel, 1993; Neary et al., 1999) at Glen Tanar increased from 34 s to almost 10 min at the soil surface and from 0 to 4 min 2 cm below the soil surface. Furthermore, average maximum soil temperatures during burning at Glen Tanar increased by 158 °C at the soil surface and by 27 °C 2 cm below the soil surface (189 and 40 °C, respectively). These values are higher than those previously reported at 1 cm below the soil surface in *Calluna* heathland managed burning (30–70 °C; Hobbs and Gimingham, 1984a) and suggest that burning under drought conditions could have important implications for vegetation regeneration in dry *Calluna* heathlands.

Although ecological interpretation of total heat is difficult because different combinations of maximum temperatures and duration can produce the same value, higher heating and duration of the heating is associated with drying of organic soils, thus facilitating their ignition (Hartford and Frandsen, 1992). The higher total heat at the soil surface combined with the lower soil moisture content in drought plots indicate that burning in drought conditions in dry *Calluna* heathlands could facilitate the ignition of the organic soil layer and potentially lead to substantial carbon emissions (Davies et al., 2013) and severe alteration to the habitat (Maltby et al., 1990). The lack of soil combustion in the experiments may be due the generally high soil moisture contents (Figure 5.2) relative to the critical soil moisture content for self-sustained smouldering combustion (125–150 % for peat, Rein et al., 2008; Prat-Guitart et al., 2016). Drought had a much smaller effect on fire-induced soil heating at Braehead Moss: average soil maximum temperatures during the fire remained very low (15 °C at the top of the soil and 10 °C 2 cm below) and far from temperatures that could directly impact plant tissue, seeds or soil microorganisms (> 50 °C, Neary et al., 1999). This is likely due to the higher soil moisture content, which requires more energy per temperature increase (higher heat capacity) than dry soil (Abu-Hamdeh, 2003; Busse et al., 2010). In addition, the higher insulation provided by the thicker M/L layer (Table 5.4; see also Chapter 3) and the lower energy output as suggested by the lower M/L layer consumption (Figure 5.3) may have also played a role. However, it is important to note that drought was simulated over small areas and soil water may have moved from surrounding areas at the bog. Drought at the site scale may therefore lead to lower superficial soil moisture content and increased fire severity than that reported here.

5.4.3 Environmental controls on fire intensity and fire severity

Burnt branch tip diameter was primarily controlled by site, fuel load and moisture content of the M/L layer (Table 5.5, Figure 5.5). Pre-fire fuel load at Glen Tanar was substantially higher than at Braehead Moss, and therefore the larger burnt branch tip diameter at Glen Tanar could indicate greater fire intensity as a result of higher fuel availability. This is supported by previous research on *Calluna* moorland, which reported an association between fuel load and fire intensity (Hobbs and Gimingham, 1984a; Davies et al., 2010b). However, significant differences in burnt branch tip diameter could also be related to the larger pre-fire stems at Glen Tanar. Although pre-fire stem diameter may relate to *Calluna* developmental stage and fuel load, and so fire intensity, as I do not have detailed fuel structure and *Calluna* morphology data from the two sites, comparison of intensity between them is not possible. Nevertheless, I can more readily examine the effects of the drought treatment within each site. Larger burnt branch tip diameters were correlated with low M/L layer moisture content. Low M/L layer moisture content may have resulted in a larger amount of fuel available for combustion, larger energy release above ground and enhanced drying of large woody stems, thus increasing their combustion. It is surprising that burnt branch tip diameter, which has been shown to be an adequate estimator of fire intensity (Moreno and Oechel, 1989; Whight and Bradstock, 2000), was not related to wind speed, given the importance of wind speed in determining rate of spread in *Calluna* heathlands (Davies et al., 2009) and that rate of spread is often the key control on fire intensity on a given habitat (Alexander, 1982). It is possible that high intensity but low flame residence time at high wind speeds, and low intensity but longer flame residence time, thus leading to residual smouldering, at low wind speeds resulted in similar fuel consumption.

The most important environmental variables controlling the consumption of the M/L layer were its moisture content and wind speed (Table 5.5, Figure 5.6). Wind has been found to facilitate shrubland ground fuel ignition when the ignition source is within the litter bed, but to hinder it when the ignition is on top as heat transfer downwards decreases (Plucinski and Anderson, 2008). The fact that M/L layer consumption increased with wind speed therefore suggests that combustion advanced predominantly horizontally, rather than vertically from surface ignitions. My results could also indicate that, when burning under drought conditions (i.e. when the FMC of the M/L layer is below ca. 150 %, when most M/L layer consumption was observed), higher wind speed could be an important control on M/L layer consumption through increased drying and heating of the M/L layer.

The most important variables controlling fire-induced soil heating (as total heat) were the thickness of the M/L layer and the moisture content of the M/L layer and soil. The negative relationship between the thickness of the M/L layer and fire-induced soil heating indicates the importance of the M/L layer in insulating soil from temperature pulses (Section 3.3.1). In addition, high moisture content of the M/L layer possibly prevented or limited its combustion (Davies and Legg, 2011), while soil moisture content likely reduced soil heating by increasing soil heat capacity and energy required for evaporation (Busse et al., 2005, 2010). Both when considering consumption of the M/L layer and fire-induced soil heating as fire severity indicators, the highest fire severity occurred when the moisture content of the M/L layer was below approximately 150 % (Figure 5.6). This is a higher threshold than the 70 % FMC value identified previously for substantial M/L layer consumption in a *Calluna* heathland (Davies and Legg, 2011), possibly due to the smaller area of the test ignition plots (2 × 2 m) compared to the test fires here.

5.4.4 Effect of drought on post-fire soil thermal dynamics

Burning increased daily and seasonal soil thermal ranges, as previous research has reported for UK *Calluna* moorlands (Brown et al., 2015) and Canadian northern peatlands (Kettridge et al., 2012). M/L layer combustion was likely a key control on altered post-fire soil thermal dynamics, as the thickness of the M/L layer is the main fuel structure variable explaining variation in post-fire soil thermal dynamics within the same site (i.e. for similar edaphic and fuel structure characteristics) in *Calluna* heathlands (Section 3.3.2). Combustion of the M/L layer reduces its capacity to insulate soil temperatures from variation in air temperature and solar radiation, and can lead to important changes in ground surface albedo, especially if the dark organic soil is exposed (López-Saldaña et al., 2015). The thicker M/L layer and lower consumption of the M/L layer during burning at Braehead Moss likely contributed to the lower alteration to post-fire soil thermal dynamics in the raised bog compared to the dry heath (Figure 5.8). However, given the differences in soil moisture content and thickness of the organic soil horizons between both sites, and the importance of water in regulating thermal dynamics due to its large thermal inertia, hydrological differences between the sites were probably key in explaining differences in post-fire soil thermal dynamics. This may be supported by the fact that differences in post-fire soil thermal dynamics between both sites were larger for daily temperature range than for mean daily temperature. The influence of the large thermal inertia of water at Braehead Moss would be expected to dampen shorter-term (daily) temperature fluctuation, rather than altering longer-term seasonal patterns, which may be more influenced by differences in climate between the sites (Zhuang et al., 2002).

Post-fire mean daily soil temperature patterns were similar in no-drought (low severity) and drought (higher severity) plots (Figure 5.10, Table 5.6): both showed larger seasonal changes in mean daily temperature than unburnt locations, which suggests that the additional effect that drought had on the consumption of the M/L layer was negligible compared to the general fire-induced changes to *Calluna* moorland structure (i.e. removal of the *Calluna* canopy). However, at Glen Tanar, burning under drought conditions resulted in a significantly greater daily temperature range compared to burning under no-drought conditions. Therefore the additional variation in fuel structure caused by higher severity fires under drought conditions (mainly changes in the M/L layer thickness) had a significant effect on short-term (within day) soil thermal dynamics, but it did not have an observable effect on longer-term, seasonal patterns in soil thermal dynamics, indicating the greater importance of climate on longer-term thermal dynamics. Such increased daily temperature range could lead to higher soil carbon cycling due to its non-linear relationship with soil temperature, although the effect would likely be small given the limited range. For example, for a mean daily temperature of 12 °C, soil respiration would be 4 % higher if daily range was 8 °C compared to 1 °C (Lloyd and Taylor, 1994).

Differences in post-fire soil thermal dynamics between treatments led to higher accumulated heat in the soil in burnt than in unburnt plots at Glen Tanar during spring and summer (Figure 5.11). Such higher soil temperature during the growing season could facilitate regeneration of recently-burnt plants with living parts entirely below ground. A greater soil temperature range could also have an effect on post-fire vegetation regeneration by stimulating seed germination (Thompson and Grime, 1983).

5.5 Conclusions

Simulated drought increased fire effects more strongly at the dry heath (Glen Tanar) compared to the raised bog (Braehead Moss) site. At the dry heath, drought lowered the moisture content of the M/L layer and the soil, which resulted in significantly higher M/L layer consumption and soil heating. Such changes led to alteration of post-fire soil thermal dynamics: drought plots showed higher mean daily range than no-drought burnt plots, although there were no differences in post-fire mean daily temperatures. At the raised bog, the simulated drought lowered the moisture content of the M/L layer, but did not have an effect on soil moisture content. Compared to the dry heath, fire-induced soil heating and alteration of post-fire soil thermal dynamics were very low at the raised bog. Increased consumption of the M/L layer and higher soil heating occurred when the moisture content of the M/L layer was below 150 %. Low soil moisture content and high wind speed also contributed to higher fire severity. The results suggest that, with regards to fire severity, heathlands are significantly more sensitive to drought than bogs, and that, in a context of climate change where increased summer droughts are projected, *Calluna* heathlands community composition and carbon stores may be more at risk than bogs.

Chapter 6

Higher fire severity does not alter increased short-term soil carbon emission in a *Calluna* heathland and a raised bog

Abstract

Large amounts of carbon are stored in northern peatlands. Wildfire severity is projected to increase across northern regions due to predicted drier conditions, and there is concern this will lead to higher post-fire belowground carbon losses to the atmosphere. I monitored soil carbon dynamics in a dry heath and a raised peat bog after experimental fires. The fires were conducted along a severity gradient achieved by simulating drought in 2 × 2 m plots, while other plots were burnt under ambient conditions. Ecosystem respiration (ER), net ecosystem exchange (NEE), methane flux (CH_4) and concentration of dissolved organic carbon (DOC, measured at the raised bog only) were monitored up to two years after burning. Burning altered average NEE from a net carbon sink (-0.33 μmol m^{-2} s^{-1} in unburnt plots) to a carbon source (0.50 μmol m^{-2} s^{-1} in burnt plots) at the dry heath and at the raised bog (-0.38 and 0.16 μmol m^{-2} s^{-1}, respectively) during the first

two years post-fire. Burning also increased CH_4 flux at the raised bog (e.g. from 1.16 to 25.3 nmol m^{-2} s^{-1} in the summer, when it accounted for 79 % of the CO_2-equivalent emission) but had no effect on soil water DOC concentration. For all soil carbon dynamics measurements, soil temperature, soil moisture and vegetation cover were important, often interacting, controlling mechanisms. Response of soil carbon dynamics to increased fire severity in drought plots was similar to plots burnt under ambient conditions. Thus higher fire-induced ground fuel consumption and soil heating after drought did not further alter controlling mechanisms of soil C cycling compared to regular managed burning.

6.1 Introduction

Soils are the largest terrestrial carbon (C) store, with global C stocks estimated at ca. 1500 Pg of C in the upper 1 m, and 2400 Pg in the upper 2 m (Stockmann et al., 2013; Scharlemann et al., 2014). In comparison, biomass pools are estimated at 360–560 Pg C (Stockmann et al., 2013; Liu et al., 2015) and atmospheric pools, at 832 Pg C (IPCC, 2013). Peatlands store a disproportionately large amount of C (ca. 600 Pg C; Yu et al., 2010; Page et al., 2011; Yu, 2012) relative to their area (ca. 3 % of the global land surface) and so there is interest in evaluating the potential impact of environmental change on their C stores. For instance, land-use changes leading to drier peat have resulted in C losses from tropical peatlands (Hooijer et al., 2012; Konecny et al., 2016). However, most peat (500 Pg C, Yu, 2012) is stored in northern regions, where it may be particularly vulnerable to changes triggered by the projected warmer and drier climate (IPCC, 2013; Cook et al., 2014) such as permafrost melt and increased CO_2 emissions (Dorrepaal et al., 2009) and increased wildfire activity (Turetsky et al., 2002; Flannigan et al., 2009; Turetsky et al., 2015), and could potentially contribute to a positive feedback with climate change (Heimann and Reichstein, 2008).

Fire can directly impact on belowground C stores during high severity fires where peat or organic soil layers are ignited (Turetsky et al., 2011b; Davies et al., 2013). But even in normal hydrological conditions in northern peatlands (Waddington et al., 2015) when peat moisture content is high and does not ignite (> 150 %; Prat-Guitart et al., 2016), fire can alter the mechanisms controlling soil C dynamics. Fire-induced plant mortality reduces root and aboveground respiration and can lower ecosystem respiration (ER, heterotrophic soil respiration and autotrophic respiration from roots and aboveground plant structures) (Hanson et al., 2000; Janssens et al., 2001; Moore et al., 2002). The lower supply of labile substrate from root exudates can also reduce microbial respiration (Artz, 2013). In addition, burning has been associated with warmer soils (Chapter 3; Chapter 5; Zhuang et al., 2002; Kettridge et al., 2012; Brown et al., 2015) which may increase C cycling, leading to higher ER (Dunfield et al., 1993; Lloyd and Taylor, 1994; Freeman et al., 2001b; Dorrepaal et al., 2009). Furthermore, a shallower post-fire water table (Wieder et al., 2009; Clay et al., 2012), possibly due to reduced evapotranspiration, and thus lower oxygen availability in the superficial peat could decrease soil respiration (Artz, 2013) and dissolved organic carbon (DOC) production (Moore, 2013) and increase methane (CH_4) flux (Moore and Dalva, 1993; Morris et al., 2002). Altered post-fire soil microbiology (Dooley and Treseder, 2012; Wang et al., 2012; Sun et al., 2016) is also likely to lead to changes in soil C dynamics. Post-fire changes in vegetation community composition (Chapter 4) can impact on soil C dynamics due to differences in C cycling between plant functional groups (Ward et al., 2009; Kip et al., 2010; Strack et al., 2016), changes to associated microbial communities (Bragazza et al., 2015) and substrate for decomposition (Bragazza et al., 2013), and altered transport mechanisms including ebullition and plant-mediated flux (Coulthard et al., 2013; Gray et al., 2013).

Wildfires have been reported to decrease the C sink in boreal peatlands, both due to fuel combustion and to altered post-fire peat C dynamics, i.e. reduced primary productivity and increased respiration due to warmer peat and fertilization from ash (Turetsky et al., 2002). Peat bogs can become net

C sources after a fire, switching back to net C sinks as vegetation regenerates (e.g. 13 years, peak C sink at 75 years; Wieder et al., 2009). For established vegetation, net ecosystem exchange (NEE, ER minus photosynthesis) increases (i.e. larger carbon source or smaller carbon sink) with age: in a blanket bog, NEE was higher in 50-year burnt plots than in 20-year burnt plots, in turn higher than in 10-year burnt plots (Ward et al., 2007; Clay et al., 2010). Work on the effect of burning on CH_4 flux has not shown clear patterns, with research on blanket bogs reporting no short-term (< 3 years) change (Taylor, 2015) and long-term (10 years) decline (Ward et al., 2007) following managed fires. In addition, DOC concentration has been found to be higher in streams draining catchments where managed burning had taken place (Ramchunder et al., 2013), but no differences have been found at the plot level (Armstrong et al., 2012; Clay et al., 2012). Methodological differences between catchment and plot studies have been proposed to explain the contradictory results (Holden et al., 2012), but clear evidence of the effect of burning on DOC is still lacking.

In the UK, peat bogs contain the largest amount of belowground C ($>$ 550 Tg C, 35 % of belowground C in the upper 0.5 m of all terrestrial ecosystems), but dwarf shrub heathlands also store a substantial amount (125 Tg C, 7 %; Ostle et al., 2009). Carbon deposits in heathlands may actually be more vulnerable to fire given the apparent lower resilience of these habitats to drought (Chapter 5; Davies et al., 2016a). Moreover, these are semi-natural habitats often managed by prescribed burning (Dodgshon and Olsson, 2006; Allen et al., 2016) and prone to wildfires (Legg et al., 2007). While dry conditions have been linked to high severity fires, i.e. where peat ignites leading to large C losses (Turetsky et al., 2011a; Davies et al., 2013), few studies have focused on the effect of variation in fire severity on post-fire belowground C dynamics. This is a significant gap in our understanding given the potential for increased fire severity across northern regions in response to climate change. I aimed to investigate the effect of a fire severity gradient on soil carbon dynamics by completing experimental fires in two UK habitats: an upland dry heath and a lowland raised bog (see Section 2.1). Although both sites have similar above-ground vegetation structure, dominated by dense *Calluna* and a continuous bryophyte layer, they are at either extremes of an ecohydrological gradient. Soils at the dry heath were well-drained peaty podzols with an organic horizon < 10 cm, but the peat at the raised bog was > 1 m deep and saturated throughout most of its profile. My specific objectives were to: (i) understand how soil carbon dynamics (ER, NEE, CH_4 flux and DOC concentration) respond to a gradient of fire severity resulting from moisture content manipulation (Chapter 5); (ii) investigate how responses to fire vary across the sites' ecohydrological gradient; and (iii) quantify the impact of interacting environmental variables on soil C dynamics. A greater understanding of the effect of higher fire severity on soil C dynamics is important for predicting potential impacts of altered fire regimes on soil carbon stores, and to inform management strategies to minimise carbon loss.

6.2 Materials and methods

6.2.1 Simulating a range of fire severities

I completed ten experimental fires at Glen Tanar and nine at Braehead Moss between the 10th of September 2013 and the 13th of November 2014. In each fire, two 2×2 m rain-out shelters had been installed three to four months before the fires. I used M/L layer consumption and soil heating as indicators of fire severity. Fire severity was higher in treated (drought) than in untreated (no-drought) burnt plots, and at the dry heath (Glen Tanar) than at the raised bog (Braehead Moss). Chapter 5 provides more information on the experimental design and on fire severity differences between treatments and sites.

6.2.2 Vegetation cover

I visually estimated the percentage cover of broad plant functional groups (shrubs, graminoids and bryophytes) and type of substrate (litter and duff/bare soil) within the collars used for measuring CO_2 and CH_4 fluxes at both sites (for gas flux data), and in a central 1 m^2 of each plot in Braehead Moss (for DOC data). Glen Tanar was surveyed in April 2015 and Braehead Moss in September 2015.

6.2.3 Soil temperature and moisture content

Soil temperature during the gas flux and DOC measurements period was measured using soil temperature loggers deployed as per Section 5.2.1. Soil temperature measurements at 2 h intervals were averaged across plots within each treatment and site. Soil temperature data was not available for some gas flux and DOC sampling due to sampling occurring outwith the soil temperature measurement period or due to temperature logger malfunction. I estimated missing soil temperatures in each site by correlating the observed soil temperatures with soil temperatures measured in nearby weather stations (Aboyne, 13 km east of the Glen Tanar site, and Drumalbin, 13 km south of Braehead Moss; Met Office, 2012). The linear models included an interaction between soil temperature at 10 cm at the weather station, treatment and hour of the day as explanatory variables. Soil temperature measurements were available for all gas flux sampling dates at Braehead Moss, but needed to be estimated for 21 % of the gas flux sampling dates at Glen Tanar. 53 % of the soil temperatures associated with DOC sampling at Braehead Moss had to be estimated.

Moisture content of the soil surface (approximately top 6 cm) was estimated using a soil moisture meter (Hydrosense^{TM}, Campbell Scientific, see Section 2.2 for calibration details), taking three measurements near the location of each collar.

6.2.4 Gas fluxes

The closed static non-steady-state chamber method was used to estimate gas fluxes. Here, ground-atmosphere gas flux is calculated on the basis of the gas concentration change with time in a closed volume (Bekku et al., 1995). I inserted opaque plastic collars into the ground at a randomly-chosen location in each plot, and in an unburnt control, at least two weeks before taking the first gas flux measurements. Each collar had an area of 0.0962 m^2, and mean height of 0.21 m (SD = 0.024 m) above ground. A cylindrical clear plastic chamber (height = 0.46 m, diameter = 0.39 m) was secured to the top of the collar with clamps. Mean headspace volume was 0.075 m^3, SD = 0.003 m^3. Foam was used in the interspace between collar and chamber to prevent leaks. The chamber contained a five-volt fan, and air temperature and relative humidity sensors. A photosynthetically active radiation (PAR) sensor was mounted on top and orientated perpendicular to the ground (Figure 6.1). Due to instrument malfunction, I used two different analysers to measure the change of gas concentration in the chamber space: a Los Gatos Research Ultraportable Greenhouse Gas Analyser (CO_2, CH_4, H_2O) and a Vaisala GMP343 Carbon Dioxide Probe (CO_2 only), both with a 1 s measurement rate. Plastic tubing connected the Los Gatos analyser to the chamber and air was continually circulated with a pump integrated in the instrument, whilst the Vaisala analyser was mounted directly on top of the chamber. Tubing volume was negligible (< 0.1 % of headspace volume) and not taken into account for gas flux calculation. I used the Los Gatos analyser from August 2014 to April 2015, and the Vaisala analyser from June to October 2015 (Appendix D.1 provides details on sampling effort and average weather conditions in each sampling day).

Closure times ranged between four and five minutes. In each plot I took a measurement with the chamber uncovered for estimating NEE (and CH_4 when the Los Gatos analyser was used), and a "dark" measurement with a black opaque polyethylene cover over the chamber for ER. By convention, negative NEE values indicate a C sink. The chamber was opened for ventilation for

Figure 6.1: Closed chamber during net ecosystem exchange (NEE) and CH_4 flux measurements in Braehead Moss, with the Los Gatos Research analyser in operation.

at least one minute prior to each measurement. Gas fluxes (F, μmol m^{-2} s^{-1}) were calculated (Levy et al., 2011; Equation 6.1) from the sequence of gas concentration measurements over time in each chamber closure.

$$F = \frac{dC}{dt_0} \cdot \frac{\rho V}{A} \tag{6.1}$$

where dC/dt_0 is the initial change in concentration (in μmol mol^{-1} s^{-1}) as estimated by a regression model, ρ is the air density (mol m^{-3}), V is the volume of the headspace (volume of the closed chamber and volume of the collar above the ground, in m^{-3}), and A is the area of ground delimited by the collar (m^{-2}).

Increase in water vapour concentration in the chamber during the closure time has a dilution effect on the gas concentration measurement, and therefore water vapour needs to be accounted for and the gas concentration calculated on a dry air basis. The Los Gatos analyser corrected the concentration measurement internally. For the Vaisala analyser gas concentration measurements were corrected as follows:

$$C_{dry} = \frac{C_{moist}}{1 - C_{H_20}} \tag{6.2}$$

where C_{dry} and C_{moist} are CO_2 concentrations (in μmol mol^{-1}) in dry and moist air, respectively, and C_{H_20} is the water vapour concentration in mol mol^{-1}.

The initial change in concentration (dC/dt_0) can be estimated using a range of linear and non-linear modelling approaches (Levy et al., 2011). The simplest and most widely-used approach is linear regression, which provides an adequate estimate of initial change in concentration when the change in concentration is constant during the closure time, as was observed (see Appendix D.2 for an example of a long closure showing a linear response), and so linear regression was used. Air density (ρ) varies with pressure and air temperature, and was calculated using Equation 6.3.

$$\rho = \frac{P}{R \cdot T} \tag{6.3}$$

where ρ is air density (in mol m^{-3}), P is the air pressure (in Pa), R is the specific gas constant for dry air (in J kg^{-1} K^{-1}), and T is the average air temperature in the chamber (in K).

6.2.5 Dissolved Organic Carbon

Measurement of soil water DOC concentration was limited to the raised bog site (Braehead Moss) as insufficient soil water could be sampled from the thin and free-draining soils of Glen Tanar. Soil water was sampled and water table depth measured using a network of PVC dip-wells with an internal diameter of 1.9 cm perforated at a frequency of 1–2 cm from 10 cm to 60 cm below the peat surface (Figure 6.2). Depth of the open part of the dip-well was designed to include water table fluctuation on the basis of a pilot study, and was slightly shallower than in previous research on effects of burning on peatland DOC (ca. 0–100 cm; Clay et al., 2012; Worrall et al., 2013b; Armstrong et al., 2015). Depth of measurement could have an effect on observed DOC concentration due to higher sensitivity of shallow soil water to environmental variables in peatlands (Clark et al., 2008; Holden et al., 2012). I manually inserted a dip-well centrally within each 2 × 2 m treatment area of each plot and in two unburnt locations (controls) near each fire.

I took soil water samples approximately every two months from October 2013 to November 2015, emptying the dip-wells 24 h before taking the samples. The depth of the water table was recorded to the nearest cm before emptying the dip-wells. The samples were later filtered using pre-combusted 0.7 μm glass fibre filters (Fischerbrand) and stored in low-density polyethylene (LDPE) bottles in the dark at 3 °C for two to four months until the carbon concentration was analysed with a total carbon analyser (Thermolox™, Analytical Sciences).

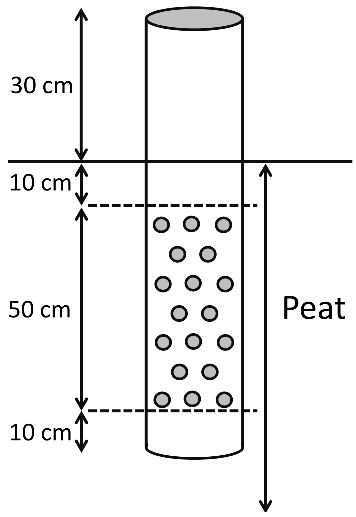

Figure 6.2: Diagram of the installation of a dip-well. Small circles indicate perforated area.

6.2.6 Data analysis

I used R 3.2.2 (R Core Team, 2015) for all statistical analysis and plotting. The function "lme" in the package *nlme* (Pinheiro et al., 2015) was used for fitting linear mixed effects models and "r.squaredGLMM" in *MuMIn* (Barton, 2015) to calculate marginal R^2 (variance explained by fixed effects) and conditional R^2 (variance explained by both fixed and random effects). Table 6.1 shows the environmental variables available for modelling carbon dynamics. The variance inflation factor (VIF) among covariates was used to detect multicollinearity (function "vif" in *usdm*; Naimi, 2015). Final model selection was based on the Akaike information criterion (AIC). Section 2.5 provides more information on data analysis. Gas flux estimates for which the 95 % confidence intervals of the regression line included zero were considered zero in order to exclude spurious estimates due to measurement inaccuracy.

Ecosystem Respiration

The effect of fire severity (treatment levels: unburnt, no-drought and drought) on ER within the same site and climatic conditions (season levels: spring,

Table 6.1: Environmental variables used as fixed effects in modelling Ecosystem Respiration (ER), Net Ecosystem Exchange (NEE), methane (CH_4) emissions and/or concentration of dissolved organic carbon (DOC).

Variable	Details
Soil *T*	Temperature (°C) 2 cm below the soil surface, averaged for site and treatment, important for C cycling as metabolic activity is temperature-dependent (Lloyd and Taylor, 1994; Smith et al., 2007; Dorrepaal et al., 2009).
Soil MC	Soil moisture content (top 6 cm; in % dry base), related to oxygen availability and substrate transport (Kalbitz et al., 2000; Smith et al., 2007; Strack et al., 2008; Levy et al., 2012).
Water table	Depth of the water table below the peat surface in Braehead Moss (cm). Controls similar mechanisms as soil moisture content.
t since fire	Time since burning, in days. Fire dates are provided in Table 5.1. Related to productivity of vegetation and microbial community (Wieder et al., 2009; Dooley and Treseder, 2012; Wang et al., 2012; Köster et al., 2016).
PAR	Average photosynthetic active radiation during the NEE measurement, in μmol m^{-2} s^{-1}. Controls photosynthesis (Wieder et al., 2009; Appendix D.2).
Shrubs	Percentage cover of shrubs in collars (for gas flux analysis) or plots (for [DOC]); dominated by *Calluna* but with *Erica cinerea* and *Erica tetralix* also present. Plant functional type is an important control on C dynamics (Ward et al., 2009; Gray et al., 2013).
Graminoid	Percentage cover of graminoids in collars or plots; principally *Eriophorum vaginatum* at Braehead Moss and *Deschampsia flexuosa* at Glen Tanar.
Bryophytes	Percentage cover of bryophytes in collars or plots; dominated by *Hypnum jutlandicum* and *Plerozium shcerebi* in unburnt plots and *Polytrichum juniperinum*, *Dicranum scoparium* and *Campylopus introflexus* in burnt plots.
Litter	Percentage cover of plant litter in collars or plots, important as substrate for decomposition (Bragazza et al., 2013).
Duff	Percentage cover of duff or bare soil in collars or plots.
Site	Glen Tanar (dry heath) or Braehead Moss (raised bog). Ecosystem type can greatly influence C cycling through variables not accounted for here such as belowground C (Levy et al., 2012).
Treatment	Drought and no-drought burnt plots, and unburt plots, i.e. higher severity, low severity fires and unburnt controls.
Season	Spring (March–May), summer (June–August), autumn (September–November) and winter (December–February).
Instrument	Gas analyser, either Los Gatos Research GHG analyser or Vaisala CO_2 probe. Included in ER and NEE models to account for the possible effect of using different analysers.

summer and autumn) was analysed by fitting a linear mixed effects model with an interaction between site (Glen Tanar, a dry heath, and Braehead Moss, a raised bog), treatment and season as fixed effects, plot within fire as random effects and a constant variance function to account for the heterogeneity of variance between different seasons. Multiple comparisons were performed on the basis of 95 % confidence intervals of differences between means, using the variance of the full model and a Bonferroni correction (3 treatments $\times$ 2 sites $\times$ 3 seasons = 18 comparisons) for the t value.

The effect of interacting environmental variables (Table 6.1) on ER was investigated using a linear mixed effects model. Given the importance of soil temperature and moisture content in explaining variation in C dynamics (Lloyd and Taylor, 1994; Kalbitz et al., 2000; Smith et al., 2007; Strack et al., 2008; Dorrepaal et al., 2009; Levy et al., 2012), the initial model included an interaction between both and site, treatment, instrument and cover of plant functional type and substrate as fixed effects (Table 6.2). The influence of time since fire on ER is related to post-fire recovery of ecosystem functions such as soil microbial activity, which may depend on fire severity. Since variation of fire severity between treatments was different in each site (see Section 5.3.2) I considered that the effect of time since fire may interact with treatment and site.

Net ecosystem exchange

The effect of fire severity on NEE was analysed following the same approach as for ER. To study the effect of environmental variables on NEE, in addition to the interactions already considered for ER, an interaction between photosynthetic active radiation (PAR), treatment and vegetation cover (shrubs, graminoids and bryophytes) was also included in the fixed part of the linear mixed effects model of NEE (Table 6.2). As with ER, plot within fire was included as a random effect and a constant variance function was used to account for the different residual variances at Glen Tanar and at Braehead Moss.

Table 6.2: Full (before model selection) linear mixed effects model specifications for analysing the effect of environmental variables (Table 6.1) on ecosystem respiration, net ecosystem exchange and concentration of dissolved organic carbon. All models included plot within fire as random effects.

Response	Fixed effects in full model
ER	Soil T × Soil MC × (Site + Treatment + Instrument + Shrub + Graminoid + Bryophyte + Litter + Duff) + t since fire × Site × Treatment
NEE	Soil T × Soil MC × (Site + Treatment + Instrument + Shrub + Graminoid + Bryophyte + Litter + Duff) + t since fire × Site × Treatment + PAR × Treatment × (Shrub + Graminoid + Bryophyte)
log([DOC])	Soil T × WT depth × (Treatment + Shrub + Graminoid + Bryophyte + Litter) + t since fire × Treatment

Methane flux

High abundance of zeros made statistical analysis of methane flux data using linear regression impossible. A graphical analysis based on boxplots is presented instead.

Dissolved organic carbon concentration

I analysed the effect of fire severity on DOC concentration in different seasons by fitting a linear mixed effects model with an interaction between treatment and season as fixed effects and plot within fire as a random effect. The function "glht" in *multcomp* was used to perform simultaneous tests on differences between treatments within seasons. For analysing the effect of environmental variables, DOC concentration was log-transformed and the fixed effect structure followed the one used for ER, except site and instrument were not included and soil moisture content was substituted by water table depth (Table 6.2).

6.3 Results

6.3.1 Vegetation cover

Burning led to lower cover of shrubs in the gas flux collars (mean across both sites ± standard deviation was 26.8 ± 24.7 % in unburnt and 7.1 ± 7.8 % in burnt plots) and of bryophytes (80.2 ± 18.1 % in unburnt and 14.4 ± 20.2 % in burnt plots), while graminoids had similar cover in unburnt (4.0 ± 5.5 %) and burnt plots (4.8 ± 10.3 %) (Figure 6.3). The low fire severity treatment (no-drought plots) had similar cover of shrubs (5.3 ± 4.7 %), graminoids (4.3 ± 5.4 %) and bryophytes (17.5 ± 22.6 %) than the higher severity (drought) treatment (8.8 ± 9.7 %, 5.4 ± 13.6 % and 11.4 ± 17.3 %, respectively). Litter cover was highest in no-drought plots (52.5 ± 29.4 %), and cover of duff/bare soil was highest in drought plots (60.7 ± 35.0 %). The sum of litter and duff/bare soil made up most of the cover in burnt plots collars (78 % at Glen Tanar, 63 % at Braehead Moss). I found similar patterns of post-fire vegetation cover in 1 m^2 plots at Braehead Moss (used for analysis of DOC concentration) except for the higher shrub cover in unburnt plots (ca. 65 % versus 30 % in collars; see Appendix D.3).

6.3.2 Soil temperature and moisture content

The models for estimating soil temperatures had an R^2 of 0.96 for Glen Tanar and 0.94 for Braehead Moss (see Appendix D.4 for details). A complete analysis and discussion of post-fire soil thermal dynamics (excluding estimated values) is provided in Sections 5.3.4 and 5.4.4. Post-fire soil temperature patterns were different at both sites (Figure 6.4). At Glen Tanar, burnt plots had larger annual temperature extremes, and daily temperature fluctuation was higher in drought plots than in no-drought, in turn higher than unburnt. At Braehead Moss, temperature patterns were similar in all treatments. Air in the chamber during the gas flux measurement was always warmer than the soil, but the temperature difference between air and soil was greater in unburnt

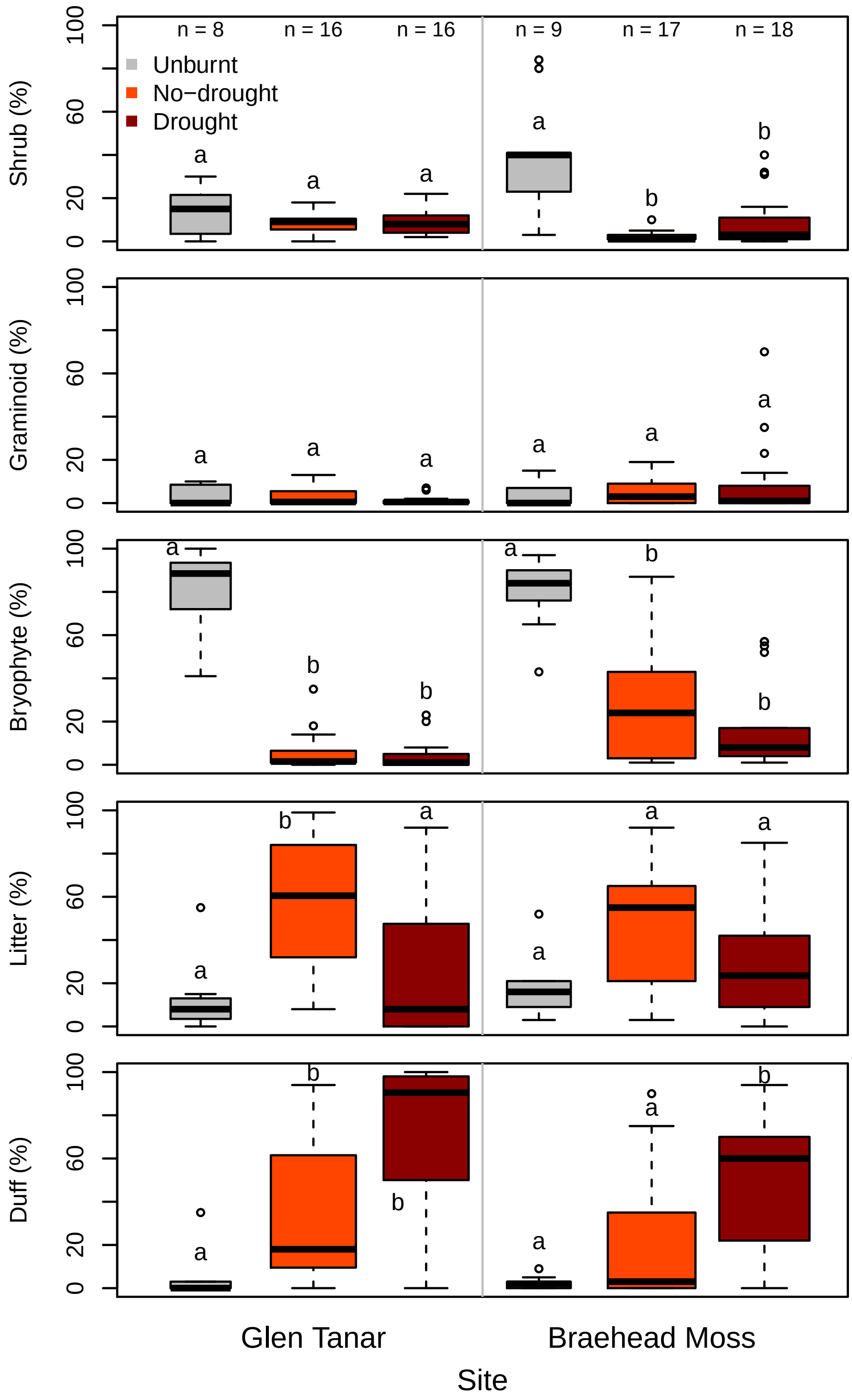

Figure 6.3: Post-fire vegetation cover in gas flux collars per fire severity treatment and site. n indicates number of observations. Different letters above boxes indicate significant differences between treatments within the same site and vegetation/substrate type ($\alpha = 0.05$). Model details can be found in Appendix D.3.

than in burnt plots (e.g. at Glen Tanar, average soil and air temperatures in unburnt plots were 9.6 and 18.0 °C, respectively, while they were 13.2 and 17.7 °C in drought plots; see Appendix D.5 for detailed information).

Moisture content of the top soil during the gas flux measurements was higher at Braehead Moss (average = 330 %) than at Glen Tanar (275 %), but differences between treatments within the same site were generally small and it was only during spring at Glen Tanar that drought plots had significantly lower soil moisture content (Figure 6.5). There was weak statistical evidence (t-value = -1.8, p-value = 0.07) that average water table at Braehead Moss was lower in unburnt (20.6 cm below the soil surface) than in burnt plots (16.0 cm in no-drought and 16.5 cm in drought); differences between treatments within the same season were not significant (Figure 6.6).

6.3.3 Ecosystem respiration

Seasonal average ER in unburnt plots at Glen Tanar ranged between 0.58 (spring) and 1.7 μmol m^{-2} s^{-1} (summer) (Figure 6.7; summary statistics are provided in Appendix D.7). At Braehead Moss, average ER in unburnt plots was slightly higher and ranged between 0.85 (spring) and 2.05 μmol m^{-2} s^{-1} (summer). Pairwise comparisons between treatments indicated significantly higher ER in unburnt than in burnt plots for all seasons considered, both at Glen Tanar and at Braehead Moss. ER in drought plots was significantly greater than in no-drought plots in autumn at Glen Tanar (0.52 versus 0.87 μmol m^{-2} s^{-1}), but all other differences between fire severity treatments within the same season and site were statistically non-significant. Burning seemed to reduce heterogeneity in ER.

There was high multicollinearity between cover of bryophytes, litter and duff in collars, and duff was dropped from further analysis of environmental variables (Appendix D.8 provides VIF details). Model selection retained most variables in the full model but excluded some high level interactions (Table 6.3). Soil temperature and soil moisture content were key controls on ER, as indicated by their presence in most interacting terms in the model

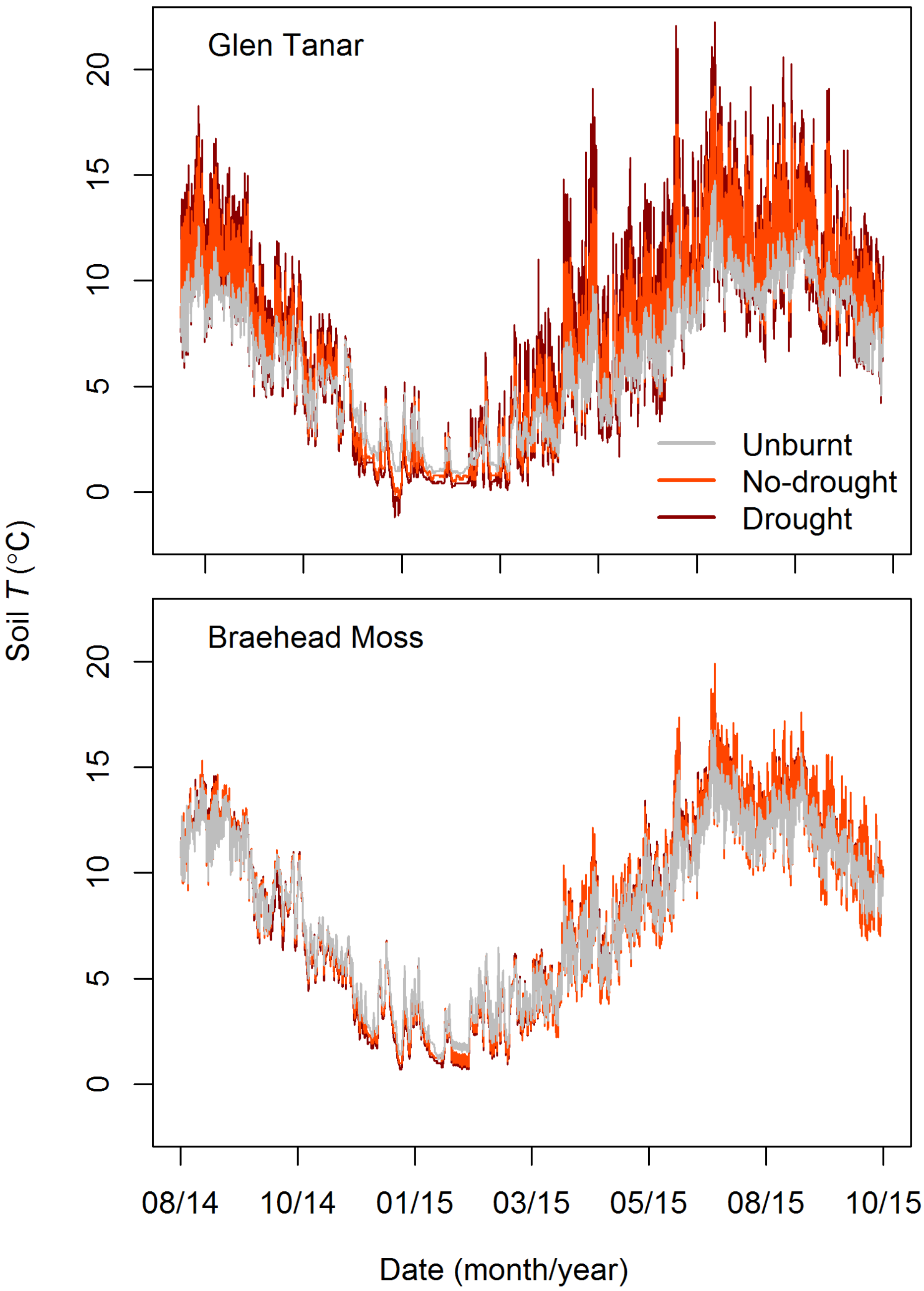

Figure 6.4: Soil temperature 2 cm below the soil surface during the gas flux measurement period. Grey lines are bi-hourly soil temperature averages in unburnt plots; light red, no-drought burnt plots; dark red, drought burnt plots. At Glen Tanar mean summer temperature was 9.8 °C (unburnt) and 11.5 °C (boh burnt treatments); at Braehead Moss it was 12.1 °C (unburnt), 12.7 °C (no-drought) and 12.9 °C (drought).

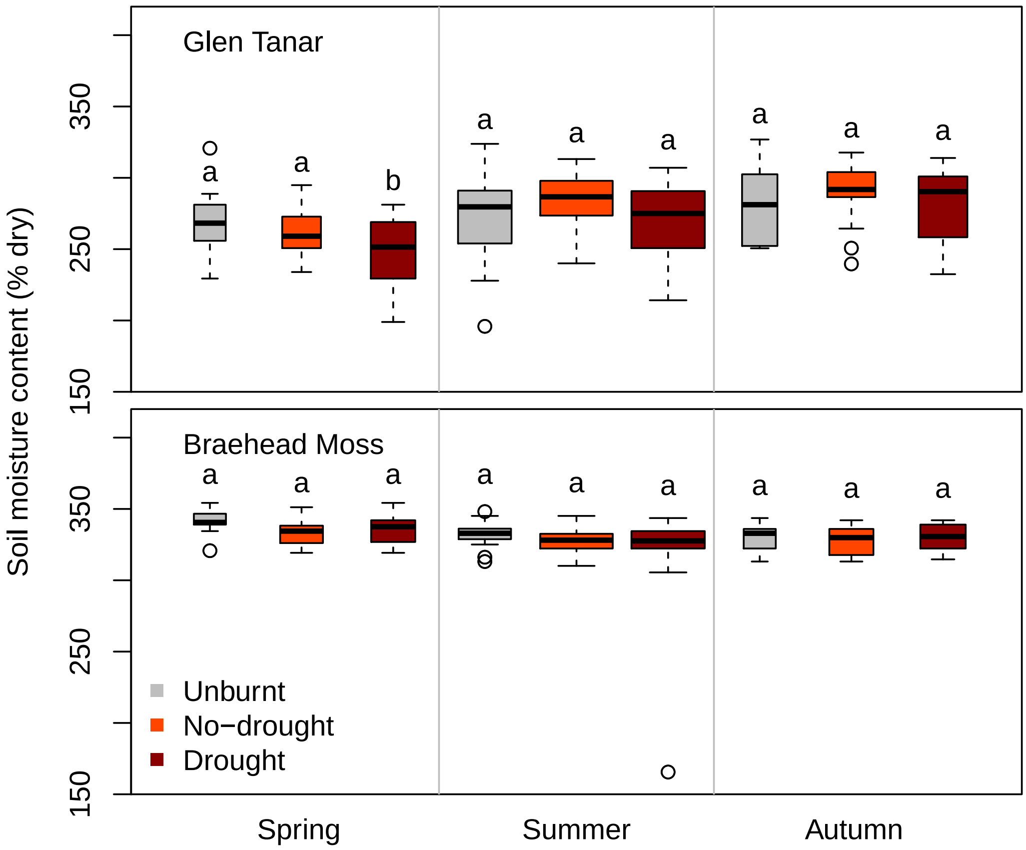

Figure 6.5: Moisture content of the top 6 cm of soil during gas flux measurements in unburnt and both burnt plots (no-drought and drought) at Glen Tanar and Braehead Moss per season (spring: March–May, summer: June–August, autumn: September–November), showing small differences between treatments. Width of the boxes is proportional to the number of observations (16–86 at Glen Tanar; 18–94 at Braehead Moss). Different letters above boxes indicate significant differences between treatments within the same site and season ($\alpha = 0.05$). Model details can be found in Appendix D.6.

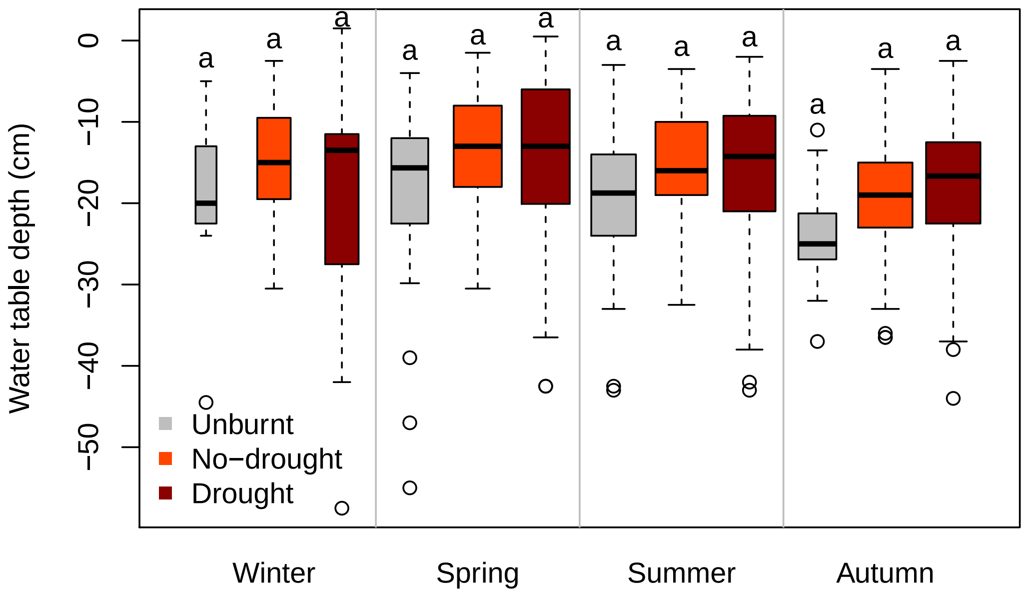

Figure 6.6: Water table depth at Braehead Moss during DOC monitoring, for each season (winter: December–February, spring: March–May, summer: June–August, autumn: September–November) treatment (unburnt, no-drought, drought). Width of the box is proportional to the number of observations (min = 11, max = 74). Different letters above boxes indicate significant differences between treatments within the same season ($\alpha = 0.05$). Overall differences between unburnt and burnt plots, with plot within fire as random effect, were weakly significant (p-value = 0.07). Model details can be found in Appendix D.6.

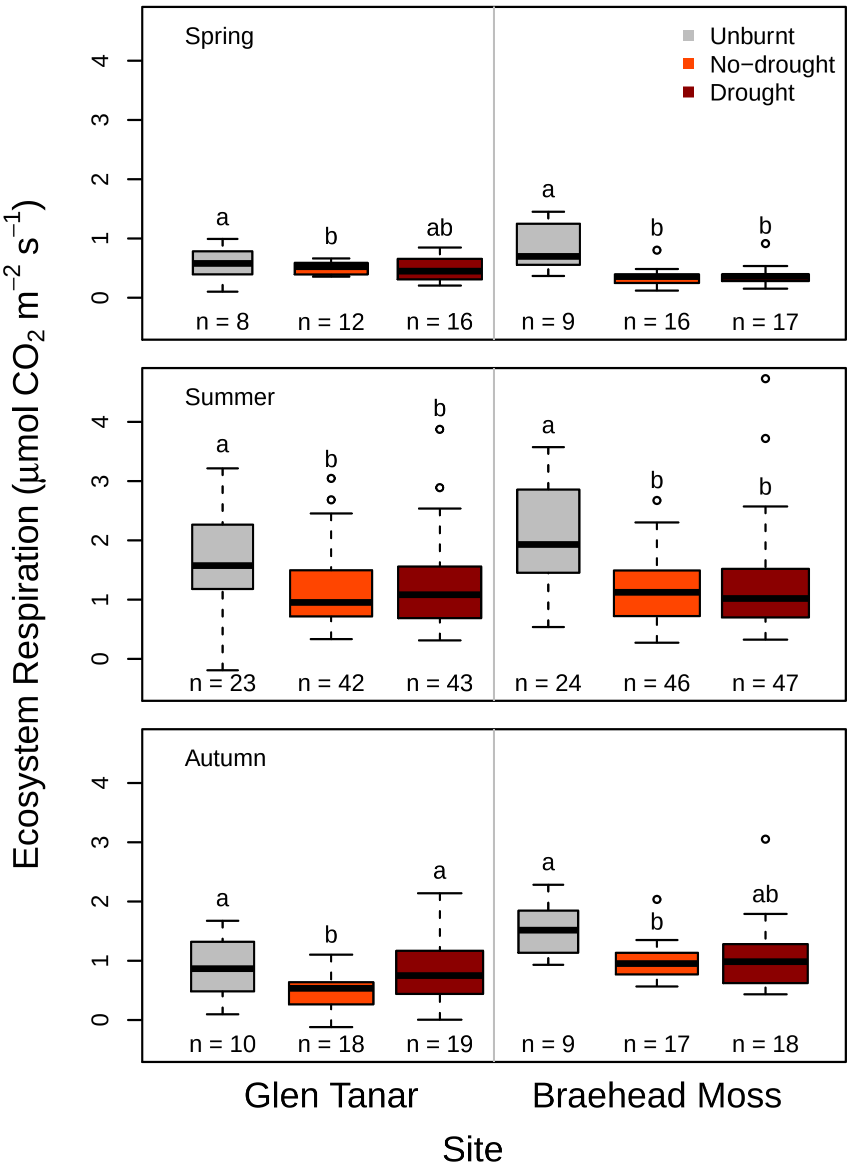

Figure 6.7: Ecosystem respiration per treatment, season (spring: March–May, summer: June–August, autumn: September–November) and site. n indicates number of observations. Within each season and site, different letters above the boxplots indicate statistically significant differences between treatments. Summary statistics and model details are provided in Appendix D.7.

Table 6.3: Optimal linear mixed effects model specifications (after model selection) for ecosystem respiration, net ecosystem exchange and concentration of dissolved organic carbon. All models included plot within fire as random effects. See variables definitions in Table 6.1.

Response	Fixed effects in optimal model
ER	Soil T × Soil MC × (Site + Shrub + Graminoid + Instrument) + t since fire × (Site + Treatment) + Soil T × Bryophyte
NEE	Soil T × (Shrub + Instrument + Graminoid) + Soil MC × (Shrub + Graminoid + Site) + Treatment × (PAR + t since fire + Graminoid)
log([DOC])	Soil T × WT depth + Treatment × t since fire + Shrub + Bryophyte

(Table 6.4). I performed a sensitivity analysis to test the effect of variation of soil temperature, soil moisture content and treatment on ER (Figure 6.8). ER increased with soil temperature, and this increase was stronger for unburnt plots than for burnt plots, and greater (steeper slopes) at Brahead Moss than at Glen Tanar. Soil moisture had a negative relationship with ER at both sites, but had a small effect on the relationship between ER and soil temperature. Increases in ER between 5 °C and 15 °C (Q_{10} or temperature sensitivity of ER) ranged from approximately 1.4 (burnt plots in dry conditions at Glen Tanar) to 3.5 (unburnt plots in moist conditions at Braehead Moss).

Table 6.4: Details of the model of ecosystem respiration as a function of environmental variables (see environmental variables in Table 6.1; model formula in Table 6.3). Marginal R^2 (variance explained by fixed effects) was 0.81 and conditional R^2 (both fixed and random effects) was 0.86.

	Value	Std.Error	DF	t-value	p-value
(Intercept)	-0.32804	1.48800	290	-0.220	0.826
Soil.T	0.12676	0.11267	290	1.125	0.262
Soil.MC	0.00276	0.00503	290	0.549	0.583
Site(BM)	4.38424	2.29272	15	1.912	0.075
Graminoid	-0.17522	0.09943	62	-1.762	0.083
Shrub	0.12217	0.07317	62	1.670	0.100
Days.since.fire	-0.00017	0.00032	290	-0.516	0.606
Tr(No-drought)	0.07257	0.19837	62	0.366	0.716
Tr(Drought)	-0.10602	0.20298	62	-0.522	0.603
Instrument(Vaisala)	2.46208	0.55671	290	4.423	<0.001
Bryophyte	-0.00559	0.00287	62	-1.947	0.056
Soil.T : Soil.MC	-0.00038	0.00039	290	-0.973	0.331
Soil.T : Site(BM)	-0.52131	0.17230	290	-3.026	0.003
Soil.T : Graminoid	0.01787	0.00759	290	2.354	0.019
Soil.T : Shrub	-0.00958	0.00595	290	-1.611	0.108
Soil.MC : Site(BM)	-0.01463	0.00727	290	-2.012	0.045
Soil.MC : Graminoid	0.00049	0.00029	290	1.693	0.092
Soil.MC : Shrub	-0.00042	0.00022	290	-1.868	0.063
Days.since.fire : Tr(No-drought)	-0.00090	0.00029	290	-3.145	0.002
Days.since.fire : Tr(Drought)	-0.00057	0.00029	290	-1.976	0.049
Site(BM) : Days.since.fire	0.00147	0.00030	290	4.942	<0.001
Soil.T : Instrument(Vaisala)	0.03889	0.01303	290	2.984	0.003
Soil.MC : Instrument(Vaisala)	-0.00752	0.00161	290	-4.671	<0.001
Soil.T : Bryophyte	0.00070	0.00021	290	3.324	<0.001
Soil.T : Soil.MC : Site(BM)	0.00158	0.00055	290	2.865	0.004
Soil.T : Soil.MC : Graminoid	-0.00005	0.00002	290	-2.064	0.040
Soil.T : Soil.MC : Shrub	0.00004	0.00002	290	2.009	0.046

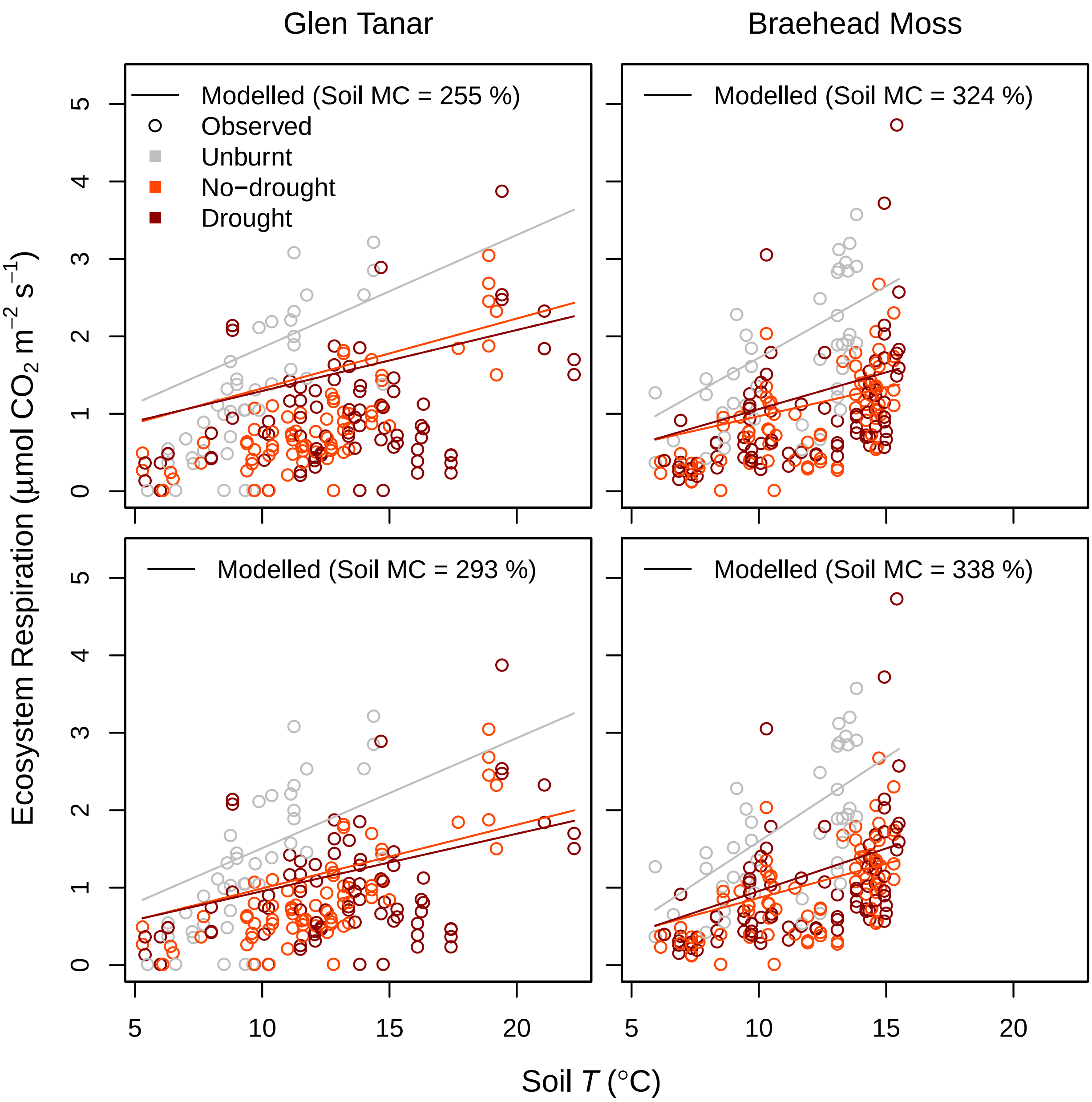

Figure 6.8: Observed (circles) and modelled (lines) ecosystem respiration against soil temperature at Glen Tanar (left) and Braehead Moss (right). The model is detailed in Table 6.4. Modelled values were calculated for different treatments and for (top) low soil moisture content within each site (first quartile) and (bottom) high moisture content (third quartile). Modelled values were calculated for average values of plant cover within each treatment, overall average of time since fire (480 days) and the Vaisala analyser.

6.3.4 Net ecosystem exchange

Seasonal average NEE in unburnt plots at Glen Tanar ranged between 0.18 μmol m^{-2} s^{-1} in spring and -0.78 μmol m^{-2} s^{-1} in autumn (Figure 6.9; summary statistics are provided in Appendix D.9). Seasonal NEE patterns in unburnt plots at Braehead Moss were similar and ranged between 0.18 (spring) and -0.64 (autumn) μmol m^{-2} s^{-1}. NEE was lower (i.e. stronger C sink or lower C emission) in unburnt than in burnt plots during summer and autumn: unburnt plots were, on average, a net sink of CO_2 (NEE was -0.54 μmol m^{-2} s^{-1} at Glent Tanar and -0.57 μmol m^{-2} s^{-1} at Braehead Moss) while burnt plots were a source (0.34 μmol m^{-2} s^{-1} at Glen Tanar, 0.08 μmol m^{-2} s^{-1} at Braehead Moss) (Figure 6.9). Burning appeared to reduce NEE heterogeneity at Glen Tanar, but not at Braehead Moss. In burnt plots, NEE was highest in summer rather than in spring (as in unburnt plots). Differences between fire severity treatments (drought versus no-drought) were not statistically significant.

As with ER, duff cover was dropped from the analysis of environmental variables due to multicollinearity. The optimal model showed that, in addition to soil temperature and moisture content, treatment and cover of vascular plants were important controls on NEE (Table 6.5). The relationship between soil temperature, soil moisture content and treatment in controlling NEE was explored using a sensitivity analysis (Figure 6.10). NEE had a positive relationship with soil temperature: warmer soils were associated with increased ground to atmosphere CO_2 flux. NEE in both burnt treatments responded similarly to soil temperature. Higher soil moisture led to lower NEE at Glen Tanar, but had little effect at Braehead Moss. NEE was lower at Braehead Moss than at Glen Tanar, especially at lower soil moisture contents. Higher PAR resulted in lower NEE: for conditions represented in Figure 6.10 (i.e. for a range of soil temperature and soil moisture conditions, and for the different treatments), increased PAR from 379 to 1237 μmol m^{-2} s^{-1} (first to third quartile of all PAR data) lowered NEE in unburnt plots by 0.70–0.88 μmol m^{-2} s^{-1} (variation represents response to different sites, soil temperature and

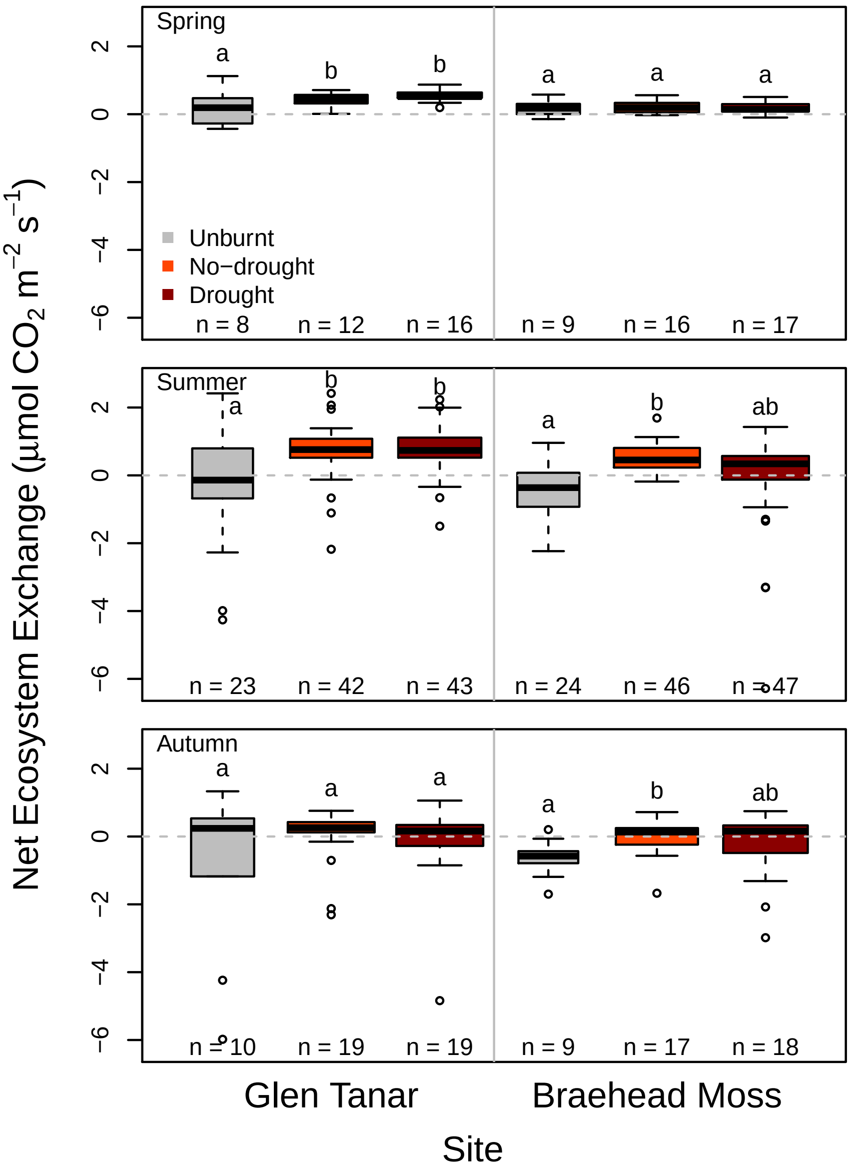

Figure 6.9: Net ecosystem exchange per treatment, season (spring: March–May, summer: June–August, autumn: September–November) and site. n indicates number of observations. Within each season and site, different letters above the boxplots indicate statistically significant differences between treatments. Summary statistics and model details are provided in Appendix D.9.

soil moisture content), by 0.20–0.32 μmol m^{-2} s^{-1} in no-drought plots and by 0.52–0.56 μmol m^{-2} s^{-1} in drought plots.

Table 6.5: Details of the model of net ecosystem exchange as a function of environmental variables (see environmental variables in Table 6.1; model formula in Table 6.2). Marginal R^2 (variance explained by fixed effects) was 0.59 and conditional R^2 (variance explained by both fixed and random effects) was 0.61.

	Value	Std.Error	DF	t-value	p-value
(Intercept)	7.944	1.189	296	6.682	<0.001
Tr(No-drought)	-0.686	0.357	63	-1.921	0.059
Tr(Drought)	-0.232	0.354	63	-0.657	0.513
PAR	-0.001	0.000	296	-5.070	<0.001
Days.since.fire	-0.002	0.001	296	-3.618	<0.001
Soil.MC	-0.023	0.004	296	-6.430	<0.001
Shrub	-0.113	0.044	63	-2.570	0.013
Graminoid	-0.200	0.074	63	-2.692	0.009
Site(BM)	-8.617	1.277	15	-6.750	<0.001
Soil.T	0.047	0.026	296	1.828	0.069
Instrument(Vaisala)	-1.469	0.310	296	-4.739	<0.001
Tr(No-drought) : PAR	0.001	0.000	296	2.827	0.005
Tr(Drought) : PAR	0.000	0.000	296	0.919	0.359
Tr(No-drought) : Days.since.fire	0.001	0.001	296	2.416	0.016
Tr(Drought) : Days.since.fire	0.001	0.001	296	0.908	0.365
Soil.MC : Shrub	0.000	0.000	296	3.073	0.002
Soil.MC : Graminoid	0.001	0.000	296	2.842	0.005
Soil.MC : Site(BM)	0.028	0.004	296	6.712	<0.001
Shrub : Soil.T	-0.003	0.001	296	-3.066	0.002
Soil.T : Instrument(Vaisala)	0.117	0.026	296	4.439	<0.001
Graminoid : Soil.T	-0.003	0.001	296	-2.311	0.022

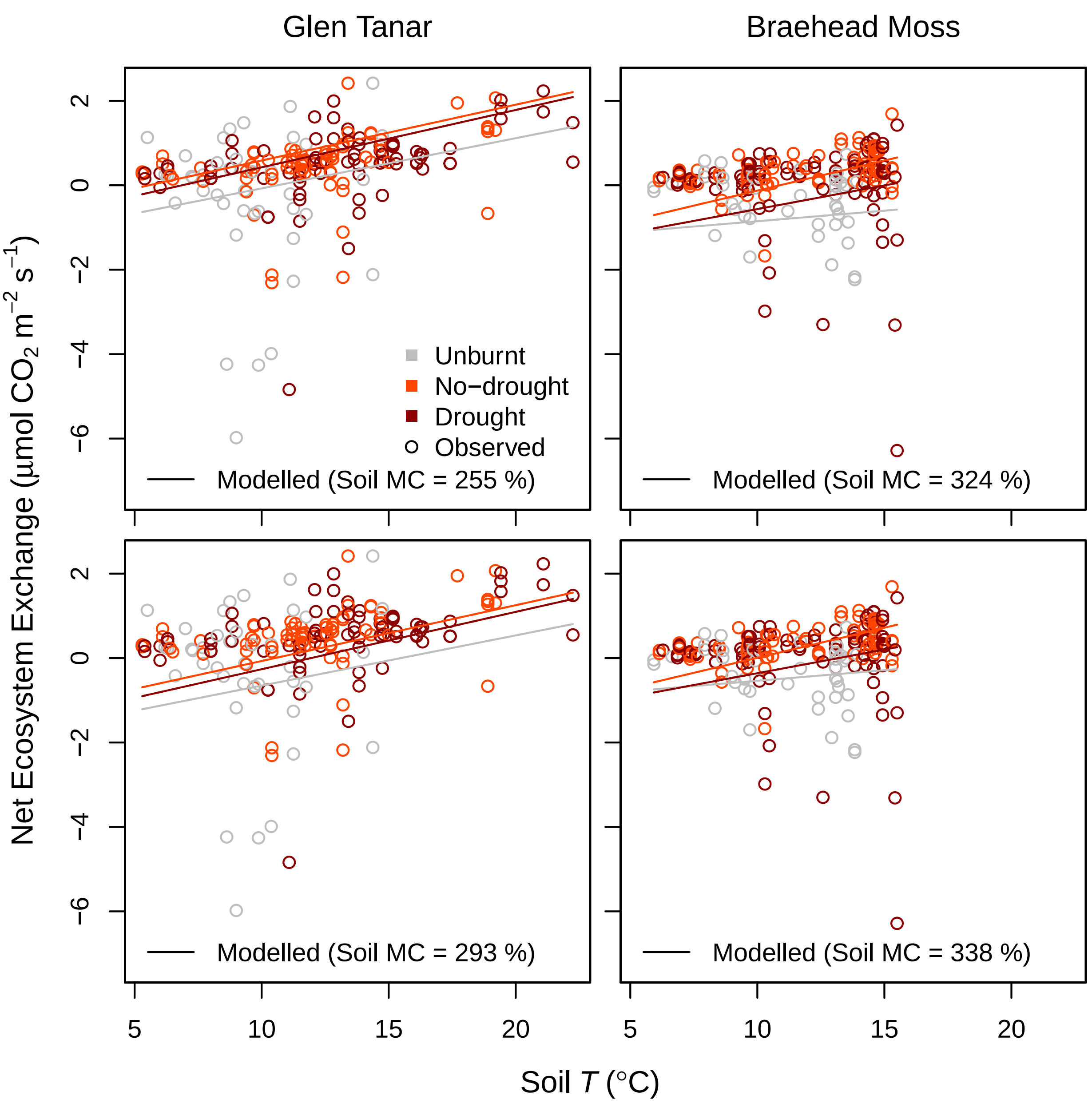

Figure 6.10: Observed (circles) and modelled (lines) net ecosystem exchange against soil temperature at Glen Tanar (left) and Braehead Moss (right). The model is detailed in Table 6.5. Modelled values were calculated for different treatments, average plant cover within each treatment, (top) low soil moisture content within each site (first quartile) and (bottom) high moisture content (third quartile), average PAR in each site (899 μmol m^{-2} s^{-1} at Glen Tanar and 718 μmol m^{-2} s^{-1} at Braehead Moss), overall average time since fire (480 days) and the Vaisala analyser.

6.3.5 Methane flux

Methane fluxes were generally negligible at Glen Tanar, and were only detectable in unburnt plots during autumn (Figure 6.11; summary statistics are provided in Appendix D.10). At Braehead Moss, average CH_4 emissions in unburnt plots were 0.3 (spring) and 1.2 (summer) nmol m^{-2} s^{-1}. Methane fluxes at Braehead Moss were larger in burnt than in unburnt plots, especially during the summer (1.2 nmol m^{-2} s^{-1} in unburnt, 25.3 nmol m^{-2} s^{-1} burnt plots). There was a high variability in methane fluxes in burnt plots at Braehead Moss (e.g. average standard deviation in the summer was 57.2 nmol m^{-2} s^{-1}), including three extreme measurements (92, 168 and 212 nmol m^{-2} s^{-1}) during the summer. Considering CH_4 has a global warming potential (GWP) over 100 years 28 times higher than CO_2 (IPCC, 2013), summer CH_4 flux at Braehead Moss increased net CO_2-equivalent emission from burnt plots by 0.6–0.7 μmol m^{-2} s^{-1} (79 % of total flux). CH_4 contribution to CO_2-equivalent flux at Glen Tanar was close to zero. Appendix D.11 provides detailed information on CO_2-equivalent fluxes.

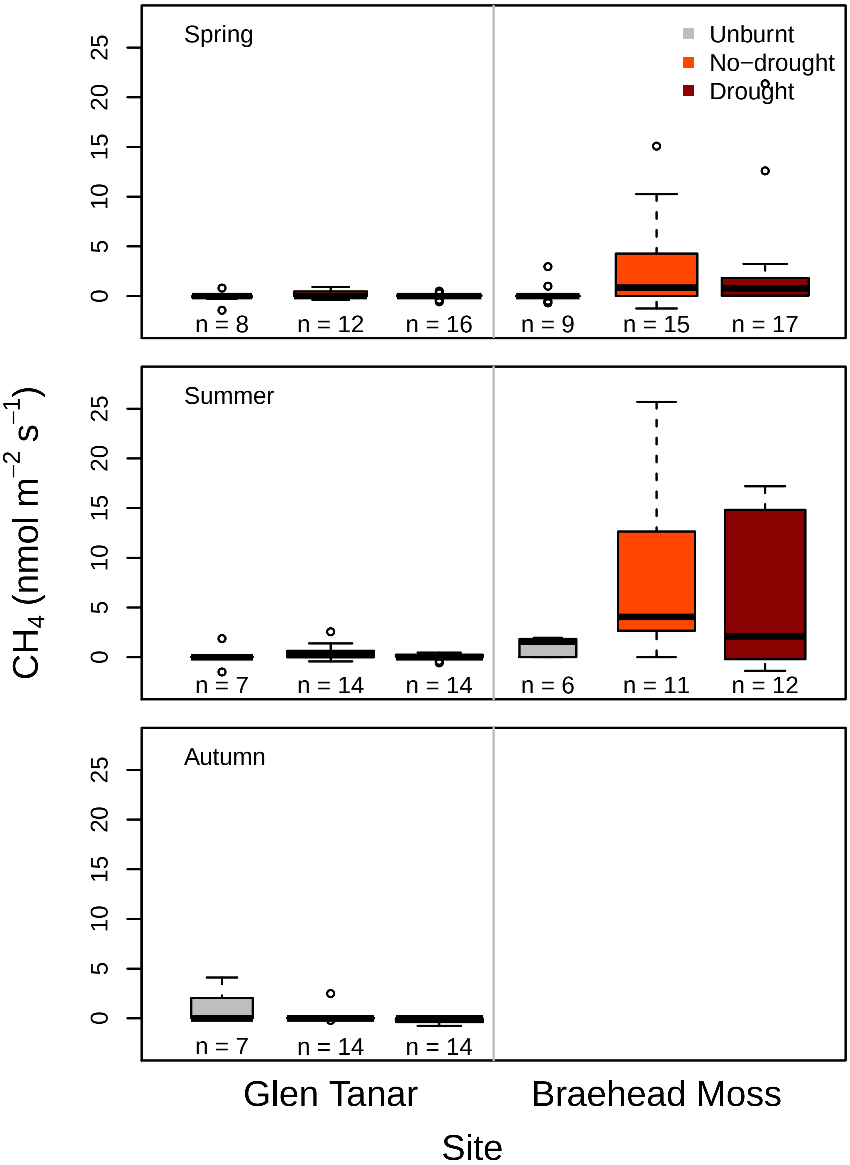

Figure 6.11: Methane flux per treatment, season (spring: March–May, summer: June–August, autumn: September–November) and site. *n* indicates number of observations. Extreme summer measurements at Braehead Moss (92 nmol m^{-2} s^{-1}, drought plot; 168 nmol m^{-2} s^{-1}, drought plot; 212 nmol m^{-2} s^{-1}, no-drought plot) not shown. Summary statistics, as well as boxplots of methane fluxes measured in the dark showing similar results as presented here for light conditions, are provided in Appendix D.10.

6.3.6 Dissolved organic carbon

Burning had no effect on DOC concentration within any season (Figure 6.12). Seasonal DOC concentration in each treatment remained relatively constant in winter, spring and summer (around 131 mgC l^{-1} in unburnt, 120 mgC l^{-1} in no-drought and 122 mgC l^{-1} in drought plots) and increased in autumn (155 mgC l^{-1} in unburnt and 143 mgC l^{-1} in both burnt plots). Overall mean DOC concentration was 137 mgC l^{-1} in unburnt plots, 128 mgC l^{-1} in no-drought plots and 129 mgC l^{-1} in drought plots. Variability was higher in unburnt plots (SD = 47.0 mgC l^{-1}) than in burnt plots (29.2 mgC l^{-1} in no-drought, 31.6 in drought mgC l^{-1}). Detailed information on seasonal variation of DOC concentration in each fire severity treatment is provided in Appendix D.12.

Soil temperature, water table depth, treatment, time since fire and shrub and bryophyte cover were retained as fixed effects in the optimal model for DOC concentration (Table 6.6). I used a sensitivity analysis to explore the interacting effect of soil temperature, water table depth, fire severity treatment and time since fire on DOC concentration (Figure 6.13). Higher water table was associated with lower DOC concentration, especially at low soil temperatures. DOC concentration in unburnt plots increased during the measurement period, while it remained constant in burnt plots.

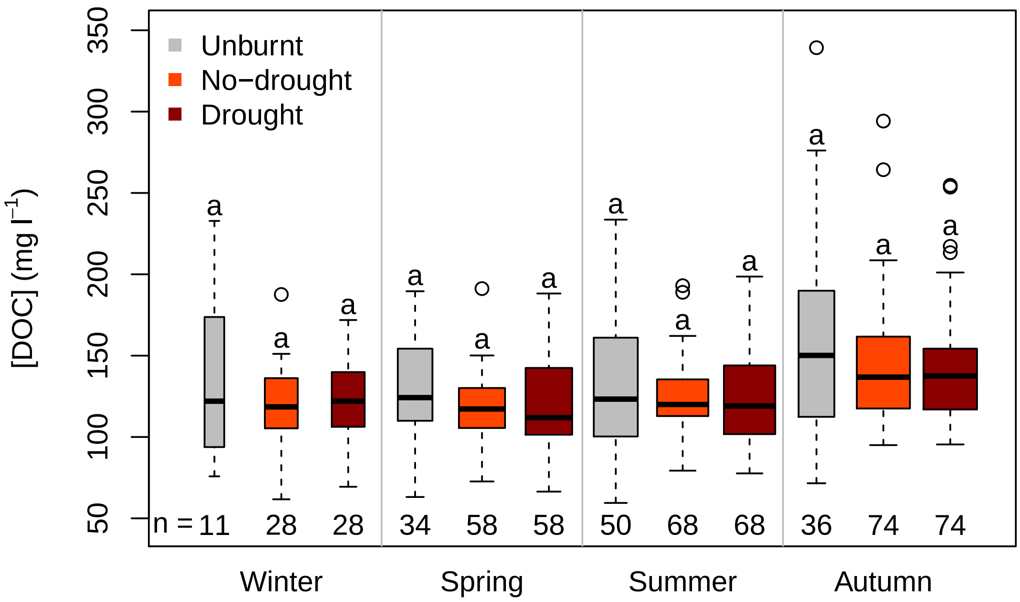

Figure 6.12: Concentration of dissolved organic carbon per treatment at Braehead Moss grouped by season (winter: December–February, spring: March–May, summer: June–August, autumn: September–November). Number of observations are indicated below each boxplot. Within each season, different letters above the boxplots indicate statistically significant differences between treatments. Summary statistics and model and pairwise comparisons details can be found in Appendix D.12.

Table 6.6: Details of the final model of dissolved organic carbon concentration as a function of environmental variables (see environmental variables in Table 6.1; model formula in Table 6.3). Marginal R^2 (variance explained by fixed effects) was 0.21 and conditional R^2 (variance explained by both fixed and random effects) was 0.53.

	Value	Std.Error	DF	t-value	p-value
(Intercept)	5.9403	0.227	437	26.204	<0.001
Soil.T	0.0028	0.005	437	0.573	0.567
WT	-0.0097	0.003	437	-3.455	<0.001
Tr(No-drought)	-1.0995	0.211	36	-5.201	<0.001
Tr(Drought)	-1.0697	0.210	36	-5.084	<0.001
Days.since.fire	-0.0003	0.000	437	-2.828	0.005
Bryophyte	-0.0026	0.001	36	-2.016	0.051
Shrub	-0.0133	0.003	36	-4.034	<0.001
Soil.T : WT	0.0005	0.000	437	1.957	0.051
Tr(No-drought) : Days.since.fire	0.0004	0.000	437	3.196	0.001
Tr(Drought) : Days.since.fire	0.0003	0.000	437	2.237	0.026

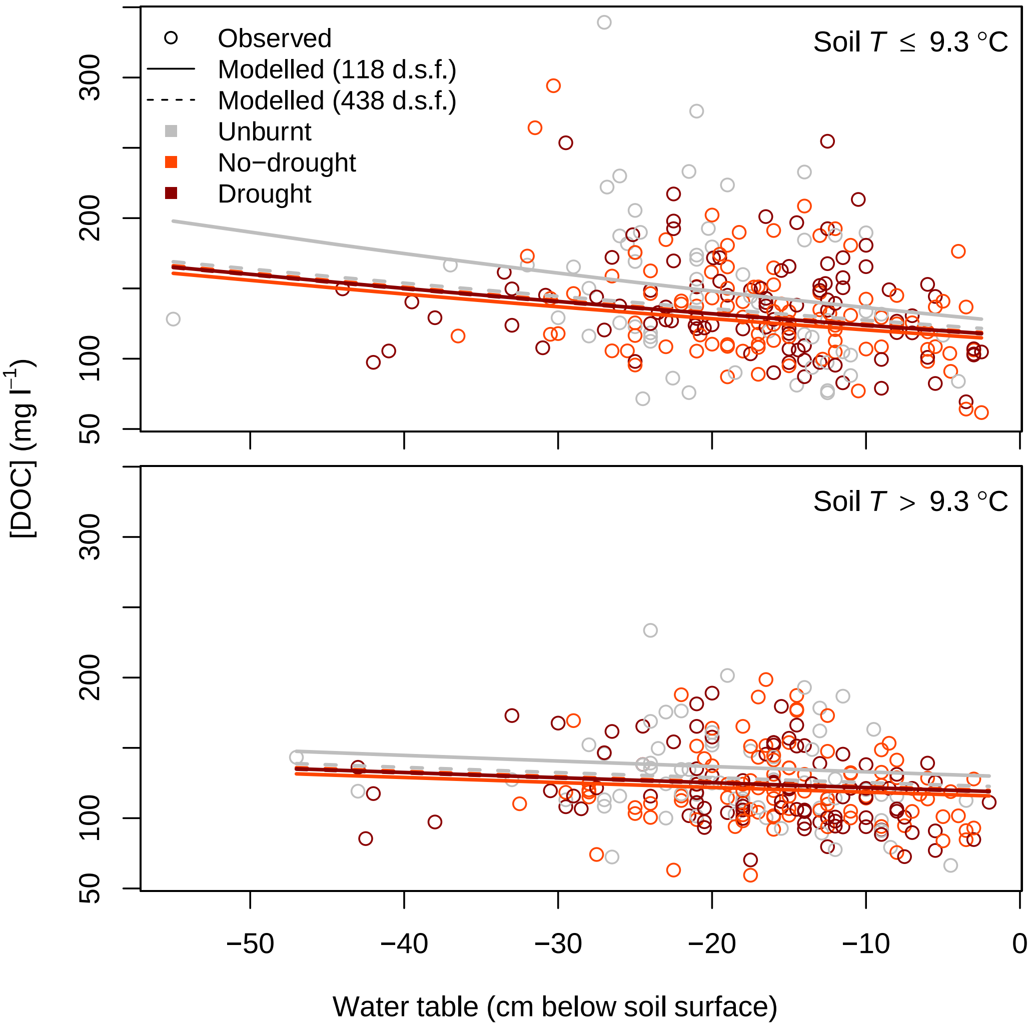

Figure 6.13: Observed (circles) and modelled (lines) dissolved organic carbon concentration against depth of the water table at Braehead Moss (see Table 6.6 for model details). The top plot shows observed [DOC] measurements when the soil temperature was below the mean soil temperature (9.3 °C), and the bottom, when it was above 9.3 °C. Modelled [DOC] used a soil temperature of 6.2 °C (mean soil temperature below 9.3 °C, top plot), 13.0 °C (mean soil temperature above 9.3 °C, bottom plot), and a combination of treatment and days since fire (d.s.f): 25 % quartile, 118 d.s.f., in dotted lines, and 75 % quartile, 438 d.s.f., in solid lines. Modelled unburnt 438 d.s.f. was increased by 3 units to aid visibility.

6.4 Discussion

6.4.1 Vegetation cover

Burning decreased cover of shrubs at Braehead Moss, but not at Glen Tanar (Figure 6.3). This may be an effect of inserting the collar as *Calluna* was prostate and had long stems at Glen Tanar, and was therefore difficult to keep within the collar area. Vegetation survey of the whole plot gave a more reliable assessment of the effect of burning on *Calluna* (Appendix D.3). Graminoids had similar cover across treatments at the time of survey, likely due to their fast recovery after disturbance (Hobbs and Legg, 1984). Burning greatly reduced bryophyte cover at both sites, with no difference between lower (no-drought) and higher fire severity treatments (drought). Cover of litter was greatest in no-drought plots, and duff/bare soil in drought plots. This could be due to the lower pre-fire moisture content of the M/L layer in drought than in no-drought burnt plots, which resulted in increased M/L layer consumption and thus greater exposure of duff/bare soil in drought plots (Figure 5.6 in Section 5.3.3).

6.4.2 Ecosystem Respiration

Seasonal variation in ER in unburnt plots (0.58–1.7 μmol m^{-2} s^{-1} at Glen Tanar, 0.85–2.05 μmol m^{-2} s^{-1} at Braehead Moss) was similar to other studies in UK shrub-dominated peatland, e.g. 0.8–2.3 μmol m^{-2} s^{-1} (Chapman and Thurlow, 1996), 1.2–2.7 μmol m^{-2} s^{-1} (Ward et al., 2007). Burning decreased ER (Figure 6.7), probably a result of reduced vegetation-induced respiratory processes, both heterotrophic and autotrophic (Curiel-Yuste et al., 2004) and altered post-fire soil microbiology (Wang et al., 2012). In contrast to these results, work on an upland blanket bog at the Moor House Nature Reserve in northern England found no short-term (< 18 months) differences in ER between burnt plots and unburnt plots (Clay et al., 2010; Ward et al., 2012). Similarly, no short-term (< 3 years) effect of fire on ER was found in three sites across Scotland ranging from wet heath to blanket bog (Taylor, 2015). However, research on Moor House Nature Reserve found that longer-term ER in 9-year burnt plots was higher than in unburnt (Ward et al., 2007), which may indicate that established post-fire vegetation promotes faster C cycling than mature communities. Decreased post-fire vegetation activity could explain the lower variability in respiration in burnt plots, as the heterogeneity in vegetation composition, superimposed on heterogeneity of abiotic factors, may have had a smaller contribution to respiration.

Similar ER was found after higher severity burning (drought plots) and lower severity burning (no-drought plots), except at Glen Tanar during autumn when ER was higher in drought plots, i.e. increased soil heating (Figure 6.4; Section 5.3.4) and consumption of the M/L layer in drought plots had little effect on respiratory processes. Given the importance of fire severity in controlling post-fire soil microbiology (Dooley and Treseder, 2012; Wang et al., 2012; Ward et al., 2012), and the similar cover of vegetation functional groups in both burnt treatments (Figure 6.3), this suggests that the higher severity treatment did not substantially alter soil microbial communities: average maximum soil temperature during the fire was under 40 °C 2 cm below the top of the soil (Section 5.3.2), more often below the temperatures required to kill bacteria and fungi (ca. 90 °C, Neary et al., 1999), particularly at Braehead Moss. However, the fact that ER at Glen Tanar was higher in drought plots, where particularly high soil temperature was measured (Section 5.3.2), than in no-drought plots during autumn could indicate an effect of high fire severity on seasonal activity of the soil microbial community. Perhaps the positive effect of higher fire severity on ER was due to stimulation of microbial activity by warmer soil and more nutrients (Dooley and Treseder, 2012) and could only be detected after the period of maximal microbial growth during the summer (Wardle, 1998).

Modelling of ER with environmental variables revealed ER was controlled by interacting biotic and abiotic factors (Table 6.4; Figure 6.8), as has been previously reported (Ward et al., 2013; Armstrong et al., 2015). Soil temperature and soil moisture content were the predominant environmental factors regulating such interactions. Temperature is directly related to metabolic rates (Lloyd and Taylor, 1994) and underpins all components of ER (Chapman and Thurlow, 1996; Ryan et al., 1997). The larger Q_{10} at Braehead Moss could be due to the different soil thermal regime compared to Glen Tanar. The thicker M/L layer and higher soil moisture of Braehead Moss dampened diurnal soil thermal fluctuation (Figure 6.4), and so soil temperature remained relatively cold for warm air temperatures (Appendix D.5). Such warm air temperature may have increased above ground autotrophic respiration and resulted in a higher apperent Q_{10} at Braehead Moss. Q_{10} range (1.4–3.5) was similar to the Q_{10} range of soil respiration reported in a variety of habitats (1.3–3.3, Raich and Schlesinger, 1992). ER was higher at lower values of soil moisture content, likely a result of the faster C turnover in oxic conditions (Blodau et al., 2004). Cover of shrubs and graminoids interacted with soil temperature and soil moisture in controlling ER. This is in line with previous studies which have highlighted the importance of vascular plants on C cycling, both in terms of respiratory and assimilatory processes (Ward et al., 2013; Armstrong et al., 2015).

6.4.3 Net Ecosystem Exchange

Seasonal NEE variation in unburnt plots at Glen Tanar (-0.78–0.18 μmol m^{-2}) (Figure 6.9) showed a wider range than that reported for a temperate heath (-0.4 to -0.25 μmol m^{-2}; Larsen et al., 2007). Seasonal NEE patterns in unburnt plots at Braehead Moss (-0.64–0.18 μmol m^{-2} s^{-1}) also showed a wider range than previous studies from UK peatlands (-0.50 to -0.17 μmol m^{-2} s^{-1}, Ward et al., 2007; -0.68 to -0.30 μmol m^{-2} s^{-1}, Armstrong et al., 2015). Burning increased NEE (Figure 6.9). Taking into account the generally higher ER values in unburnt plots, this shows that burning induced a decrease in respiration and a larger decrease in photosynthesis which resulted in a net increase in ground to atmosphere CO_2 flux. The decreased photosynthesis can be explained by fire-induced mortality of, and damage to, vascular and cryptogamic vegetation (Figure 6.3).

NEE was similar in drought and in no-drought plots. This suggests that the increased fire-induced soil heating in drought plots did not have any additional effects on soil microbiology above that associated with lower severity management fires. Furthermore, the altered ground vegetation and microclimate conditions in drought plots, particularly at Glen Tanar (e.g. higher cover of bare ground and altered post-fire soil thermal dynamics, Figure 6.3, Section 5.3.4) compared to no-drought plots did not have an effect on NEE.

Modelled NEE showed a positive relationship with soil temperature (Figure 6.10), indicating that respiration dominated over photosynthesis at warmer temperatures. Such observation is in agreement with the observed relationship between ER and soil temperature, where high soil temperatures were associated with high ER, but differs from reported decreased NEE (stronger carbon sink) in warmer conditions (Larsen et al., 2007; Ward et al., 2007). However, these research refer to medium-term post-fire conditions (Ward et al., 2007) or long-term unburnt (Larsen et al., 2007), which suggest that, as vegetation regenerates, warmer conditions lead to a greater increase in photosynthesis than in ER.

The importance of vegetation on NEE was apparent from the significance of shrub and graminoid cover in the model (Table 6.5). Shrubs and graminoid cover were associated with lowered NEE, especially in warmer soils, as indicated by the interaction with soil temperature. Increased C processing in vascular plants may have promoted photosynthesis (Ward et al., 2013; Armstrong et al., 2015), and the interaction between cover and soil temperature may be due to the seasonal variation in plant activity: photosynthesis will be larger in warmer months when PAR is also higher, decreasing NEE. The importance of vegetation cover in NEE may explain the larger NEE variance in unburnt plots compared to burnt plots (Figure 6.9) because of the fast response of vegetation to changing weather conditions (e.g. PAR, see Appendix D.2). The effect of PAR lowering NEE was higher in unburnt than in burnt plots as would be expected given the higher vegetation cover (and photosynthesis) in unburnt plots.

6.4.4 Methane

Methane flux was negligible at Glen Tanar in spring and summer, and only in autumn did unburnt plots show small (1.4 nmol m^{-2} s^{-1}) emission values (Figure 6.11). Besides their low C store, the thin soils of Glen Tanar were probably not conducive to the anaerobic conditions needed for CH_4 production. Negative fluxes (-0.02 to -0.17 nmol m^{-2} s^{-1}) were recorded in spring an autumn, indicating some CH_4 consumption due to aerobic methanotrophic bacteria (Lai, 2009). CH_4 flux in unburnt plots was also small at Braehead Moss (e.g. 1.2 nmol m^{-2} s^{-1} during the summer) and on the lower end of those reported for peatlands across the UK (average 12.2, minimum 0.4, maximum 27.4 nmol m^{-2} s^{-1}; Levy et al., 2012).

Burning increased post-fire CH_4 emission at Braehead Moss. No substantial differences in CH_4 flux between drought and no-drought burnt plots at Braehead Moss were apparent (Figure 6.11), not surprising given the low fire-induced soil heating measured at the site (Section 5.3.4) and the small differences in post-fire vegetation cover between both burnt treatments (Figure 6.3). Burning has been observed to reduce CH_4 production in peatlands by decreasing methanotrophic bacteria (Chen et al., 2008). However, given the primary importance of vegetation in controlling CH_4 flux (Levy et al., 2012; Gray et al., 2013) and the low fire-induced soil heating measured at Braehead Moss (Section 5.3.2), fire-induced change in vegetation was likely a key variable in explaining differences between treatments. For example, vascular plants can promote methanotroph activity through diffusion of oxygen to the root zone (Ström et al., 2005). Vegetation can also have a direct effect on CH_4 flux by facilitating its transport from anaerobic peat layers to the atmosphere, therefore bypassing methanotrophs. This is especially the case with aerenchymatous species such as *E. vaginatum* (Greenup et al., 2000; McNamara et al., 2008). In addition to a substantial reduction in shrub cover, burning led to a small increase in cover of graminoids at Braehead Moss, dominated by *E. vaginatum*, from 4.6 % to 7.2 % (Figure 6.3) and so this may have increased the flux. Vegetation can also have an effect on abiotic factors that are important controls on CH_4: reduced post-fire plant cover, especially from vascular plants, can decrease evapotranspiration and lead to a lower water table (Figure 6.6; Wieder et al., 2009; Clay et al., 2012), thus enhancing soil aerobic conditions which reduce CH_4 production and increase CH_4 consumption.

The observed effect of burning on CH_4 flux at Braehead Moss contrasts with work on UK peatlands reporting no differences between unburnt and burnt plots up to three years after fire (Taylor, 2015). Such disparity is probably related to the complexity of interrelated factors controlling carbon cycling (Armstrong et al., 2015) and to their heterogeneity, including fire severity, thus making isolating fire effects difficult. Longer-term research has observed lower CH_4 flux in 9-year burnt plots than in plots unburnt for 50 years (Ward et al., 2007). Successional dynamics in both vegetation and microbial communities are likely key in explaining post-fire CH_4 flux.

The seasonality of the CH_4 flux (the largest emission was observed during the summer) indicates soil temperature was an important controlling mechanism (Levy et al., 2012). Extreme summer CH_4 emission occurred in both burnt plots, suggesting that burning could facilitate episodic ebullition events. The mechanisms involved could be related to increased post-fire CH_4 production, as discussed above, leading to a higher gas concentration in the soil thus promoting bubble formation, and/or to altered transport (e.g. as a result of changes in hydrology) (Baird et al., 2004). Enhanced CH_4 production in burnt plots during the summer, in combination with the variety of mechanisms of transport and consumption that can control the flux, could explain the larger heterogeneity in CH_4 flux in burnt plots compared to unburnt. Even though summer CH_4 flux was 10 times lower than the positive NEE in burnt plots at Braehead Moss, it represented 79 % of the CO_2-equivalent flux.

6.4.5 Dissolved organic carbon

Mean seasonal soil water DOC concentration at Braehead Moss ranged between 120–155 mgC l^{-1}, larger than averages reported for blanket peatlands in northern England: 40 mg l^{-1} (Ward et al., 2007), 45 mg l^{-1} (Clay et al., 2009) (both at the Moor House Nature Reserve), and 97.2 mg l^{-1} (Clay et al., 2012). Seasonal patterns of DOC indicated higher concentrations in autumn, likely a result of higher DOC production during the summer and its flushing due to higher water tables in the autumn (Kalbitz et al., 2000) (Figure 6.12). Burning had no effect on DOC concentration, indicating that combined fire effects including fire-induced soil heating, decreased plant activity, altered soil thermal dynamics and hydrology were not important controls. Previous research on UK peatlands also found no long-term effect of burning on soil water DOC concentration (Ward et al., 2007; Clay et al., 2009, 2012), although lower DOC concentration was found in recently burnt plots ($<$ 2 years) compared to *Calluna*-dominated plots (23.4 versus 42.0 mg l^{-1}) at a blanket bog in northern England (Armstrong et al., 2012). Variability was consistently lower in burnt plots compared to unburnt, which may be a consequence of reduced plant community heterogeneity post-fire, thus resulting in a more homogenous contribution of plant photosynthate to DOC (Trinder et al., 2008).

The interaction between soil temperature and water table depth had a weakly significant effect on DOC concentration: at low temperatures, deeper water table led to higher DOC concentration (Table 6.6, Figure 6.13). In contrast, at high soil temperatures the effect of water table was negligible across the three treatments. Higher and more variable DOC concentration was found when soil temperature was low than when it was high. Such temperature effects could be explained by lower temperature sensitivity of DOC production compared to CO_2, i.e. when temperature increases, the rate at which organic matter joins the DOC pool (through desorption of soil organic matter, decomposition of plant material by microorganisms or exudation of roots) increases less than the rate at which this organic matter is respired producing CO_2 (Moore, 2013).

Although lower water table depth was generally correlated with higher DOC concentration (Figure 6.13), the relationship between DOC concentration and water table is likely a complex one: while enhanced aerobic processes at low water tables may increase DOC production due to higher microbial and plant activity (Freeman et al., 2001b, 2004; Strack et al., 2008), respiration is also higher in these conditions (Moore and Dalva, 1993). Moreover, anaerobic conditions can facilitate the production of water-soluble intermediate metabolites during organic matter decomposition which contribute to DOC (Kalbitz et al., 2000; Blodau et al., 2004).

Shrub and bryophyte cover significantly decreased DOC concentration. Differences in soil microbial populations, which vary with vegetation type (Bragazza et al., 2015), or differences in fresh plant tissue and plant exudates, which are important sources of carbon cycling (Blodau et al., 2004; Tipping et al., 2010), could be controlling mechanisms. A possible explanation is that higher vegetation cover, particularly of vascular plants, led to increased evapotranspiration, lower water table and enhanced soil aerobic conditions (Figure 6.6), thus favouring respiration over DOC production. However, previous research found a positive correlation between biomass of vascular plants, microbial biomass and DOC concentration (Bragazza et al., 2015).

Differences in DOC concentration between treatments were more apparent at low soil temperatures (Figure 6.13), which may be due to increasing CO_2/DOC production ratios with increasing temperatures as noted above. At colder soil temperatures, burnt plots showed a similar rate of DOC concentration increase with lower water tables, while the rate was higher in unburnt plots. Given the low soil heating recorded during the fires, the direct effect on post-fire DOC concentration was probably small and observed differences were likely predominantly driven by indirect post-fire effects such as a change in microclimate (although changes in thermal dynamics were small, Figure 6.4) or in vegetation cover (Appendix D.3). The larger values in unburnt plots suggest a larger contribution from plant photosynthate (Trinder et al., 2008).

It is possible that the similarity between both burnt treatments is related to the relatively small size of the plots, thus allowing soil water mixing with surrounding areas. For example, hydraulic conductivity in raised bogs can be ca. 10^{-4} m s^{-1} (8.6 m d^{-1}) at 20 cm depth and ca. 10^{-5} m s^{-1} at 50 cm depth (Fraser et al., 2001; Baird et al., 2008). Furthermore, response of DOC concentration to burning may have been stronger at shallower depths than the range I sampled (10–60 cm; Figure 6.6) (Holden et al., 2012). Future studies should investigate this, e.g. using an array of dip-wells at different depths.

Time since fire had little effect on DOC concentration in both burnt treatments but was correlated with lower DOC concentration in unburnt plots, especially at low soil temperatures. This is difficult to interpret if time since fire is understood as recovering ecosystem functioning to pre-fire status (e.g. soil microbiology, vegetation regeneration). However if, as noted previously, direct fire effects were minimal due to low soil heating, and indirect fire effects (e.g. post-fire vegetation cover) were accounted for in other variables of the model, time since fire could indicate a drift of the ecosystem due to environmental variability. For example, overcast weather could have predominated in the second half of the measuring period, leading to lower plant activity and altered DOC production in unburnt plots with high cover of vascular plants, but with little effect on burnt plots. Therefore, while the undisturbed bog had generally lower DOC concentration two years after sampling started than at the start, burnt plots remained unchanged, suggesting a disconnect with environmental change.

6.5 Conclusions

Burning decreased ecosystem respiration during the first two years following fires, but decreased photosynthesis more strongly, resulting in higher net ecosystem exchange (ground to atmosphere CO_2 flux) compared to unburnt plots. While mean net ecosystem exchange in unburnt plots was similar at the dry heath and the raised bog (-0.33 and -0.38 μmol m^{-2} s^{-1}, respectively), post-fire flux was larger at the dry heath (0.50 versus 0.16 μmol m^{-2} s^{-1}). Methane flux was close to zero at the dry heath. At the raised bog, burning increased methane flux substantially, especially during summer (1.16 nmol m^{-2} s^{-1} in unburnt and 25.3 nmol m^{-2} s^{-1} in burnt plots), when it represented 79 % of the CO_2-equivalent flux. Although comparatively few CH_4 flux data was available, the results suggest a similar impact of burning on net carbon emission at the dry heath and at the raised bog. Burning did not induce short-term changes in dissolved organic carbon concentration at the raised bog. Generally, the effect of higher fire severity on soil carbon dynamics did not differ from regular managed burning, and suggests that variation in fire severity such as that resulting from drier ground fuels has negligible effect on short-term soil carbon dynamics in the context of managed burning. Alteration of short-term soil carbon dynamics is more likely where there is extensive consumption of ground fuels and/or ignition of organic soil layers (i.e. wildfires) leading to substantial changes in soil microclimate (Chapter 3). It is possible that altered soil carbon dynamics resulting from variation in fire severity may become apparent in the longer term through changes in vegetation community composition. This information could be useful to managers wanting to use higher severity fires to promote vigorous regeneration of vascular plants (Chapter 4) while concerned about preserving carbon stocks. In addition, my findings may contribute to land-atmosphere carbon modelling by improving estimates of post-fire belowground carbon losses from heathlands and peatlands.

Chapter 7

Conclusions

Increasing human pressure on the natural environment is resulting in rapid environmental change in many ecosystems. *Calluna* moorlands are internationally recognised for their conservation value and often overlay large stores of belowground carbon. This research focused on the effect of higher severity fires, likely to intensify on UK *Calluna*-dominated habitats under current predictions of climate change. An altered fire regime could fundamentally change the ecology of these fire-prone ecosystems and increase carbon emission from their organic soils. Through research such as that presented here, which manipulates fuel structure and moisture content to produce fires of different severity and seeks to understand changes in post-fire community composition and soil carbon dynamics, we improve our understanding of the impact of higher severity fires on ecosystem services. This information is vital to help land managers select the best conditions for burning to achieve specific objectives whilst maximising our landscapes natural capital and retaining high quality ecosystem services.

7.1 Contribution of the thesis to research on peatland fire ecology

I aimed to improve our understanding of how ecosystem response scales across variation in fire severity on *Calluna* heathlands and peat bogs. I focused on four different aspects: the role of the moss and litter layer in controlling fire-induced soil heating and post-fire soil thermal dynamics (Chapter 3); disturbance severity controls on vegetation regeneration (Chapter 4); effect of drought on fire intensity, fire severity and post-fire soil thermal dynamics (Chapter 5); and the effect of fire severity on soil carbon dynamics (Chapter 6).

The study of the moss and litter layer (**Chapter 3**) is important as this layer regulates the non-linear relationship between fire intensity and fire severity, and influences post-fire microclimate and seedbed structure. Although the moss and litter layer insulates soil and below-ground biomass from radiative heating during the passage of a flaming fire front, few studies have explicitly quantified how soil heating is affected by variation in ground fuel structure in the context of managed burning on heather moorland (Davies et al., 2010b). Where the moss and litter layer was removed from a dry heath, average maximum soil surface temperature during burning increased three-fold (from 21 °C to 73 °C) and time above the ecologically important 50 °C threshold (Neary et al., 1999) increased from 11 s to 58 s (Section 3.3.1). Such quantitative information on soil heating during managed burning is crucial for understanding post-fire vegetation regeneration in *Calluna* heathlands (Chapter 4).

Similarly, the study of the effect of vegetation structure on soil microclimate — a controlling mechanism on belowground carbon dynamics (Lloyd and Taylor, 1994; Dorrepaal et al., 2009) and vegetation regeneration (Santana et al., 2010) — on *Calluna* moorlands has been limited (e.g. Mallik, 1986; Brown et al., 2015) and Chapter 3 has helped to fill this research gap. I found that fire, and particularly simulated higher severity fire through moss and litter layer removal, led to larger diurnal and annual temperature fluctuations in a dry heathland (Section 3.3.2). A simple model based on soil temperature led to a prediction that high severity fires would lead to larger annual soil respiration rates (Section 3.3.3) as a result of higher soil temperatures in warmer months. However, less extreme M/L layer alteration resulted in small differences in observed ecosystem respiration between higher and lower severity burnt plots (Chapter 6). Although only a small amount of data on soil thermal dynamics after wildfires was available, similar patterns to those found after high severity fires suggest consumption of the moss and litter layer may be a controlling mechanism of soil thermal dynamics after wildfires. This is in agreement with previous research in boreal peatlands which have demonstrated the importance of altered ground fuels after wildfires on soil thermal dynamics (Zhuang et al., 2002; Kettridge et al., 2012). The quantitative information on the relationship between fire severity and post-fire soil thermal dynamics provided here could contribute to better estimates of carbon fluxes from organic soils in relation to land use (e.g. Smith et al., 2007).

Previous field studies have investigated post-fire vegetation regeneration in heather moorlands (Mallik and Gimingham, 1983; Hobbs and Gimingham, 1984b; Hobbs and Legg, 1984; Velle et al., 2012) and in relation to variation in fire severity (Legg et al., 1992; Davies et al., 2010b), but mechanisms relating to the fire itself (ground heating, germination cues, fertilization) and to the altered environment (microclimate, seed bed structure) have remained confounded. The gradient of fire severity established in Chapter 3, together with the cutting treatments, allowed investigation of both direct fire effects (seed and plant tissue mortality and stimulation of seed germination due to heating, smoke and ash effects) and the subsequent altered environment (changes in microclimate and in the seedbed structure) on vegetation regeneration (**Chapter 4**). Low fire severity was important in shaping post-fire community composition over and above the effect of removing the *Calluna* canopy (i.e. by cutting) by promoting ericoids, forbs, graminoids and acrocarpous mosses (Section 4.3.1). In high severity fires, the change of substrate from moss and litter layer to bare soil also promoted ericoids, forbs and graminoids (Mallik et al., 1984b; Davies et al., 2010b), but increased fire-induced soil heating reduced their abundance and increased that of acrocarpous mosses (Section 4.3.2). The fire severity gradient led to contrasting dominant mechanisms of ericoid regeneration (*Calluna*, *Erica cinerea* and *Erica tetralix*): whilst removed (consumed) moss and litter layer generally led to higher ericoid abundance, high fire-induced soil heating resulted in low abundance of seedlings (Section 4.3.3). Abundance of ericoids after high severity fires in heather moorlands depends on a balance between improved substrate conditions (Mallik et al., 1984b; Davies et al., 2010b), stimulation of seed germination (Whittaker and Gimingham, 1962; Måren et al., 2009; Santana et al., 2010) and plant and seed mortality (Whittaker and Gimingham, 1962; Schimmel and Granström, 1996). Higher abundance of ericoids was observed after higher severity experimental fires (Section 4.3.3), which suggests that managed fires where there is increased consumption of the moss and litter layer but where heat pulses into the soil are limited promote ericoid regeneration. This can happen when the soil remains wet (Chapter 3, Chapter 5).

In Chapters 3 and 4 I produced a range of fire severities by manipulating vegetation structure. By manipulating fuel moisture content instead (**Chapter 5**) I was able to study the effect of drought on fire severity, and therefore improve our conceptual model of moorland responses to climate change. Experimentation at two sites, a dry heath and a raised bog, allowed comparison between different *Calluna*-dominated habitats with contrasting soil properties and hydrological regimes. Quantitative field measurements of fire effects in low to moderately severe fires in bogs (e.g. managed fires or wildfires where the peat is not consumed) are particularly limited, and so my results inform the debate over effects of burning on UK peatlands (Glaves et al., 2013; Davies et al., 2016b). During drought treaments fuel moisture content decreased most in the moss and litter (Section 5.3.1). Lower moss, litter and soil moisture contents at the dry heath resulted in significantly increased moss and litter layer consumption (particularly when moisture content was below 150 %) and incrased soil heating (e.g. time above 50 °C at the soil surface was 34 s in untreated and almost 10 min in drought plots at the dry heath, Section 5.3.2). The important contribution of the combustion of the moss and litter layer to increasing fire-induced soil heating was apparent through comparison with the lower soil heating measured in Chapter 3, where higher severity was achieved by removing the moss and litter layer. The higher consumption of the moss and litter layer also resulted in increased post-fire soil thermal range (Section 5.3.4). In contrast to the dry heath, the drought treatment did not lower surface soil moisture content at the raised bog which, together with the thicker moss and litter layer and its lower consumption, explains the low fire-induced soil heating measured (average maximum temperatures remained below 15 °C) and the similarity of post-fire soil thermal dynamics between untreated and drought plots. Given the large thermal inertia of wet soils (Busse et al., 2010), ecohydrological differences between sites (soil moisture and the depth of the organic layer, and thus water storage, were much higher at the raised bog) likely played a key role in controlling both fire-induced soil heating and post-fire soil thermal dynamics. Raised bogs appear to be more resilient to drought and subsequent fire than dry heath, and thus the carbon stored in thin organic layers under dry heaths may be more at risk during higher severity fires, and in a drier climate, than that stored in deep peat. However, drought can have a larger effect on fire severity in peatlands that have been subjected to interacting disturbances such as drainage (Sherwood et al., 2013).

Previous research has reported contradictory results on the effect of burning on peatland carbon dynamics. For example, short-term post-fire (up to 3 years) methane flux was found to be similar to that from unburnt (Taylor, 2015) while longer-term (9 years) post-fire methane flux was found to be lower than unburnt (Ward et al., 2007). Burning was observed to increase dissolved organic carbon concentration in streams (Ramchunder et al., 2013) but no effect was observed in soil water (Clay et al., 2010; Holden et al., 2012). Furthermore, soil carbon flux data from dry heaths is scarce.

Chapter 6 therefore makes a valuable contribution to research by presenting new information while introducing novel components such as the drought simulation, which allowed investigation of the role of fire severity on soil carbon dynamics. Burning decreased ecosystem respiration and photosynthesis, the latter to a greater extent, resulting in a switch from net CO_2 sink to net loss during summer and autumn, and in greater net CO_2 loss during winter, at both sites (Section 6.3.4). Methane flux was negligible at the dry heath but after burning this flux increased at the raised bog (Section 6.3.5), where it contributed to a substantial amount of CO_2 equivalent flux during the summer. Conversely, soil water dissolved organic carbon concentration at the raised bog was not altered by fire (Section 6.3.6). No differences in short-term soil carbon dynamics between normal and increased fire severity treatments were apparent in any of the measurements, except for larger ecosystem respiration in the dry heath during autumn. In addition to burning, soil temperature, soil moisture content (or water table depth) and vegetation cover were important controls on soil carbon fluxes. The importance of such ecosystem controls has been observed elsewhere in UK and boreal peatlands (Dorrepaal et al., 2009; Wieder et al., 2009; Levy et al., 2012). My results show that burning increased short-term carbon fluxes both at the dry heath and at the raised bog. However, increased fire severity, at least within the range of conditions captured by this study, had no additional effect.

This research improves our understanding of moisture content and fuel structure controls on fire severity, and subsequent effects on vegetation regeneration and soil carbon dynamics (Figure 1.3, Table 7.1). My results indicate that drought increases fire severity through lowering the moisture content of ground fuels and soil. Increase in fire-induced soil heating in drought plots was substantial and ecologically significant at the dry heath, but not at the raised bog, where high moisture content and thick moss and litter layers kept soil heating low. This suggests impacts of higher severity fires following drought on vegetation community composition and soil carbon dynamics may be more important in dry heaths than in raised bogs. Higher disturbance severity led to significant differences in community composition at the dry heath, which could have an effect on the conservation value of these habitats. Although no short-term differences in soil carbon dynamics between higher and lower fire severity were observed, the differences in community composition could lead to altered carbon dynamics in the longer term.

7.2 Future research directions

7.2.1 Developing tools to forecast fire severity

My research has demonstrated the importance of ground fuels (the moss and litter layer) in controlling fire effects in *Calluna*-dominated habitats. Such importance is not surprising given that it can represent a substantial proportion of the total fuel above the soil (e.g. 18–61 %; Table C.2) and that it lies at the surface of the soil where it has a key role regulating plant establishment and soil microclimate. The moss and litter layer controls fuel available for combustion and influences fire behaviour and fire-induced soil heating, post-fire soil thermal dynamics and vegetation regeneration (Chapter 3, Chapter 4 and Chapter 5). Furthermore, results from the climate manipulation experiment indicate that it is the fuel layer most susceptible to drought.

Being able to forecast the moisture content of the moss and litter layer could be a powerful tool to advice managed burning to achieve specific objectives, including that burning is completed in safe conditions, and to make provisions towards addressing wildfire risk. The Met Office Fire Severity Index, based on the widely-used Canadian Forest Fire Weather Index System (Van Wagner, 1987), is the forecasting system currently used in England and Wales to identify conditions in which very high severity fires are likely. Previous research has highlighted the limitations of the Met Office Fire Severity Index for predicting fire behaviour and has suggested using the

Table 7.1: Thesis objectives (see Section 1.5) and summary of findings.

Research objective	Findings
1. Quantify the role of fuel structure in driving variation in indicators of fire severity (e.g. soil heating)	- M/L layer substantially reduced fire-induced soil heating. - Diurnal and annual soil temperature fluctuations were larger after simulated high severity fires (M/L layer removed). - Soil thermal dynamics were similar after simulated high severity fires and after wildfires. - Differences in soil thermal dynamics due to fire severity led to increased modelled soil respiration.
2. Assess the effect of drought on altering flammability of *Calluna* fuels and on subsequent variation in fire severity	- At the dry heath, lowered M/L layer and soil moisture led to substantial M/L consumption and soil heating. - At the raised bog, lowered M/L layer moisture increased M/L layer consumption but soil heating remained low. - Higher severity altered post-fire soil thermal dynamics at the dry heath but not at the raised bog.
3. Determine differences in post-fire vegetation community composition in response to variation in disturbance severity	- Managed burning increased abundance of ericoids, forbs, graminoids and acrocarpous mosses compared with cut plots, dominated by pleurocarpous mosses. - Increase of bare soil cover in high severity fires promotes ericoids, forbs and graminoids but higher soil heating favours acrocarpous mosses.
4. Quantify the effect of variation in fire severity on post-fire soil carbon dynamics	- Burning reduced photosynthesis more than respiration, resulting in a switch from CO_2 sink to source at both sites in the short term. - Burning increased CH_4 emission at the raised bog. - Dissolved organic carbon at the raised bog was not altered by burning. - No differences in soil carbon dynamics between lower and higher severity treatments were observed.

Canadian system for forecasting moisture content (Legg et al., 2007; Davies et al., 2016a). The Fine Fuel Moisture Code of the Forest Fire Weather Index System may be of particular value since it uses simple daily weather data (air temperature and relative humidity at noon, average wind speed and 24 h accumulated rain) to estimate the moisture content of litter and other dead fine fuels, and can be adapted to a variety of fuel types (de Groot et al., 2005; Wotton and Beverly, 2007). Although designed for dead fine fuels with no active regulation of moisture, the Fine Fuel Moisture Code may perform well for mosses due to their lack of a well-developed root system.

Similarly, the moisture content of the soil may be critical in regulating fire-induced soil heating and ignition of organic layers (Chapter 5), and therefore the ability to use weather forecasts to predict when low soil moisture content could lead to severe fires would be useful for land managers and wildfire services. Again, some success may come from using a moisture code from the Canadian Forest Fire Weather Index System such as the Drought Code, which is designed to simulate wetting and drying of deep layers of compact organic matter. Therefore, further research needs to correlate the moisture content of the different fuel layers in *Calluna*-dominated habitats to meteorological variation (as captured, for example, by a moisture code of the Canadian system) so that fire behaviour can be forecasted.

7.2.2 Developing a mechanistic model of post-fire soil thermal dynamics

I generated quantitative information on the extent to which soil thermal dynamics can be affected by fire by simulating high severity fires where all ground fuels are consumed (Chapter 3) and by varying pre-fire moisture content to achieve a range of moss and litter layer combustion rates (Chapter 5). Although the results from the dry heath and the raised bog sites allow some estimation of how soil thermal dynamics in UK *Calluna*-dominated habitats respond to fire, generalisation of the results is difficult due to site-specific responses dependent on vegetation canopy density, depth and composition of the moss and litter layer, and bulk density and organic matter content of the soil organic layer. Therefore, a valuable extension of this work could be to develop a mechanistic model of the post-fire changes in the ground energy balance including changes in canopy and ground vegetation cover and altered hydrology. Such models have been developed for peatlands and are based on energy transfers by conduction and advection of vapour (Kettridge and Baird, 2008; Kettridge et al., 2012). A one-dimensional model that expresses temperature as a function of depth requires inputs for calculating the thermal conductivity (soil porosity, volumetric moisture content and fraction of organic matter) and the surface energy balance (surface albedo and light extinction coefficient resulting from the vascular vegetation cover) (Kettridge et al., 2012).

7.2.3 Investigating post-fire community composition following drought

I found that post-fire community composition following simulated higher severity fires differed from that following managed fires carried out under normal moisture conditions (Chapter 4). Logistically, changes in vegetation regeneration in response to a gradient of fire severity following drought (Chapter 5) could only be investigated in terms of broad plant functional groups during this thesis (Chapter 6). Increase in soil cover at the expense of moss and litter was identified in Chapter 4 as an important driver of variation in post-fire vegetation regeneration. Thus, the higher post-fire soil cover observed in drought-treated plots (Figure 6.3) suggests that vegetation regeneration in these higher fire severity plots could follow similar trends as those identified in Chapter 4, e.g. higher abundance of vascular plants when compared to lower fire severity (non-drought) plots. A multivariate analysis of the post-fire community composition could provide more detailed information on the effect of a gradient of fire severity on vegetation regeneration, i.e. response of individual species, and quantify the effect on diversity.

It is also important to understand better if the differences in post-fire vegetation community observed as a result of variation in fire severity are time-limited. In Chapter 4 I related variation in fire severity to short-term changes in community composition (after three growing seasons), but it is unclear how long-lived these changes will be and whether higher severity fires could ultimately lead to substantially different long-term community compositions. With the exception of extreme severity fires where organic soil layers ignite (Maltby et al., 1990; Legg et al., 1992), research on *Calluna* moorlands has found that initial post-fire floristic composition can determine medium-term (7–8 years) differences in community composition (Hobbs and Gimingham, 1984b; Velle et al., 2012), but that eventual re-assertion of *Calluna* dominance leads to homogenous mature communities (Harris et al., 2011). Further research on how composition dynamics vary according to a disturbance severity would contribute to a better understanding of potential effects of an altered fire regime on the ecology of *Calluna*-dominated habitats.

7.2.4 Further study of the effect of fire severity on soil carbon dynamics

In Chapter 6 I compared post-fire soil carbon flux between fire severity treatments (higher severity after drought, low fire severity and unburnt controls) over a year thus encompassing annual variation. Nevertheless, winter data, as well as night-time data, was lacking, making it difficult to estimate an annual carbon budget for the sites. Moreover, methane flux was an important contribution to total carbon flux at the raised bog during summer, but difficulties with the instrument meant few data was available, and only during spring and summer. Therefore some uncertainties remain as to what the response of the methane flux was to meteorological variation. Although the main objective of estimating the effect of fire severity on soil carbon dynamics was achieved, further gas flux measurements, especially methane, under a wider range of conditions would provide a more accurate assessment of the impact of fire on soil carbon dynamics.

All carbon dynamics measurements (ecosystem respiration, net ecosystem exchange, methane and dissolved organic carbon) were significantly influenced by vegetation cover. Such relationship could be further explored with a long-term monitoring of the site, as suggested above for post-fire community composition. For instance, although no short-term differences in carbon dynamics were observed in response to the fire severity gradient, it is possible that, given that fire severity can shape community composition, such differences could be observed later in the succession as autotrophic respiration and photosynthesis had a greater contribution to soil carbon dynamics (Wieder et al., 2009). Furthermore, considering that vascular plants may induce greater soil carbon loss (Walker et al., 2016), the greater abundance of shrubs after higher severity fires (Chapter 4) could potentially lead to larger soil carbon emissions from soils. However, fire-derived increase in carbon losses may be compensated for in the long-term by higher plant assimilation (Wieder et al., 2009; Clay et al., 2010, 2015). Longer-term monitoring of vegetation regeneration, as well as of the evolution of post-fire soil thermal dynamics, are needed to confidently assess the effect of increased fire severity on *Calluna* moorlands.

I only examined the effects of higher severity on soil carbon dynamics in the context of managed burning where extensive loss of the moss and litter and ignition of the organic layer did not take place. But given the important effect of wildfires where organic soil layers ignite on controlling mechanisms of soil carbon dynamics such as soil temperature, water table (Kettridge et al., 2015) and vegetation cover (Maltby et al., 1990), it is likely that fire severity effects are apparent at higher severities, i.e. wildfires (Davies et al., 2016a). Therefore, further research needs to investigate the relationship between fire severity and post-fire soil carbon dynamics at the higher end of severity. This could be achieved by assessing fire severity in wildfires (Davies et al., 2016a) and relating its variation to measurements of soil carbon dynamics.

7.3 Implications for moorland management

- Low severity managed burning (where there was minimal alteration to the moss and litter layer) promoted higher abundance of vascular plants and acrocarpous mosses than cutting, where pleurocarpous mosses were dominant (Chapter 4). This suggests that, if the objective of burning is to increase the abundance of a wider variety of plant functional types, burning may be preferable to cutting. With regards to *Calluna* regeneration, burning and cutting resulted in similar *Calluna* abundance.

- Abundance of vascular plants, including dominant ericoids, was higher when the substrate was bare soil rather than moss and litter, even when ground heating was relatively high and hindered regeneration (Chapter 4). Therefore higher severity prescribed burns that consume the moss and litter layer may be preferable if the primary management objective is vigorous ericoid regeneration. In this case burning should take place when the soil moisture content is high (> 200 %, see Chapter 5) to minimise high fire-induced ground heating that can damage vegetative and seedling regeneration.

- Fire severity in terms of fire-induced soil heating was much higher at the dry heath than at the raised bog despite similar above-ground fuel structure. Thicker moss layers and, particularly, deep wetter soils resulted in low ground heating, much below thresholds of damage to plant tissue or soil microbial community, and low alteration to post-fire soil thermal dynamics.

- My results suggest that higher severity burning in dry heaths where total combustion of the moss and litter layer takes place leads to warmer soils, which could result in higher short-term soil carbon emissions compared to managed burning where the moss and litter layer does not ignite (Chapter 3). When higher severity managed burning resulted in only partial moss and litter layer combustion, post-fire soil carbon emissions were similar to than from normal managed burning where the moss and litter layer was little altered (Chapter 6).

- Land managers need to consider the potential trade-offs that result from burning under different fire severity conditions. While higher severity fires that achieve a greater proportion of moss and litter layer consumption may facilitate *Calluna* regeneration, the associated alteration of post-fire soil thermal dynamics could also increase carbon loss.

Appendix A

Chapter 3

A.1 Fuel structure variance partitioning

Table A.1: Variance partitioning of fuel characteristics in "between fire" and "within fire". Variance is expressed as % of total variance.

	Between	Within
Total fuel (kg m^{-2})	59	41
Fine fuel (kg m^{-2})	54	46
Bulk density (kg m^{-3})	62	38
Height (m)	7	93
M/L thickness (cm)	30	70

A.2 Differences between both M/L layer present treatments

Table A.2: Details of models examining differences in temperature metrics (total heat, maximum temperatures and slopes of the heating and cooling limbs of the temperature-time curves) between both treatments where the M/L was present at the time of the fire. The mixed effects models included treatment (levels: burnt plots and burnt plots where the M/L layer was removed after the fire) as fixed effect and fire as random effects. Separate models were fitted for different depths of soil temperature measurement (soil surface or 2 cm below).

Response	Depth (cm)	Term	Value	Std.Error	DF	t-value	p-value
Total Heat (°C.s)	0	(Intercept)	70.25	13.06	20	5.38	<0.001
		Treatment	12.53	15.80	20	0.79	0.437
	2	(Intercept)	33.75	8.59	18	3.93	<0.001
		Treatment	4.07	7.41	18	0.55	0.590
Maximum T (°C)	0	(Intercept)	2.49	0.27	20	9.04	<0.001
		Treatment	0.22	0.30	20	0.72	0.482
	2	(Intercept)	1.82	0.17	18	10.83	<0.001
		Treatment	0.01	0.08	18	0.17	0.863
Heating slope (λ)	0	(Intercept)	-6.10	1.35	20	-4.52	<0.001
		Treatment	1.13	1.64	20	0.69	0.499
	2	(Intercept)	-8.45	1.29	18	-6.53	<0.001
		Treatment	-0.52	1.00	18	-0.52	0.612
Cooling slope (λ)	0	(Intercept)	-7.39	1.27	20	-5.84	<0.001
		Treatment	0.49	1.45	20	0.34	0.740
	2	(Intercept)	-10.74	0.13	18	-82.37	<0.001
		Treatment	0.18	0.18	18	1.00	0.331

A.3 Heterogeneity of variance at different depths of measurement

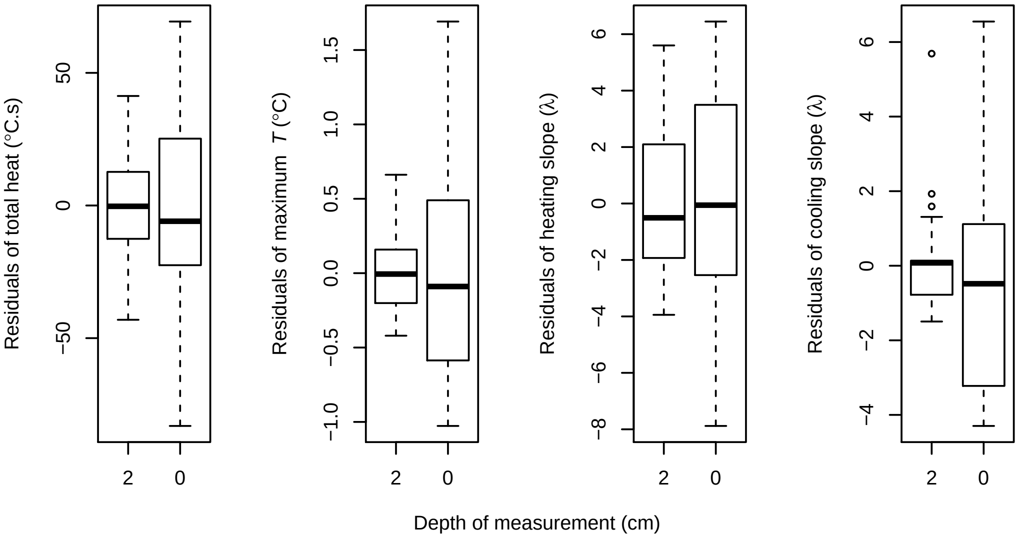

Figure A.1: Distribution of the residuals of models examining differences in temperature metrics between treatments (burnt plots and burnt plots where the M/L layer was removed before and after the fire) by depth of measurement (soil surface and 2 cm below).

A.4 Differences in post-fire thermal dynamics by type of fire

Table A.3: Model details of post-fire mean daily temperature increase as a function of mean daily temperature in the unburnt plot and fire type associated with each paired plot. The factor "fire type" had three levels: wildfires (the base level), low severity experimental fires ("ML") and simulated high severity experimental fires (where the M/L layer was removed "M/L.removed").

Response	R^2m	R^2c	Fixed effects	DF	t-value	p-value
ΔMDT	0.41	0.65	Intercept	2550	-3.98	<0.001
			MDT.unburnt		4.68	<0.001
			ML		2.28	0.023
			ML.removed		1.43	0.154
			MDT.unburnt:ML		-2.14	0.032
			MDT.unburnt:ML.removed		-0.19	0.849

Appendix B

Chapter 4

B.1 Rare species

Table B.1: List of rare species excluded from analysis, including the percentage of plots in which they were present.

Species	% plots
Luzula multiflora	4.2
Cephalozia connivens	4.2
Barbilophozia barbata	2.8
Thuidium tamariscinum	1.4
Unidentified graminoid 2	2.8
Unidentified liverwort	2.8
Unidentified graminoid 3	1.4

B.2 Stress plots

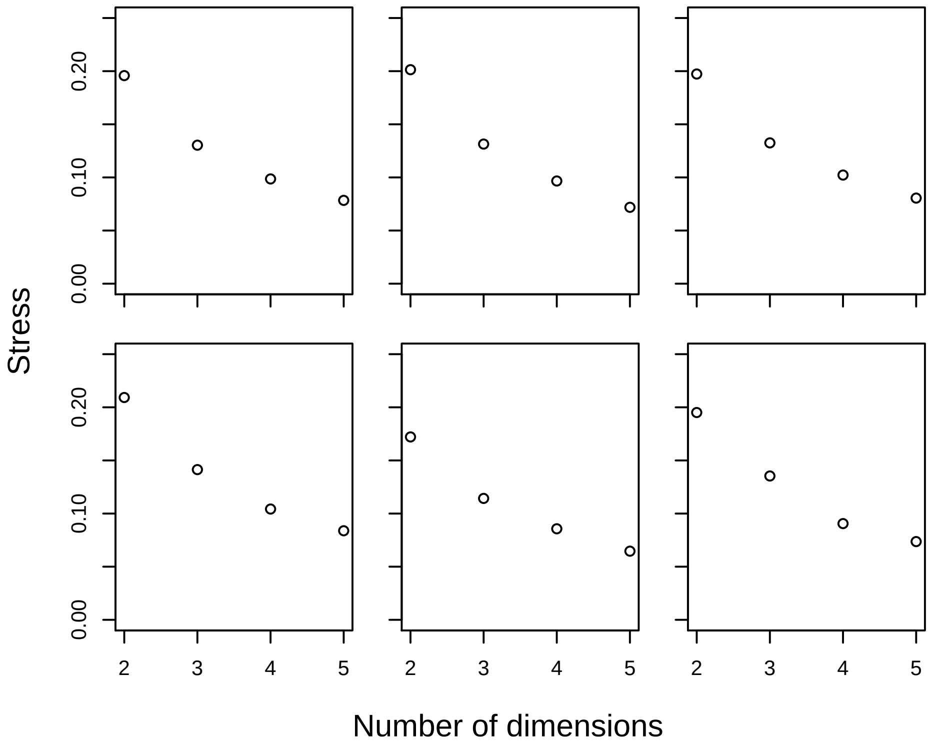

Figure B.1: Stress values of NMDS ordination of frequency data (top row) and cover data (bottom row) against number of dimensions. The three ordinations tested were: (left) all treatments (Figure 4.3, Appendix B.3), (centre) only unburnt, cut and burnt plots (Figure 4.4, Appendix B.4), and (right) cut and burnt treatments where the M/L layer was removed (Figure 4.5, Appendix B.5).

B.3 3-D ordination diagrams for all treatments

Frequency

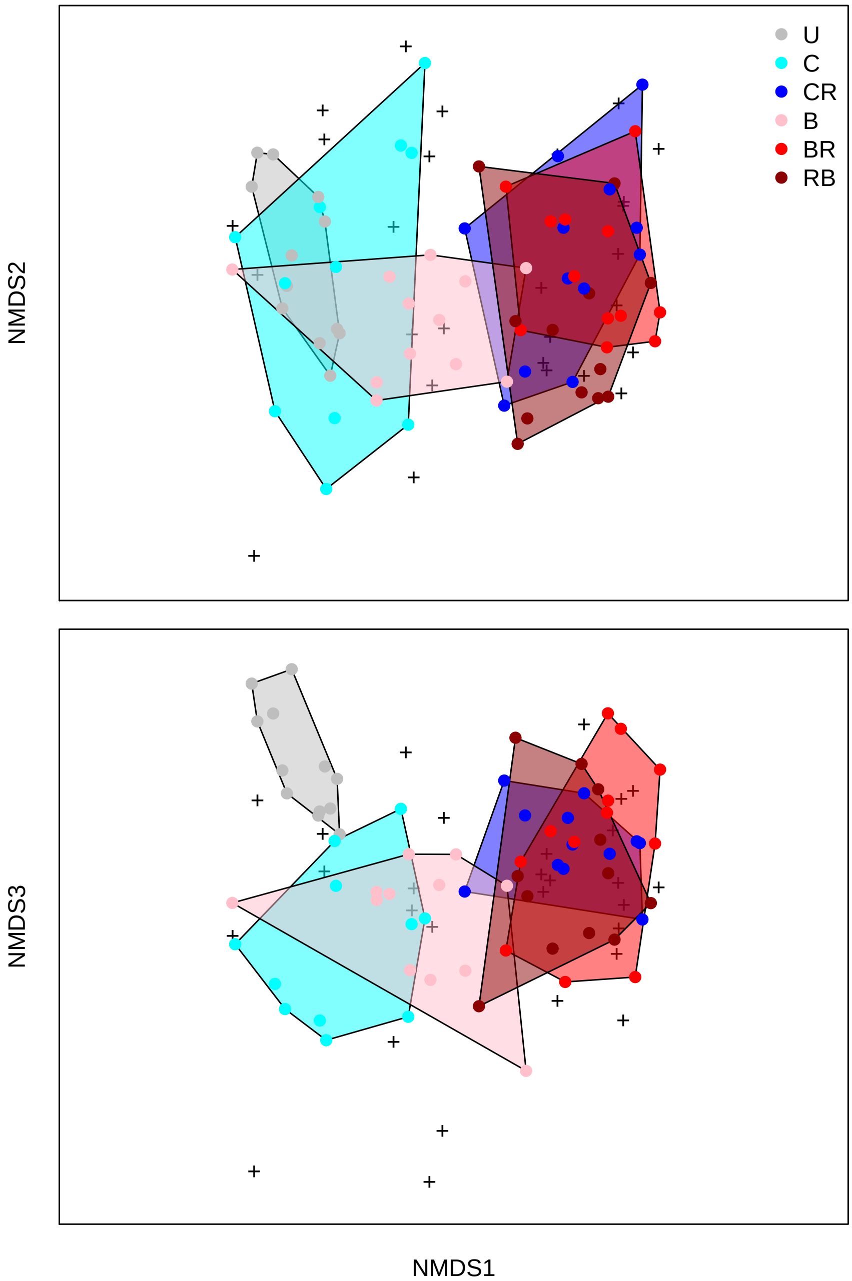

Figure B.2: NMDS ordination of plots grouped by treatment (U: unburnt; C: cut; CR: cut, M/L layer removed; B: burnt; BR: burnt, M/L layer removed after the fire; RB: burnt, M/L layer removed before the fire) in axes 1 vs 2 (top) and 1 vs 3 (bottom); species indicated by "+". Ordination stress was 0.13.

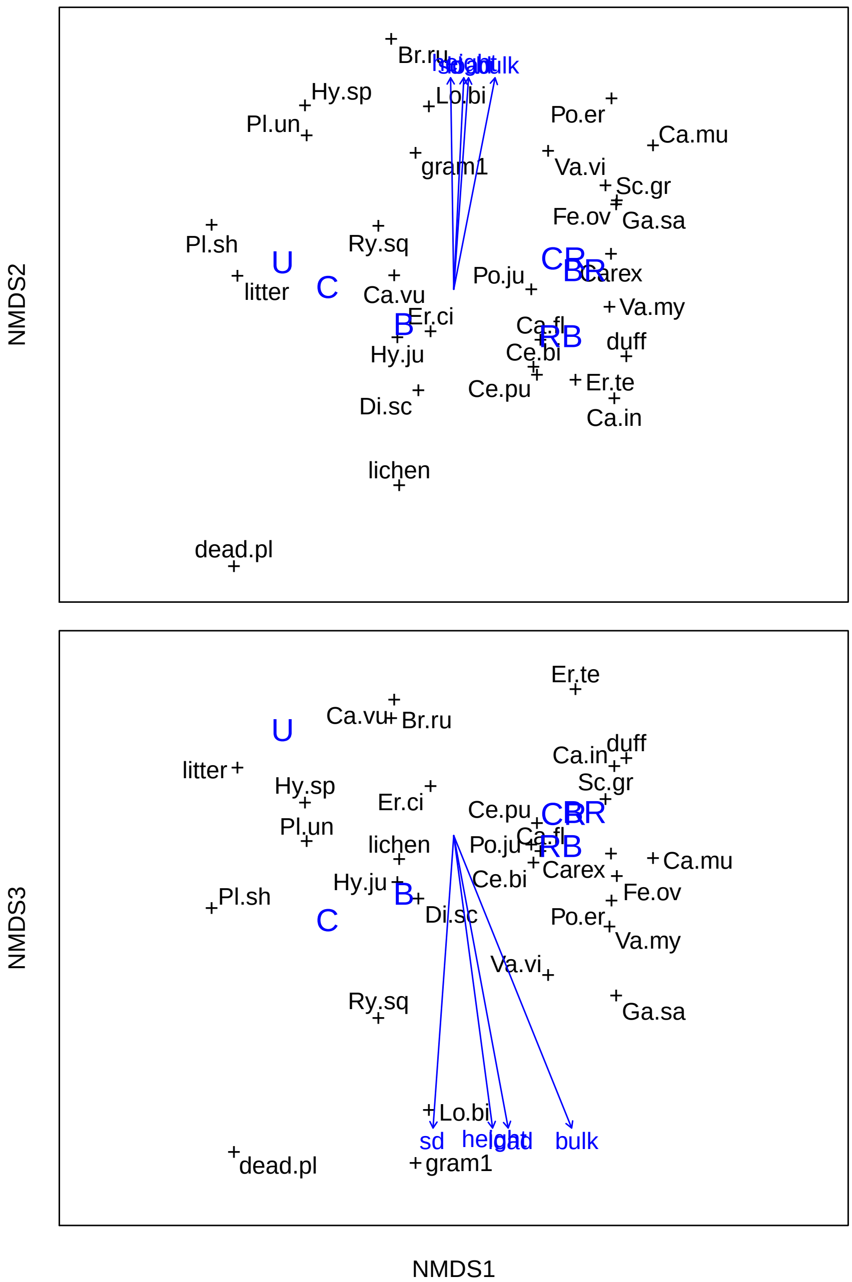

Figure B.3: NMDS ordination of species (codes follow Table 4.3) in axes 1 vs 2 (top) and 1 vs 3 (bottom) with centroid (averages) of treatment levels (U: unburnt; C: cut; CR: cut, M/L layer removed; B: burnt; BR: burnt, M/L layer removed after the fire; RB: burnt, M/L layer removed before the fire) and direction of correlation with pre-disturbance *Calluna* structure measurements. Ordination stress was 0.13.

Cover

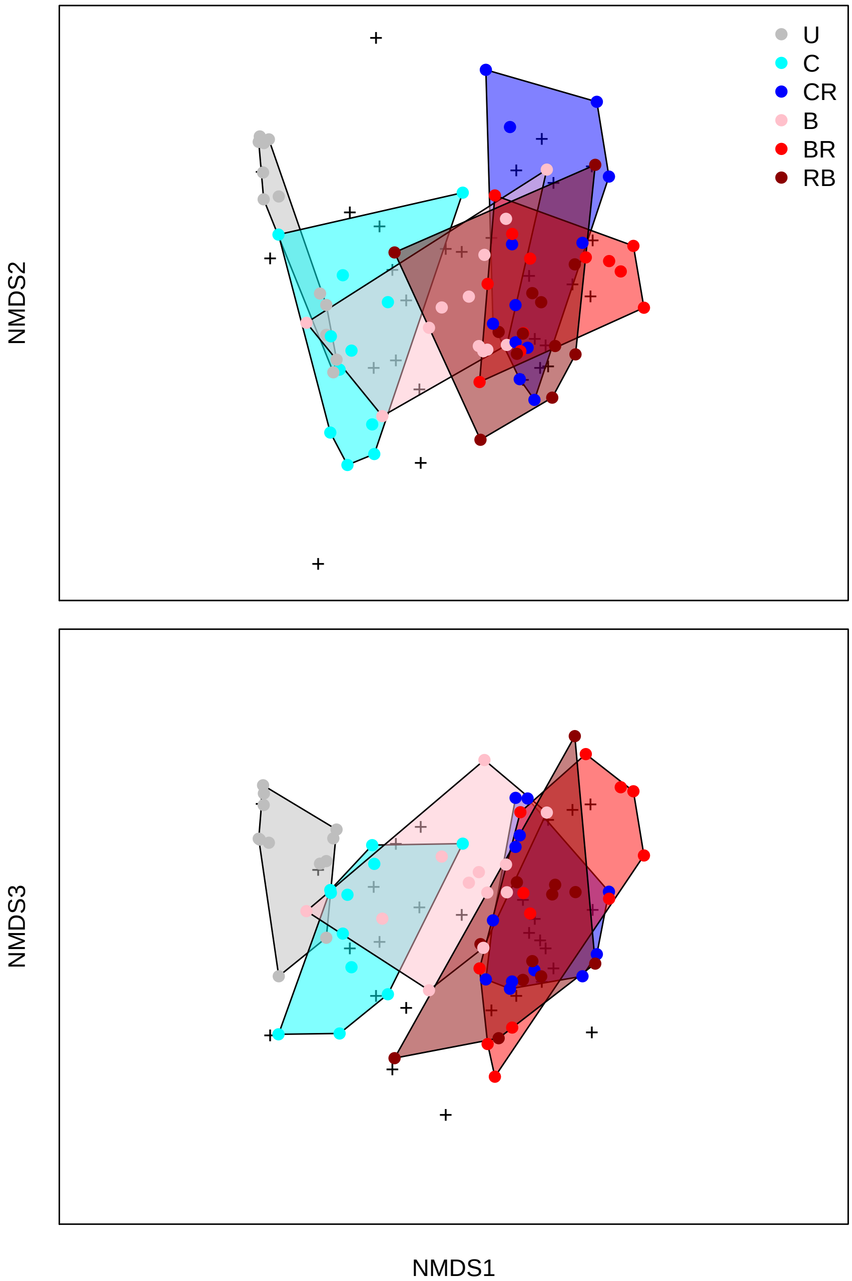

Figure B.4: NMDS ordination of plots grouped by treatment (U: unburnt; C: cut; CR: cut, M/L layer removed; B: burnt; BR: burnt, M/L layer removed after the fire; RB: burnt, M/L layer removed before the fire) in axes 1 vs 2 (top) and 1 vs 3 (bottom); species indicated by "+". Ordination stress was 0.14.

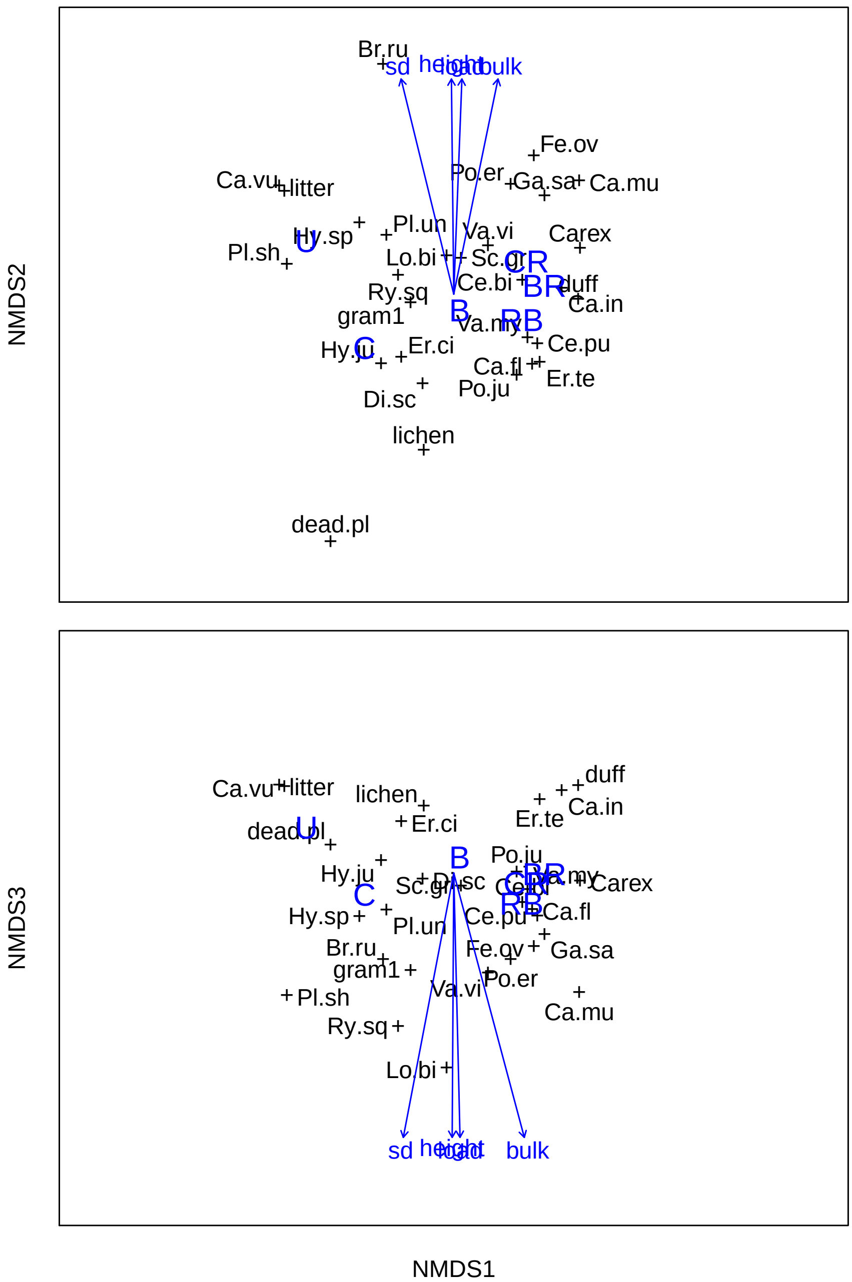

Figure B.5: NMDS ordination of species (codes follow Table 4.3) in axes 1 vs 2 (top) and 1 vs 3 (bottom) with centroid (averages) of treatment levels (U: unburnt; C: cut; CR: cut, M/L layer removed; B: burnt; BR: burnt, M/L layer removed after the fire; RB: burnt, M/L layer removed before the fire) and direction of correlation with pre-disturbance *Calluna* structure measurements. Ordination stress was 0.14.

B.4 3-D ordination diagrams of low severity disturbance treatments

Frequency

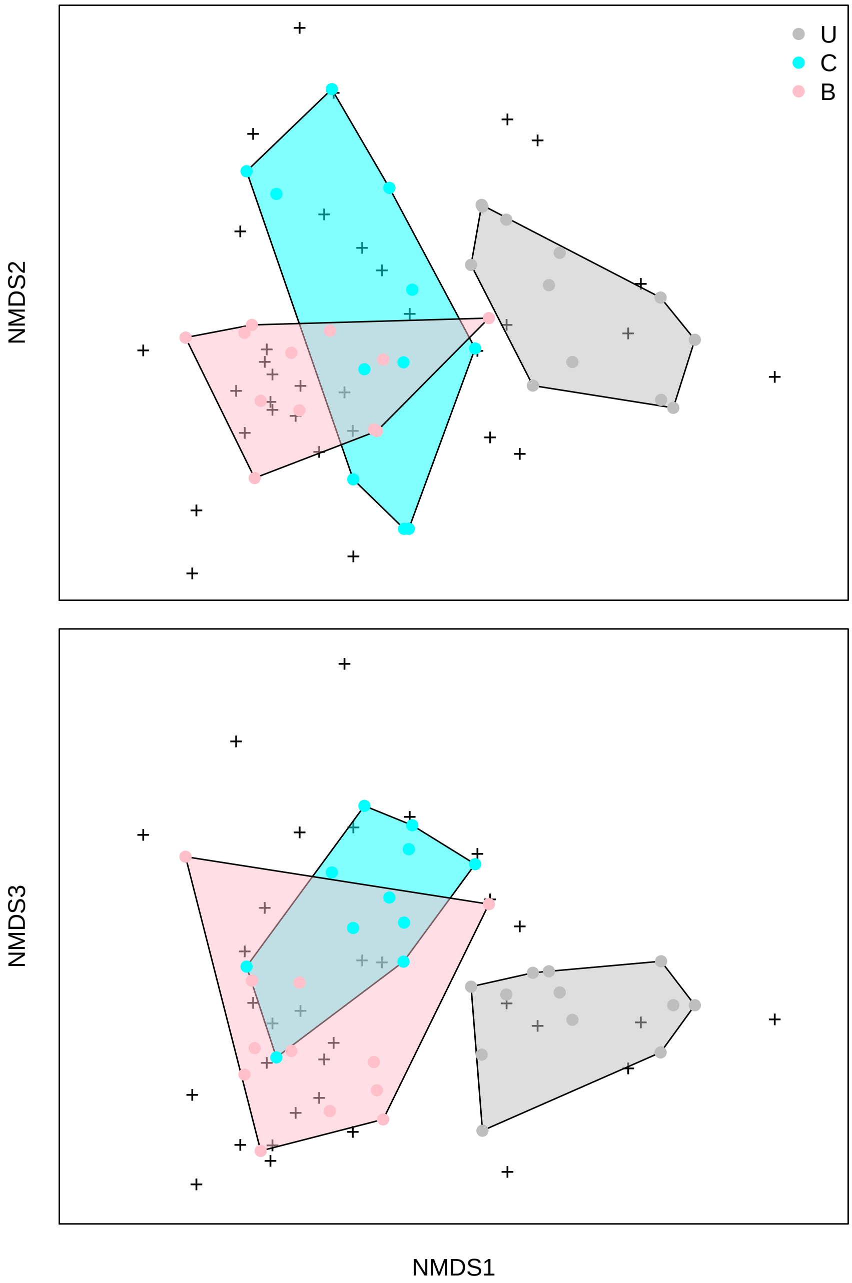

Figure B.6: NMDS ordination of plots grouped by treatment (U: unburnt; C: cut; B: burnt) in axes 1 vs 2 (top) and 1 vs 3 (bottom); species indicated by "+". Ordination stress was 0.13.

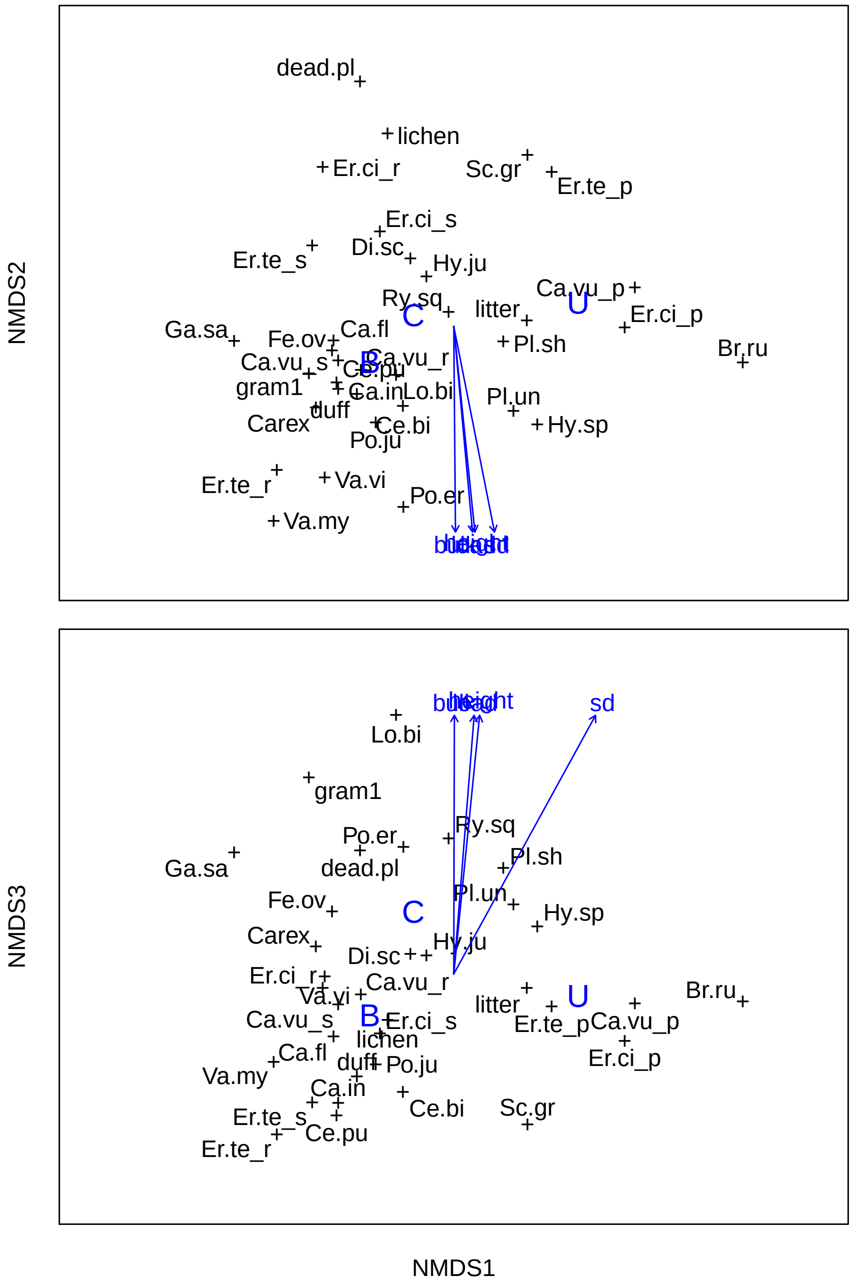

Figure B.7: NMDS ordination of species (codes follow Table 4.3) in axes 1 vs 2 (top) and 1 vs 3 (bottom) with centroid (averages) of treatment levels (U: unburnt; C: cut; B: burnt) and direction of correlation with pre-disturbance *Calluna* structure measurements. Ordination stress was 0.13.

Cover

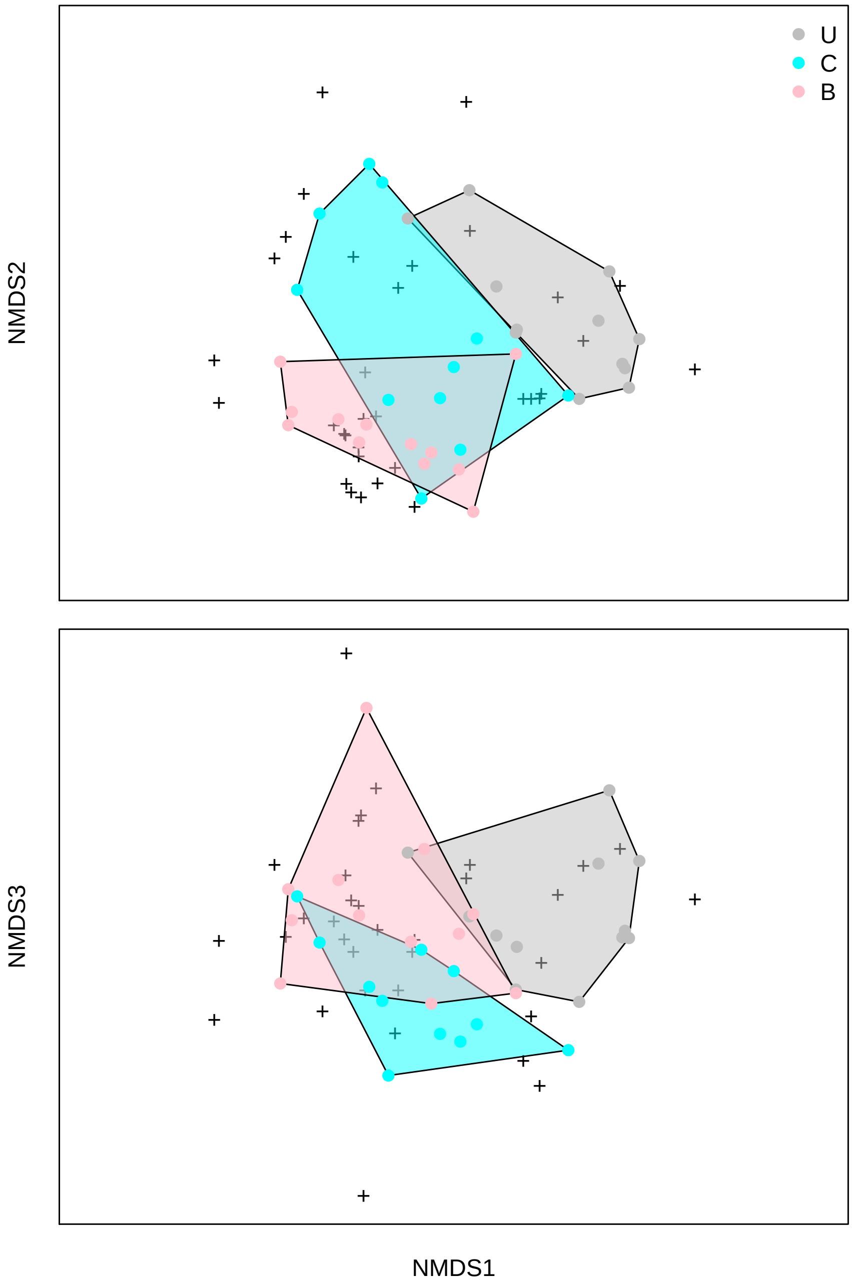

Figure B.8: NMDS ordination of plots grouped by treatment (U: unburnt; C: cut; B: burnt) in axes 1 vs 2 (top) and 1 vs 3 (bottom); species indicated by "+". Ordination stress was 0.11.

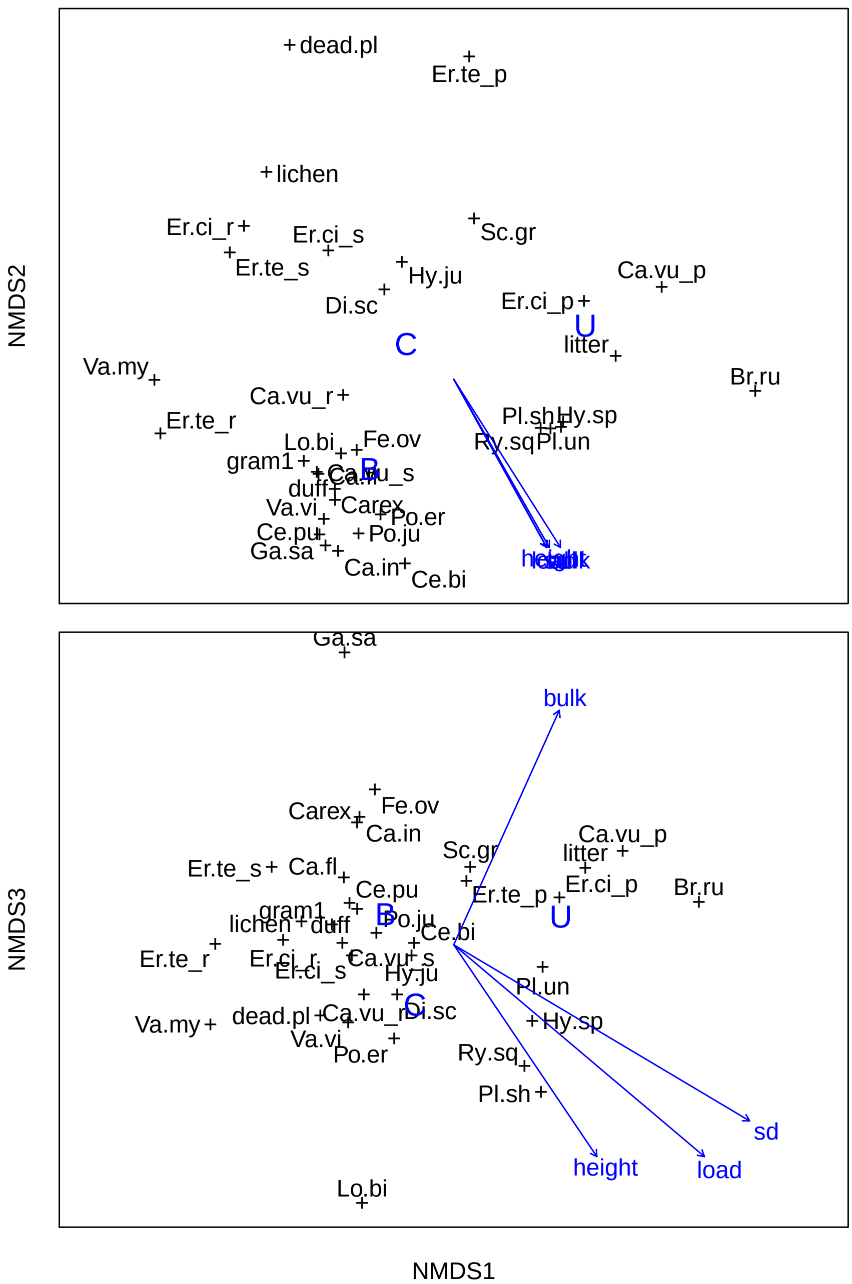

Figure B.9: NMDS ordination of species (codes follow Table 4.3) in axes 1 vs 2 (top) and 1 vs 3 (bottom) with centroid (averages) of treatment levels (U: unburnt; C: cut; B: burnt) and direction of correlation with pre-disturbance *Calluna* structure measurements. Ordination stress was 0.11.

B.5 3-D ordination diagrams of high severity disturbance treatments

Frequency

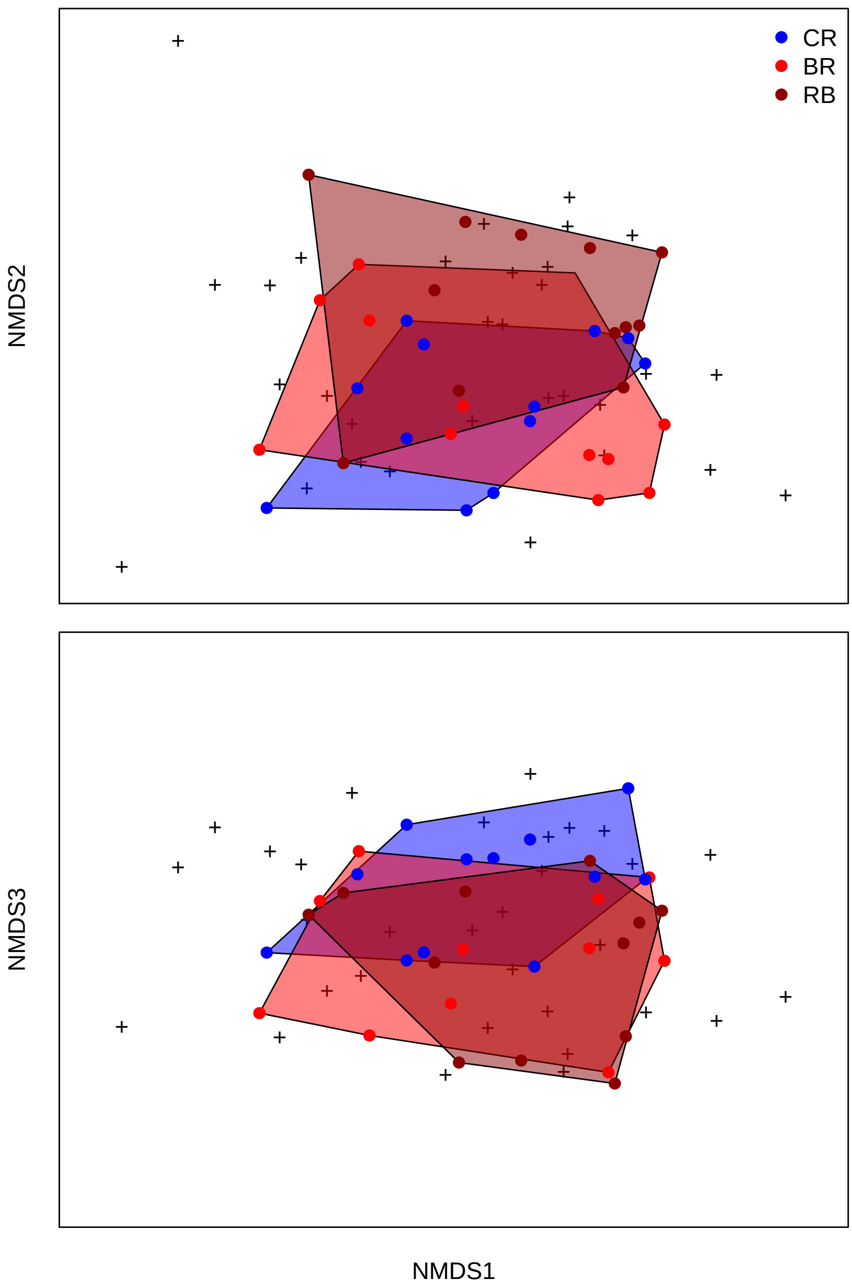

Figure B.10: NMDS ordination of plots grouped by treatment (CR: cut, M/L layer removed; BR: burnt, M/L layer removed after the fire; RB: burnt, M/L layer removed before the fire) in axes 1 vs 2 (top) and 1 vs 3 (bottom); "+" indicates species. Ordination stress was 0.13.

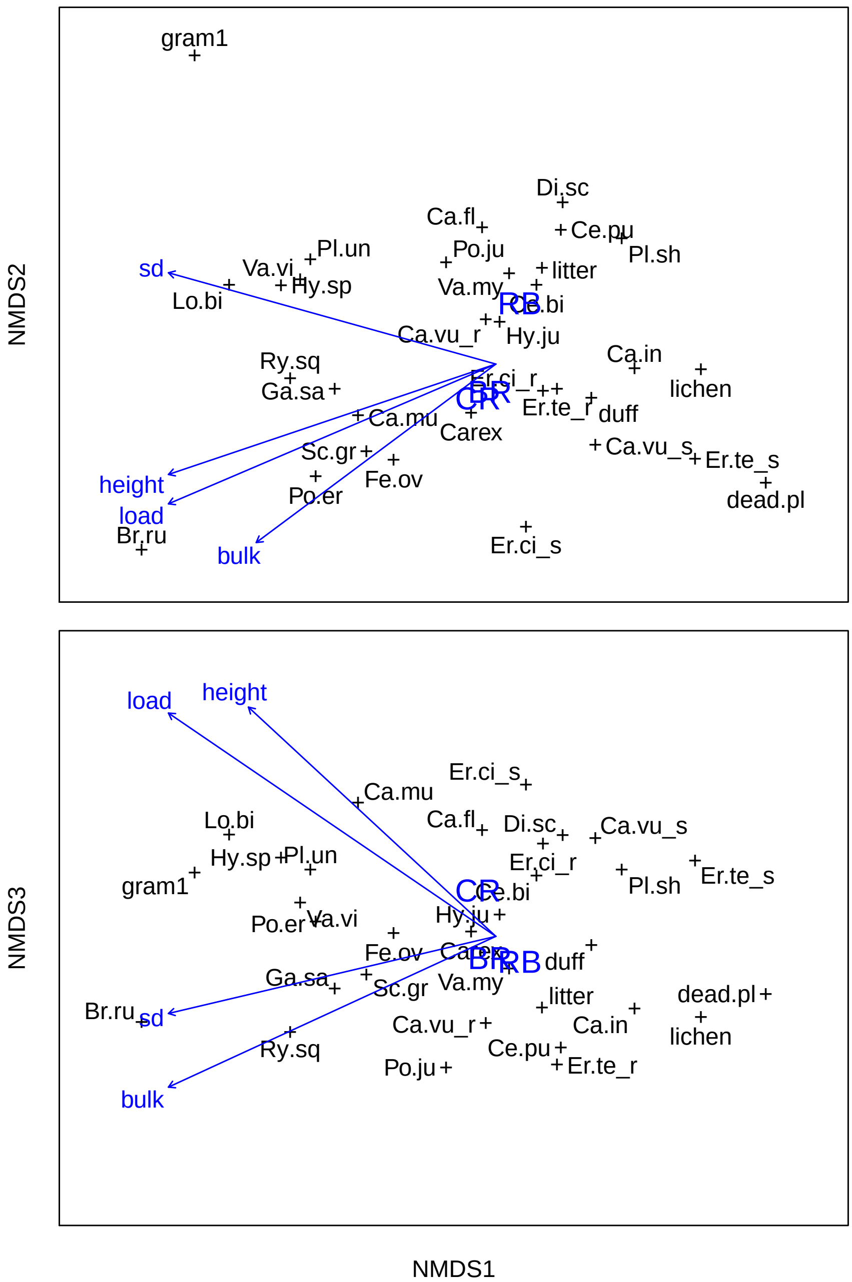

Figure B.11: NMDS ordination of species (codes follow Table 4.3) in axes 1 vs 2 (top) and 1 vs 3 (bottom) with centroid (averages) of treatment levels (CR: cut, M/L layer removed; BR: burnt, M/L layer removed after the fire; RB: burnt, M/L layer removed before the fire) and direction of correlation with pre-disturbance *Calluna* structure measurements. Ordination stress was 0.13.

Cover

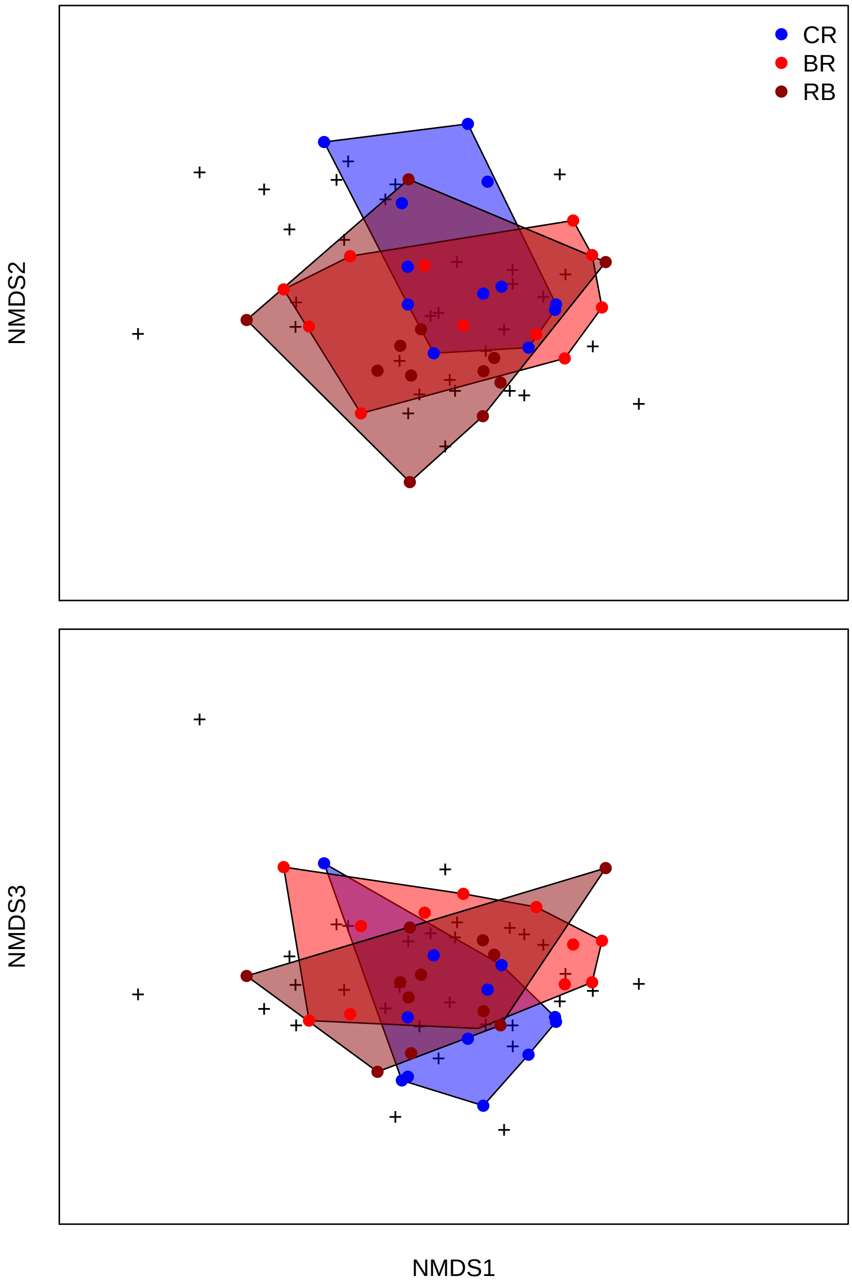

Figure B.12: NMDS ordination of plots grouped by treatment (CR: cut, M/L layer removed; BR: burnt, M/L layer removed after the fire; RB: burnt, M/L layer removed before the fire) in axes 1 vs 2 (top) and 1 vs 3 (bottom); "+" indicates species. Ordination stress was 0.14.

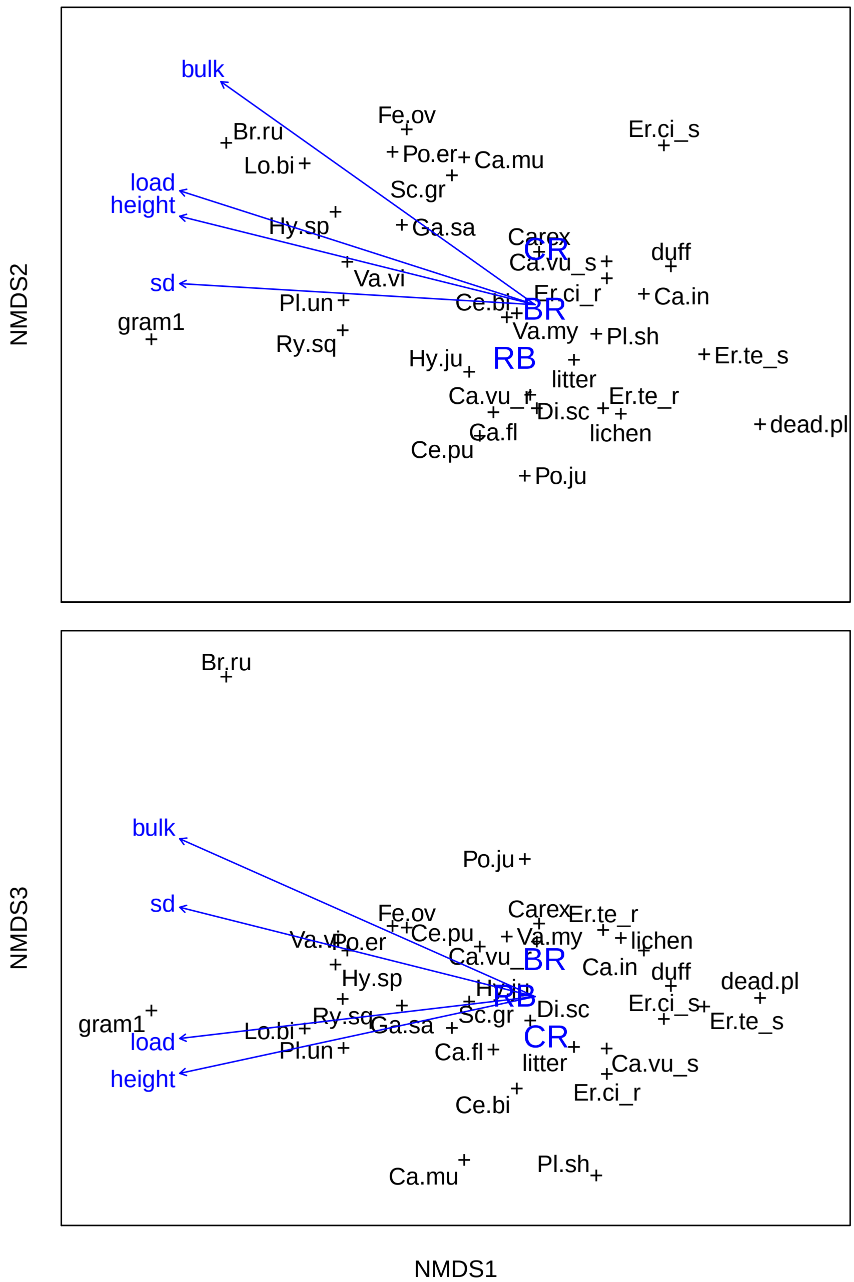

Figure B.13: NMDS ordination of species (codes follow Table 4.3) in axes 1 vs 2 (top) and 1 vs 3 (bottom) with centroid (averages) of treatment levels (CR: cut, M/L layer removed; BR: burnt, M/L layer removed after the fire; RB: burnt, M/L layer removed before the fire) and direction of correlation with pre-disturbance *Calluna* structure measurements. Ordination stress was 0.14.

B.6 PERMANOVA and analyses of group dispersion

Low severity treatments

Frequency

Table B.2: PERMANOVA of the frequency dissimilarity matrix including unburnt, cut and burnt plots.

	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Treatment	2	2.62	1.31	7.73	0.001
Residuals	33	5.60	0.17		
Total	35	8.22			

Table B.3: Pairwise PERMANOVA of the frequency dissimilarity matrix including unburnt, cut and burnt plots. P-values <0.017 indicates statistical significance at the 95 % level (Bonferroni), in bold.

	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Burnt vs cut plots					
Treatment	1	0.24	0.24	2.89	**0.001**
Residuals	22	1.84	0.08		
Total	23	2.09			
Burnt vs unburnt plots					
Treatment	1	0.66	0.66	9.12	**0.001**
Residuals	22	1.60	0.07		
Total	23	2.26			
Cut vs unburnt plots					
Treatment	1	0.69	0.69	7.84	**0.001**
Residuals	22	1.95	0.09		
Total	23	2.64			

Table B.4: Analysis of group dispersion of the frequency dissimilarity matrix including unburnt, cut and burnt plots.

	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Groups	2	0.05	0.02	3.15	0.0562
Residuals	33	0.24	0.01		

Table B.5: Pairwise comparisons of group dispersions in the frequency dissimilarity matrix including unburnt, cut and burnt plots.

	Difference	Lower CI	Upper CI	p-value
C-U	0.088	0.002	0.173	0.044
B-U	0.045	-0.040	0.131	0.406
B-C	-0.042	-0.128	0.044	0.457

Cover

Table B.6: PERMANOVA of the cover dissimilarity matrix including unburnt, cut and burnt plots.

	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Treatment	2	2.61	1.30	6.91	0.001
Residuals	33	6.23	0.19		
Total	35	8.83			

Table B.7: Pairwise PERMANOVA of the cover dissimilarity matrix including unburnt, cut and burnt plots. P-values <0.017 indicates statistical significance at the 95 % level (in bold).

	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Burnt vs cut plots					
Treatment	1	0.23	0.23	2.64	**0.002**
Residuals	22	1.95	0.09		
Total	23	2.18			
Burnt vs unburnt plots					
Treatment	1	0.62	0.62	7.40	**0.001**
Residuals	22	1.85	0.08		
Total	23	2.47			
Cut vs unburnt plots					
Treatment	1	0.57	0.57	5.60	**0.001**
Residuals	22	2.23	0.10		
Total	23	2.80			

Table B.8: Analysis of group dispersion of the cover dissimilarity matrix including unburnt, cut and burnt plots.

	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Groups	2	0.03	0.01	0.81	0.4531
Residuals	33	0.51	0.02		

High severity treatments

Frequency

Table B.9: PERMANOVA of the frequency dissimilarity matrix including cut plots where the M/L layer was removed and burnt plots where the M/L layer was removed after or before the fire.

	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Treatment	2	0.51	0.25	1.58	0.001
Residuals	33	5.33	0.16		
Total	35	5.84			

Table B.10: Pairwise PERMANOVA of the frequency dissimilarity matrix including cut plots where the M/L layer was removed and burnt plots where the M/L layer was removed after or before the fire. P-values <0.017 indicates statistical significance at the 95 % level (in bold).

	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Cut, M/L removed vs Burnt, M/L removed after fire					
Treatment	1	0.06	0.06	1.17	0.081
Residuals	22	1.22	0.06		
Total	23	1.28			
Cut, M/L removed vs Burnt, M/L removed before fire					
Treatment	1	0.13	0.13	2.36	**0.001**
Residuals	22	1.17	0.05		
Total	23	1.29			
Burt, M/L removed after vs before fire					
Treatment	1	0.08	0.08	1.30	0.033
Residuals	22	1.28	0.06		
Total	23	1.35			

Table B.11: Analysis of group dispersion of the frequency dissimilarity matrix including cut plots where the M/L layer was removed and burnt plots where the M/L layer was removed after or before the fire.

	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Groups	2	0.01	0.00	0.79	0.4612
Residuals	33	0.19	0.01		

Cover

Table B.12: PERMANOVA of the cover dissimilarity matrix including cut plots where the M/L layer was removed and burnt plots where the M/L layer was removed after or before the fire.

	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Treatment	2	0.65	0.33	1.57	0.013
Residuals	33	6.82	0.21		
Total	35	7.48			

Table B.13: Pairwise PERMANOVA of the cover dissimilarity matrix including cut plots where the M/L layer was removed and burnt plots where the M/L layer was removed after or before the fire. P-values <0.017 indicates statistical significance at the 95 % level (in bold).

	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Cut, M/L removed vs Burnt, M/L removed after fire					
Treatment	1	0.13	0.13	1.68	**0.013**
Residuals	22	1.74	0.08		
Total	23	1.87			
Cut, M/L removed vs Burnt, M/L removed before fire					
Treatment	1	0.16	0.16	2.19	**0.006**
Residuals	22	1.65	0.07		
Total	23	1.81			
Burt, M/L removed after vs before fire					
Treatment	1	0.06	0.06	0.76	0.494
Residuals	22	1.71	0.08		
Total	23	1.77			

Table B.14: Analysis of group dispersion of the cover dissimilarity matrix including cut plots where the M/L layer was removed and burnt plots where the M/L layer was removed after or before the fire.

	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Groups	2	0.02	0.01	0.76	0.4743
Residuals	33	0.48	0.01		

B.7 Mechanisms of *Calluna* regeneration

Table B.15: Details of the generalised linear mixed effects model investigating the interaction between mechanimsm of regeneration (resprout or seedling) and treatment (unburnt, U; cut, C; cut where the M/L layer was removed, CR; burnt, B; burnt where the M/L layer was removed after the fire, BR; burnt where the M/L layer was removed before the fire, RB) on *Calluna* frequency.

	Estimate	Std. Error	z value	$Pr(>\|z\|)$
(Intercept)	0.00	0.20	0.00	1.000
treatmentC	1.80	0.25	7.21	<0.001
treatmentCR	2.63	0.25	10.52	<0.001
treatmentB	1.50	0.25	6.00	<0.001
treatmentBR	3.19	0.25	12.75	<0.001
treatmentRB	3.06	0.25	12.22	<0.001
typeseedling	-0.00	0.29	-0.00	1.000
treatmentC:typeseedling	-0.65	0.35	-1.83	0.067
treatmentCR:typeseedling	0.44	0.35	1.24	0.215
treatmentB:typeseedling	0.03	0.35	0.08	0.938
treatmentBR:typeseedling	-1.09	0.35	-3.07	0.002
treatmentRB:typeseedling	-1.42	0.35	-4.02	<0.001

Table B.16: Details of multiple comparison tests examining differences between levels of treatment (unburnt, U; cut, C; cut where the M/L layer was removed, CR; burnt, B; burnt where the M/L layer was removed after the fire, BR; burnt where the M/L layer was removed before the fire, RB) within mechanisms of regeneration (resprout or seedling) in a generalised linear mixed effects model testing the effect of the interaction between the two on frequency of *Calluna* (see Table B.15).

	Estimate	Std. Error	z value	Pr(> $\|z\|$)
resprout:C - U	1.80	0.25	7.21	<0.001
resprout:CR - U	2.63	0.25	10.52	<0.001
resprout:B - U	1.50	0.25	6.00	<0.001
resprout:BR - U	3.19	0.25	12.75	<0.001
resprout:RB - U	3.06	0.25	12.22	<0.001
resprout:CR - C	0.83	0.20	4.05	0.001
resprout:B - C	-0.30	0.20	-1.48	0.893
resprout:BR - C	1.39	0.20	6.79	<0.001
resprout:RB - C	1.25	0.20	6.13	<0.001
resprout:B - CR	-1.13	0.20	-5.54	<0.001
resprout:BR - CR	0.56	0.20	2.74	0.130
resprout:RB - CR	0.43	0.20	2.08	0.501
resprout:BR - B	1.69	0.20	8.27	<0.001
resprout:RB - B	1.56	0.20	7.62	<0.001
resprout:RB - BR	-0.13	0.20	-0.65	1.000
seedling:C - U	1.15	0.25	4.62	<0.001
seedling:CR - U	3.07	0.25	12.27	<0.001
seedling:B - U	1.53	0.25	6.11	<0.001
seedling:BR - U	2.10	0.25	8.41	<0.001
seedling:RB - U	1.63	0.25	6.53	<0.001
seedling:CR - C	1.91	0.20	9.38	<0.001
seedling:B - C	0.37	0.20	1.83	0.693
seedling:BR - C	0.95	0.20	4.64	<0.001
seedling:RB - C	0.48	0.20	2.34	0.319
seedling:B - CR	-1.54	0.20	-7.55	<0.001
seedling:BR - CR	-0.97	0.20	-4.74	<0.001
seedling:RB - CR	-1.44	0.20	-7.03	<0.001
seedling:BR - B	0.57	0.20	2.81	0.107
seedling:RB - B	0.11	0.20	0.52	1.000
seedling:RB - BR	-0.47	0.20	-2.30	0.350

B.8 Pre-disturbance vegetation structure

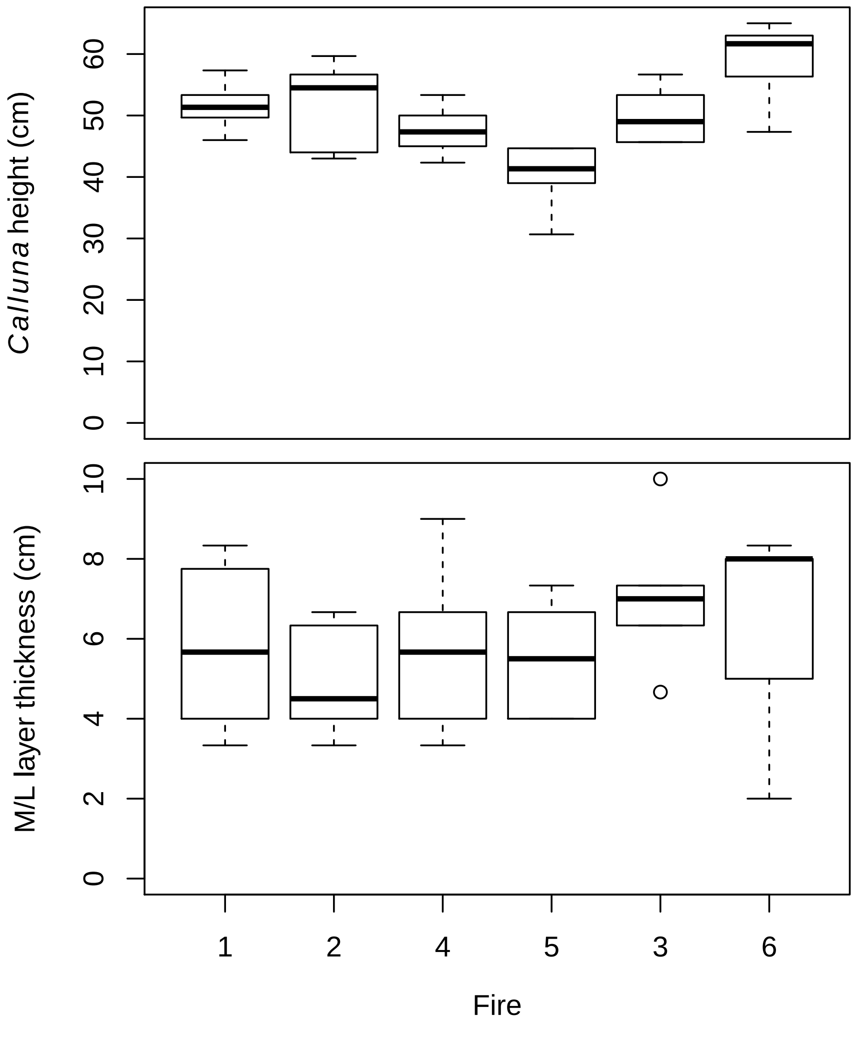

Figure B.14: *Calluna* height and M/L layer thickness in plots within the fire area, before M/L layer manipulation and burning.

Appendix C

Chapter 5

C.1 Pre-fire fuel structure and weather

Table C.1: Variance partitioning of fuel characteristics in "between fire" and "within fire" variance at Glen Tanar and Braehead Moss, expressed as % of total variance.

	Glen Tanar		Braehead Moss	
	Between	Within	Between	Within
Total fuel (kg m^{-2})	11	89	37	63
Fine fuel (kg m^{-2})	6	94	38	62
Bulk density (kg m^{-3})	27	73	38	62
Height (m)	7	93	2	98
M/L thickness (cm)	0	100	10	90

Table C.2: Fire-level average and standard deviation (in parentheses) of fuel structure at Glen Tanar and Braehead Moss, estimated with the FuelRule method. See Section 2.2 for details.

Fire	Maximum height (m)	Biomass above M/L (kg m^{-2})	Fine fuel above M/L (kg m^{-2})	M/L thickness (cm)	Biomass M/L (kg m^{-2})
			Glen Tanar		
1	0.47 (0.03)	1.7 (0.07)	0.81 (0.03)	4.3 (1.1)	0.53 (0.16)
2	0.47 (0.05)	1.7 (0.09)	0.82 (0.03)	4.5 (1.4)	0.56 (0.20)
3	0.46 (0.02)	1.7 (0.11)	0.82 (0.04)	3.8 (1.0)	0.45 (0.15)
4	0.45 (0.02)	1.6 (0.09)	0.81 (0.04)	3.0 (0.9)	0.34 (0.13)
5	0.49 (0.01)	1.8 (0.07)	0.86 (0.04)	2.7 (0.1)	0.30 (0.01)
6	0.48 (0.01)	1.6 (0.06)	0.78 (0.03)	4.6 (0.4)	0.58 (0.06)
7	0.44 (0.02)	1.6 (0.10)	0.78 (0.04)	2.7 (0.2)	0.30 (0.03)
8	0.48 (0.04)	1.6 (0.09)	0.80 (0.04)	3.9 (1.1)	0.47 (0.16)
9	0.50 (0.03)	1.7 (0.16)	0.83 (0.06)	3.2 (0.7)	0.36 (0.10)
10	0.46 (0.05)	1.7 (0.15)	0.82 (0.05)	2.4 (0.6)	0.25 (0.08)
			Braehead Moss		
1	0.52 (0.06)	1.2 (0.19)	0.60 (0.08)	17.6 (2.5)	2.46 (0.37)
2	0.48 (0.02)	1.3 (0.09)	0.65 (0.03)	14.6 (3.3)	2.02 (0.48)
3	0.51 (0.04)	1.3 (0.12)	0.63 (0.05)	14.8 (4.0)	2.04 (0.57)
4	0.47 (0.03)	1.4 (0.14)	0.69 (0.06)	9.2 (5.2)	1.24 (0.75)
5	0.50 (0.06)	1.4 (0.10)	0.71 (0.04)	10.9 (3.9)	1.49 (0.56)
6	0.46 (0.04)	1.2 (0.15)	0.62 (0.07)	11.5 (5.0)	1.57 (0.73)
7	0.51 (0.01)	1.6 (0.10)	0.77 (0.06)	6.7 (2.8)	0.87 (0.41)
8	0.47 (0.04)	1.7 (0.38)	0.81 (0.16)	6.8 (3.6)	0.89 (0.52)
9	0.48 (0.05)	1.4 (0.07)	0.69 (0.02)	6.1 (1.6)	0.79 (0.24)

Table C.3: 24 h accumulated rainfall (from noon), and moisture codes from the Canadian Fire Weather Index (FWI) system (Van Wagner, 1987), which uses daily weather data (air temperature, air relative humidity and wind speed at noon, plus 24 h accumulated rainfall) to estimate the moisture content of different types of fuel. Weather data for Glen Tanar was obtained from Aboyne weather station, and for Braehead Moss, from Drumalbin weather station (Met Office, 2012). The Fine Fuel Moisture Code estimates the moisture content of litter and other dead fine fuels, the Duff Moisture Code, of loosely compacted, decomposing organic matter, and the Drought Code, of deep layers of compact organic matter. Larger values indicate drier conditions. FWI codes were calculated using R package *fwi.fbp* (Wang et al., 2016).

Fire	Date	Raifall (mm)	FFMC	DMC	DC
		Glen Tanar			
1	2013-09-10	0.0	82	16	401
2	2013-09-10	0.0	82	16	401
3	2013-09-24	0.0	84	18	440
4	2013-09-24	0.0	84	18	440
5	2013-10-30	0.0	82	2	322
6	2014-03-11	0.0	79	2	3
7	2014-03-11	0.0	79	2	3
8	2014-04-11	0.0	86	13	54
9	2014-09-03	0.0	85	10	227
10	2014-09-03	0.0	85	10	227
		Braehead Moss			
1	2013-10-10	0.0	74	1	269
2	2013-10-10	0.0	74	1	269
3	2013-10-11	0.0	77	1	271
4	2014-04-16	0.0	80	5	27
5	2014-04-16	0.0	80	5	27
6	2014-04-25	0.0	78	11	51
7	2014-10-16	2.6	62	3	258
8	2014-10-16	2.6	62	3	258
9	2014-11-13	3.0	50	0	158

C.2 Fuel moisture content

Table C.4: Summary statistics of fuel moisture content for different sites, fuel layers and treatments.

Site	fuel	Treatment	Mean (SD)	Min	Max	n
GT	*Calluna* live	No-drought	117 (35)	76	165	10
		Drought	121 (38)	71	181	10
	Calluna dead	No-drought	39 (31)	16	97	7
		Drought	33 (22)	13	71	8
	M/L layer	No-drought	271 (180)	25	694	20
		Drought	117 (72)	22	267	20
	Soil	No-drought	221 (60)	139	326	20
		Drought	190 (79)	107	364	20
BM	*Calluna* live	No-drought	84 (6)	74	93	9
		Drought	82 (11)	64	102	9
	Calluna dead	No-drought	26 (7)	15	34	9
		Drought	23 (6)	14	31	9
	M/L layer	No-drought	365 (248)	64	699	17
		Drought	112 (101)	24	310	18
	Soil	No-drought	357 (30)	303	393	18
		Drought	341 (42)	209	394	18

Table C.5: Details of linear mixed effects models investigating the effect of the interaction between site (Glen Tanar and Braehead Moss) and treatment ("Tr": no-drought or drought) on fuel moisture content in different fuel layers.

	Value	Std.Error	DF	t-value	p-value	R^2m	R^2c
			Calluna live				
Intercept	83.56	7.71	19	10.83	<0.001	0.29	0.96
Site(GT)	26.01	11.89	15	2.19	0.045		
Trt(Drought)	-1.78	2.59	19	-0.69	0.500		
Site(GT) : Tr(Drought)	5.83	6.54	19	0.89	0.384		
			Calluna dead				
Intercept	25.89	5.74	15	4.51	<0.001	0.11	0.98
Site(GT)	12.89	8.71	15	1.48	0.160		
Trt(Drought)	-2.44	1.31	14	-1.87	0.082		
Site(GT) : Tr(Drought)	-3.31	3.77	14	-0.88	0.395		
			Moss and litter layer				
Intercept	370.04	50.26	54	7.36	<0.001	0.29	0.68
Site(GT)	-98.55	67.74	17	-1.45	0.164		
Trt(Drought)	-258.21	38.22	54	-6.76	<0.001		
Site(GT) : Tr(Drought)	103.51	49.02	54	2.11	0.039		
			Soil				
Intercept	357.04	18.34	55	19.47	<0.001	0.62	0.93
Site(GT)	-136.45	25.36	17	-5.38	<0.001		
Trt(Drought)	-16.14	8.26	55	-1.95	0.056		
Site(GT) : Tr(Drought)	-14.23	11.75	55	-1.21	0.231		

Table C.6: Multiple comparison tests examining differences in FMC in different fuel layers between levels of treatment (no-drought or drought) within the same site (Glen Tanar or Braehead Moss) and between sites within the same treatment. The linear mixed effects models tested the effect of the interaction between treatment and site on fuel moisture content of different fuel layers (see Table C.5).

	Estimate	Std. Error	z value	p value
Calluna live				
Drought vs No-drought in BM	-1.8	2.6	-0.69	0.880
Drought vs No-drought in GT	4.0	6.0	0.67	0.886
GT vs BM in Drought	26.0	11.9	2.19	0.096
GT vs BM in No-drought	31.8	11.9	2.68	0.026
Calluna dead				
Drought vs No-drought in BM	-2.4	1.3	-1.87	0.189
Drought vs No-drought in GT	-5.8	3.5	-1.63	0.301
GT vs BM in Drought	12.9	8.7	1.48	0.385
GT vs BM in No-drought	9.6	8.6	1.11	0.627
Moss and litter layer				
Drought vs No-drought in BM	-258.2	38.2	-6.76	<0.001
Drought vs No-drought in GT	-154.7	30.7	-5.04	<0.001
GT vs BM in Drought	-98.5	67.7	-1.45	0.409
GT vs BM in No-drought	5.0	67.4	0.07	1.000
Soil				
Drought vs No-drought in BM	-16.1	8.3	-1.95	0.161
Drought vs No-drought in GT	-30.4	8.4	-3.63	<0.001
GT vs BM in Drought	-136.5	25.4	-5.38	<0.001
GT vs BM in No-drought	-150.7	25.4	-5.94	<0.001

C.3 Fire intensity and fire severity models

Table C.7: Details of the linear mixed effects model investigating differences in burnt branch tip diameter between sites (Glen Tanar and Braehead Moss), and treatments ("Tr": no-drought and drought). R^2 marginal was 0.57 and R^2 conditional, 0.79.

	Value	Std.Error	DF	t-value	p-value
(Intercept)	3.540	0.151	54	23.44	<0.001
Site(BM)	-1.360	0.219	17	-6.20	<0.001
Tr(No-drought)	-0.561	0.121	54	-4.62	<0.001
Site(BM) : Tr(No-drought)	0.364	0.178	54	2.05	0.046

Table C.8: Multiple comparison tests examining differences in burnt branch tip diameter between levels of treatment (no-drought or drought) within the same site (Glen Tanar or Braehead Moss) and between sites within the same treatment. See Table C.7 for model details.

Comparison	Estimate	Std. Error	z-value	p-value
Drought vs No-drought in GT	-0.561	0.12	-4.62	<0.001
Drought vs No-drought in BM	-0.196	0.13	-1.51	0.379
GT vs BM in Drought	-1.360	0.22	-6.20	<0.001
GT vs BM in No-drought	-0.995	0.22	-4.51	<0.001

Table C.9: Details of the linear mixed effects model investigating differences in M/L layer consuption between sites (Glen Tanar and Braehead Moss), and treatments ("Tr": no-drought and drought). R^2 marginal was 0.50 and R^2 conditional, 0.97.

	Value	Std.Error	DF	t-value	p-value
(Intercept)	2.306	0.388	54	5.95	<0.001
Site(BM)	-0.860	0.563	17	-1.53	0.145
Tr(No-drought)	-1.623	0.295	54	-5.49	<0.001
Site(BM) : Tr(No-drought)	0.310	0.429	54	0.72	0.473

Table C.10: Multiple comparison tests examining differences in fire-induced M/L layer consumption between levels of treatment (no-drought or drought) within the same site (Glen Tanar or Braehead Moss) and between sites within the same treatment. See Table C.9 for model details.

Comparison	Estimate	Std. Error	z-value	p-value
Drought vs No-drought in GT	-1.623	0.30	-5.49	<0.001
Drought vs No-drought in BM	-1.312	0.31	-4.21	<0.001
GT vs BM in Drought	-0.860	0.56	-1.53	0.361
GT vs BM in No-drought	-0.550	0.38	-1.46	0.397

Table C.11: Details of linear mixed effects models investigating the effect the interaction between site (Glen Tanar and Braehead Moss) and treatment ("Tr": unburnt, no-drought and drought) on different temperature metrics, at the soil surface or 2 cm below.

	Value	Std.Error	DF	t-value	p-value	R^2m	R^2c
	log(Total heat (°C.s)), 2 cm depth						
Intercept	9.56	0.38	47	25.47	<0.001	0.41	0.69
Site(BM)	-1.96	0.55	17	-3.58	0.002		
Tr(No-drought)	-1.26	0.32	47	-3.92	<0.001		
Site(BM) : Tr(No-drought)	0.07	0.48	47	0.15	0.880		
	log(Total heat (°C.s)), soil surface						
Intercept	10.69	0.34	49	31.16	<0.001	0.52	0.69
Site(BM)	-1.84	0.51	17	-3.58	0.002		
Tr(No-drought)	-1.23	0.34	49	-3.63	<0.001		
Site(BM) : Tr(No-drought)	-0.82	0.53	49	-1.55	0.126		

	log(Maximum T (°C)), 2 cm depth						
Intercept	2.94	0.16	50	18.07	<0.001	0.35	0.90
Site(BM)	-0.65	0.23	17	-2.82	0.012		
Tr(No-drought)	-0.49	0.12	50	-4.17	<0.001		
Site(BM) : Tr(No-drought)	0.35	0.16	50	2.11	0.040		
	log(Maximum T (°C)), soil surface						
Intercept	4.24	0.27	53	15.47	<0.001	0.59	0.80
Site(BM)	-1.64	0.40	17	-4.08	<0.001		
Tr(No-drought)	-1.11	0.25	53	-4.37	<0.001		
Site(BM) : Tr(No-drought)	0.77	0.38	53	2.06	0.045		
	log(t above 50°C), 2 cm depth						
Intercept	-2.15	0.61	51	-3.53	<0.001	0.16	0.29
Site(BM)	-2.46	0.86	17	-2.85	0.011		
Tr(No-drought)	-2.48	0.73	51	-3.37	0.001		
Site(BM) : Tr(No-drought)	2.48	1.05	51	2.35	0.023		
	log(t above 50°C), soil surface						
Intercept	0.96	0.91	53	1.06	0.293	0.30	0.49
Site(BM)	-5.57	1.33	17	-4.19	<0.001		
Tr(No-drought)	-4.07	0.97	53	-4.22	<0.001		
Site(BM) : Tr(No-drought)	4.07	1.43	53	2.85	0.006		
	log(Heating slopes (λ)), 2 cm depth						
Intercept	-5.04	1.20	51	-4.18	<0.001	0.36	0.62
Site(BM)	-3.89	1.72	17	-2.26	0.037		
Tr(No-drought)	-1.89	1.11	51	-1.70	0.096		
Site(BM) : Tr(No-drought)	-3.08	1.60	51	-1.93	0.059		
	log(Heating slopes (λ)), soil surface						
Intercept	-2.11	0.97	53	-2.18	0.034	0.46	0.54
Site(BM)	-3.76	1.43	17	-2.63	0.018		
Tr(No-drought)	0.42	1.19	53	0.35	0.727		
Site(BM) : Tr(No-drought)	-5.58	1.75	53	-3.18	0.002		
	log(Cooling slopes (λ)), 2 cm depth						
Intercept	-7.96	0.93	49	-8.54	<0.001	0.34	0.52
Site(BM)	-6.12	1.30	17	-4.70	<0.001		
Tr(No-drought)	-3.11	1.00	49	-3.11	0.003		
Site(BM) : Tr(No-drought)	3.11	1.41	49	2.20	0.032		
	log(Cooling slopes (λ)), soil surface						
Intercept	-3.27	1.09	53	-3.01	0.004	0.37	0.43
Site(BM)	-6.51	1.60	17	-4.07	<0.001		

Tr(No-drought)	-3.04	1.38	53	-2.21	0.031
Site(BM) : Tr(No-drought)	0.35	2.04	53	0.17	0.866

Table C.12: Multiple comparison tests examining differences in temperature metrics at the soil surface or 2 cm below between levels of treatment (no-drought and drought) within the same site (Glen Tanar and Braehead Moss) and between sites within the same treatment. The linear mixed effects models tested the effect of the interaction between treatment and site on temperature metrics (see Table C.11).

Comparison	Estimate	Std. Error	z-value	p-value
log(Total heat (°C.s)), 2 cm depth				
Drought vs No-drought in GT	-1.262	0.322	-3.916	<0.001
Drought vs No-drought in BM	-1.189	0.358	-3.321	0.004
GT vs BM in Drought	-1.956	0.546	-3.584	0.001
GT vs BM in No-drought	-1.883	0.547	-3.442	0.002
log(Total heat (°C.s)), soil surface				
Drought vs No-drought in GT	-1.227	0.338	-3.633	0.001
Drought vs No-drought in BM	-2.044	0.403	-5.076	<0.001
GT vs BM in Drought	-1.838	0.513	-3.581	0.001
GT vs BM in No-drought	-2.655	0.516	-5.144	<0.001
log(Maximum T (°C)), 2 cm depth				
Drought vs No-drought in GT	-0.489	0.117	-4.172	<0.001
Drought vs No-drought in BM	-0.142	0.115	-1.240	0.544
GT vs BM in Drought	-0.654	0.232	-2.824	0.017
GT vs BM in No-drought	-0.307	0.180	-1.706	0.267
log(Maximum T (°C)), soil surface				
Drought vs No-drought in GT	-1.109	0.254	-4.368	<0.001
Drought vs No-drought in BM	-0.337	0.276	-1.219	0.561
GT vs BM in Drought	-1.643	0.403	-4.078	<0.001
GT vs BM in No-drought	-0.872	0.254	-3.431	0.002
t above 50°C, 2 cm depth				
Drought vs No-drought in GT	-2.476	0.735	-3.371	0.003
Drought vs No-drought in BM	0.000	0.755	0.000	1.000
GT vs BM in Drought	-2.459	0.863	-2.851	0.017
GT vs BM in No-drought	0.017	0.864	0.020	1.000
log(t above 50°C), soil surface				

Drought vs No-drought in GT	-4.071	0.965	-4.217	<0.001
Drought vs No-drought in BM	-0.000	1.053	-0.000	1.000
GT vs BM in Drought	-5.567	1.330	-4.187	<0.001
GT vs BM in No-drought	-1.497	1.330	-1.126	0.626
log(Heating slopes (λ)), 2 cm depth				
Drought vs No-drought in GT	-1.889	1.113	-1.697	0.276
Drought vs No-drought in BM	-4.971	1.144	-4.343	<0.001
GT vs BM in Drought	-3.893	1.725	-2.257	0.085
GT vs BM in No-drought	-6.975	1.726	-4.040	<0.001
log(Heating slopes (λ)), soil surface				
Drought vs No-drought in GT	0.417	1.187	0.352	0.981
Drought vs No-drought in BM	-5.158	1.291	-3.994	<0.001
GT vs BM in Drought	-3.757	1.428	-2.631	0.032
GT vs BM in No-drought	-9.333	1.428	-6.536	<0.001
log(Cooling slopes (λ)), 2 cm depth				
Drought vs No-drought in GT	-3.115	1.003	-3.107	0.007
Drought vs No-drought in BM	-0.000	0.996	-0.000	1.000
GT vs BM in Drought	-6.122	1.304	-4.695	<0.001
GT vs BM in No-drought	-3.008	1.280	-2.350	0.067
log(Cooling slopes (λ)), soil surface				
Drought vs No-drought in GT	-3.044	1.378	-2.209	0.094
Drought vs No-drought in BM	-2.699	1.498	-1.801	0.225
GT vs BM in Drought	-6.512	1.599	-4.073	<0.001
GT vs BM in No-drought	-6.167	1.599	-3.857	<0.001

C.4 Post-fire M/L layer thickness

Table C.13: Details of the linear mixed effects model investigating differences in post-fire M/L thickness above the soil temperature loggers between sites (Glen Tanar and Braehead Moss), and treatments ("Tr": unburnt, no-drought and drought). A constant variance function was used for site. R^2 marginal was 0.29 and R^2 conditional, 0.44.

	Value	Std.Error	DF	t-value	p-value
(Intercept)	4.900	0.683	20	7.17	<0.001
Site(BM)	0.743	1.245	10	0.60	0.564
Tr(No-drought)	-1.500	0.541	20	-2.77	0.012
Tr(Drought)	-3.900	0.541	20	-7.21	<0.001
Site(BM) : Tr(No-drought)	0.571	1.414	20	0.40	0.690
Site(BM) : Tr(Drought)	4.900	1.414	20	3.46	0.002

Table C.14: Multiple comparisons of differences in post-fire thickness of the M/L layer above the soil temperature loggers between sites (Glen Tanar and Braehead Moss) and treatments (unburnt, no-drought and drought).

	Estimate	Std. Error	z-value	p-value
GT:nodrought - unburnt	-1.50	0.54	-2.77	0.03
GT:drought - unburnt	-3.90	0.54	-7.21	0.00
GT:drought - nodrought	-2.40	0.54	-4.44	0.00
BM:nodrought - unburnt	-0.93	1.31	-0.71	0.94
BM:drought - unburnt	1.00	1.31	0.77	0.92
BM:drought - nodrought	1.93	1.31	1.48	0.51

C.5 Post-fire soil thermal dynamics models

Table C.15: Details of the mean daily temperature and daily temperature range harmonic models for unburnt, no-drought and drought plots, at Glen Tanar and Braehead Moss.

Site	Response	Treatment	DF	R^2m	R^2c	Fixed effects	t-value	p-value
GT	MDT	Unburnt	1503	0.91	0.91	Intercept	66.48	<0.001
						cos	-11.94	<0.001
						sin	-34.45	<0.001
		No-drought	1345	0.90	0.90	Intercept	55.16	<0.001
						cos	-16.95	<0.001
						sin	-32.37	<0.001
		Drought	1503	0.88	0.88	Intercept	60.50	<0.001
						cos	-19.64	<0.001
						sin	-34.65	<0.001
	DTR	Unburnt	1503	0.35	0.38	Intercept	16.06	<0.001
						cos	-17.40	<0.001
						sin	-4.79	<0.001
		No-drought	1345	0.45	0.55	Intercept	8.25	<0.001
						cos	-18.22	<0.001
						sin	-12.62	<0.001
		Drought	1503	0.52	0.55	Intercept	14.52	<0.001
						cos	-24.15	<0.001
						sin	-14.38	<0.001
BM	MDT	Unburnt	1501	0.92	0.92	Intercept	83.92	<0.001
						cos	-18.34	<0.001
						sin	-37.55	<0.001
		No-drought	1583	0.91	0.91	Intercept	80.48	<0.001
						cos	-19.63	<0.001
						sin	-37.76	<0.001
		Drought	1501	0.91	0.91	Intercept	70.30	<0.001
						cos	-18.44	<0.001
						sin	-34.42	<0.001
	DTR	Unburnt	1501	0.17	0.42	Intercept	6.46	<0.001
						cos	-13.21	<0.001
						sin	-4.78	<0.001
		No-drought	1583	0.10	0.58	Intercept	4.25	<0.001

				cos	-11.21	<0.001
				sin	-5.16	<0.001
Drought	1501	0.18	0.43	Intercept	7.30	<0.001
				cos	-12.76	<0.001
				sin	-7.10	<0.001

Table C.16: Average amplitude and phase of modelled sinusoidal post-fire soil thermal dynamics. Variance in parentheses. Same letters within treatment and column indicate non-statistically significant differences between sites ($\alpha = 0.05$).

	Mean Daily Temperature		Daily Temperature Range	
	Amplitude	Phase	Amplitude	Phase
		Unburnt		
Glen Tanar	4.49 (0.015) a	162 (3.39) a	0.90 (0.0025) a	105 (181) a
Braehead Moss	5.09 (0.015) b	157 (2.19) a	0.82 (0.0034) a	112 (134) a
		No-drought		
Glen Tanar	5.60 (0.024) a	153 (3.74) a	2.42 (0.012) a	125 (24.4) a
Braehead Moss	5.60 (0.017) a	156 (2.07) a	1.03 (0.007) b	118 (110) a
		Drought		
Glen Tanar	5.78 (0.021) a	150 (3.42) a	3.85 (0.019) a	120 (20.4) a
Braehead Moss	5.80 (0.022) a	155 (2.60) a	1.04 (0.0051) b	121 (66.4) a

C.6 Models of growing degree hours

Glen Tanar

Table C.17: Details of the linear mixed effects model investigating the effect of the interaction between season ("Se": spring, summer, autumn and winter), and treatment ("Tr": unburnt, no-drought and drought) on daily average growing degree hours at Glen Tanar.

	Value	Std.Error	DF	t-value	p-value
(Intercept)	3.009	0.520	43	5.79	<0.001
Se(Spring)	54.733	6.543	43	8.36	<0.001
Se(Summer)	187.769	3.989	43	47.07	<0.001
Se(Autumn)	163.794	10.970	43	14.93	<0.001
Tr(No-drought)	-1.185	0.704	43	-1.68	0.100
Tr(Drought)	-0.461	0.704	43	-0.65	0.516
Se(Spring) : Tr(No-drought)	22.090	9.254	43	2.39	0.021
Se(Summer) : Tr(No-drought)	44.020	5.979	43	7.36	<0.001
Se(Autumn) : Tr(No-drought)	2.193	15.514	43	0.14	0.888
Se(Spring) : Tr(Drought)	35.010	9.254	43	3.78	<0.001
Se(Summer) : Tr(Drought)	48.127	5.642	43	8.53	<0.001
Se(Autumn) : Tr(Drought)	18.902	15.514	43	1.22	0.230

Table C.18: Multiple comparisons of differences in daily growing degree hours between treatment levels within each season at Glen Tanar.

	Estimate	Std. Error	z-value	p-value
winter:nodrought - unburnt	-1.18	0.70	-1.68	0.61
winter:drought - unburnt	-0.46	0.70	-0.65	1.00
winter:drought - nodrought	0.72	0.70	1.03	0.96
spring:nodrought - unburnt	20.90	9.23	2.27	0.22
spring:drought - unburnt	34.55	9.23	3.74	0.00
spring:drought - nodrought	13.64	9.23	1.48	0.76
summer:nodrought - unburnt	42.83	5.94	7.21	0.00
summer:drought - unburnt	47.67	5.60	8.52	0.00
summer:drought - nodrought	4.83	5.94	0.81	0.99
autumn:nodrought - unburnt	1.01	15.50	0.07	1.00
autumn:drought - unburnt	18.44	15.50	1.19	0.91
autumn:drought - nodrought	17.43	15.50	1.12	0.94

Braehead Moss

Table C.19: Details of the linear mixed effects model investigating the effect of the interaction between season ("Se": spring, summer, autumn and winter), and treatment ("Tr": unburnt, no-drought and drought) on daily average growing degree hours at Braehead Moss.

	Value	Std.Error	DF	t-value	p-value
(Intercept)	17.808	2.791	60	6.38	<0.001
Se(Spring)	83.845	4.078	60	20.56	<0.001
Se(Summer)	215.705	6.817	60	31.64	<0.001
Se(Autumn)	158.290	19.650	60	8.06	<0.001
Tr(No-drought)	-4.735	2.221	60	-2.13	0.037
Tr(Drought)	-6.252	2.366	60	-2.64	0.010
Se(Spring) : Tr(No-drought)	4.190	5.659	60	0.74	0.462
Se(Summer) : Tr(No-drought)	17.142	9.576	60	1.79	0.078
Se(Autumn) : Tr(No-drought)	7.723	27.767	60	0.28	0.782
Se(Spring) : Tr(Drought)	12.616	5.717	60	2.21	0.031
Se(Summer) : Tr(Drought)	24.927	9.610	60	2.59	0.012
Se(Autumn) : Tr(Drought)	21.566	28.901	60	0.75	0.458

Table C.20: Multiple comparisons of differences in daily growing degree hours between treatment levels within each season at Braehead Moss.

	Estimate	Std. Error	z-value	p-value
winter:nodrought - unburnt	-4.73	2.22	-2.13	0.29
winter:drought - unburnt	-6.25	2.37	-2.64	0.09
winter:drought - nodrought	-1.52	2.22	-0.68	1.00
spring:nodrought - unburnt	-0.54	5.20	-0.10	1.00
spring:drought - unburnt	6.36	5.20	1.22	0.90
spring:drought - nodrought	6.91	5.20	1.33	0.85
summer:nodrought - unburnt	12.41	9.31	1.33	0.85
summer:drought - unburnt	18.67	9.31	2.00	0.38
summer:drought - nodrought	6.27	9.31	0.67	1.00
autumn:nodrought - unburnt	2.99	27.68	0.11	1.00
autumn:drought - unburnt	15.31	28.81	0.53	1.00
autumn:drought - nodrought	12.33	28.81	0.43	1.00

Appendix D

Chapter 6

D.1 Gas flux sampling

Table D.1: Gas flux sampling effort, including the date the sampling was made, site (Glen Tanar and Braehead Moss), the gas analyser used (Los Gatos Research Ultra-Portable GHG analyser and Vaisala GMP343 Carbon Dioxide Probe), number of plots sampled, average air temperature and relative humidity in the chamber and average photosynthetic active radiation during deployments.

Date	Site	Instrument	Plots	Air T (°C)	RH (%)	PAR (μmol m^{-2} s^{-1})
2014-08-23	GT	Los Gatos	20	14.7	79	816
2014-08-24	GT	Los Gatos	15	19.8	64	799
2014-08-26	BM	Los Gatos	20	26.0	64	1193
2014-08-27	BM	Los Gatos	10	24.1	53	1217
2014-11-27	GT	Los Gatos	5	4.9	99	20
2014-11-28	GT	Los Gatos	10	6.2	99	61
2015-04-04	BM	Los Gatos	23	14.8	83	582
2015-04-05	BM	Los Gatos	19	22.7	68	1127
2015-04-18	GT	Los Gatos	23	26.5	40	1207
2015-04-21	GT	Los Gatos	13	25.9	38	1415
2015-06-27	BM	Vaisala	30	20.7	81	663
2015-06-28	BM	Vaisala	14	19.6	92	1114
2015-07-03	GT	Vaisala	18	26.5	68	1811
2015-07-04	GT	Vaisala	19	19.5	85	566
2015-08-09	BM	Vaisala	28	18.8	85	466
2015-08-10	BM	Vaisala	15	19.7	90	570
2015-08-15	GT	Vaisala	19	15.2	91	533
2015-08-16	GT	Vaisala	17	17.4	80	804
2015-09-24	GT	Vaisala	33	13.0	79	916
2015-10-09	BM	Vaisala	24	14.8	89	427
2015-10-10	BM	Vaisala	20	13.5	93	381

D.2 Long closure test

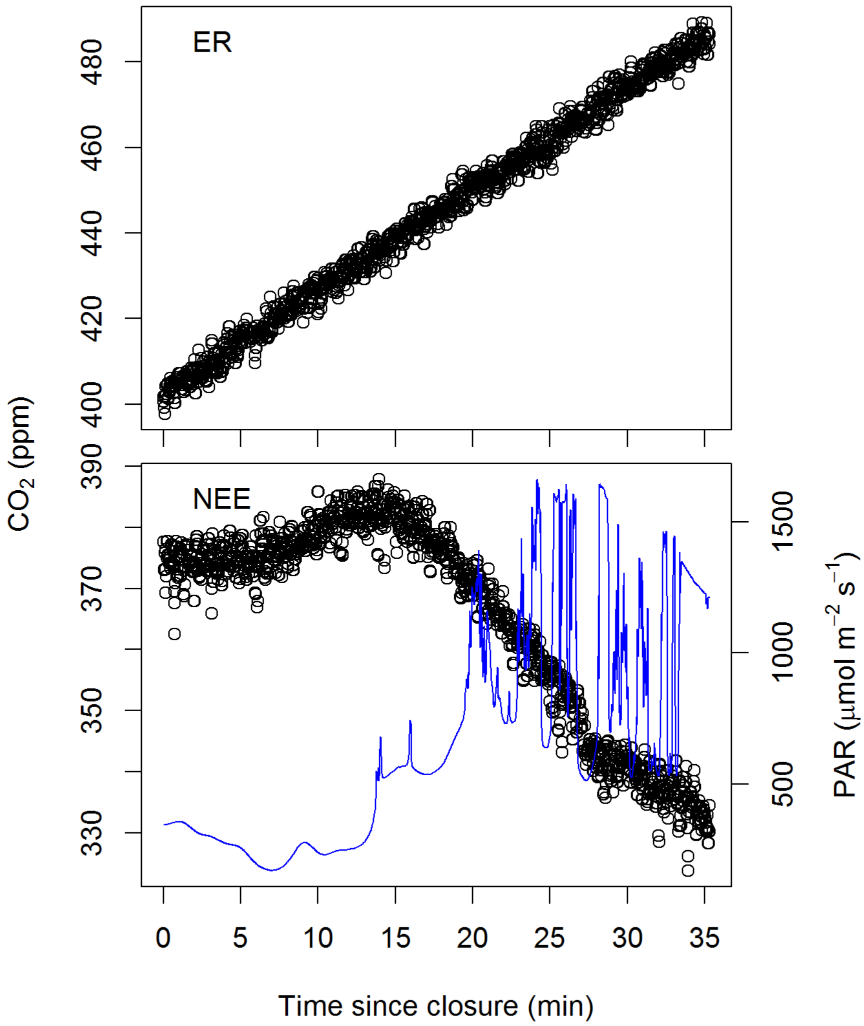

Figure D.1: CO_2 concentration during two long closure deployments: one using a covered chamber (ecosystem respiration, ER, top plot, showing a linear increase in CO_2 concentration with time) and the other one with the uncovered clear chamber (net ecosystem exchange, NEE, bottom plot). Both measurements were completed in the same unburnt plot in Braehead Moss using a Vaisala probe, in October 2015 (ER) and August 2015 (NEE). Photosynthetically active radiation (PAR, blue line) was included in the NEE plot to illustrate its effect on the balance between respiratory and assimilatory CO_2 processes.

D.3 Post-fire vegetation cover

Table D.2: Details of the linear mixed effects model investigating the effect of the interaction between site (Glen Tanar and Braehead Moss), and treatment ("Tr": unburnt, no-drought and drought) on cover of vegetation in gas flux collars. Separate models were fitted to each broad plant functional type / substrate cover. Fire was included as a random effect.

	Value	Std.Error	DF	t-value	p-value	R^2m	R^2c
			Shrub				
(Intercept)	1.476	0.62	69	2.37	0.020	0.33	0.41
Tr(No-drought)	0.267	0.66	69	0.41	0.686		
Tr(Drought)	0.440	0.67	69	0.66	0.512		
Site(BM)	1.841	0.84	69	2.19	0.032		
Tr(No-drought) : Site(BM)	-2.955	0.91	69	-3.26	0.002		
Tr(Drought) : Site(BM)	-2.470	0.92	69	-2.69	0.009		
			Graminoid				
(Intercept)	-0.741	0.82	69	-0.90	0.371	0.06	0.20
Tr(No-drought)	0.238	0.91	69	0.26	0.794		
Tr(Drought)	-0.227	0.91	69	-0.25	0.804		
Site(BM)	0.411	1.07	69	0.38	0.703		
Tr(No-drought) : Site(BM)	0.559	1.25	69	0.45	0.657		
Tr(Drought) : Site(BM)	0.667	1.26	69	0.53	0.597		
			Bryophyte				
(Intercept)	4.374	0.10	69	42.32	<0.001	0.47	0.48
Tr(No-drought)	-3.590	0.40	69	-9.08	<0.001		
Tr(Drought)	-4.248	0.40	69	-10.54	<0.001		
Site(BM)	-0.052	0.12	69	-0.42	0.677		
Tr(No-drought) : Site(BM)	1.864	0.55	69	3.39	0.001		
Tr(Drought) : Site(BM)	2.120	0.55	69	3.82	<0.001		
			Litter				
(Intercept)	1.694	0.49	69	3.43	0.001	0.57	0.58
Tr(No-drought)	2.166	0.54	69	4.02	<0.001		
Tr(Drought)	-0.661	0.79	69	-0.84	0.403		
Site(BM)	0.934	0.68	69	1.38	0.172		
Tr(No-drought) : Site(BM)	-1.252	0.74	69	-1.69	0.096		
Tr(Drought) : Site(BM)	0.527	1.08	69	0.49	0.627		

			Duff				
(Intercept)	-0.698	0.76	69	-0.92	0.360	0.33	0.41
Tr(No-drought)	3.490	0.89	69	3.94	<0.001		
Tr(Drought)	4.302	0.83	69	5.21	<0.001		
Site(BM)	0.454	0.99	69	0.46	0.647		
Tr(No-drought) : Site(BM)	-2.214	1.22	69	-1.81	0.075		
Tr(Drought) : Site(BM)	-0.620	1.13	69	-0.55	0.587		

Table D.3: Multiple comparisons of vegetation cover in gas flux collars between treatment levels within levels of season. See Table D.2 for model details.

	Estimate	Std.Error	z-value	p-value
		Shrub		
GT:nodrought - unburnt	0.267	0.66	0.41	0.992
GT:drought - unburnt	0.440	0.67	0.66	0.952
GT:drought - nodrought	0.173	0.37	0.47	0.986
BM:nodrought - unburnt	-2.688	0.62	-4.31	<0.001
BM:drought - unburnt	-2.030	0.63	-3.22	0.007
BM:drought - nodrought	0.658	0.35	1.86	0.269
		Graminoid		
GT:nodrought - unburnt	0.238	0.91	0.26	0.999
GT:drought - unburnt	-0.227	0.91	-0.25	0.999
GT:drought - nodrought	-0.465	0.68	-0.69	0.946
BM:nodrought - unburnt	0.797	0.86	0.92	0.858
BM:drought - unburnt	0.440	0.86	0.51	0.982
BM:drought - nodrought	-0.357	0.65	-0.55	0.976
		Bryophyte		
GT:nodrought - unburnt	-3.590	0.40	-9.08	<0.001
GT:drought - unburnt	-4.248	0.40	-10.54	<0.001
GT:drought - nodrought	-0.658	0.55	-1.20	0.690
BM:nodrought - unburnt	-1.726	0.38	-4.51	<0.001
BM:drought - unburnt	-2.128	0.38	-5.60	<0.001
BM:drought - nodrought	-0.403	0.53	-0.76	0.919
		Litter		
GT:nodrought - unburnt	2.166	0.54	4.02	<0.001
GT:drought - unburnt	-0.661	0.79	-0.84	0.891

GT:drought - nodrought	-2.827	0.65	-4.34	<0.001
BM:nodrought - unburnt	0.914	0.51	1.79	0.306
BM:drought - unburnt	-0.134	0.74	-0.18	1.000
BM:drought - nodrought	-1.048	0.62	-1.70	0.358
Duff				
GT:nodrought - unburnt	3.490	0.89	3.94	<0.001
GT:drought - unburnt	4.302	0.83	5.21	<0.001
GT:drought - nodrought	0.811	0.67	1.21	0.693
BM:nodrought - unburnt	1.276	0.84	1.51	0.485
BM:drought - unburnt	3.682	0.78	4.73	<0.001
BM:drought - nodrought	2.406	0.65	3.72	0.001

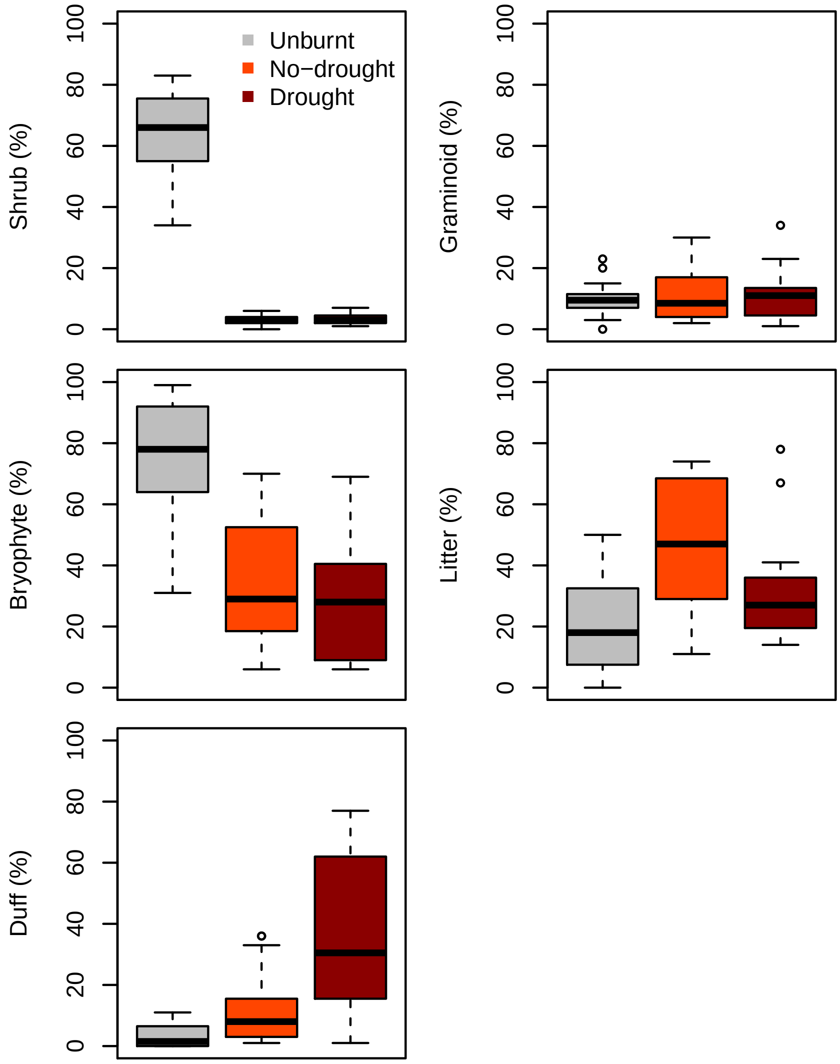

Figure D.2: Post-fire vegetation cover in Braehead Moss plots, for each treatment (unburnt, no-drought and drought). Number of observations was 16 in all treatments within each vegetation type. Differences between treatments were similar to those found in gas flux collars (Figure 6.3).

D.4 Predicted soil temperature models

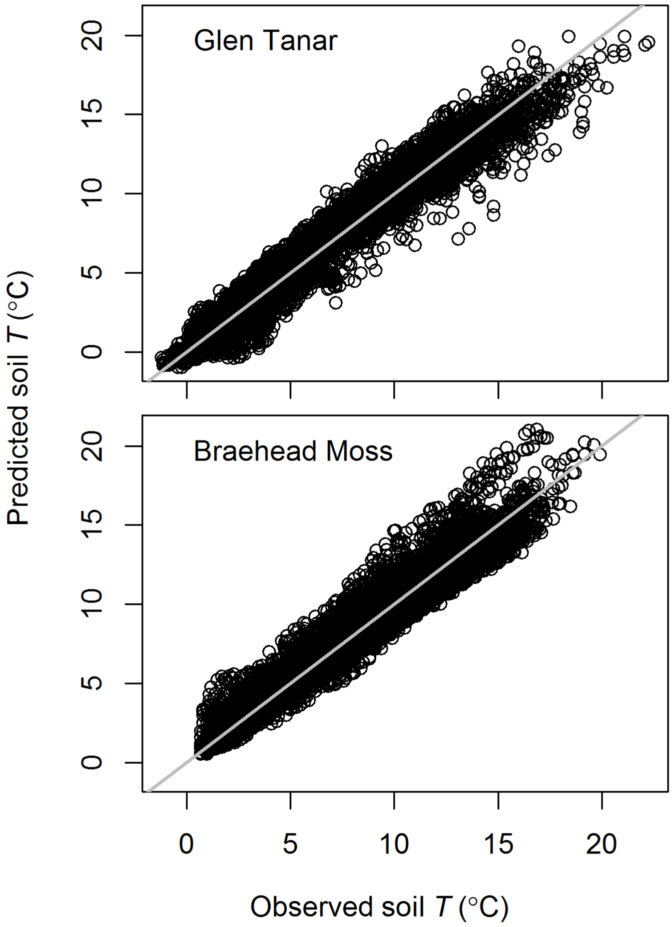

Figure D.3: Observed against predicted soil temperatures at Glen Tanar (top) and at Braehead Moss (bottom). The linear model used to predict soil values included an interaction between soil temperature at 10 cm recorded at a nearby weather station (Aboyne for Glen Tanar and Drumalbin for Braehead Moss), hour of the day (only even hours were used, as soil temperature was recorded bi-hourly from 00:00) and treatment (drought / no-drought / unburnt plots). R^2 was 0.96 for Glen Tanar and 0.94 for Braehead Moss. In grey, the line of perfect agreement.

D.5 Soil temperature vs air temperature

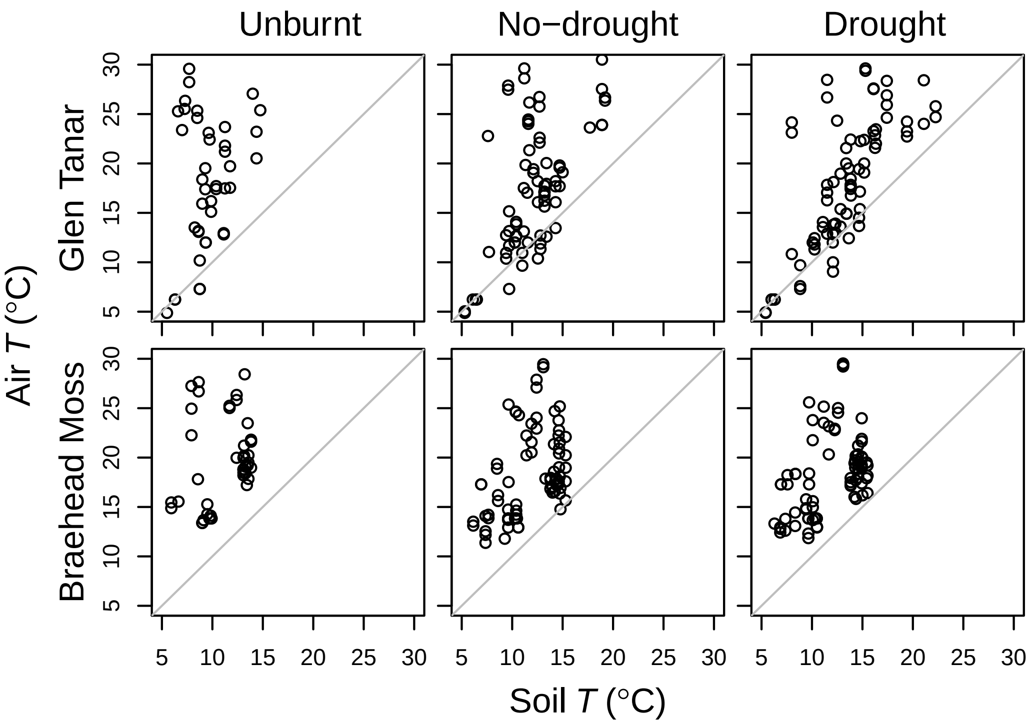

Figure D.4: Comparison of soil temperature against air temperature inside the gas flux chamber during ER measurements, showing larger differences between air and soil temperature in unburnt plots. Line indicates perfect agreement.

D.6 Soil moisture content and water table

Table D.4: Details of the linear mixed effects models investigating the effect of the interaction between season ("Se": spring, summer and autumn), and treatment ("Tr": unburnt, no-drought and drought) on soil moisture content. Separate models were fitted for the different sites (Glen Tanar and Braehead Moss). Plot within fire was included as a random effect. R^2 marginal and R^2 conditional were 0.16 and 0.74 (Glen Tanar) and 0.13 and 0.66 (Braehead Moss).

	Value	Std.Error	DF	t-value	p-value
	Glen Tanar				
(Intercept)	270.081	7.32	337	36.87	<0.001
Se(Summer)	5.051	2.75	337	1.84	0.067
Se(Autumn)	12.427	3.36	337	3.70	<0.001
Tr(No-drought)	-8.229	5.40	30	-1.53	0.138
Tr(Drought)	-21.649	5.29	30	-4.10	<0.001
Se(Summer) : Tr(No-drought)	15.075	3.53	337	4.27	<0.001
Se(Autumn) : Tr(No-drought)	14.603	4.26	337	3.43	<0.001
Se(Summer) : Tr(Drought)	18.434	3.38	337	5.45	<0.001
Se(Autumn) : Tr(Drought)	21.987	4.14	337	5.32	<0.001
	Braehead Moss				
(Intercept)	339.904	2.65	352	128.10	<0.001
Se(Summer)	-8.010	1.59	352	-5.03	<0.001
Se(Autumn)	-10.517	1.88	352	-5.59	<0.001
Tr(No-drought)	-6.848	2.94	33	-2.33	0.026
Tr(Drought)	-3.764	2.91	33	-1.29	0.205
Se(Summer) : Tr(No-drought)	1.746	1.95	352	0.90	0.370
Se(Autumn) : Tr(No-drought)	5.255	2.31	352	2.27	0.024
Se(Summer) : Tr(Drought)	0.494	1.93	352	0.26	0.799
Se(Autumn) : Tr(Drought)	4.441	2.29	352	1.94	0.053

Table D.5: Multiple comparisons of soil moisture content between treatment levels within levels of season. See Table D.4 for model details.

	Estimate	Std.Error	z-value	p-value
Glen Tanar				
spring:nodrought - unburnt	-8.23	5.40	-1.53	0.482
spring:drought - unburnt	-21.65	5.29	-4.10	<0.001
spring:drought - nodrought	-13.42	4.45	-3.02	0.018
summer:nodrought - unburnt	6.85	5.35	1.28	0.648
summer:drought - unburnt	-3.22	5.34	-0.60	0.977
summer:drought - nodrought	-10.06	4.40	-2.29	0.121
autumn:nodrought - unburnt	6.37	5.88	1.08	0.776
autumn:drought - unburnt	0.34	5.84	0.06	1.000
autumn:drought - nodrought	-6.04	4.84	-1.25	0.670
Braehead Moss				
spring:nodrought - unburnt	-6.85	2.94	-2.33	0.111
spring:drought - unburnt	-3.76	2.91	-1.29	0.638
spring:drought - nodrought	3.08	2.40	1.28	0.643
summer:nodrought - unburnt	-5.10	2.61	-1.96	0.239
summer:drought - unburnt	-3.27	2.58	-1.27	0.655
summer:drought - nodrought	1.83	2.14	0.85	0.898
autumn:nodrought - unburnt	-1.59	2.89	-0.55	0.984
autumn:drought - unburnt	0.68	2.86	0.24	1.000
autumn:drought - nodrought	2.27	2.37	0.96	0.848

Table D.6: Details of the linear mixed effects model investigating the effect of the interaction between season ("Se": winter, spring, summer and autumn), and treatment ("Tr": unburnt, no-drought and drought) on water table detph at Braehead Moss. Plot within fire was included as a random effect. R^2 marginal was 0.02 and R^2 conditional was 0.44.

	Value	Std.Error	DF	t-value	p-value
(Intercept)	-16.876	3.365	530	-5.01	<0.001
Se(Spring)	-1.294	3.204	530	-0.40	0.686
Se(Summer)	-2.140	3.090	530	-0.69	0.489
Se(Autumn)	-5.783	3.112	530	-1.86	0.064
Tr(No-drought)	1.921	3.997	38	0.48	0.634
Tr(Drought)	-1.971	3.997	38	-0.49	0.625
Se(Spring) : Tr(No-drought)	1.613	3.808	530	0.42	0.672
Se(Summer) : Tr(No-drought)	1.204	3.663	530	0.33	0.743
Se(Autumn) : Tr(No-drought)	1.972	3.679	530	0.54	0.592
Se(Spring) : Tr(Drought)	4.938	3.808	530	1.30	0.195
Se(Summer) : Tr(Drought)	5.213	3.663	530	1.42	0.155
Se(Autumn) : Tr(Drought)	6.657	3.679	530	1.81	0.071

Table D.7: Multiple comparisons of water table values between treatment levels within levels of season. See Table D.6 for model details.

	Estimate	Std. Error	z-value	p-value
Winter:No-drought - Unburnt	1.92	4.00	0.48	1.00
Winter:Drought - Unburnt	-1.97	4.00	-0.49	1.00
Winter:Drought - No-drought	-3.89	3.21	-1.21	0.81
Spring:No-drought - Unburnt	3.53	2.33	1.52	0.61
Spring:Drought - Unburnt	2.97	2.33	1.27	0.77
Spring:Drought - No-drought	-0.57	2.21	-0.26	1.00
Summer:No-drought - Unburnt	3.12	2.07	1.51	0.61
Summer:Drought - Unburnt	3.24	2.07	1.57	0.57
Summer:Drought - No-drought	0.12	2.03	0.06	1.00
Autumn:No-drought - Unburnt	3.89	2.13	1.83	0.39
Autumn:Drought - Unburnt	4.69	2.13	2.20	0.20
Autumn:Drought - No-drought	0.79	2.02	0.39	1.00

D.7 Ecosystem respiration

Table D.8: Summary statistics of ecosystem respiration for different sites, seasons and treatments.

Site	Season	Treatment	Mean (SD)	Min	Max	n
GT	Spring	Unburnt	0.58 (0.29)	0.10	0.99	8
		No-drought	0.51 (0.11)	0.36	0.66	12
		Drought	0.48 (0.21)	0.21	0.85	16
	Summer	Unburnt	1.71 (0.89)	-0.19	3.22	23
		No-drought	1.13 (0.65)	0.33	3.05	42
		Drought	1.22 (0.76)	0.31	3.87	43
	Autumn	Unburnt	0.88 (0.52)	0.10	1.67	10
		No-drought	0.52 (0.32)	-0.12	1.10	18
		Drought	0.87 (0.59)	0.01	2.14	19
BM	Spring	Unburnt	0.85 (0.40)	0.37	1.45	9
		No-drought	0.34 (0.16)	0.12	0.80	16
		Drought	0.37 (0.17)	0.15	0.91	17
	Summer	Unburnt	2.06 (0.86)	0.54	3.57	24
		No-drought	1.15 (0.56)	0.27	2.67	46
		Drought	1.22 (0.82)	0.32	4.73	47
	Autumn	Unburnt	1.53 (0.45)	0.93	2.28	9
		No-drought	0.98 (0.35)	0.57	2.04	17
		Drought	1.07 (0.62)	0.43	3.05	18

Table D.9: Details of the linear mixed effects model investigating the effect of the interaction between season ("Se": Spring, Summer and Autumn), site (Glen Tanar and Braehead Moss) and treatment ("Tr": unburnt, no-drought and drought) on ecosystem respiration. R^2 marginal was 0.27 and R^2 conditional was 0.32.

	Value	Std.Error	DF	t-value	p-value
(Intercept)	0.486	0.091	298	5.362	<0.001
Site(BM)	0.367	0.125	15	2.942	0.010
Tr(No-drought)	0.002	0.108	63	0.017	0.987
Tr(Drought)	-0.005	0.103	63	-0.047	0.963
Se(Spring)	1.235	0.156	298	7.895	<0.001
Se(Summer)	0.431	0.160	298	2.699	0.007
Site(BM) : Tr(No-drought)	-0.529	0.146	63	-3.616	<0.001
Site(BM) : Tr(Drought)	-0.489	0.142	63	-3.451	0.001
Site(BM) : Se(Spring)	-0.033	0.218	298	-0.151	0.880
Site(BM) : Se(Summer)	0.250	0.229	298	1.089	0.277
Tr(No-drought) : Se(Spring)	-0.606	0.197	298	-3.078	0.002
Tr(Drought) : Se(Spring)	-0.527	0.194	298	-2.723	0.007
Tr(No-drought) : Se(Summer)	-0.407	0.201	298	-2.022	0.044
Tr(Drought) : Se(Summer)	-0.081	0.197	298	-0.409	0.683
Site(BM) : Tr(No-drought) : Se(Spring)	0.229	0.272	298	0.840	0.402
Site(BM) : Tr(Drought) : Se(Spring)	0.178	0.270	298	0.660	0.510
Site(BM) : Tr(No-drought) : Se(Summer)	0.350	0.287	298	1.222	0.223
Site(BM) : Tr(Drought) : Se(Summer)	0.114	0.282	298	0.404	0.687

D.8 Variance inflation factor

Table D.10: Variance inflation factors for the different environmental covariates (Table 6.1) before and after removing duff cover.

Duff included		Duff removed	
Variable	VIF	Variable	VIF
Soil.T	1.1	Soil.T	1.1
Soil.MC	1.2	Soil.MC	1.2
PAR	1.1	PAR	1.1
Days.since.fire	1.1	Days.since.fire	1.1
Shrub	1.2	Shrub	1.2
Graminoid	1.9	Graminoid	1.2
Bryophyte	14.4	Bryophyte	1.4
Litter	14.1	Litter	1.2
Duff	17.9		

D.9 Net ecosystem exchange

Table D.11: Summary statistics of net ecosystem exchange for different sites, seasons and treatments.

Site	Season	Treatment	Mean (SD)	Min	Max	n
GT	Spring	Unburnt	0.18 (0.53)	-0.43	1.13	8
		No-drought	0.43 (0.19)	0.01	0.71	12
		Drought	0.54 (0.17)	0.20	0.87	16
	Summer	Unburnt	-0.31 (1.66)	-4.26	2.42	23
		No-drought	0.72 (0.77)	-2.18	2.42	42
		Drought	0.81 (0.72)	-1.50	2.23	43
	Autumn	Unburnt	-0.78 (2.42)	-5.98	1.33	10
		No-drought	0.00 (0.84)	-2.31	0.76	19
		Drought	-0.17 (1.23)	-4.84	1.06	19
BM	Spring	Unburnt	0.18 (0.25)	-0.14	0.58	9
		No-drought	0.20 (0.16)	-0.03	0.56	16
		Drought	0.17 (0.16)	-0.10	0.51	17
	Summer	Unburnt	-0.49 (0.85)	-2.23	0.96	24
		No-drought	0.52 (0.37)	-0.18	1.69	46
		Drought	0.00 (1.32)	-6.28	1.43	47
	Autumn	Unburnt	-0.64 (0.57)	-1.70	0.20	9
		No-drought	0.00 (0.55)	-1.67	0.72	17
		Drought	-0.20 (0.99)	-2.98	0.75	18

Table D.12: Details of the linear mixed effects model investigating the effect of the interaction between season ("Se": Spring, Summer and Autumn), site (Glen Tanar and Braehead Moss) and treatment ("Tr": unburnt, no-drought and drought) on net ecosystem exchange. R^2 marginal was 0.17 and R^2 conditional, 0.22.

	Value	Std.Error	DF	t-value	p-value
(Intercept)	0.185	0.087	299	2.13	0.034
Site(BM)	-0.002	0.119	15	-0.02	0.984
Tr(No-drought)	0.254	0.106	63	2.40	0.019
Tr(Drought)	0.359	0.101	63	3.57	<0.001
Se(Summer)	-0.493	0.201	299	-2.46	0.015
Se(Autumn)	-1.009	0.357	299	-2.83	0.005
Site(BM) : Tr(No-drought)	-0.227	0.143	63	-1.58	0.119
Site(BM) : Tr(Drought)	-0.371	0.139	63	-2.67	0.010
Site(BM) : Se(Summer)	-0.178	0.280	299	-0.63	0.526
Site(BM) : Se(Autumn)	0.185	0.518	299	0.36	0.721
Tr(No-drought) : Se(Summer)	0.774	0.251	299	3.08	0.002
Tr(Drought) : Se(Summer)	0.752	0.248	299	3.03	0.003
Tr(No-drought) : Se(Autumn)	0.548	0.442	299	1.24	0.216
Tr(Drought) : Se(Autumn)	0.287	0.441	299	0.65	0.516
Site(BM) : Tr(No-drought) : Se(Summer)	0.218	0.349	299	0.62	0.533
Site(BM) : Tr(Drought) : Se(Summer)	-0.231	0.346	299	-0.67	0.504
Site(BM) : Tr(No-drought) : Se(Autumn)	0.075	0.641	299	0.12	0.907
Site(BM) : Tr(Drought) : Se(Autumn)	0.166	0.637	299	0.26	0.795

D.10 Methane flux

Table D.13: Summary statistics of methane flux for different sites, seasons and treatments.

Site	Season	Treatment	Mean (SD)	Min	Max	n
GT	Spring	Unburnt	-0.26 (0.86)	-1.66	0.80	8
		No-drought	0.27 (0.38)	-0.39	0.92	12
		Drought	-0.00 (0.34)	-0.58	0.50	16
	Summer	Unburnt	0.10 (0.98)	-1.49	1.87	7
		No-drought	0.48 (0.78)	-0.43	2.56	14
		Drought	0.12 (0.35)	-0.57	0.82	14
	Autumn	Unburnt	1.50 (2.26)	0.17	4.11	3
		No-drought	0.39 (1.04)	-0.21	2.49	6
		Drought	-0.17 (0.34)	-0.75	0.13	6
BM	Spring	Unburnt	0.30 (1.14)	-0.68	2.96	9
		No-drought	2.67 (4.58)	-3.05	15.09	16
		Drought	3.21 (5.51)	0.04	21.36	17
	Summer	Unburnt	1.10 (1.04)	-0.51	1.96	6
		No-drought	22.99 (60.14)	-10.32	211.89	12
		Drought	24.74 (52.13)	-1.36	168.31	12

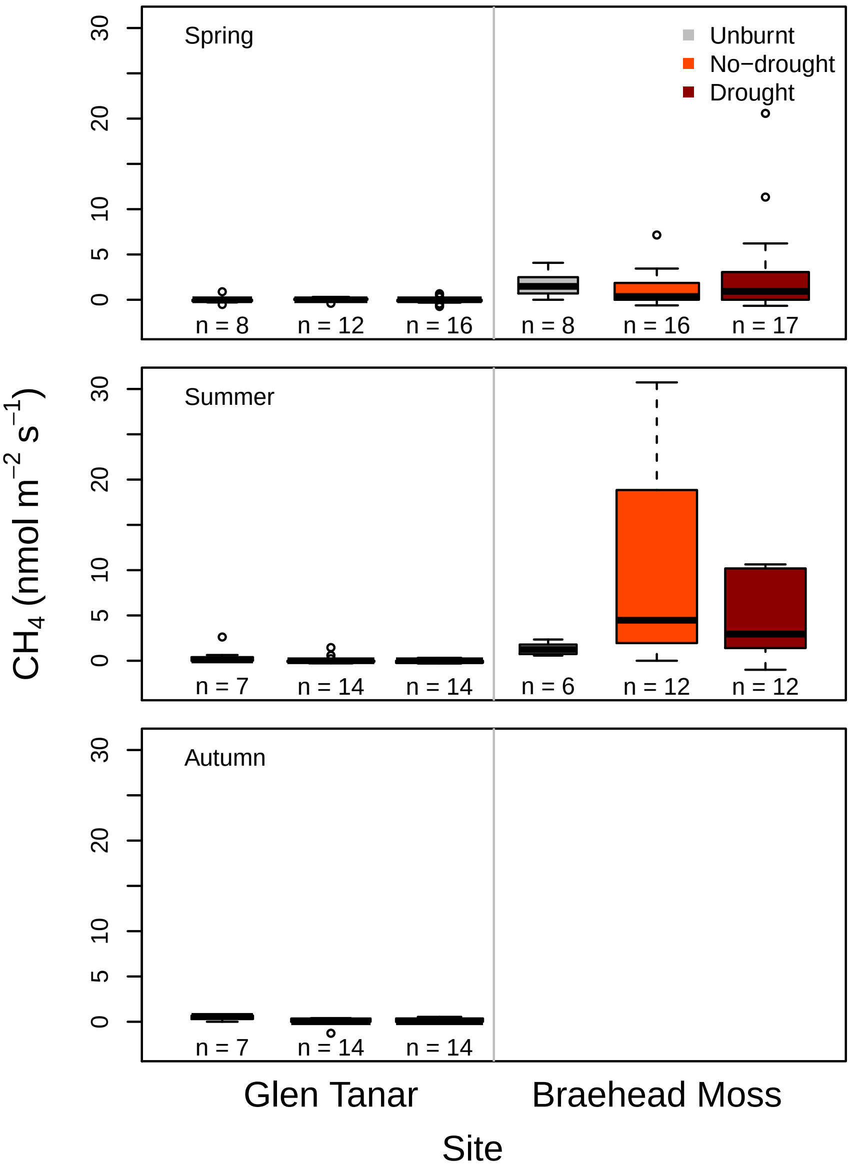

Figure D.5: Methane flux per treatment, season and site measured in the dark (covered chamber). *n* indicates number of observations. Extreme summer measurements at Braehead Moss (97 nmol m^{-2} s^{-1}, no-drought plot; 110 nmol m^{-2} s^{-1}, drought plot; 140 nmol m^{-2} s^{-1}, drought plot) not shown.

D.11 Net CO_2 equivalent flux

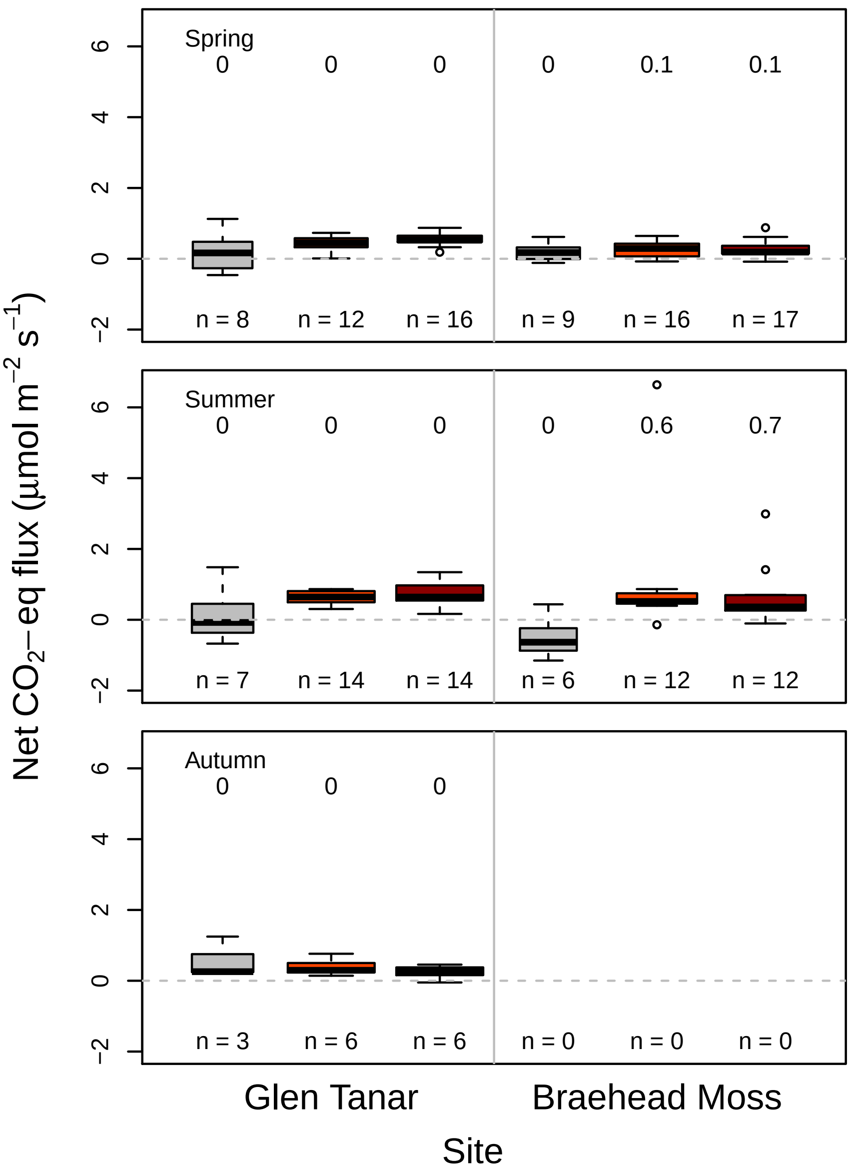

Figure D.6: Net CO_2 equivalent flux incorporating CH_4 flux (multiplied by 28 as it has 28 times the global warming potential of CO_2; IPCC, 2013) and NEE flux measured at the same time, per treatment, season and site. Numbers above the boxplots indicate CO_2-eq increase compared to NEE (i.e. due to CH_4). n indicates number of observations.

D.12 Dissolved organic carbon

Table D.14: Summary statistics of dissolved organic carbon concentration for different seasons and treatments.

Season	Treatment	Mean (SD)	Min	Max	n
Winter	Unburnt	134 (50)	76	233	10
	No-drought	119 (26)	62	188	28
	Drought	123 (28)	69	172	28
Spring	Unburnt	129 (34)	63	190	31
	No-drought	118 (21)	73	191	55
	Drought	121 (28)	66	188	56
Summer	Unburnt	130 (39)	59	234	50
	No-drought	124 (21)	79	193	68
	Drought	124 (27)	78	199	68
Autumn	Unburnt	156 (63)	72	339	33
	No-drought	143 (36)	95	294	73
	Drought	143 (35)	95	255	74

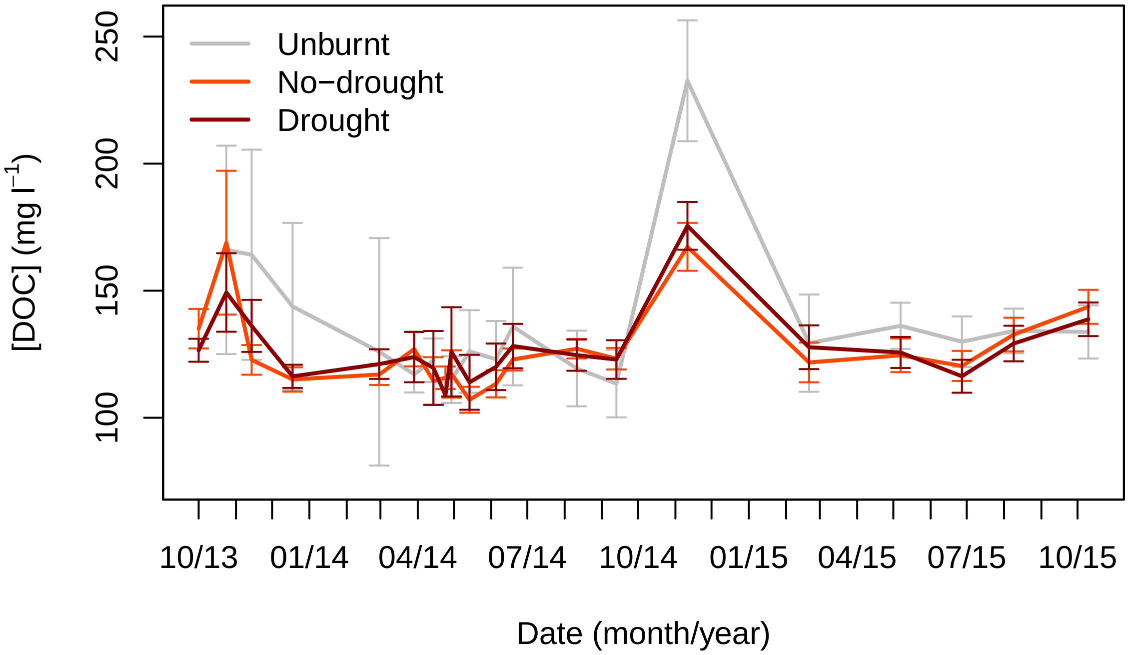

Figure D.7: Average concentration of dissolved organic carbon during the measuring period, for each fire severity treatment. Error bars, based on the standard error of the mean, also indicate sampling day.

Table D.15: Details of the linear mixed effects model investigating the effect of the interaction between season ("Se": spring, summer, autumn and winter), and treatment ("Tr": unburnt, no-drought and drought) on dissolved organic carbon concentration. R^2 marginal was 0.05 and R^2 conditional, 0.51.

	Value	Std.Error	DF	t-value	p-value
(Intercept)	4.902	0.077	517	63.99	<0.001
Se(Spring)	-0.005	0.058	517	-0.08	0.936
Se(Summer)	-0.041	0.056	517	-0.74	0.461
Se(Autumn)	0.086	0.065	517	1.31	0.190
Tr(No-drought)	-0.135	0.095	38	-1.42	0.165
Tr(Drought)	-0.104	0.095	38	-1.09	0.283
Se(Spring) : Tr(No-drought)	0.023	0.068	517	0.33	0.741
Se(Summer) : Tr(No-drought)	0.095	0.066	517	1.45	0.148
Se(Autumn) : Tr(No-drought)	0.102	0.077	517	1.32	0.186
Se(Spring) : Tr(Drought)	0.013	0.068	517	0.19	0.847
Se(Summer) : Tr(Drought)	0.054	0.066	517	0.82	0.412
Se(Autumn) : Tr(Drought)	0.067	0.077	517	0.88	0.382

Table D.16: Multiple comparisons between treatment levels within levels of season. See Table D.15 for model details.

	Estimate	Std. Error	z-value	p-value
Winter:No-drought - Unburnt	-0.00	0.06	-0.08	1.00
Winter:Drought - Unburnt	-0.04	0.06	-0.74	0.99
Winter:Drought - No-drought	-0.04	0.03	-1.33	0.78
Spring:No-drought - Unburnt	0.02	0.04	0.50	1.00
Spring:Drought - Unburnt	0.05	0.03	1.57	0.62
Spring:Drought - No-drought	0.04	0.02	1.65	0.56
Summer:No-drought - Unburnt	0.10	0.06	1.62	0.58
Summer:Drought - Unburnt	-0.03	0.05	-0.62	1.00
Summer:Drought - No-drought	-0.13	0.08	-1.54	0.65
Autumn:No-drought - Unburnt	0.05	0.04	1.12	0.90
Autumn:Drought - Unburnt	0.03	0.06	0.45	1.00
Autumn:Drought - No-drought	-0.02	0.06	-0.38	1.00

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