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The regeneration of bryophytes after the burning of dry heath and wet heath moorland on the North York Moors

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Introduction

Natural England commission a range of reports from external contractors to provide evidence and advice to assist us in delivering our duties. The views in this report are those of the authors and do not necessarily represent those of Natural England.

Background

The North York Moors are atypical uplands because of their low altitude and low rainfall. Many are intensively managed as grouse moors.

This report was commissioned to find out:

- Whether under, Common Standards Monitoring, the North York Moors Sites of Special Scientific Interest could achieve 'favourable condition'.
- What management, if any, would enable them to reach this condition.

The report concentrates on two main areas:

- The lack of bryoflora diversity and how bryoflora diversity could be enhanced using Burning Management Plans.
- The lack of bryoflora cover to protect the peat layer on further re-burning and whether 'cool burns' were possible where such a protective layer did not exist.

The findings will be used by the local Natural England team to:

- Draw up prescriptions for Higher Level Stewardship Burning Management Plans.
- To help justify the need for 'no - burn' areas on intensively managed grouse moors.
- To identify burning rotations that will maximise bryoflora diversity on moors not managed for grouse.

Note, these results only apply to the local conditions found in the North York Moors and should not automatically be extrapolated to other upland areas.

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THE REGENERATION OF BRYOPHYTES AFTER THE BURNING OF DRY AND WET HEATH; A LITERATURE REVIEW AND A FIELD STUDY CONDUCTED ON THE NORTH YORK MOORS

by

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SUMMARY

Introduction

The age at which heather is burnt influences the amount of dry matter ignited, the fire temperature and subsequent re-colonisation by both heather and the bryophyte community. On moorland managed by controlled burning, a balance needs to be reached between having a burning cycle long enough to allow re-colonisation and development of the bryophyte community without allowing too much dry matter to accumulate. If this balance is achieved, damage to the peat surface and the level of peat erosion will be kept at a minimum, whilst allowing the survival of refugia of bryophytes and encouraging post fire bryophyte recolonisation.

Objective

To investigate the regeneration of bryophytes following heather burning, including a review of the literature review and fieldwork, and try to establish an indicator to inform the decision as to when burning should occur, that is easy to apply, and will be accurate and consistent when applied.

Methods

Studies evaluating the regeneration of bryophytes after wild or managed fires were sought for the literature review by searching the electronic database Web of Science and the contents pages of relevant journals. Studies were grouped according to the pre-fire vegetation type; sand/alluvial deposits, grassland, forest/woodland and heathland.

The field study was conducted on Spaunton Moor, North York Moors. Four H12a dry heath sites were selected, with plots 1, 3, 5, 7, 10, 15, 20, and >25 years post-burn. Three M16d wet heath sites were selected with plots 3, 7 and 25 years post-burn on each site. Other ages at the wet heath sites included 10 years (1 site), 15 years (2 sites), and 20 years (2 sites) post-burn. Firstly, eight 10x10cm quadrats were surveyed on each plot. Vegetation height, percentage cover of vascular plants, and the number of growing tips and percentage cover of bryophytes were recorded. Secondly, the presence of bryophyte species was recorded every metre along three 10m transects in each plot. Species abundance was analysed using the Friedman test and principal components analysis. The presence and absence of species was analysed using TWINSPAN (Hill and Smilauer 2005). Relationships between vascular plant height (mainly heather) and abundance and bryophyte abundance were analysed using Spearman's rank correlation.

Results

Literature review

Twenty four studies were identified, one conducted on alluvial deposits/sand, two on grassland, twelve in forest/woodland, and nine on heathland. The most commonly recorded post burn coloniser was *Ceratodon purpureus*, being recorded in thirteen of the studies. Other commonly recorded species were *Funaria hygrometrica* (ten studies), *Polytrichum* species (nine studies), and *Bryum* species (seven studies). *Pohlia* was a colonising species in four studies, all of which were carried out on heathlands. Other species specific to heathland recolonisation were *Campylopus* species (three studies) and *Dicranum scoparium* (one study).

Field study

H12a dry heath Twenty three bryophyte species were recorded on the H12a sites. *Campylopus introflexus* was the most abundant bryophyte species one year post-fire. *Campylopus pyriformis*, *Cephaloziella divaricata* and *Ceratodon purpureus* were also prominent. Species restricted to younger plots were *Bryum capillare*, *Leptodontium flexifolium* and *Polytrichum juniperinum*. *Dicranum scoparium* and *Hypnum jutlandicum* were most abundant in older heather stands. Species restricted to older plots were *Barbilophozia floerkei*, *Campylopus flexuosus*, *Lophocolea bidentata*, *Mnium hornum*, *Plagiothecium undulatum* and *Rhytidiadelphus squarrosus*.

Hypnum jutlandicum significantly increased in abundance with the age of heather (p=0.002), whereas *Campylopus introflexus* (p=0.006), *Campylopus pyriformis* (p=0.041), and *Cephaloziella divaricata* (p=0.028) significantly decreased in abundance. TWINSPAN divided the H12a sites into two main groups, one predominantly of plots ten years and older, and the other mainly of plots of seven years and younger.

The height of the vascular plant canopy was negatively correlated with the number of stems of *Campylopus introflexus* (p<0.001), *Campylopus pyriformis* (p<0.001), *Cephaloziella divaricata* (p=0.004). The greatest number of stems of *Campylopus introflexus* (and acrocarpous mosses in general) were recorded when the canopy height was below 30 cm. The height of the vascular plant canopy was positively correlated with the number of stems of *Hypnum jutlandicum* (p=0.008), with the abundance of this species (and pleurocarpous mosses in general) increasing once the canopy height reached 30 cm, appearing more consistently at canopy heights over 40 cm and declining once the canopy height reached approximately 55 cm.

M16d wet heath Thirty species were recorded on the M16d sites. *Sphagnum* was most the most abundant bryophyte genus three years after burning; *Odontoshisma sphagni* and *Campylopus introflexus* were also prominent. Species restricted to younger plots were *Campylopus pyriformis*, *Calypogea fissa*, *Cephalozia connivens*, and *Kurzia pauciflora*. Species restricted to older plots were *Polytrichum commune*, *Pleurozium schreberi*, *Rhytidiadelphus squarrosus*, and *Pseudoscleropodiu purum*. *Hypnum jutlandicum* was present throughout the age range of heather, although it was more abundant in older stands.

Odontoshisma sphagni showed significant effect of the stage of heather development on abundance (p=0.048), with the greatest number of stems at the building stage. TWINSPAN divided the sites into two main groups, one generally of younger sites where *Sphagnum* was recorded, and the other older sites generally without *Sphagnum*. There was a significant correlation between the height of the vascular plant canopy and the number of stems of *Odontoschisma sphagni* (p=0.001), *Sphagnum* section *Subsecunda* (p=0.008), *Sphagnum* section *Cuspidata* (p=0.002), and *Hypnum jutlandicum* (p=0.012).

Sphagnum species and *Odontoshisma sphagni* were recorded in the greatest numbers when the canopy height was below 30 cm. *H. jutlandicum* started to increase in abundance once the canopy height reached approximately 20 cm, with the maximum abundance achieved at a canopy height of approximately 50 cm. The height of the canopy where both *Sphagnum* and *Hypnum jutlandicum* were represented, ranged from approximately 20 cm to 35 cm.

On both the dry and wet heath sites, the narrow range of canopy heights at which the bryophyte species characteristic of these habitats were present, were recorded in a wide range of ages and stages of development of heather, indicating that canopy height is a better indicator of the bryoflora than either the age or stage of heather development.

Conclusions

Implications for management

The benefit of a developed bryoflora in an area to be burnt is their water holding capacity, which moistens the bases of the heather stems, producing a cooler burn. This in turn may reduce damage to the peat surface and increase the likelihood of survival of some of the pre-burn bryophyte community, increasing the speed of recovery of the bryoflora, and limiting the colonisation of less desirable invasive species, such as *C. introflexus*. The current study highlighted the potential for promoting the spread of *Campylopus introflexus* with repeated burning, and the relationship between characteristics of the vascular plant canopy and the bryoflora. The 10-year post-burn increase in species characteristic of a mature H12a heathland is most likely an indicator to the start of the the recovery of this habitat, rather than a widespread recovery, as *C. introflexus* persists in older plots and desired species characteristic of a mature heathland were still absence. Age and stage of heather development do not seem to be good indicators of bryoflora composition. Canopy height may be a more reliable indicator to inform practice regarding a sustainable burning cycle.

Recommendations for future research

Further research is required to determine whether the canopy heights indicating a recovered bryoflora at Spaunton Moor can be extrapolated to other moors in the North York Moors and elsewhere in England. It seems promising that the same canopy height is related to a high abundance of *H. jutlandicum* on both the H12a and M16d sites. However, until this is tested experimentally on other vegetation types, and moorlands in other areas with different environmental conditions, it would be unwise to apply the results of this study to other areas.

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1 Introduction

1.1 Heathland

Gimingham (1972) defines heathlands as “territories in which trees or tall shrubs are sparse or absent, and in which the dominant life-form is that of the evergreen dwarf shrub, particularly as represented in Ericaceae”. Rodwell (1998) expands on this, and defines heathlands as “vegetation types in which sub-shrubs play the most important structural role, albeit sometimes in a dwarfed or broken canopy, with such species as *Calluna* and other ericoids (notably *Vaccinium* species and *Erica*), *Ulex minor* and *U. gallii* the usual dominants, alone or in various combinations”.

Gimingham (1972, 1988) described a cyclical process with four phases of heather growth: pioneer, building, mature and degenerate:

- Pioneer: The early stages of establishment and growth, when cover is low (~10%), and branching is regular from the axis of a single leading shoot. The heather starts as a pyramidal shape, becomes hemispherical, and gains a height of up to ~6 cm. This stage lasts for 3-6 years, and sometimes up to 10 years.
- Building: The stage where the heather becomes bushy, with branches radiating from the centre. Productivity of peripheral shoots is high and flowering is vigorous. There is usually a clear definition between short- and long-shoots, with peripheral extension taking place in the long-shoots. The heather gains a height of 50 cm or more, and is hemispherical in shape. The canopy reaches its maximum density, with cover high (90-100%). This phase lasts until plant is 15 to 20 years of age.
- Mature: The stage where extension growth is declining and green shoot production and flowering is reducing, but still high. The shape is hemispherical, but the central branches are starting to spread sideways, initiating gap formation. At this stage, the heather reaches its maximum height, although cover is slightly reduced (~75%). This stage lasts until the plant is 20-25 years old.
- Degenerate: Central branches are dying, so creating gaps. Outer branches persist, often lying flat. Some branches, partially buried in the litter, may remain alive due to adventitious rooting, therefore sustaining a ring of foliage-bearing twigs. At this stage, cover is reduced to ~40%. This happens when plant is aged between 25-30 (up to 33) years, and eventually the whole plant may die, at 30-40 years of age.

Cycles of heather occur when there is no competition from other permanent, long-term species, such as a tall shrub or tree that can establish in the gaps (Gimingham 1972).

1.2 Bryophytes

Bryophytes are present in most plant communities, but form a major component in relatively few, where vascular plants are severely limited (Bates 1998). They are generally found in groups of individuals, which have characteristic features depending on their family, genus or species (Magdefrau 1982). They have no roots, although some species have underground rhizomes (e.g. *Polytrichum* species) or root-like structures (e.g. *Takakia* species). When connected to the substrate, bryophytes are only loosely connected with rhizoids. Most absorb (and lose) water (and nutrients) over their entire surface directly into/out of the cells of leaf tissue, due to a lack of cuticular waxes (e.g. *Hypnum* species). The term bryophyte encompasses mosses (Bryophyta), liverworts (Hepatophyta) and hornworts (Anthocerotophyta).

1.2.1 Mosses

Mosses have distinct stems and leaves, with the leaves in most species arranged spirally around the stem, but are sometimes flattened in two rows (complanate). Mosses are divided into two major types, acrocarpous and pleurocarpous. Acrocaprous mosses generally have erect stems, are either not branched or sparingly branched, are of determinate growth, often growing as individuals or in tufts or cushions, and the sporophytes are produced from the tip of the main stem. Pleurocarpous mosses generally have stems that are prostate and of unlimited growth, often highly branched, forming mats or wefts, and produce on lateral branches. Throughout the report, acrocarpous mosses will be denoted (A), and pleurocarpous (P).

1.2.2 Liverworts

Liverworts are also split into two types, those forming a flattened plate of cells which are not differentiated in to stems and leaves (thallose), and those with distinct stems and leaves (leafy). Leafy liverworts tend to have leaves complanate along the stem, sometimes with a third row of smaller leaves on the ventral side of the stem (underleaves). Throughout the report, thalloid liverworts will be denoted (TL), and leafy liverworts (LL).

1.2.3 Hornworts

Hornworts are thallose, consisting of a flat plate of tissue, with or without a mid-rib, but with no distinguishable stem and leaves. Throughout the report, hornworts will be denoted (H).

1.3 Bryophyte ecology and physiology

Bryophytes are essential components of the environment, being plant pioneers, and have several important ecological roles. These include: encouraging soil formation by colonising bare areas, trapping wind blown inorganic particles (Danin & Ganor 1991) and contributing organic matter and nutrients (Bates 2000); preventing soil erosion (Danin & Ganor 1991; Rieley and others 1979); reducing temperature fluctuations in soils (Richardson 1958); reducing the rate of soil moisture loss (Van Tooren and others 1985); providing protection (Pugh 1996; Suren 1991; Varga 1992; Smrz 1992) and food for animals (Crafford & Chown 1991; Klein & Bay 1994); retaining nutrients in slowly decomposing tissue making them unavailable for use by vascular plants (Bates 1992; Berg 1984; Bowden 1991; Brock & Bregman 1989; Li & Vitt 1997; Longton 1988, 1992; Rochefort and others 1990; Shukla & Kaul 1979; Van Tooren 1988), and controlling nutrient cycling of ecosystems (Oechel & Van Cleve 1986; Rieley and others 1979). The retention of nutrients in bryophyte tissue may have a direct effect on the composition and succession of the vascular plant community.

The nutrient thought to most limit bryophyte growth is nitrogen (Chapin 1980; Tamm 1991; Robinson & Wookey 1997), especially at higher latitudes (Aerts and others 1992). Pollutant nitrogen has been shown to alter the growth and physiology of bryophytes (Bates 1987; Bates 1992; Potter and others 1995; Lee & Caporn 1998; Press and others 1998; Prins and others 1991; Aerts and others 1992; Kooijman & Kanne 1993; Näsholm and others 1994), with human activities sometimes resulting in toxic concentrations of nitrogen compounds (Lee 1998).

Like vascular plants some bryophytes, such as *Polytrichum* species (A), have a water repellent layer on their leaves, similar in structure to the early developmental stages of vascular plants cuticles (Cook & Graham 1998). This surface wax is thought to have two functions, water retention and water repellence (Clayton-Green and others 1985). Proctor (1979) examined 43 UK bryophyte species for the presence, and level of development, of epicuticular wax. Twenty of these species had surface wax present, with the layer being strongly developed in nine of these species. Most bryophytes, however, have no protective cuticle on their leaves. Nitrogen pollutants dissolve in the fluid on the surface of the plant, in direct contact to the leaf cells, allowing the pollutants to be absorbed directly into the chlorophyllose cells. The lack of cuticular waxes in many species, along with the high surface area, and lack of stomata preventing the exclusion of the atmospheric environment at night, make bryophytes susceptible to pollution (Brown 1995).

Pleurocarpous mosses and liverworts seemed to be particularly sensitive to pollutant nitrogen (Burch 2001), possibly due to the large leaf surface area increasing exposure to the pollutant. Pleurocarpous mosses leaves are also often concave and overlapping, a feature designed to retain water, which would prolong the period of contact of polluted water with the leaf surface. This may be an important factor on UK heathlands, as the regeneration of bryophyte species after burning may be adversely affected by increasing nitrogen deposition.

1.3.1 Regeneration strategies

Bryophytes are able to regenerate both sexually and asexually.

Sexual reproduction Bryophytes have male (antheridium) and female (archegonium) structures. These can be located on the same plant (monoecious), or different plants (dioecious). The antheridium produces antherozoids, which fertilises an egg contained in the archegonium. From this fertilised egg, the sporophyte develops, which contains spores. Spores are released either by the bursting of the capsule as in the liverworts, or by the removal of the lid as in most mosses. The spores germinate to produce a filamentous structure (protonema), which goes on to produce the leafy shoot (gametophyte).

Asexual reproduction Asexual reproduction can be achieved in several ways, including: production of gemmae, fragmentation of the gametophyte, and innovation production.

Gemmae Gemmae are specialised vegetative propagules produced by the gametophyte. They can be formed on thalli, stems, leaves, rhiziods or in leaf axils. Most thalloid and many leafy bryophytes produce gemmae. The gemmae are genetically identical to the parent plant.

Fragmentation of the gametophyte All bryophyte cells are capable of going on to produce a new plant. When a gametophyte is fragmented, cells of the leaves or stem produce protonemata, which go on to complete the life-cycle in the usual way, forming new gametophytes genetically identical to the parent plant. There are occasions where direct organogenesis occurs, such as the production of gametophytes from the leaf surface of Polytrichum species, bypassing the protonemal stage of the life-cycle. Some species have adapted to fully exploit gametophyte fragmentation as a means of dispersal, such as species of the genus Campylopus, which produce deciduous leaf tips that break off, and lay on the surface of the plants, until they are dispersed by wind, water or animals.

Innovations Innovations are new branches. In some circumstances, a new branch can take on the characteristics of the main stem and go on to produce a new plant. This occurs when the apical portion and active growing tip are removed or damaged. This is a particularly prominent mode of reproduction in Sphagnum species.

1.3.2 Reproductive constraints

Many bryophytes are dioecious, and the absence of, or low numbers of either male or female plants side by side in the same stand, can lead to low reproductive rates with reliance on vegetative reproduction (Longton & Hedderson 2000). As stated above, asexual reproduction produces offspring genetically identical to the parent plant. This can lead to genetic uniformity in a population, which in turn can increase the populations' vulnerability to changes in its environment. Longton (1992) stated that the incidence of rarity is highest among species that are monoecious and produce sporophytes, or are dioecious and reproduce asexually. Both of these strategies lead to lack of genetic recombination, limit genetic variability and the capacity for adaptation, either due to self-fertilisation or the failure to reproduce sexually. The same goes for liverworts, where the rarity of monoecious species may be explained by decrease in genetic variation by inbreeding (Laaka-Lindberg and others 2000).

1.4 Heathland bryophytes

Hobbs and Gimingham (1987) classified bryophytes of heathland as species with complementary strategies to *Calluna*, either as subordinate species (shade tolerant ground flora), or species appearing in the gap phases. Typical bryophytes of H12a *Calluna vulgaris – Vaccinium myrtillus* heath, *Calluna vulgaris* sub-community include *Dicranum scoparium, Hypnum jutlandicum* and *Pleurozium schreberi*, with *Hylocomium splendens, Rhytidiadelphus loreus* and *Ptilidium ciliare* also present occasionally (Rodwell 1998). Bryopytes commony recorded in M16d are *Sphagnum compactum* and *Hypnum jutlandicum* (Rodwell 1998).

Gimingham (1988) observed that bryophytes are abundant at the pioneer stage of heather growth, when other vascular plants are at their minimum, increase in cover during the mature stage, were at their maximum cover in the degenerate phase when cover of *Calluna* is ~40%, and at their lowest during the building stage, when *Calluna* cover is at its maximum. Barclay-Estrup (1970) demonstrated this pattern in the biomass of bryophytes (Table 1).

Table 1: The biomass of bryophytes in relation to the biomass and height of vascular plants during each of the four stages of heather growth (Barclay-Estrup 1970).

	Pioneer	**Building**	**Mature**	**Degenerate**
Mean age of *Calluna* (yrs)	5.7	9.0	17.1	24.0
Calluna biomass	287.2	1507.6	1923.6	1043.2
Calluna height (cm)	24.1	52.1	63.2	55.2
Biomass of other vascular plants	179.6	41.2	52.0	83.2
Biomass of bryophytes	422.4	153.2	329.6	434.4
Depth moss layer (cm)	6.0	2.4	4.1	6.3

1.5 Burning

Hobbs and Gimingham (1987) identified several reasons for the use of fire in heathlands: interrupting the ageing process of *Calluna*, keeping it young, productive and in a nutritious state; preventing the transition from heathland to scrub or woodland; a management tool; an alternative to cutting; and as part of an agricultural system, releasing nutrients.

Burning is permitted between 1 October and 15 April in the uplands (and 1 November and 31 March in the lowlands) in England (DEFRA 2007). The burning period is longer in Scotland, from 1 October to 15 April below 450 m, but 1 October to 30 April above 450 m (with possible extensions to 30 April and 15 May respectively) (SEERAD, 2001), but has recently been shortened in Wales to between 1 October and 31 March in the uplands (1 November to 15 March elsewhere) (Welsh Assembly Government 2008).

Hobbs & Gimingham (1987) stated that fires should be restricted to patches of limited size, burnt on a rotation such that all parts of an area of heathland are burned once in the course of a given period of years, and is best carried out in small patches or narrow strips rather than in large blocks, especially for grouse management. Both Mowforth and Sydes (1989) and Wood-Gee (1996) also advised burning in long narrow strips approximately 20 to 30m wide and covering an area of no greater than 2 ha for grouse management. Wood-Gee (1996) went on to say that the benefits of this burn rotation were that old/dead vegetation was removed, new growth encouraged, the height and structure of vegetation is promoted, and diversity of characteristic plant species is favoured. Disadvantages identified included the inability of slow moving or sedentary animals to escape, the destruction of food, cover and nesting material for animals, the invasion of weeds (e.g. ragwort) onto bare ground, changes in surface water run-off, reduction in evaporation and absorption, and the growth of fire-resistant species. The rapid regeneration of heather when burnt young was also highlighted by Gardner and others (1993) as regeneration was from both seeds and shoots took place, whereas when older heather was burnt, regeneration was primarily, or solely, by seed.

Mowforth & Sydes (1989) stated that the optimum burning regime would allow sufficient time for heather to regain dominance, but prevent it from accumulating much woody material. They suggest that heather should be burned at the late building/early mature phase. Wood-Gee (1996) suggested that the best time to burn heather was when it was finely branched and vigorous, as a general rule, stems no thicker than a pencil and 20-30 cm tall, so that it will regenerate freely from the buds at the base of the stems. The burn rotation thought to achieve these goals were 6-10 years on Exmoor in southern England, to 10-12 years in Aberdeenshire in northeast Scotland by Mowforth & Sydes (1989) accounting for the differences in productivity and climate, and between 8 and 15 years by Wood-Gee (1996) depending on soil, climate, exposure and level of grazing. Hobbs & Gimingham (1987) highlighted that the length of rotation may be linked to the rate of recovery of the vegetation: i.e. if *Calluna* is ready to burn at 10 years old, 1/10th of the total area would be burned each year. In practice, the strips that are burnt tend to overlap forming a mosaic of different ages and developmental stages of heather (cross-burning), therefore some areas of the heath are burnt more frequently.

Much of the North York Moors is burnt in a controlled manner to promote conditions that will support the high population densities of grouse that are required for commercial shoots (Jerram, Clayden & Rees 1998). On dry heath, the patches tend to be approximately 30 m wide and of varying length, forming a mosaic of burn patches of different ages. The frequency of burning tends to be high, and the regrowth of *Calluna* higher in the North York Moors than elsewhere in northern England. In contrast to Wood-Gee (1996), Jerram, Clayden & Rees (1998) stated that one of the main effects of burning is the reduction in species diversity, with frequent, repeated burning favouring *Calluna* over other heathland species, especially on the dry heaths, where other species are almost excluded. They go on to say that short burn cycles also result in a poorly developed bryophyte layer, citing the ‘RadHaz’ zone at the Ministry of Defence early warning station at Fylingdales, where the heather hasn’t been burnt or grazed for 30-40 years, as having a well developed bryophyte layer, whereas immediately outside the zone, where burning occurs, bryophytes are sparse.

MacDonald and others (1995) questioned the need to burn upland heathlands due to the high frequency of layering. They investigated 11 stands, 0.5 to 2 ha each, at eight sites at an altitude of 300-400 m across Scotland and northern England. They noted that the stands with strong layering were in more shaded habitats and of a younger mean age, and stated that the factors associated with layering were stem prostateness, a deeper humus rich or peaty soil, the absence or low abundance of *Hypnum* species (P) and lichens, and increased stem density and canopy vigour distal to the point of rooting. They also observed adventitious roots in over 50% of stems in all stands, with adventitious roots on over 90% of stems in six stands, and strongly developed in more than 30% of stems in seven stands.

1.5.1 Fire intensity

The amount of plant material present, composition, distribution, energy content and moisture content have all been identified as contributing to fire behaviour. Older stands of *Calluna* may be expected to burn hotter due to the abundance of fuel. Dense uniform stands, may also burn hotter, and allow the fire front to move more quickly than in patchy, degenerate stands, resulting in mature and building stands burning hottest (Hobbs & Gimingham 1984). Fritsch (1927) suggested that both the height and density of vegetation, were factors which determined fire intensity. Hobbs & Gimingham (1987) stated that the intensity of the fire may affect *Calluna* regeneration, with very high temperatures damaging or killing seeds and buds. However, underground seeds, buds or rhizomes may be afforded some protection from the fire. Therefore the regeneration strategies of heathland plants will impact on their ability to survive and regenerate after a fire.

Table 2 summarises the results of Hobbs & Gimingham (1984), showing the biomass of bryophytes, and the maximum temperatures recorded at canopy and soil level, when each stage of heather development was burnt. Regression analysis carried out by the authors showed that age, vegetation height, amount of dead material, available heat energy, *Calluna* stem density, vegetation moisture, wind speed and fire width were variables accounting for differences in fire intensity.

Whittaker (1961) used heat-sensitive paint on mica, and recorded temperatures of 220-840^{o}C at ground level during fires of mature *Calluna* heathland communities (Table 3). These results showed no relationship between fire intensity and the height of vegetation, as suggested by Hobbs & Gimingham (1984) and Fritsch (1927). Whittaker (1961) went on to provide more detailed temperatures for a *Calluna-Erica* heath, with different constituents in the ground layer. There appeared to be no relationship between the constituents of the ground layer and temperatures recorded (Table 4). Whittaker (1961) made two recordings using two pieces of mica with heat-sensitive paint. Where these agreed, one temperature was given, and where the two differed, both figures were given. However, Whittaker (1961) stated that the composition of the ground layer had an insulating effect, protecting underground parts and seeds. To demonstrate this, mor humus from a podsol, peat, *Calluna* litter, *Leucobryum glaucum* (A), *Hypnum cupressiforme* (P), *Pleurozium schreberi* (P), and *Cladonia sylvatica* had hot air blown onto them (up to 600^{o}C) and the temperature measured at 1cm depth beneath them. This showed humus, peat and *L. glaucum* to be the best insulators, and *H. cupressiforme, C. sylvatica*, and *Calluna* litter the poorest insulators.

Sedlakova & Chytry (1999) studied a dry heath in the Czech republic. They compared the regeneration after high intensity burns on dense heathland, and low intensity burns on an open heathland. After the high intensity burn, *Calluna* regeneration was from stem bases in the first and second year, and *Calluna* seedlings were prominent after 1 year. The regeneration of

Hypnum cupressiforme (P) was limited. After 6 years, the heathland was species-rich, with more gramioids, acrocarpous and pleurocarpous mosses, and lichens than the original heathland. On the two low intensity burn sites, one showed a steady increase in *Calluna* cover due to vegetative regrowth, and a species-rich heathland was restored, with graminoids, forbs, mosses, and lichens, 6 years after burning. On the second low intensity burn site, *Calluna* regeneration was limited, with only a slight increase in cover in the fourth year. A similar pattern was seen in lichens. Grasses, particularly *Festuca ovina* and *Agrostis coarctata* dominated this plot. *Calluna* regeneration by seedlings was more prominent in the high intensity burn site compared to the low intensity sites.

Table 2: The biomass of bryophytes, and the maximum temperatures recorded at canopy and soil level during the burning of the four different stages of heather development (summarised results from Hobbs & Gimingham (1984))

Pre-burn Heather Stage	Bryophytes (g m^{2})	Age (years)	Canopy (^{o}C)	Soil surface (^{o}C)
Pioneer	0	8.1	350	340
Pioneer	8	6.1	430	320
Pioneer	82	5.6	340	180
Building	24	15.4	490	280
Building	32	10.1	630	140
Building	52	11.8	620	590
Building	358	16.0	760	710
Building	390	14.1	530	550
Mature	4	14.0	660	840
Mature	96	25.7	670	600
Mature	168	17.0	640	480
Mature	168	27.0	630	160
Mature	174	23.0	690	600
Mature	250	14.5	440	560
Mature	764	25.1	740	630
Degenerate	11	32.6	790	650
Degenerate	214	39.0	340	510

Table 3: Temperatures at ground level (^{o}C) during fires, where the pre-burn vegetation was mature *Calluna* heathland (Whittaker 1961)

		Calluna			**Temperature recorded**		
Vegetation	**% cover**	**Stage**	**Height (cm)**	**Mean age (years)**	**Most often**	**Maximum**	**Minimum**
Calluna/Erica	80	M	40	15	340	640	220
Calluna/Erica	90	M	30	14	500	715	290
Calluna/Vaccinium	95	M/D	52	19	440	440	290
Calluna/Empetrum	100	M	21	14	340	715	290
Calluna	90	M	16	14	440	500	340
Calluna	90	M	15	15	340	840	290
Calluna	100	M	31	14	340	715	340

Table 4: Detailed temperatures for one heathland with a canopy of *Calluna*, and various ground layer constituents (Whittaker 1961)

	Temperature (^{o}C)	
Ground layer	**20cm above ground**	**Ground level**
None	840	290
Litter	500	340
Litter	500	340/500
Litter	500	290/340
Litter	500/715	500
Litter	640	440/500
Litter	715	340
Litter	715	640/715
Litter	715	440/500
Litter	840	290/400
Litter	840	290/340
Litter	840	715
Litter	840	640
Leucobryum glaucum	640	340
Polytrichum commune	715	500
Campylopus introflexus	715	500
Hypnum cupressiforme	715/840	500
Cladonia pyxidata	840	440/640
Erica cinerea	715/840	500

1.5.2 Post-burn conditions

During burning, nutrients are mobilised, and become more readily available. Nutrients are lost in smoke, and by leaching and soil erosion by wind and water, and are deposited in ash (Hobbs & Gimingham 1987 and references therein). Substances released in organic matter may be toxic for many bryophytes therefore a restricted number of species can survive after fire, and these tend to be nitrophilous species (Brown 1982). Southorn (1977) demonstrated in culture that *Funaria hygrometrica* (A) required high concentrations of calcium, potassium, nitrogen, and phosphorus. This may explain the widespread colonisation of this species on burn sites, as burning increases the availability of these nutrients.

1.6 Aims

The main aims of the present study were to review the literature relating to bryophyte regeneration after burning, and to undertake a field study to determine the sequence of colonisation of bryophytes after the burning of heather on dry and wet heath to try to establish an easy, accurate and consistent indicator as to when burning should occur.

2 Literature review

Studies evaluating the regeneration of bryophytes after fire were sought by searching the electronic database Web of Science, the internet and the contents pages of relevant journals. Studies of bryophyte regeneration after wild or managed fires, in any habitat, were included. Studies were grouped according to the pre-fire vegetation type; sand/alluvial deposits, grassland, forest/woodland and heathland. Twenty four studies were located and are described below.

2.1 Sand/alluvial deposits

Esposito and others (1999) investigated the regeneration of bryophytes after wild and managed (wood pile) burns on stabilised dunes of alluvial deposits and loose siliceous-calcareous sand in a coastal area north of Naples. They classified the fires as high intensity (centre, and half way between the centre and edge of the wood pile fires), and low intensity (edge of the wood pile fires and the wild fire sites).

Low intensity sites: bryophyte regeneration was dominated by vegetative growth, and *Funaria hygrometrica* (A) and *Bryum torquescens* (A) dominated early. *Barbula convoluta* (A) and *Bryum dunense* (A) were replaced by *Bryum torquescens* (A) 2-3 years after fire. *Tortella flavovirens* (A) and *Pleurochaete squarrosa* (A) appeared after 1.7 years and gained dominance over the pioneer species after 3.2 years on the lowest fire intensity sites.

High intensity sites: initial bryophyte regeneration was predominantly by spores (0.8 and 1.7 years after fire), with vegetative growth becoming dominant after later (2.7 and 3.7 years after fire). *F. hygrometrica* and *B. torquescens* took longer to recolonise the high intensity fire site (2.7 years) compared to the low intensity sites. *B. convluta* and *B. dunense* competed with *F. hygrometrica* in and became dominant after 2 years. *T. flavovirens* and *P. squarrosa* appeared after 2.7, but did not gain dominance.

Other species recorded at low frequencies, but never achieved dominance included *Bryum argenteum* (A), *B. radiculosum* (A), *B. ruderale* (A), *Cheilothela chloropus* (A), *Didymodon luridus* (A), *Fossombronia wondraczekii* (LL), *Pseudocrossidium hornschuchianum* (A) and *Riccia sorocarpa* (TL).

2.2 Grasslands

Antos and others (1983) investigated the effect of fire on ungrazed Western Montana grassland, which was dominated by *Festuca scabrella*. They had four natural wild fire sites and four unburnt control areas. All bryophytes were eliminated by fire, and after one year, *Bryum caespiticum* (A) and *Ceratodon purpureus* (A) became established. Two liverworts, *Athalamia hyalina* (TL) and *Mannia fragrans* (TL) were recorded on some burnt and also on the unburnt sites. Total bryophyte cover returned to pre-burn levels three years after the fire, however, the species composition had changed, with the cover of *B. casepiticum* and *C. purpureus* being three times greater on burnt sites than unburnt controls, and accounted for most of the bryophyte recovery. The bryophyte dominant before burning, *Brachythecium albicans* (P), achieved only 5% of the cover present on unburnt controls. Antos and others (1983) concluded that bryophytes recovered more slowly than the vascular plants, as vascular plant cover and species composition was similar on burnt and unburnt sites three years after burning.

Southorn (1976) studied rapid fire and bonfire sites on grassland, in the grounds of Royal Holloway College. On the rapid fire sites vascular plant recovery was rapid, however, bryophytes never became abundant, with species characteristic of the pre-burn vegetation recorded. On the bonfire sites, *Funaria hygrometrica*, *Ceratodon purpureus*, *Bryum argenteum* and tuberous *Bryum* species all recolonised at about the same time, however, *Funaria hygrometrica* quickly became dominant. By the second growing season, vascular plant cover increased and post-burn bryophyte species decreased, being eliminated by third growing season, when species of pre-burn vegetation were recorded.

2.3 Forests/woodland

Three studies have been published investigating recolonisation of bryophytes on burnt Euclayptus forest in Tasmania and their nutrient content (Duncan & Dalton 1982; Brasell & Mattay 1984; Brasell and others 1986). Duncan & Dalton (1982) investigated the recolonisation of bryophytes on burnt tree-felled sites, and reported that *Marchanita berteroana* (TL) and *Funaria hygrometrica* (A) provided the major vegetation cover after 6 months. These species were replaced by *Ceratodon purpureus* (A) in the second year, which became dominant, with Polytrichum juniperinum (A) also represented in the bryoflora in the second year. *P. juniperinum* increased in cover in the third year, and became the dominant bryophyte by the fourth year. Other species recorded were *Bryum sauteri* (A) which was present in first year after burn, but never in large quantities, *Campylopus introflexus* (A), *C. clavatus* (A), *C. pallidus* (A) and *Tortella calycina* (A), which all colonised in during second year.

On this same site (Brasell & Mattay 1984) reported a similar pattern of colonisation. They identified the five most important species in the first three years after burning as *Marchantia berteroana* (TL), *Funaria hygrometrica* (A), *Ceratodon purpureus* (A), *Polytrichum juniperinum* (A), and *Campylopus introflexus* (A), with *M. berteroana* and *F. hygrometrica* being the first colonisers within the first few months after the fire. *C. purpureus* was evident at end of first year, and was well established and dominant in the second year, and *F. hygrometrica* was virtually eradicated by the second summer. *M. berteroana* persisted for at least three years, but became more restricted to damper areas over time. *P. juniperinum* became established in the second year, replacing *C. purpureus* in moister areas. They also recorded other species that were present by end of third year, such as *Pohlia nutans* (A), *Tortella calycina* (A), and *Bryum* spp (A).

Brasell and others (1986) went on to investigate the tissue concentrations of nitrogen, phosphorus, potassium, calcium and magnesium. Concentrations were high in *F. hygrometrica* in plants on the new burn and 1 year post burn sites, but had decreased dramatically by 2nd year. Concentrations increased in *M. berteroana* each year for the 3 years. Concentrations were higher in *P. juniperinum* and *C. introflexus* in the second year post-burn, compared to one year post burn. Concentrations of nitrogen and magnesium increased each year for 3 years in *C. purpureus*, however, Concentrations of phosphorus, potassium, calcium increased from new burn to 1 year, then stayed same for 2nd year.

Brasell and others (1986) measured acetylene reduction in bryophyte species from burnt sites and adjacent unburnt forest. They showed that acetylene reduction increased in bryophytes from the burnt sites compared to those from the unburnt forest, indicating increased nitrogen fixation. They concluded that the bryophytes associated with the highest rates of acetylene reduction were the earliest colonisers, *M. berteroana*, *F. hygrometrica*, and *C. purpureus*.

Eversman & Horton (2004) investigated recolonisation of burned woodland substrates by lichens and mosses in Yellowstone National Park, and reported that the main mosses on burnt soil *C. purpureus* (A), *Polytrichum juniperinum* (A), *P. piliferum* (A) and *Bryum* spp (A), particularly *B. caespiticium*. No *Funaria hygrometrica* (A) was recorded.

Puche & Gimeno (2000) also investigated the dynamics of the early stages of bryophyte colonisation after burning, in Mediterranean forests of Castellon, eastern Spain. They chose three vegetation types, *Quercus suber* forest, *Pinus halepensis*/*P. pinaster* stands, and *Quercus suber*/*P. pinaster* stands and recorded the regeneration of bryophytes six times over a 30 month period. The *Quercus suber* vegetation type had traditional post-burn bryophyte species dominating after burning, such as *Funaria hygrometrica* (A). Other sites, however, had the early return of the bryophytes typical of the pre-burn vegetation, together with annuals (such as *Acaulon* spp and *Pottia* spp) and colonist species (*Bryum rubens* (A), *B. ruderale* (A), *Trichostomum crispulum* (A), *T. brachydontium* (A), and *Weissia* species (A). This difference was attributed to the intensity of the fire, with the *Quercus suber* site having undergone a high intensity ‘bonfire’ burn, whereas the other two rapid, low intensity burns.

Also in Spain (southeast) were the studies by De La Heras and others. De La Heras and others (1990) studied six sites, where *Bupleuro rigidi-Querceto rotundifoliae* (*Quercus rotundifolia* forest) and *Berberidi hispanicae-Quercerto rotundifoliae* were the vegetation types. *Homalothecio aurei-Pleurochaetetum squarrosae* was the representative bryophyte community in the area. Each site was burnt at different times, resulting in sites 1, 4, 6, 7 (2 sites) and 10 years post-burn. After 1 year, ten bryophyte species were recorded, this rose to 21 species after 4 years, and 23 species after 6 years. The two sites that were 7 years post burn had 21 and 35 bryophyte species. Thirty-nine species were recorded on the site 10 post-burn.

Bryum bicolor (A) was the most frequent species colonising after the first year, with a frequency of approximately 30%. The frequency of this species declined over time, being 19% after 4 years, 17% after 6 years, and 8.25 to 13.5% on the burn sites 7 years and older. The second most common species colonising the one year post-burn site was *Funaria hygrometrica* (A), with a frequency of 27%. The frequency of this species also decrease over time, being 18% after 4 years, 15% after 6 years, 4.5 to 8% in the burn sites 7 years and older. *Cephaloziella divaricata* (LL) had a frequency of 13% 1 year post burn, but this was reduced to 2.75% 10 years post burn. *Barbula convoluta* (A) had a frequency of 11% 1 year post burn, and remained fairly constant with a frequency of 9% 4 years and 10 years post burn. *Bryum torquescens* (A) also had a fairly consistent frequency, being 5% after 1 year, and 4 to 8.5% in the burn sites 6 and older.

De La Heras-Ibanez and others (1992) compared burnt and unburnt sites in close proximity to each other. 1x1m non-random quadrats were selected for similarity of soil, distance from river, slope, orientation, and proximity of trees and shrubs. They identified the primary colonisers when pH and organic matter are high as *F. hygrometrica, B. bicolor, B. convoluta, B. torquescens, Bryum capillare* (A) and *C. divaricata*. When organic matter and pH declined, but nitrogen availability was still high, a different group of species colonised, including *Trichostomum crispulum* (A), *Didymodon vinealis* (A), *D. fallax* (A), *Fissidens viridulus* (A). On older sites (>10 years since burn) and on control site, *Pleurochaete squarrosa* (A), *Homalothecium aureum* (P), *Weissia controversa* (A) and *Brachythecium velutinum* (P) were recorded.

De La Heras and others (1994) went on to describe 3 stages of recolonisation: colonisation, competition, and the stabilisation stage:

Colonisation stage: Characterised by *Funaria hygrometrica*, *Bryum bicolor* and *Barbula convoluta*. These are species with short life spans, high sexual reproductive effort and develop small spores (<20 µ), and this stage lasted for up to two years after the fire.

Competition stage: characterised by and increasing number of species, which displaced pioneer species.

- Early: Colonisation by competitive species with short life spans, high sexual and asexual reproductive effort, that develop small spores (<20 µ). Many of the species were not seen in the control plots, such as *Bryum capillare* (A), *B. dunense* (A), *Didymodon vinealis* (A), *D. acutus* (A), *D. insulanus* (A), *Barbula trifaria* (A), *B. unguiculata* (A), *Weissia controversa* (A), and *W. viridula* (A). A group of ephemeral species, with short life spans, sexual reproduction, and large spores (>20µ), such as *Cephaloziella divaricata* (LL), *C. baumgartneri* (LL), *Phascum cuspidatum* var. *piliferum* (A), *P. curvicolle* (A), *Acaulon triquetrum* (A), *Pottia starkeana* (A) also colonised the areas. This stage lasted for approximately two to six years after fire.
- Late: A large number of species colonising which were also seen in control plots, which displace both pioneer and competitive species, such as *Encalypta vulgaris* (A), *Pleurochaete squarrosa* (A), *Homalothecium aureum* (P), *H. sericeum* (P), *Brachythecium velutinum* (P), *Targionia hypophylla* (TL), and *Reboulia hemisphaerica* (TL). This phase lasted approximately ten years.

Stabilisation stage: Characterised by the presence of perennial species (as specified in previous, late phase of the competition stage), with longer life spans, sexual and asexual reproductive effort, and small spores (<20 µ).

De La Heras and others (1995) reported the differences between sites with north and south exposures. They reported that the number of species and seasonality was higher in north exposure sites than south. They identified three species that occurred on all the north and south exposure plots, *Funaria hygrometrica* (A), *Barbula convoluta* (A), and *Bryum bicolour* (A), each responded differently. They reported that the cover of *F. hygrometrica* remained constant over the 68 months after fire in the south, but decreased more rapidly in the north; the cover of *B. bicolour* showed little change over the 68 month period and was similar at both sites, and the cover of *B. convoluta* increased in the north, but remained less variable in the south.

De La Heras and others (1995) measured the nitrogen content of the soil 0-4 cm and 4-8 cm under dense bryophyte turfs and bare ground after fire. They reported that nitrogen increased after the fire with time under bryophytes and on bare ground, but the increase was greater in soil under bryophytes. They concluded that this was due to the association that species such as *Funaria hygrometrica* can have with blue-green algae, and therefore the high nitrogen fixation activity under those bryophyte turfs.

Schimmel & Granstrom (1996) investigated fire severity and vegetation response in a boreal Swedish forest of *Picea abies* and *Pinus sylvestris*, which had a ground flora of *Vaccinium myrtillus*, *Pleurozium schreberi* (P) and *Hylocomium splendens* (P), *Ptilium crista-castrensis* (LL), *D. scoparium* (A) and *D. polysetum* (A), some of which can be found on heathlands in the UK. To investigate the effect of the intensity of fires, Schimmel and Granstrom (1996) clipped the ground layer to ground level and then added one of four fuel levels to the burn site:

- No fuel. Smouldering extinguished immediately
- 2.5 kg fuel. Smouldering allowed for 5 minutes
- 6 kg fuel at start with another 2.5 kg during burn. Smouldering for 15 minutes
- 16 kg fuel at start with another 9 kg during burn. Smouldering for 1 hour.

On the low intensity fire sites where no fuel was added (max. ground temperatures 600^{o}C), porous mats of partially burned mosses and lichens were left, which appeared completely dead, however, in a few of these areas *Hylocomium splendens* (P) started to regenerate vegetatively. On the higher intensity fire sites, where fuel was added (max. ground temperatures 650 to 750 ^{o}C), the bryophyte layer was completely destroyed. On these sites, *Ceratodon purpureus* (A), *Polytrichum commune* (A) and *P. juniperinum* (A) became established. A few fragments of *H. splendens* were regenerating at the edges where they had dispersed from the unburnt site. *Polytrichum* species overgrew *C. purpureus*, and after two to three years *Polytrichum* species dominated.

Another study using controlled fires was conducted in oak woodland in Navarra, Northern Spain (Ariz & Indurain 1996). In this study, regeneration after slow and quick burns were compared to unburnt control areas. Early colonisers after the slow fires included *Hypnum cupressiforme* (P), *Weissia controversa* (A), *Pleuridium acuminatum* (A), *Calypogeia trichomanis* (LL), *Scleropodium purum* (P) and *Bryum* species (A). After the quick fires, early colonisers included *Hypnum cupressiforme* (P), *Polytrichum formosum* (A), *Pleuridium acuminatum* (A), *Calypogeia trichomanis* (LL), and *Bryum* species (A).

Finally, the colonisation of bryophytes at the site of a natural fire that occurred in pine woodland in 1975 in northern Germany was reported in two studies (Butin & Kappich 1980; Jahn 1980). Butin & Kappich (1980) reported that protonemata were present 2-3 months after the fire, and this was identified as *Funaria hygrometrica* (A). At this time, the first thalli of *Marchantia polymorpha* (TL) were also visible. The frequency and size of these two species increased over the next two years, producing a continuous bryophyte carpet. Two years after the burn, *Ceratodon purpureus* (A) was also present, but never achieved the same percentage cover as the other two pioneer species. Jahn (1980) reported the results from six areas of the burn sites, with each area having been studied by different researchers. Vegetation recovery was recorded in the areas between replanted trees. Within two months, *Marchantia polymorpha* was abundant. After nearly one year, *Marchantia polymorpha* had become restricted to the wetter areas, although this species persisted in these areas, and *Funaria hygrometrica* achieved an average of 60% cover. After two years, *Funaria hygrometrica* had reduced in abundance and had disappeared from some areas, and *Polytrichum juniperinum* (A) had colonised.

2.4 Heathland

Roze (1993) investigated recolonisation after a flash fire, and humus fire (burning of organic layer, destroying seed bank) on a dry heathland of *Ulex europaeus* and *Erica cinerea* in Brittany. After the flash fire, *Erica cinerea* and *Ulex europaeus* grew rapidly, with bryophytes present at a low density for more than a year, dominated by *Ceratodon purpureus* (A). After the humus fire, the ground remained completely bare for seven months. *Ulex europaeus* was first species to return, followed by *Sedum anglicum*. *Holcus lanatus* colonised, with a 30-40% cover in some sites, completely altering heathland appearance. *Erica cinerea* recolonised three years after the fire, and both *Erica cinerea* and *Ulex europaeus* slowly increased in cover, with 75-85% and 10-25% cover after five years respectively. No bryophytes became established on the humus fire sites.

A second study conducted after a natural fire on heathland in Brittany (Clement and others 1980) reported *Ceratodon purpureus* (A) and *Funaria hygrometrica* (A) as the colonising bryophytes. Three years post fire, *F. hygrometrica* had virtually disappeared, as had *Ceratodon purpureus* on some areas, and *Polytrichum piliferum* (A) and *Polytrichum formosum* (A) had increased in abundance. On areas where damage was severe, *Marchantia polymorpha* (TL) was also noted in the early stages of recolonisation. Another study conducted several years later on the same fire site (Clement and Touffet 1988) noted a continued increase in the abundance of *Polytrichum* species, particularly *P. commune* (A).

Another study conducted in Brittany on moist heathland (Gloaguen 1993) described three phases of recolonisation, which was the classification system used later by De La Heras and others (1994):

- Colonisation phase (first 2 years): *Ceratodon purpureus* (A) and *Polytrichum piliferum* (A) appeared rapidly after the fire, and became dominated after two years. *Agrostis curtisii*, *Polytrichum formosum/commune* (A), *P. juniperinum* (A), *Ulex minor*, and *Betula pendula/pubescens* also colonised in the first year. *Erica ciliaris*, *Salix atrocinerea*, *Erica cinerea*, and *Calluna* did not appear until the second year. *Funaria hygrometrica* (A) was only present in the first year in very low cover.
- Competition phase (2-8 years): During this phase there was a sharp decrease in the cover of *C. purpureus* (A) and *P. piliferum* (A), and large increases in the cover of *P. formosum/commune* (A) which became dominant.
- Stabilisation phase (8-13 years): *C. purpureus* and *P. piliferum* were absent ten years after the burn. *P. formosum/commune* was still dominant with *Ulex minor*, *Agrostic curtisii, Betula pendula/pubescens, Erica cinerea*, *Salix atrocinerea, Calluna* and *Erica ciliaris* also present.

The studies that follow were carried out in the UK. Tucker (2003) undertook a review of the impacts of heather and grassland burning in the uplands on soil, hydrology and biodiversity, concentrating on the response of the vascular plant community. Information on fire characteristics (intensity, shape and speed of burns), effects on soils and hydrology, and vascular plant responses, can be found in this publication and references therein.

Hobbs & Gimingham (1984) experimentally burnt species poor (described as a typical species poor *Callunetum*) and species rich (described as a *Arctostaphyleto*-C*allunetum*, characterised by the presence of abundant *Arctostaphylos uva-ursi*, *Erica cineria* and many herb species) heathlands in Scotland. On the species rich heathland regrowth of *Calluna* was rapid, mainly vegetatively when the heathland was burnt at the pioneer or building stage, and *Campylopus paradoxus* (A), *Ceratodon purpureus* (A), *Polytrichum juniperinum* (A), *P. piliferum* (A) established quickly. When the pre-burn vegetation was mature or degenerate, there was no vegetative regrowth of *Calluna*, and recolonisation was much slower via seedlings. *C. purpureus* became dominant in many stands. *Hylocomium splendens* (P), *Hypnum jutlandicum* (P) and *Pleurozium schreberi* (P) reappeared quickly, usually small, and infrequent, and mainly from the centre of partly burnt mats, regardless of the pre-burn stage of heather growth. *H. jutlandicum* spread rapidly in several stands and reached high frequency levels in some.

On the species poor sites, *Calluna* reached 100% frequency by the end of first season when the pre-burn vegetation was pioneer. There was less vegetative regrowth when the pre-burn vegetation was building, and virtually none when it was mature or degenerate. Seedlings were present in all stands from 2nd growing season onwards. Due to the slower regrowth of *Calluna* via seedlings, *Deschampsia flexuosa* and *Vaccinium myrtillus* increase in cover, and when the pre-burn *Calluna* was mature, become dominant. The growth of bryophytes depended upon pre-burn presence. *H. jutlandicum* (P), *D. scoparium* (A), *Plagiothecium undulatum* (P), *Polytrichum longisetum* (A) regrew from parts of unburnt colonies. Pioneer species such as *C. paradoxus* (A), *C. purpureus* (A), *Leptodontuim flexifolium* (A) and *Pohlia nutans* (A) were limited in most stands.

From these observations, Hobbs & Gimingham (1984) recommended that a burn cycle of 12-15 years provided optimal regime for maintaining community diversity on species rich heathlands, and that burning older stands decreases species diversity, with the loss of grass, forbs, and lichen species. On species poor heathland they stated that there would be a spread of rhizomatous species if present in the pre-burn community, *Calluna* re-establishment would be slower via seedlings, and bare ground would persist for several years, if old stands were burnt.

Hobbs & Gimingham (1987) stated that initial regeneration on burnt heathland was via algae, acrocarpous mosses (*Ceratodon purpureus* (A), *Polytrichum juniperinum* (A), and *P. piliferum* (A), and lichens; grasses colonised shortly after the fire; *Erica* species may become abundant before *Calluna*, and increased Ericaceaous cover, was associated with increased *Hypnum jutlandicum* (P) and *Pleurozium schreberi* (P).

In addition to grassland, Southorn (1976) studied rapid fire sites on heathlands. These were located at Chobham Common (lowland *Calluna* Heath), Morden Bog (wet lowland *Calluna* heath), South Haven Peninsula (dry and wet lowland *Calluna* heath), and Thursley Common (dry and wet lowland *Calluna* heath). Results showed acrocarpous mosses, particularly *Ceratodon purpureus* (A), *Pohlia nutans* (A), and species of *Campylopus* (A) and *Polytrichum* (A) were the most rapid colonisers. The recolonisation of dwarf shrubs was slower than that of the vascular plants of the grassland sites. Pleurocarpous mosses and leafy liverworts appeared later in the succession when angiosperm cover was more complete.

Coppins & Shimwell (1971) studied eight sites at Skipwith Common and one site at Allerthorpe Common, both dry, lowland heathlands in Yorkshire, managed by burning since 1940. Bryophytes or lichens with a biomass of apparently greater than 0.05 g in a 20x20 cm quadrat, were dried and weighed. Bryophytes present in smaller quantities were represented by a + and valued as 0.01 g in the calculation of the plot biomass. Table 5 summarises the results of Coppins & Shimwell (1971), with the mean age of *Calluna* and its stage of growth, and the dominant and subordinate species of bryophytes present.

In 1976, a severe moorland fire at Rosedale Moor on the North York Moors destroyed the surface vegetation and caused major alterations to the underlying soils and peat of *Calluna*-dominated moorland. Before the fires, the vegetation was dominated by a mosaic of even-aged stands of *Calluna* managed as grouse moor, blanket bog on the deeper peat and *Calluna-Vaccinium* heath on the shallow organic and mineral soils. Since the fire, vegetation surveys have been undertaken at permanent, marked, sites by Maltby and others (1990):
Pioneer phase (1976-1979): *Ceratodon purpureus* (A), *Pohlia nutans* (A) and *Dicranella heteromalla* (A) colonised, with *Polytrichum piliferum* (A) appearing during the third season

Table 5: Summary of the results of Coppins & Shimwell (1971), showing the bryophyte species, and % contribution of dominant species to total bryophyte biomass

***Calluna* Age (Mean Years)**	***Calluna* Stage**	**Dominant bryophyte species**	**Subordinate bryophyte species**
5.8	Pioneer	*Gymnocolea inflata* (LL) (63) *Pohlia nutans* (A) (35)	*Calypogeia fissa* (LL) *Campylopus flexuosus* (A) *Campylopus pyriformis* (A) *Cephalozia bicuspidata* (LL) *Cephalozia connivens* (LL) *Cephaloziella spp* (LL)
6.7	Pioneer	*Pohlia nutans (75)*	*Cephalozia bicuspidata* (18) *Gymnocolea inflata* (6) *Calypogeia fissa* *Cephaloziella spp* *Orthodontium lineare* (A)
9.6	Pioneer /Building	*Pohlia nutans (76)*	*Lepidozia setacea* (LL) *(12)* *Cephalozia bicuspidate* (11) *Calypogeia fissa* *Cephalozia connivens* *Cephaloziella spp* *Gymnocolea inflata* *Orthodontium lineare*
12.9	Building	*Pohlia nutans* (99.5)	*Campylopus pyriformis* *Cephaloziella spp* *Gymnocolea inflata* *Orthodontium lineare*
16.5	Building	*Pohlia nutans* (56) *Cephalozia connivens* (31)	*Calypogeia fissa* (12) *Campylopus flexuosus* *Campylopus pyriformis* *Cephalozia bicuspidata* *Cephaloziella spp* *Gymnocolea inflata* *Orthodontium lineare*
20.8	Mature	*Orthodontium lineare* (58)	*Dicranum scoparium* (A) (13) *Cephaloziella* spp (11) *Pohlia nutans* (10) *Gymnocolea inflata* (5) *Calypogeia fissa* *Campylopus pyriformis* *Cephalozia bicuspidate* *Cephalozia connivens* *Lepidozia reptans* (LL)
23.4	Mature	*Pohlia nutans* (32) Mixed liverworts (29)	*Cephalozia connivens* (17) *Calypogeia fissa* (7) *Cephaloziella* spp (5) *Orthodontium lineare* (5) *Odontoschisma denudatum* (LL) (3) *Dicranum scoparium* (2) *Aulocomnium androgynum* *Campylopus pyriformis* *Cephalozia bicuspidata* *Kindbergia praelonga* (*Eurhynchium praelongum*) (P) *Gymnocolea inflata* *Lepidozia setacea*
23.4	Mature/ Degenerate	*Campylopus flexuosus* (54)	*Lepidozia setacea* (17) *Odontoschisma denudatum* (17) *Orthodontium lineare* (4) *Pohlia nutans* (4) *Gymnocolea inflata* (3) *Calypogeia fissa* *Campylopus pyriformis* *Cephalozia bicuspidata* *Cephalozia connivens* *Cephaloziella* spp
19.0	Degenerate /Pioneer	*Orthodontium lineare* (63) *Odontoschisma denudatum* (25)	*Cephaloziella* spp (5) *Pohlia nutans* (5) *Calypogeia fissa* *Campylopus flexuosus* *Campylopus pyriformis* *Cephalozia connivens* *Gymnocolea inflata* *Lepidozia setacea*

Rapid development phase (1979-1982): Rapid substrate and ecological change, with the expansion of *Polytrichum* species (A), *P. piliferum* being the most prominent *Polytrichum* species on ashed surfaces initially, reaching its maximum cover in 1980-1981, and then decreasing in cover in 1982 as *P. commune* expanded. On intact peat surfaces, *P. commune* was the most prominent *Polytrichum* species initially. By 1982, virtually none of the intact peat surface was exposed. On ash surfaces, *Ceratodon purpureus* declined dramatically, being replaced by *Polytrichum commune*. Residual charred peat was first colonised by *P. piliferum*, followed by *P. commune*. Granulated peat was colonised by *Polytrichum* spp. Exposed stone and regolith was colonised by *Dicranella heteromalla*, *P. piliferum* and *P. commune*. By 1982 *P. piliferum* was the dominant species. *D. heteromalla* and *Pohlia nutans* obtained peak in 1981, but by 1982 were largely dead and replaced by *P. piliferum* and *Calluna*.

Consolidation phase (1982-1986): Characterised by changes in relative proportions of species rather than continued change in overall cover. There was a progressive increase in *P. commune* and decline in *P. piliferum* and other mosses. By 1984, *D. heteromalla* and *P. nutans* had disappeared, although nearly 65% of cover was bryophyte dominated communities, ~6% vascular plant and nearly 30% bare ground/peat.

Another paper by Thomas and others (1994) reported the chemical and physiological constraints on moss establishment from spores on experimental plots that recreated the conditions after the 1976 fires, i.e. superficial charring (SF); Charring of fibrous peat and the removal of 5-10 cm of organic matter (CF); Charring of thinner (<40 cm) well-humified peat, and the removal of 4-10 cm of organic matter (CH), and complete ashing of about 25 cm of humified peat (AH). The temperature of the burning peat was 750 ^{o}C on SF, 683 ^{o}C on CF, 1140 ^{o}C on CH, and 750 ^{o}C on AH. Bryophyte regeneration greatest on AH and CH. The species present were *Polytrichum* species, *Dicranella heteromalla*, *Funaria hygrometrica*, *Ceratodon purpureus*, *Campylopus pyriformis*, *Pohlia nutans*, *Calypogeia fissa*, and *Cephalozia bicuspidata*.

2.5 Summary of results from previous studies

To make between study comparisons easier, the primary colonising species recorded in the above studies are summarised for each habitat in Table 6A to 6D.

Table 6: A summary of the primary colonising species at the sites reported in the literature review

A. Alluvial deposits and sand

(Esposito and others 1999)	**Low intensity burn** *Funaria hygrometrica* (A) and *Bryum torquescens* (A), replaced by *Tortella flavovirens* (A) and *Pleurochaete squarrosa* (A)	**High intensity burn** *Funaria hygrometrica* (A) and *B.torquescens* (A), replaced by *Barbula convluta* (A) and *Bryum dunense* (A)

C. Grassland

(Antos and others 1983)	*Bryum caespiticum* and *Ceratodon purpureus*	
(Southorn 1976)	**Low intensity burn** Species characteristic of the pre-burn vegetation	**High intensity burn** *F. hygrometrica* (A) dominant, with *C. purpureus* (A), *Bryum argenteum* (A) and tuberous *Bryum* species (A) present

B. Forest/woodland

(Duncan and Dalton 1982)	*Marchanita berteroana* (TL) and *F. hygrometrica* (A) replaced by *Ceratodon purpureus* (A) along with *Polytrichum juniperinum* (A)	
(Brasell & Mattay 1984)	*M. berteroana* (TL) and *F. hygrometrica* (A), replaced by *C. purpureus* (A)	
(Brasell and others 1986)	*M. berteroana* (TL), *F. hygrometrica* (A), and *C. purpureus* (A)	
(Eversman & Horton 2004)	*C. purpureus* (A), *P. juniperinum* (A), *Polytrichum piliferum* (A) and *Bryum* species (A), particularly *B. caespiticium*	
(Puche & Gimeno 2000)	**Low intensity burn** Bryophytes typical of the pre-burn vegetation, plus such as *Acaulon* species (A) and *Pottia* species (A), and colonist species *Bryum rubens* (A), *B. ruderale* (A), *Trichostomum crispulum* (A), *T. brachydontium* (A) and *Weissia* species (A)	**High intensity burn** *F. hygrometrica* (A)
(De La Heras and others 1990)	*Bryum bicolour* (A) and *F. hygrometrica* (A)	
(De La Heras-Ibanez and others 1992)	*F. hygrometrica* (A), *B. bicolour* (A), *B. convoluta* (A), *B. torquescens* (A), *Bryum capillare* (A) and *Cephaloziella divaricata* (LL).	
(De La Heras and others 1994)	*F. hygrometrica* (A), *B. bicolour* (A) and *B. convoluta* (A).	
(Schimmel & Granstrom 1996)	**Low intensity burn** *Hylocomium splendens* (P)	**High intensity burn** *C. purpureus* (A), *Polytrichum commune* (A) and *P. juniperinum* (A)
(Butin & Kappich 1980)	*Funaria hygrometrica* (A), *Marchantia polymorpha* (TL) and *Ceratodon purpureus* (A)	
(Jahn 1980)	*Funaria hygrometrica* (A), *Marchantia polymorpha* (TL) and *Polytrichum juniperinum* (A)	
(Ariz & Indurain 1996)	**Slow fires** *Hypnum cupressiforme* (P), *Weissia controversa* (A), *Pleuridium acuminatum* (A), *Calypogeia trichomanis* (LL), *Scleropodium purum* (P) and *Bryum* species (A)	**Quick fires** *Hypnum cupressiforme* (P), *Polytrichum formosum* (A), *Pleuridium acuminatum* (A), *Calypogeia trichomanis* (LL), and *Bryum* species (A).

D. Heathland

Brittany (Roze 1993)	**Low intensity burn** *C. purpureus* (A)	**High intensity burn** No bryophytes
Brittany (Gloaguen 1993)	*C. purpureus* (A) and *P. piliferum* (A)	
Brittany (Clement and others 1980)	*Ceratodon purpureus* (A), *Funaria hygrometrica* (A) *Polytrichum piliferum* (A), *Polytrichum formosum* (A) and *Marchantia polymorpha* (TL)	
UK (Hobbs & Gimingham 1984)	Species rich, pioneer or building preburn: *Campylopus paradoxus* (A), *C. purpureus* (A), *P. juniperinum* (A), *P. piliferum* (A) established quickly. Species rich, mature or degenerate preburn: *C. purpureus* (A) became dominant in many stands. *H splendens* (P), *Hypnum jutlandicum* (P) and *Pleurozium schreberi* (P) Species poor: depended upon pre-burn presence. *H. jutlandicum* (P), *Dicranum scoparium* (A), *Plagiothecium undulatum* (P), and *Polytrichum longisetum* (A). Pioneer species such as *C. paradoxus* (A), *C. purpureus* (A), *Leptodontuim flexifolium* (A) and *Pohlia nutans* (A) limited in most stands	
UK (Hobbs & Gimingham 1987)	*C. purpureus* (A), *P. juniperinum* (A) and *P. piliferum* (A)	
UK (Southorn 1976)	*C. purpureus* (A), *P. nutans* (A), and *Campylopus* (A) and *Polytrichum* (A) species	
UK (Coppins & Shimwell 1971)	*Gymnocolea inflata* (LL) and *P. nutans* (A)	
UK (Maltby and others 1990)	*C. purpureus* (A), *P. nutans* (A) and *Dicranella heteromalla* (A), with *P. piliferum* (A) appearing during the third season	
Recreated post fire conditions (Thomas and others 1994)	*Polytrichum* species (A), *D. heteromalla* (A), *F. hygrometrica* (A), *C. purpureus* (A), *Campylopus pyriformis* (A), *P. nutans* (A), *Calypogeia fissa (LL)*, and *Cephalozia bicuspidata* (LL)	

From these tables it can be seen that the most commonly recorded post burn coloniser was *Ceratodon purpureus*, being recorded in thirteen of the studies. The next most common was *Funaria hygrometrica*, recorded in ten studies, *Polytrichum* species in nine studies, and *Bryum* species in seven studies. *Pohlia* was a colonising species in four studies, all of which were carried out on heathlands. Other species specific to heathland recolonisation were *Campylopus* species (three studies) and *Dicranum scoparium* (one study).

3 Field study: methods

3.1 Site description

The North York Moors is the most easterly area of moorland in Britain, and one of the largest continuous tracts of heather moor in the British Isles (Jerram, Clayden & Rees 1998). Jerram (1998) described the extent and characteristics of Spaunton Moor, as extending from Hutton-le-Hole and Lastingham, north to Rosedale Head. The moor reaches its highest point of 410m, at its northernmost point at the narrow, steep sided Blakey ridge. This ridge expands south east of Thorgill Head into a broad plateaux, Shooting House Hill. The ground slopes southwards from Shooting House Hill and is divided into a series of rounded ridges by four south flowing streams, Hutton Beck, Loskey Beck, Hole Beck and Tranmire Beck. Further detailed descriptions of the topography, geology, soil and bioclimate of Spaunton Moor are given in Jerram (1998).

The high moorland of Blakey Ridge and Shooting House Hill is covered by dry heath, H12a *Calluna vulgaris-Vaccinium myrtillus* heath, *Calluna* sub-community and H9c *Calluna vulgaris-Deschampsia flexuosa* heath, species-poor sub-community (Jerram 1998). H12a is the principal plant community of the higher elevations of the Spaunton Moor. *Calluna* dominates, with *Vaccinium myrtillus* occasional to frequent in the sub community. On Spaunton Moor, dry heath H12a (*Calluna vulgaris – Vaccinium myrtillus* heath, *Calluna vulgaris* sub-community) accounts for approximately 50% of the total moorland area and the wet heath M16, 20% (Figure 1). The area in hectares covered by each vegetation type on Spaunton Moor is given in Table 7.

Figure 1: The percentage of each vegetation type present on Spaunton Moor

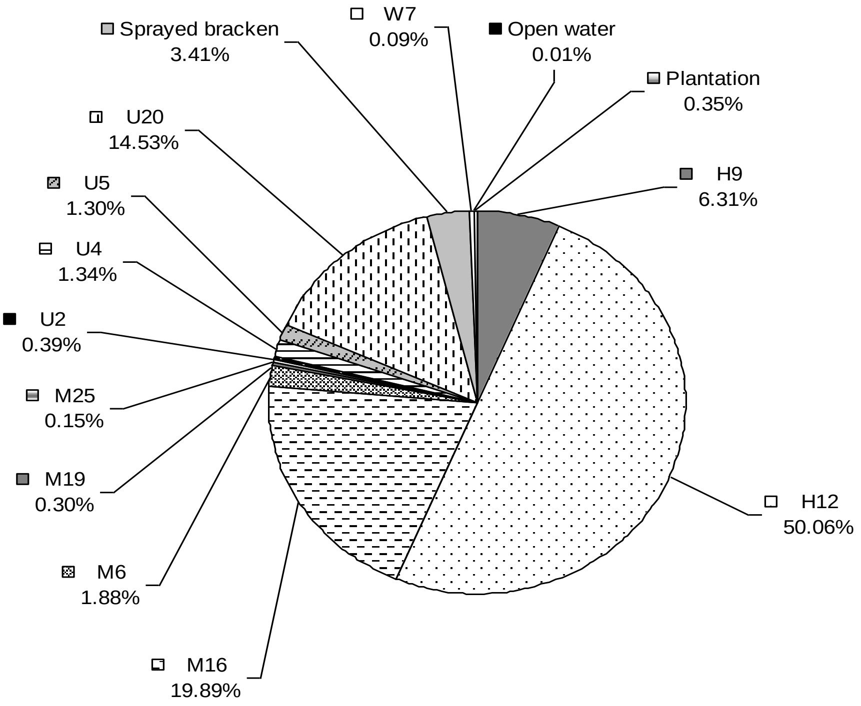


Table 7: The vegetation types on Spaunton Moor, and number of hectares covered by each has a range of vegetation types (Jerram 1998)

NVC type	Vegetation type	Hectares
H9	*Calluna vulgaris – Deschampsia flexuosa* heath	214
H12	*Calluna vulgaris – Vaccinium myrtillus* heath	1696.8
M16	*Erica tetralix – Sphagnum compactum* wet heath	674.2
M6	*Carex echinata – Sphagnum recurvum/ auriculatum* mire	63.6
M19	*Calluna vulgaris – Eriophorum vaginatum* blanket mire	10
M25	*Molinia caerulea – Potentilla erecta* mire	5
U2	*Deschampsia flexuosa* grassland	13.1
U4	*Festuca ovina – Agrostis capillaris – Galium saxatile* acid grassland	45.3
U5	*Nardus stricta – Galium saxatile* grassland	44.2
U20	*Pteridium aquilinum – Galium saxatile*	492.5
W7	Alder – ash woodland	3
Sprayed bracken		115.5
Open water		0.5
Plantation		12
	Total	3389.7

3.2 Selection of plots

Potential sites were identified, and the final sites chosen by consensus between the author, an English Nature representative, the land owner and the keeper. Sites were selected that were deemed ‘typical’ for the respective NVC type and where areas of heather of different ages were in close proximity to each other so that the effect of potential confounding factors such as slope, aspect, altitude and environmental conditions, were reduced.

Four H12a sites were selected. Each site consisted of eight plots which had been burnt 1, 3, 5, 7, 10, 15, 20 or over 25 years previously. Three M16d sites were selected where five or six plots of different ages were in close proximity to one another. As the wet heath has been less intensively managed, the age structure was less well developed. As a consequence, only 3, 7 and 25 years post-burn were represented on all three sites. The other ages represented were 5 (2 sites), 10 (1 site), 15 (2 sites), and 20 (2 sites) years post-burn. One site had two plots 7 years post-burn that varied considerable in the level of soil moisture, demonstrating that the M16d wet heath on Spaunton Moor was a mosaic which was comprised of areas of varying moisture levels along the moisture gradient. Rather than choosing to survey either the wetter or drier of these plots, both were surveyed and designated 7yrD (7 years dry) and 7yrW (7 years wet). The same occurred on a second site with plots that were 25 years post-burn, and again, both were surveyed (25yrD and 25yrW).

As far as possible, burns of degenerate heather were avoided. However, these areas were only easily identified from the remnants of heather stems at the very early stages of recolonisation. A wooden stake, with a label indicating the age of burn, was placed in the centre of each plot. Maps showing the location of each site, and the position of the plots in relation to each other within each site, are given in Appendix 1.

3.3 Surveying techniques

Eight 10x10 cm quadrats were surveyed using a pre-defined arrangement, 1 m and 2 m from the central stake, north, south, east, and west of the stake, precluding the subjective selection of ‘typical’ quadrats. Within each 10x10 cm quadrat, vegetation height, percentage cover of vascular plants, and the number of growing tips and percentage cover of bryophytes were recorded. Where there were a large number of very small bryophytes or a mixture of species, which made it difficult to count the growing tips in the field, the entire 10x10 cm surface was collected. This was kept moist, the bryophytes were counted using a dissecting microscope, and the sample replaced within 4 days. The number of growing tips was used for several reasons:

- Acrocarpous mosses are generally unbranched; each plant tends to have a single growing tip. A pleurocarpous moss can have several leading edges, and determining whether these are from the same plant or not, particularly when there is a dense mat of plants, is very difficult.
- Plants of the same species may produce different numbers of growing tips depending upon the environmental conditions. When conditions are favourable, one plant may produced a substantially greater number of growing tips compared to one growing in less favourable conditions. Therefore, the number of growing tips gives a better indication as to the suitability of the environment for that species.
- Counting growing tips is a quantitative measure that can be readily analysed statistically.

Percentage cover is a subjective measure which can vary between recorders. However, percentage cover is still a useful measure, particularly with bryophytes, as a large number of growing tips of a small acrocarpous species may cover a very small area, whereas a few pleurocarpous mosses can cover a much larger area. Therefore, percentage cover gives a ‘sense of proportion’.

Ideally, we wanted to obtain a dataset comprising a large number of quadrats, recorded quantitatively as described above, to provide a representative picture of the abundance of each bryophyte species. However, due to the patchiness of the bryophyte flora, and the restrictions of time and resources, it was considered impractical to record such a large number of quadrats. As it was deemed important to gain an overview of the bryophyte flora present, to determine whether any particular species was under- or over-represented in the dataset obtained by surveying the quadrats, three 10m transects, spaced 2m apart, were surveyed in each plot. The presence of bryophyte species was recorded at each metre along each transect, resulting in thirty potential ‘hits’ per plot. This method of recording would also give a better overview of the bryophyte flora for use in the TWINSPAN analysis (see below). To avoid edge effects, no surveying was conducted within 2m of the edge of the selected area. Examples of the record sheets used are given in Appendix 2.

Nomenclature follows that of Smith (2004) for the mosses, and Paton (1999) for the liverworts. Previous, familiar, nomenclature is given in brackets in Table 8 where deemed to be helpful. Due to the variation of *Sphagnum* species in the field, *Sphagnum* species were grouped into their taxonomic sections for analysis, rather than being analysed by species (Table 9). This reduces the potential for error, whilst maintaining some insight into the distribution of the different morphological types that would be lost if all *Sphagnum* species were grouped together.

3.4 Analysis

Species abundance in relation to the age post-burn or stage of heather development was analysed using the Friedman test. This test was chosen in preference over the Kruskal-Wallis test, as the Friedman test takes into account the dependency between plots when a block design such as the one used in the current study is employed; samples have to be independent to be analysed using the Kruskal-Wallis test.

Abundance data was used in a principal components analysis, to identify groups of species, and try to determine which factors are common to those species grouped together that may be influential in the distribution of species across the age of burns.

The presence of species recorded along the three transects was used to group the plots on the basis of species composition using the TWINSPAN classification program (Hill and Smilauer 2005). No weight was given to any species, and default options were used for the number of pseudospecies.

The relationships between vegetation height and area cover of vascular plants with bryophyte abundance were analysed using the non-parametric Spearman's rank correlation. This was also used to analyse relationships between bryophyte species.

4 Field study: results

4.1 Bryophytes recorded on the sites at Spaunton Moor.

Thirty-nine bryophyte species were recorded in total, 23 species on the H12a sites, and 30 species on the M16d sites (Table 8).

Table 8: Acrocaprous mosses, pleurocarpous mosses, leafy liverworts and *Sphagnum* species that were present (+) or absent (-) on the H12a and M16d moorland sites surveyed on Spaunton Moor

Acrocarpous mosses		
	H12a	**M16d**
Aulacomium palustre	-	+
Bryum capillare	+	-
Campylopus flexuosus (*paradoxus*)	+	-
Campylopus introflexus	+	+
Campylopus pyriformis	+	+
Ceratodon purpureus	+	-
Dicranum scoparium	+	+
Leptodontium flexifolium	+	-
Leucobryum glaucum	+	+
Mnium hornum	+	-
Orthodontium lineare	+	-
Pohlia nutans	+	+
Polytrichastrum (*Polytrichum*) *formosum*	+	+
Polytrichum commune	+	+
Polytrichum juniperinum	+	-

Pleurocarpous mosses		
	H12a	**M16d**
Brachythecium rutabulum	+	+
Hylocomium splendens	-	+
Hypnum jutlandicum	+	+
Kindbergia praelonga (*Eurhynchium praelongum*)	+	+
Plagiothecium undulatum	+	+
Pleurozium schreberi	+	+
Pseudoscleropodium (*Scleropodium*) *purum*	-	+
Rhytidiadelphus squarrosus	+	+

Leafy liverworts		
	H12a	**M16d**
Barbilophozia floerkei	+	-
Calypogeia fissa	-	+
Cephalozia connivens	-	+
Cephaloziella divaricata	+	+
Gymnocolea inflata	-	+
Kurzia pauciflora	-	+
Lophocolea bidentata	+	-
Odontoschisma sphagni	-	+

***Sphagnum* species**		
	H12a	**M16d**
Sphagnum denticulatum (*auriculatum*)	-	+
Sphagnum capillifolium	-	+
Sphagnum compactum	-	+
Sphagnum palustre	-	+
Sphagnum papillosum	-	+
Sphagnum recurvum	-	+
Sphagnum subnitens	-	+
Sphagnum tenellum	-	+

Table 9: Classification of the *Sphagnum* species recorded on the M16d moorland into their respective taxonomic sections (Smith 2004)

***Sphagnum* section**	**Species recorded**
Sphagnum	*S. palustre*, *S. papillosum*
Rigida	*S. compactum*
Acutifolia	*S. capillifolium*, *S. subnitens*
Cuspidata	*S. recurvum*, *S. tenellum*
Subsecunda	*S. denticulatum*

As can be seen from the Table 8, the M16d moorland had fewer acrocarpous mosses, but a greater number of pleurocarpous mosses and liverworts. Fourteen species were recorded on both the H12a and M16d moorland sites. Nine species were recorded only on the H12a sites, and 16 only on the M16d sites, of which eight were *Sphagnum* species.

4.2 H12a dry heath

4.2.1 Bryophyte abundance on the H12a moorland

Campylopus introflexus was most the most abundant bryophyte species the first year post-fire, with *C. pyriformis*, *Cephaloziella divaricata* and *Ceratodon purpureus* also prominent (Table 10). *C. introflexus* persisted throughout the age range, albeit in small numbers in the older stands of heather. *C. divaricata* and *C. pyriformis* also persisted, except in the oldest stands. Other species present only in the younger sites included *Bryum capillare*, *Leptodontium flexifolium* and *Polytrichum juniperinum*. Species restricted to older plots included *Barbilophozia floerkei*, *Campylopus flexuosus*, *Lophocolea bidentata*, *Mnium hornum*, *Plagiothecium undulatum* and *Rhytidiadelphus squarrosus*. *D. scoparium* and *H. jutlandicum* were most abundant in the older stands of heather, however, they were occasionally present in younger stands, where they seem to have survived the heather burning process, rather than recolonisation of burnt ground occurring.

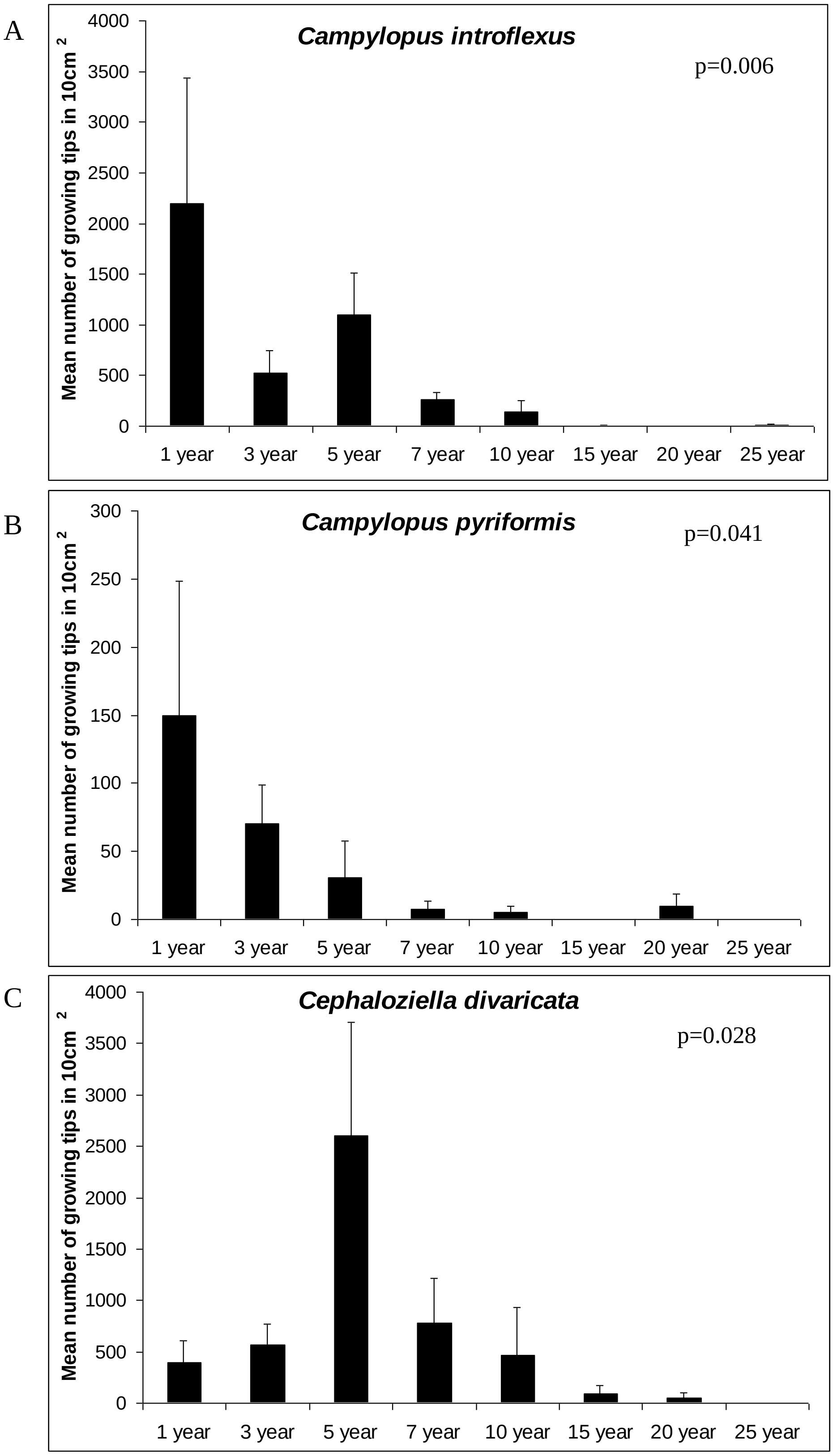
The mean number of stems recorded in a 10x10 cm quadrat for each age since last burn are given in Table 10, and at each stage of heather development in Table 11. Abundance is presented graphically when a statistically significant difference between age of last burn or stage of heather development was detected; standard errors are provided on the graphs for these distributions.

Four species showed a statistically significant difference in abundance in relation to age (Figure 2). *Hypnum jutlandicum* increased in abundance with the increasing age of heather (p=0.002), and *Campylopus introflexus* (p=0.006), *Campylopus pyriformis* (p=0.041), and *Cephaloziella divaricata* (p=0.028) decreased in abundance. *Dicranum scoparium* showed a strong trend towards an increase in abundance with increasing age of the heather stand (p=0.053), therefore the distribution of this species is also represented graphically (Figure 2).

Table 10: The mean number of growing tips recorded in a 10x10 cm area for each species, on each age of burn on the H12a moorland. Each age post-burn was represented on all four sites surveyed

	Years since previous burn							
	1	**3**	**5**	**7**	**10**	**15**	**20**	**25**
Acrocarpous mosses								
Bryum capillare	1.0	0	0	0	0	0	0	0
Campylopus flexuosus	0	0	0	0	8.5	5.3	0	13.8
Campylopus introflexus	2200.8	525.5	1096.8	266.0	140.3	3.5	2.5	11.3
Campylopus pyriformis	150.0	70.3	31.0	7.3	5.0	0	9.5	0
Ceratodon purpureus	188.5	0	0	0	0	0	0	0
Dicranum scoparium	0	0	1.0	0	5.8	3.0	3.3	15.5
Leptodontium flexifolium	5.8	2.3	0	0	0	0	0	0
Mnium hornum	0	0	0	0	0	0.5	0	0
Pohlia nutans	4.5	10.8	1.0	0	0.5	0	0	0
Polytrichastrum formosum	0	0	0	3.3	0.8	0	0	0
Polytrichum juniperinum	2.5	0	0	0	0	0	0	0
Pleurocarpous mosses								
Brachythecium rutabulum	0	0	0	0.3	2.5	0	3.3	0
Kindbergia praelonga	1.5	0	0	1.0	3.0	2.5	2.5	4.3
Hypnum jutlandicum	4.0	1.5	0	0	95.3	111.5	39.0	373.0
Plagiothecium undulatum	0	0	0	0	0	0.8	0	1.5
Rhytidiadelphus squarrosus	0	0	0	0	4.3	0	4.0	0
Leafy liverworts								
Barbilophozia floerkei	0	0	0	0	0	0.8	0	0
Cephaloziella divaricata	396.5	562.3	2601.8	779.0	467.5	86.5	49.5	0
Lophocolea bidentata	0	0	0	0.3	18.3	2.5	23.8	15.3
Number of species	10	6	5	7	12	10	9	7

Figure 2: The mean number of growing tips recorded in a 10x10 cm area of A) *Campylopus introflexus*, B) *Campylopus pyriformis*, C) *Cephaloziella divaricata*, D) *Hypnum jutlandicum*, and E) *Dicranum scoparium* for each age on the H12a dry heath sites.



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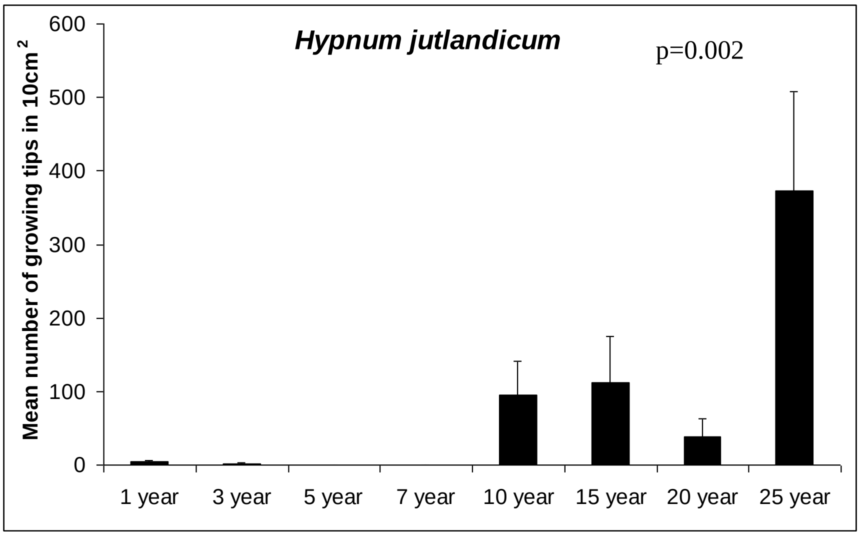

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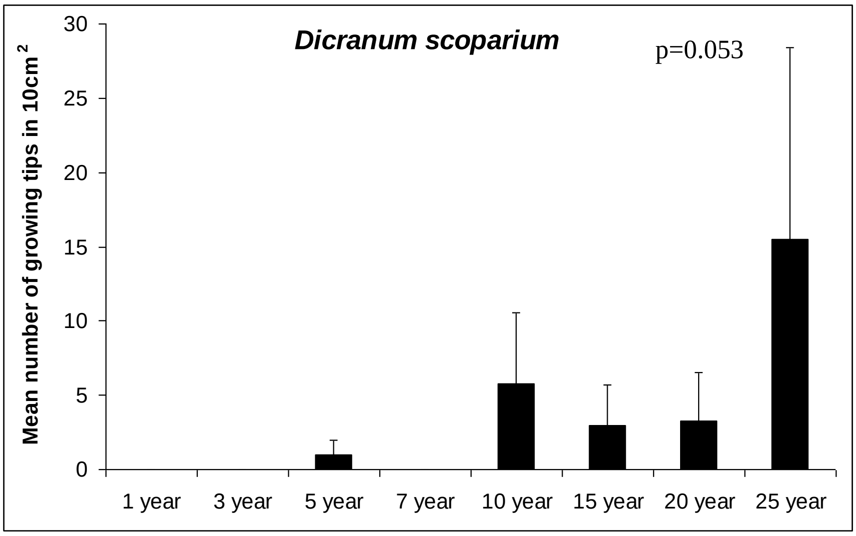
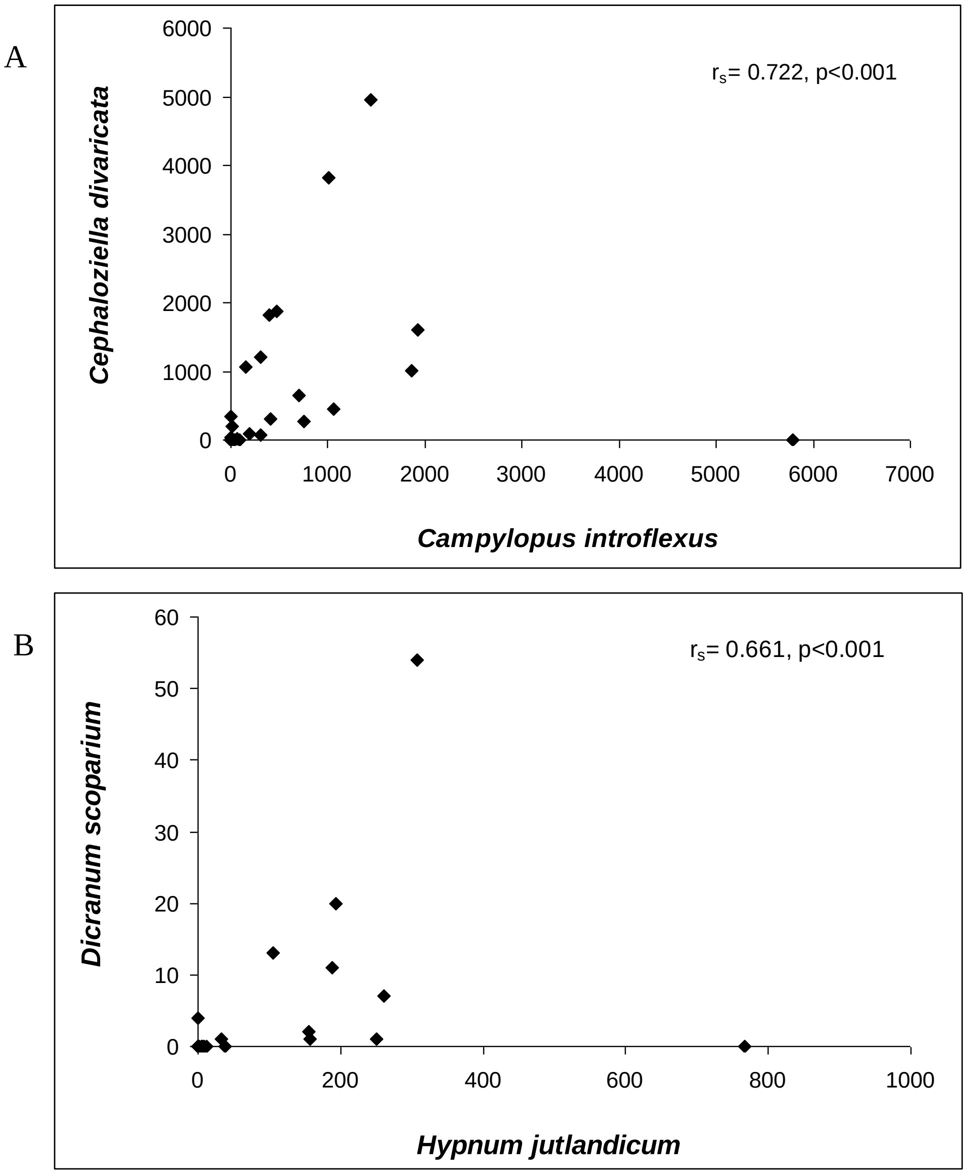


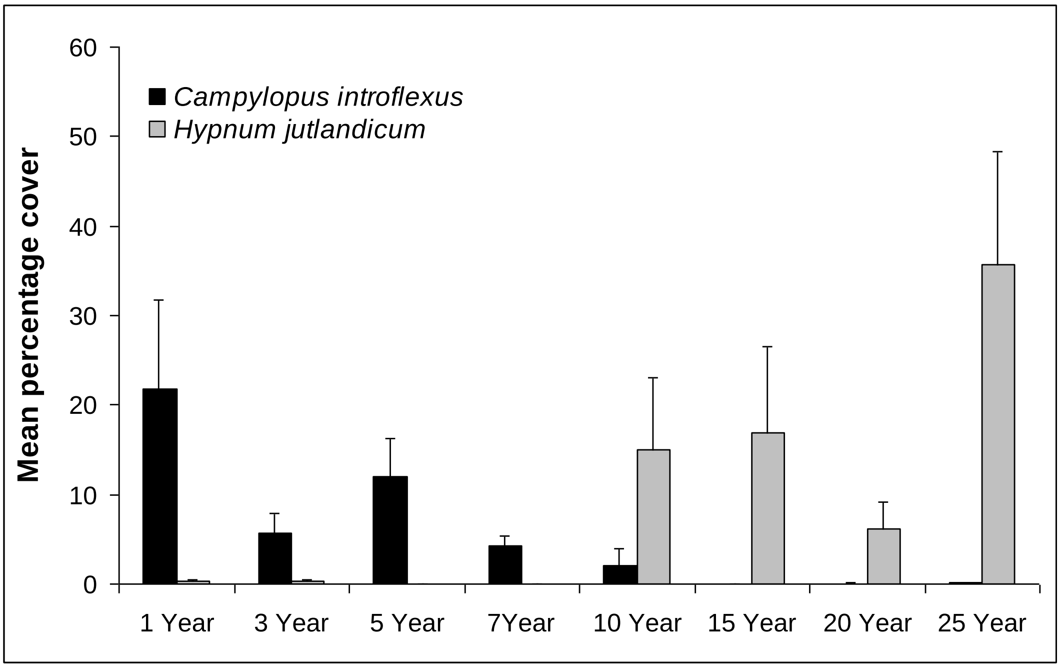
From these graphs it can be seen that there is some similarity between the pattern of abundance of *C. introflexus* and *C. divaricata*, and also between *H. jutlandicum* and *D. scoparium*. During the survey of the H12a sites, *C. divaricata* was most commonly found growing between the stems of *C. introflexus*, and there is a strong positive correlation between these two species (Figure 3A). There was also a strong positive correlation between the number of stems of *H. jutlandicum* and *D. scoparium* (Figure 3B).

Figure 3: The correlation between the number of growing tips of A) *Campylopus introflexus* and *Cephaloziella divaricata* and B) *Hypnum jutlandicum* and *Dicranum scoparium* on the H12a sites.



Although the mean number of stems of *C. introflexus* recorded in the 1 year old plots is substantially greater than the number of stems of *H. jutlandicum* recorded in the 25 year plots (2200.8 and 373 growing tips, respectively) due to the branching, creeping, pleurocarpous growth form of *H. jutlandicum* the mean percentage area covered by this species on the 25 year plots is nearly double that of *C. introflexus* on the 1 year plots (Figure 4).

Figure 4: The mean percentage area cover of *Campylopus introflexus* and *Hypnum jutlandicum* for each age post-burn on the H12a sites.



When species were grouped together (acrocarpous, pleurocarpous, mosses, liverworts, and bryophytes), there was a statistically significant effect of age on the abundance of acrocarpous mosses (p=0.009), pleurocarpous mosses (p=0.005), and all mosses (p=0.038), but not liverworts or all bryophytes (Figure 5).

By combining the results for the sites at each stage of heather growth, we get a clearer picture of the preference for each species (Table 11). The pioneer stages are dominated by *C. introflexus*, *C. divaricata* and *C. pyriformis*, with other species characteristic of post fire or disturbance recolonisation present, such as *C. purpureus*, *L. flexifolium*, *P. juniperinum*, and *P. nutans*. Species initially recorded in the building stage included *C. flexuosus*, *D. scoparium* and *L. bidentata*, and these species increased in abundance with increasing heather maturity. Of the four species that showed a statistically significant difference in the number of growing tips in relation to age, three continued to show a statistically significant difference in abundance when the sites were group in relation to the stage of heather development: *H. jutlandicum* (p=0.008), *C. introflexus* (p=0.017), and *C. divaricata* (p=0.013) (Figure 6).

All three groups of bryophytes that showed a statistically significant difference in the number of growing tips in relation to age, continued to show a statistically significant difference in the number of growing tips when the sites were grouped in relation to the stage of heather development. In addition, the distribution of liverworts became statistically significant once the sites were grouped by stage of heather development: acrocarpous mosses (p=0.017), pleurocarpous mosses (p=0.026), all mosses (p=0.050), and liverworts (p=0.017), but not all bryophytes (Figure 7).

Figure 5: The mean number of growing tips recorded in a 10x10 cm area of A) acrocarpous mosses, B) pleurocarpous mosses, and C) total number of moss stems, for each age on the H12a dry heath sites

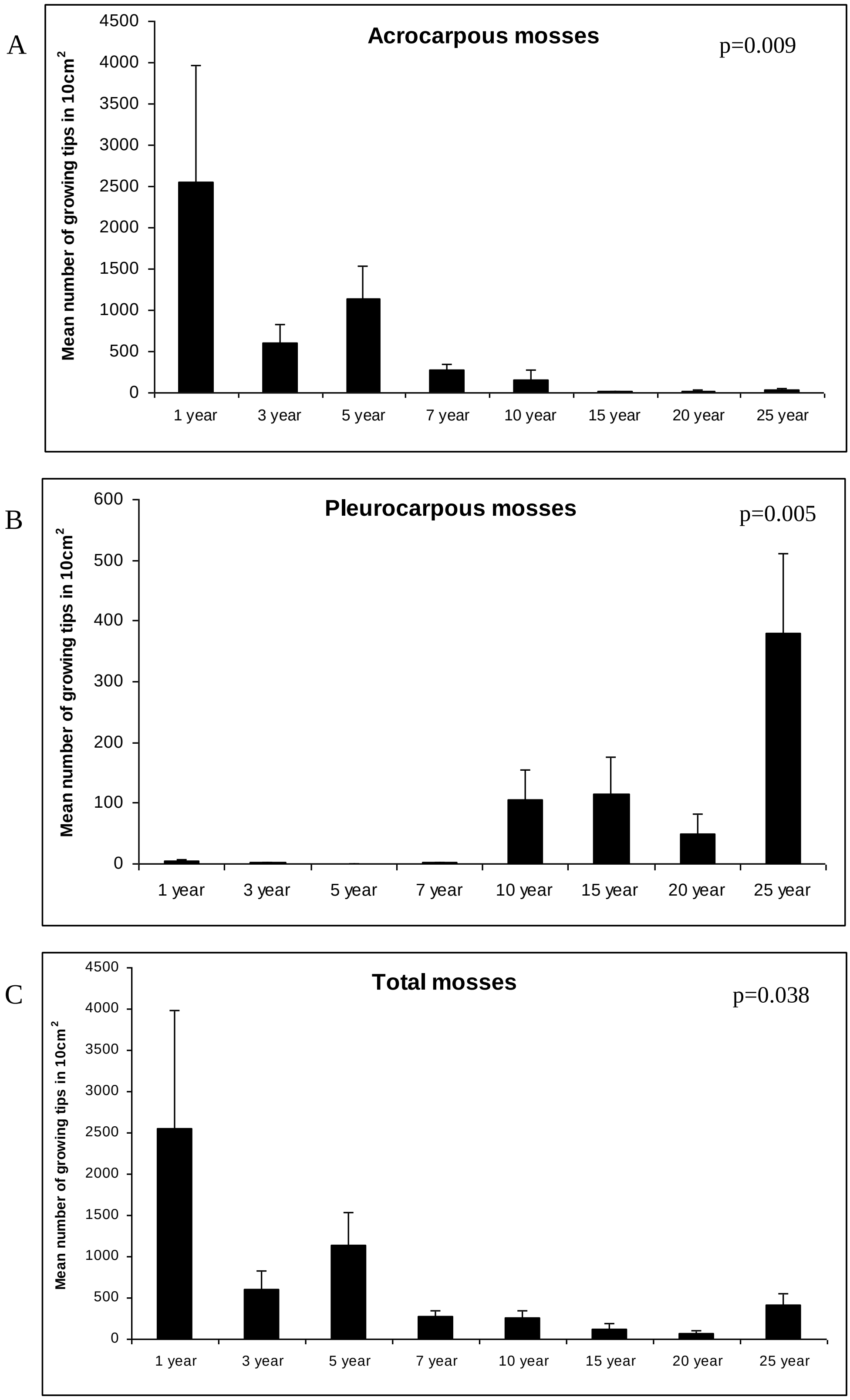


Table 11: The mean number of growing tips recorded in a 10x10 cm area for each species, for each stage of heather growth on the H12a sites

	Stage of heather growth			
	Pioneer (2 plots per site - 8 plots in total)	**Building** (3 plots per site - 12 plots in total)	**Mature** (2 plots per site – 8 plots in total)	**Degenerate** (1 plot per site – 3 plots in total)
Acrocarpous mosses				
Bryum capillare	0.5	0	0	0
Campylopus flexuosus	0	2.8	2.6	13.8
Campylopus introflexus	1363.1	501.0	3.0	11.3
Campylopus pyriformis	110.1	14.4	4.8	0
Ceratodon purpureus	94.3	0	0	0
Dicranum scoparium	0	2.3	3.1	15.5
Leptodontium flexifolium	4.0	0	0	0
Mnium hornum	0	0	0.3	0
Pohlia nutans	7.6	0.5	0	0
Polytrichastrum formosum	0.0	1.3	0.0	0.0
Polytrichum juniperinum	1.3	0.0	0.0	0.0
Pleurocarpous mosses				
Brachythecium rutabulum	0	0.9	1.6	0
Kindbergia praelonga	0.8	1.3	2.5	4.3
Hypnum jutlandicum	2.8	31.8	75.3	373.0
Plagiothecium undulatum	0	0	0.4	1.5
Rhytidiadelphus squarrosus	0.0	2.0	2.0	0.0
Leafy liverworts				
Barbilophozia floerkei	0	0	0.4	0
Cephaloziella divaricata	479.4	1282.8	68.0	0
Lophocolea bidentata	0	6.2	13.1	15.3
Number of species	10	12	13	7

Figure 6: The mean number of growing tips recorded in a 10x10 cm area of A) *Campylopus introflexus*, B) *Cephaloziella divaricata* and C) *Hypnum jutlandicum*, for each stage of heather growth in the H12a dry heath sites

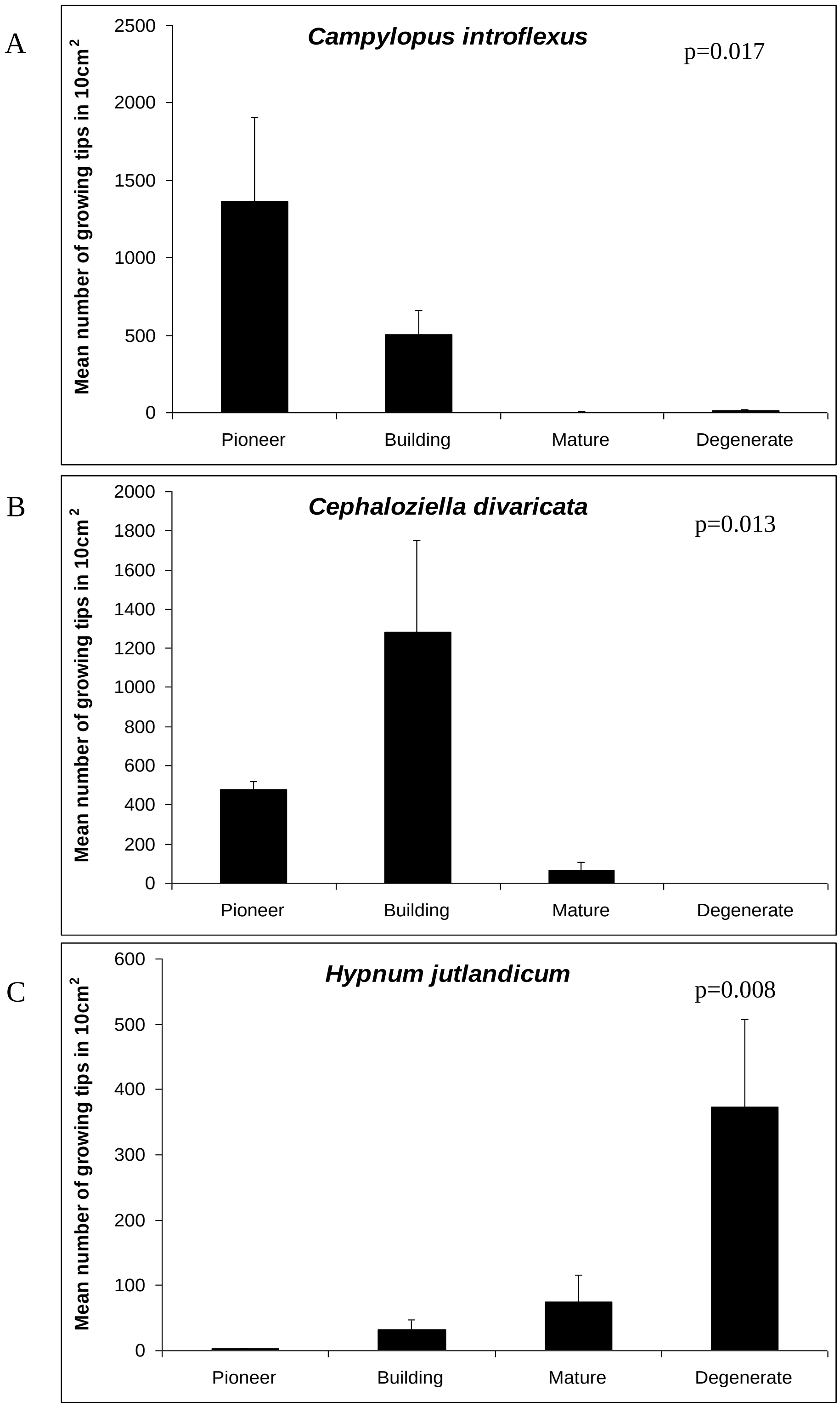
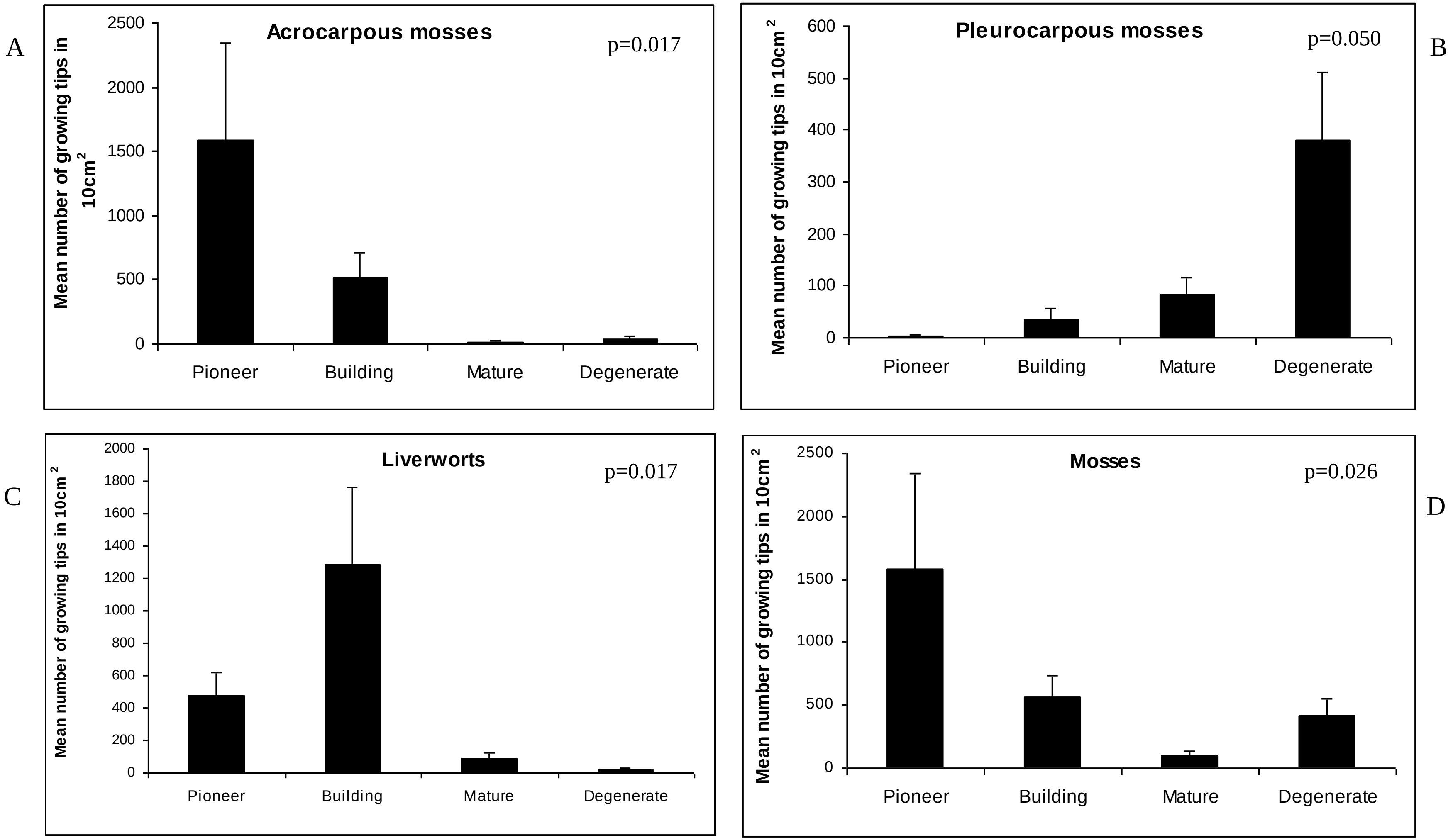
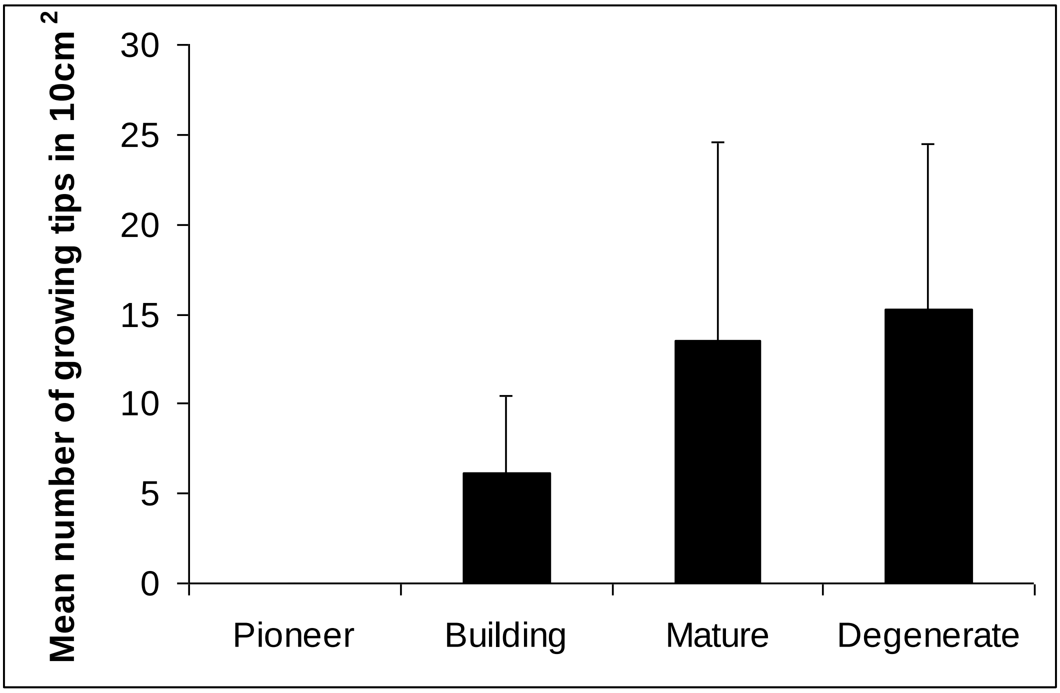


Figure 7: The mean number of growing tips recorded in a 10x10 cm area of A) acrocarpous mosses, B) pleurocarpous mosses, C) liverworts and D) the total number of moss stems, for each stage of heather growth on the H12a dry heath sites



The distribution of liverworts may seem unexpected, as generally liverworts require some shade and humidity. *C. divaricata*, however, is one of the more desiccation tolerant liverworts, often growing between the stems of other bryophytes, and heavily influences the distribution plot for the liverworts. When this species is removed, and the mean number of *B. floerkei* and *L. bidentata* stems are plotted (Figure 8), it can be seen that the distribution of these liverworts is very different, with none in the exposed pioneer sites, and an increase in numbers in the more mature stages of heather development.

Figure 8: The mean number of growing tips recorded in a 10x10 cm area of the liverworts Barbilophozia floerkei and Lophocolea bidentata in each stage of heather development on the H12a sites

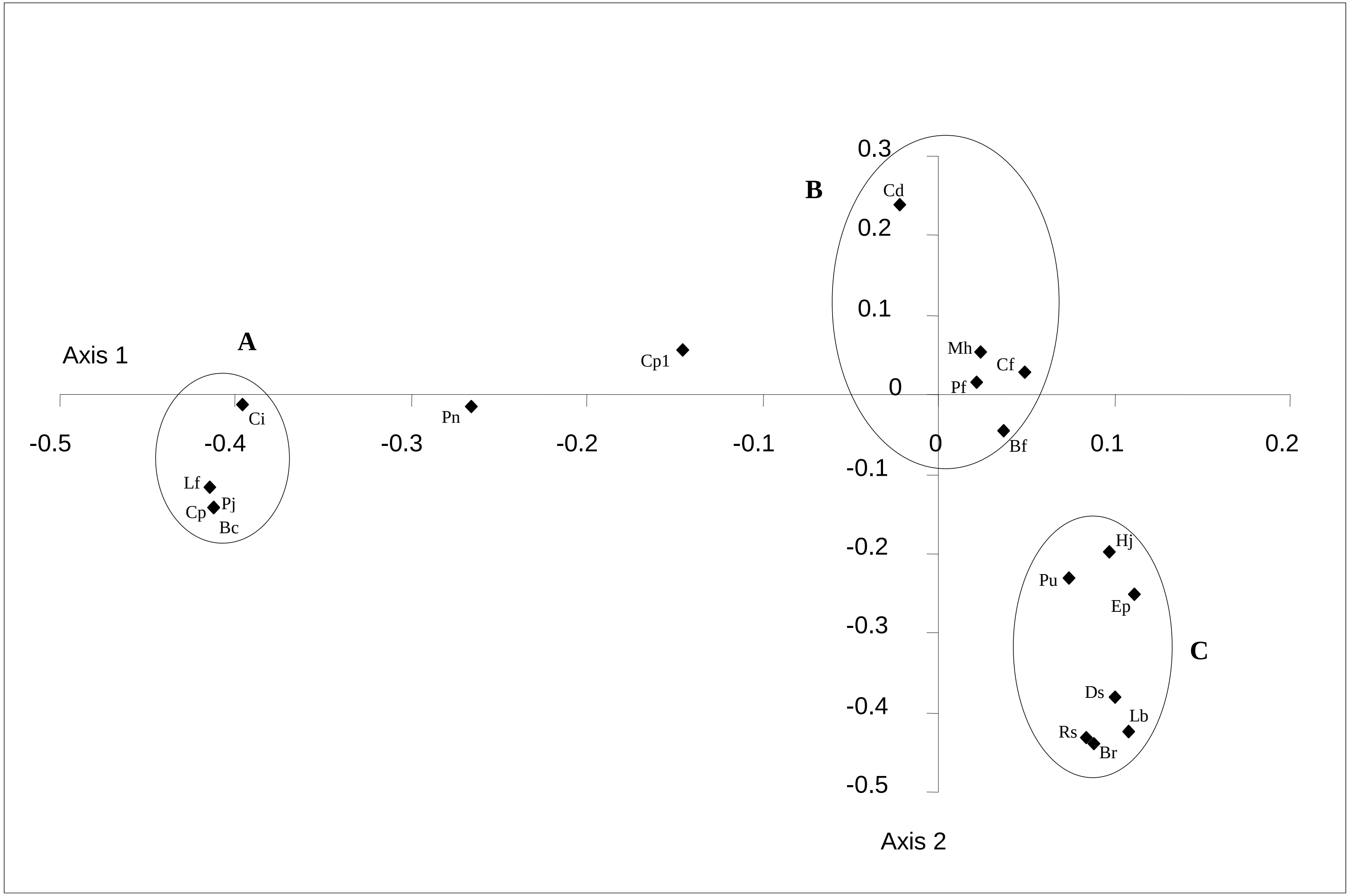


There was no statistically significant effect of age or stage of heather growth on the number of species recorded.

The abundance data was used to conduct a principal components analysis (Figure 9). The first two axes account for 27.6% and 15.6% of the variation, with eigenvalues of 5.238 and 2.959 respectively. The eigenvalue gives an indication as to the degree of separation. The higher the eigenvalue, the bigger the difference between the groups being separated. There are three distinct groups of species, which seem to be grouped in relation to shade and humidty tolerance:

- Group A contains *Campylopus introflexus* (Ci); *Leptodontium flexifolium* (Lf); *Polytrichum juniperinum* (Pj); *Ceratodon purpureus* (Cp2); and *Bryum capillare* (Bc). These are species characteristic of pioneer habitats such as post-fire or disturbed sites, or dry and exposed habitats.

Figure 9: Principle components analysis showing first two principal component axes, and the grouping of species recorded on the H12a sites



- Group C contains *Hypnum jutlandicum* (Hj); *Plagiomnium undulatum* (Pu); *Kindbergia praelonga* (*Eurhynchium praelongum*) (Ep); *Dicranum scoparium* (Ds); *Lophocolea bidentata* (Lb); *Rhytidiadelphus squarrosus* (Rs), and *Brachythecium rutabulum* (Br). These are species typical of more mature heathland, and thrive in more shaded habitats and elevated humidity that the canopy cover provides.
- Group B contains *Cephaloziella divaricata* (Cd); *Mnium hornum* (Mh); *Polytrichastrum formosum* (Pf); *Campylopus flexuosus* (Cf), and *Barbilophozia floerkei* (Bf). These species are desiccation tolerant to some degree, more so than groups C, but less so than group A.
- *Pohlia nutans* (Pn) and *Campylopus pyriformis* (Cp1) are intermediate between Group A and B, and are pioneer species, but may be less desiccation tolerant than those in group A, but more so than those in group B.

4.2.2 Presence and absence of species on the H12a moorland

Overall, the data from the presence and absence survey shows the same trends in species abundance as the stem counts used in the previous section (Table 12). Some species were recorded in one data set and not the other. *Bryum capillare, Mnium hornum, Polytrichum juniperinum* and *Brachythecium rutabulum* were recorded in the quadrats, but not on the presence and absence transects. *Leucobryum glaucum, Orthodontium lineare,* and *Pleurozium schreberi* were recorded on the presence and absence transects, but not in the quadrats. In addition, *Campylopus flexuosus* was recorded only on sites of 10 years and older during the stem counts, however, on the presence and absence data it was only recorded in the 5 year old sites. *B. rutabulum* was recorded on the 7, 10 and 20 year old sites during the stem counts, but was present in all but the 5 year sites on the presence and absence data. This demonstrates the patchy nature of bryophyte growth on the H12a sites, and the value of recording using both methods; patchy distributions may mean that they are more, or less, widely distributed, over a greater range of ages, than either data set alone would have implied.

The presence and absence data was used to classify the similarity of sites in relation to species composition and abundance using the TWINSPAN program (Hill and Smilauer 2005). The dendrogram produced by TWINSPAN shows two main groups at the first division with an eigenvalue of 0.495 (Figure 10). The eigenvalue gives an indication as to the degree of separation. The higher the eigenvalue, the bigger the difference between the groups being separated.

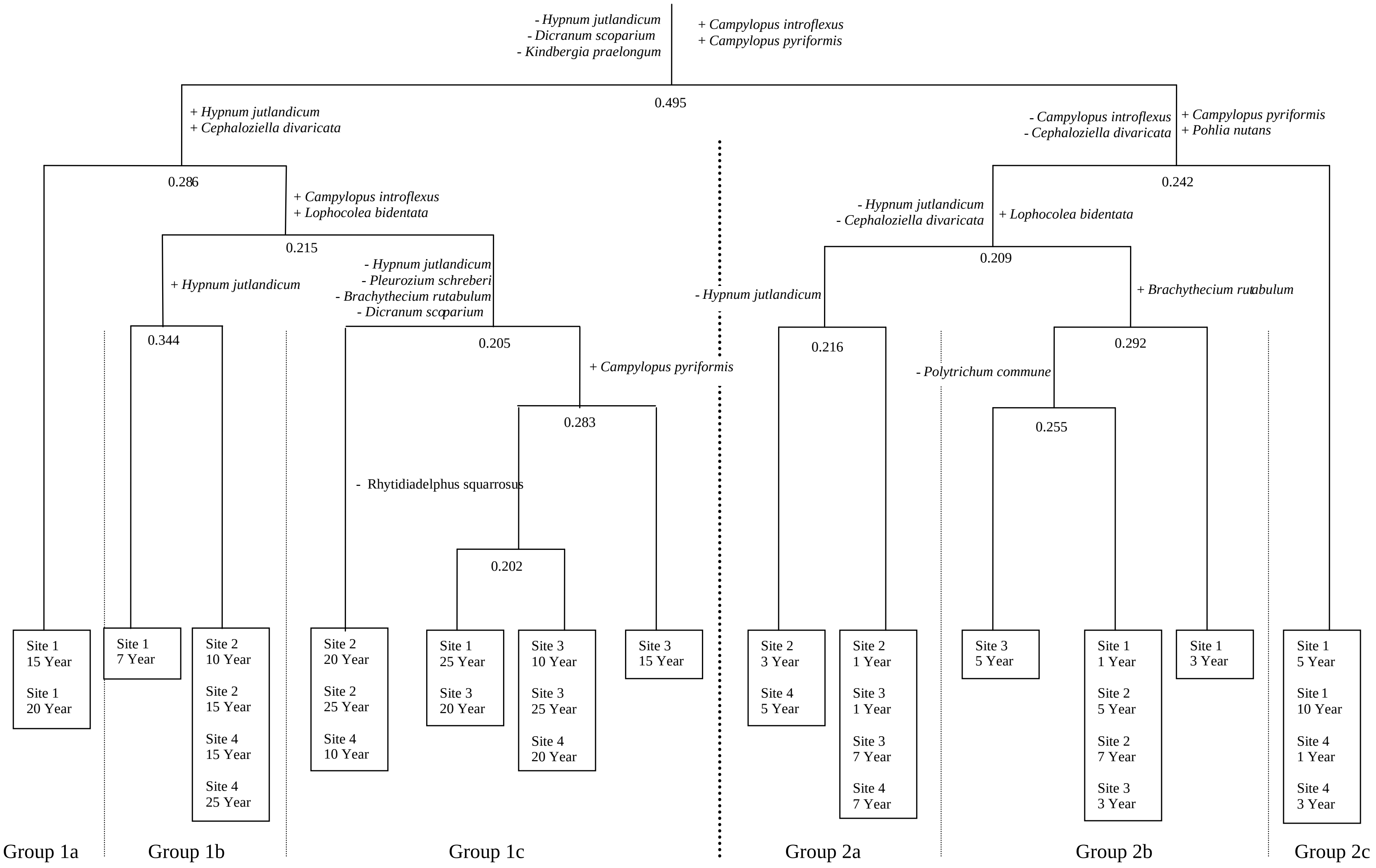
Group 1 predominantly includes sites of ten years and older, with a single seven year site, but nothing younger. Group 2 predominantly includes sites of seven years and younger, with a single ten year site, but nothing older. Therefore, the initial division seems to split the plots to those older and younger than approximately10 years. This could be inferred as the stage when the pioneer heathland is starting to be replaced by a mature heathland, with the colonisation of species such as *H. jutlandicum* and *D. scoparium* and a reduction in the abundance of *C. introflexus* and *C. divaricata*.

Table 12: Mean number of hits (out of a possible 30) for each species on each age since last burn on the H12a sites. Each age is represented on all fours sites surveyed

	Time since last burn (Years)							
	1	**3**	**5**	**7**	**10**	**15**	**20**	**25**
Acrocarpous mosses								
Campylopus flexuosus	0	0	0.25	0	0	0	0	0
Campylopus introflexus	21.00	16.75	9.25	9.75	2.25	1.25	1.25	1.00
Campylopus pyriformis	2.00	3.75	1.00	1.25	1.00	0.50	0	0
Ceratodon purpureus	2.25	0	0	0	0	0	0	0
Dicranum scoparium	0	0.25	0.25	0.50	1.50	1.00	3.50	3.75
Leucobryum glaucum	0	0	0	0	0.50	0	0.25	0
Orthodontium lineare	0	0	0	0	0	0	0	0.25
Pohlia nutans	0.75	1.00	0.25	0.25	0	0	0	0
Polytrichum commune	0	0	0.25	0	0	0	0	0
Pleurocarpous mosses								
Brachythecium rutabulum	0.25	1.25	0.00	0.75	1.75	1.75	1.25	1.25
Kindbergia praelonga	1.00	0.25	0	0	2.50	3.50	1.25	2.00
Hypnum jutlandicum	0.75	2.50	4.00	1.50	13.00	12.50	12.50	18.50
Plagiothecium undulatum	0	0	0	0	0	0.75	0	0.75
Pleurozium schreberi	0	0	0	0	0	0.25	0.50	0.50
Rhytidiadelphus squarrosus	0	0	0	0	0.50	0	0.50	0.25
Leafy liverworts								
Barbilophozia floerkei	0	0	0	0	0	0	0.25	0
Cephaloziella divaricata	9.00	7.25	11.50	8.00	2.75	1.25	1.75	1.00
Lophocolea bidentata	0	0.25	0.75	0	1.00	2.00	2.50	2.50
Number of species	8	9	9	7	10	10	11	11

Group 1 can be further divided into three main groups. Group 1a is separated early on this side of the dendrogram with an eigenvalue of 0.286. The two sites in this group have no *C. introflexus*, very low abundance of *H. jutlandicum* and no *D. scoparium*. As *H. jutlandicum* is present and *C. introflexus* absent, the sites are more similar to others in group 1 than group 2, but the much lower abundance of *H. jutlandicum* separates these two sites from the others in the group. Group 1b differs from group 1c by the complete lack of *C. introflexus*, and a high abundance of *L. bidentata*. Within group 1c, three sites are separated due to the presence of *B. rutabulum* on these three sites.

Figure 10: Dendrogram showing TWINSPAN classification of the H12a sites on the basis of species presence or absence



Group 2 is split into three main groups. Four sites are grouped together and separated early on this side of the dendrogram with an eigenvalue of 0.242 (Group 2c), due to the presence of *P. nutans*, and a lower abundance of *C. introflexus* and *C. divaricata*. Group 2a differs from group 2b in relation to the abundance of *H. jutlandicum*, with the sites in group 2a having this species present. Within group 2b, one site is separated from the others (Site 1, 3 year) due to the high proportion of *C. pyriformis* on this site.

4.2.3 Association between bryophytes and vascular plants on the H12a sites

The height of the vascular plant canopy had a statistically significant negative correlation with the number of stems of *C. introflexus* ($p<0.001$), *C. pyriformis* ($p<0.001$), *C. divaricata* ($p=0.004$), and a statistically significant positive correlation with the number of stems of *H. jutlandicum* ($p=0.008$) (Figure 11).

C. introflexus, *C. pyriformis*, and *C. divaricata* were recorded in the greatest numbers when the canopy height was below 30cm. Conversely *H. jutlandicum* started to increase in abundance once the canopy height reached 30cm. At a canopy height of 30 cm there were sites with very high abundance of *H. jutlandicum*, however, this species did not appear in the bryoflora consistently until a canopy height of over 40cm was reached.

When species were grouped together (Figure 12), canopy height had a statistically significant negative correlation with acrocarpous mosses ($p<0.001$), all mosses ($p<0.001$), liverworts ($p=0.018$) and all bryophytes ($p<0.001$), and a positive correlation with pleurocarpous mosses ($p=0.011$). As the majority of the pioneer species are acrocarpous mosses, and the majority of the species characteristic of mature heathland are pleurocarpous mosses, the canopy height at which the dominance of acrocarpous mosses declines and pleurocarpous mosses increases may give an indication as to the progression from a pioneer heathland to a mature heathland. Again, this appears to be approximately 30 cm, with pleuorcarpous mosses being more consistently recorded when the canopy is 40 cm or over, mirroring the distributions of *C. introflexus* and *H. jutlandicum*, the most abundant species in these groups of mosses.

When we consider the canopy height for each age since last burn (Table 13), the median values show that a canopy of 40 cm is achieved at 10 years post burn, supporting the results of the TWINSPAN analysis, that separated the sites based on the maturity of the heathland into those older and younger than 10 years. However, when the ranges of canopy heights recorded are taken into consideration, heather 5 years and older achieved this height. When the canopy height for each stage of heather development is calculated (Table 14), a canopy height of 40 cm seems to encompass some stands in the building, mature and degenerate stages of heather development.

Figure 11: The relationship between the number of growing tips of A) *Campylopus introflexus*, B) *Campylopus pyriformis*, C) *Cephaloziella divaricata*, and D) *Hypnum jutlandicum*, and the height of the vascular plant canopy on the H12a sites

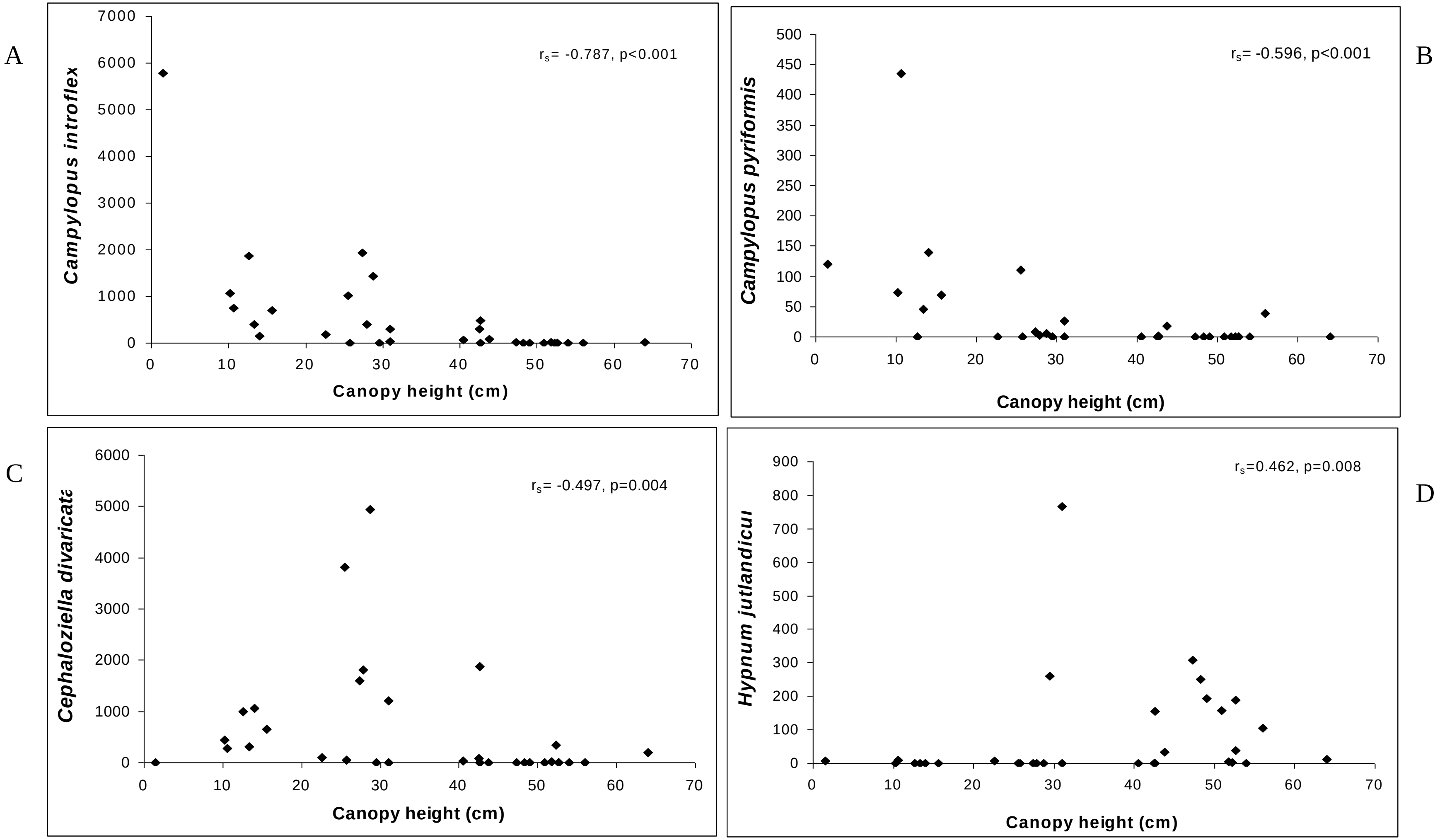
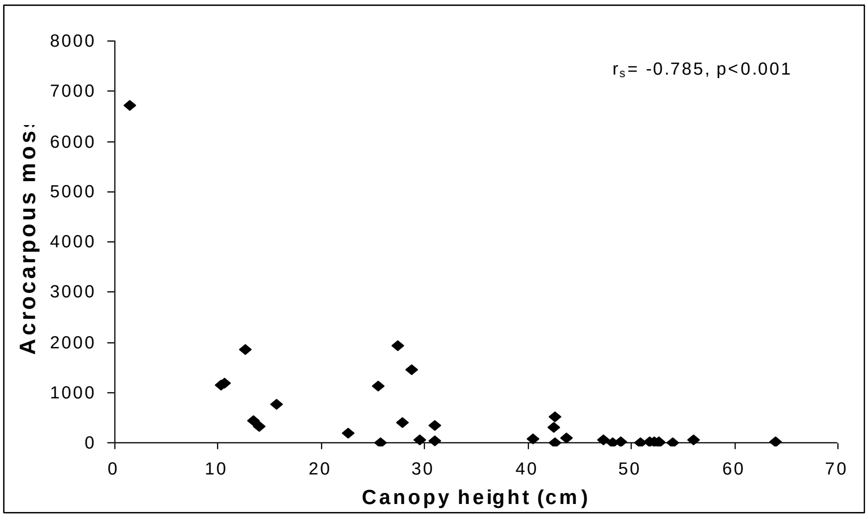


Figure 12: The relationship between the number of growing tips of A) acrocarpous mosses, B) pleurocarpous mosses, C) total number of moss stems, D) liverworts, and E) total number of bryophyte stems, and the height of the vascular plant canopy on the H12a sites

A



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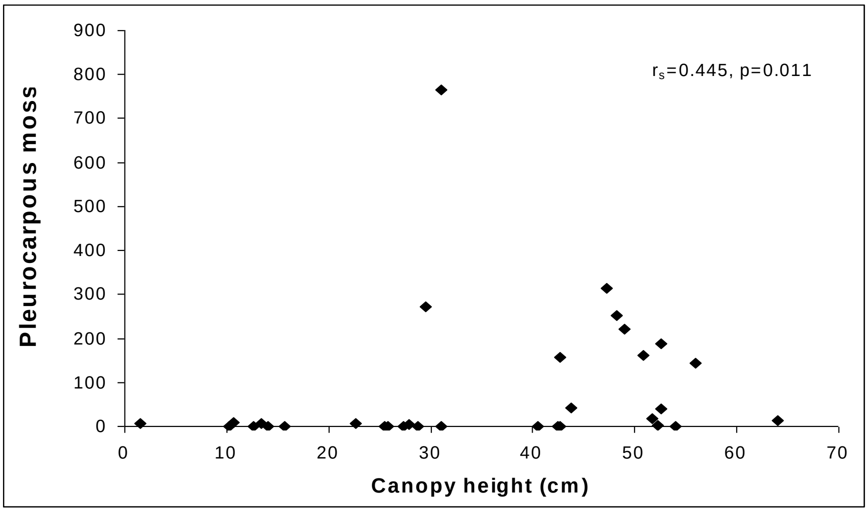
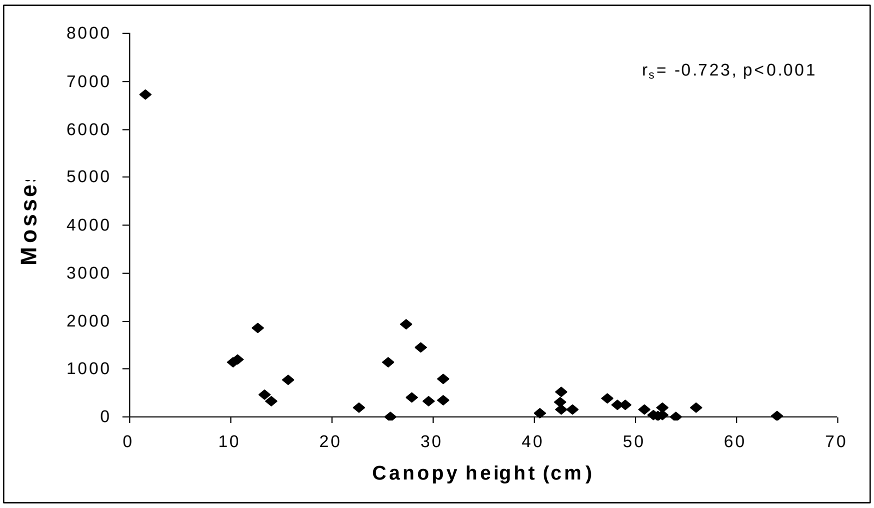


C



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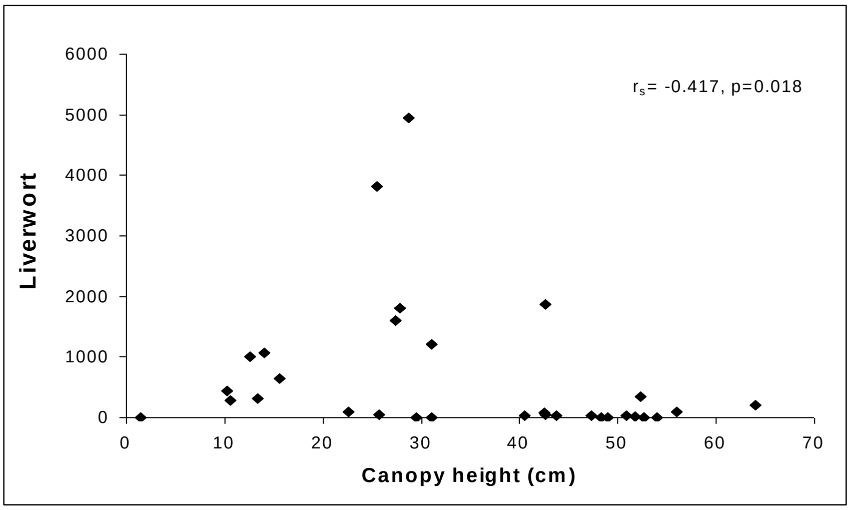

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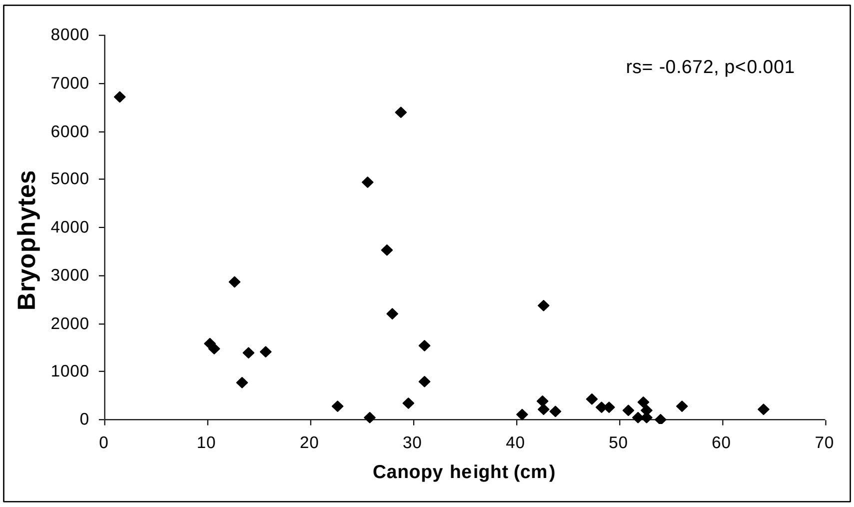


Table 13: Median height of vascular plant canopy and range for each age since last burn on the H12a sites

Year	Median cm (range)
1	10.5 (0 to 23)
3	14.5 (2 to 39)
5	27 (14 to 42)
7	36 (21 to 50)
10	45 (25 to 58)
15	51 (33 to 66)
20	57.5 (22 to 74)
25	42 (6 to 65)

Table 14: Median height of vascular plant canopy and range for each stage of heather development on the H12a sites

Stage	Median cm (range)
Pioneer	12 (0 to 39)
Building	35 (14 to 58)
Mature	54.5 (22 to 74)
Degenerate	42 (6 to 65)

The percentage cover of all vascular plants had a statistically significant negative correlation with the number of growing tips of *Campylopus introflexus* (p=0.003) (Figure 13). When species were grouped together, vascular plant cover had a statistically significant negative correlation with acrocarpous mosses (p=0.005), and all mosses (p=0.007) (Figure 14). There were no statistically significant correlations between bryophyte abundance and the percentage cover of *Erica* species.

Figure 13: The association between the percentage cover of all vascular plants and the number of growing tips of *Campylopus introflexus* on the H12a sites

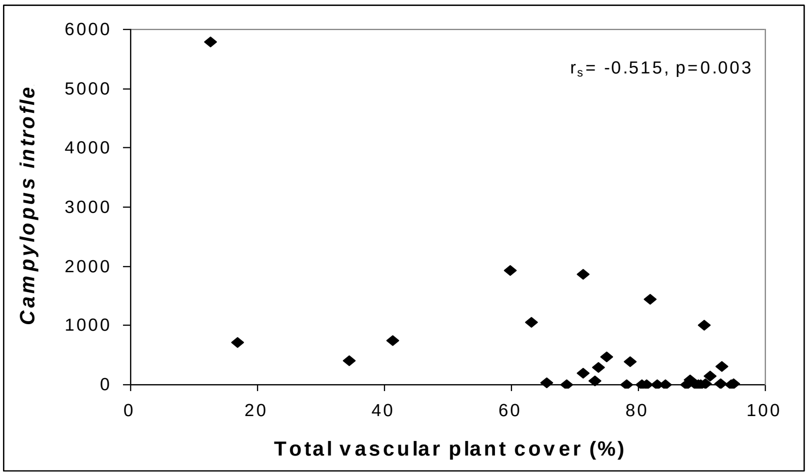
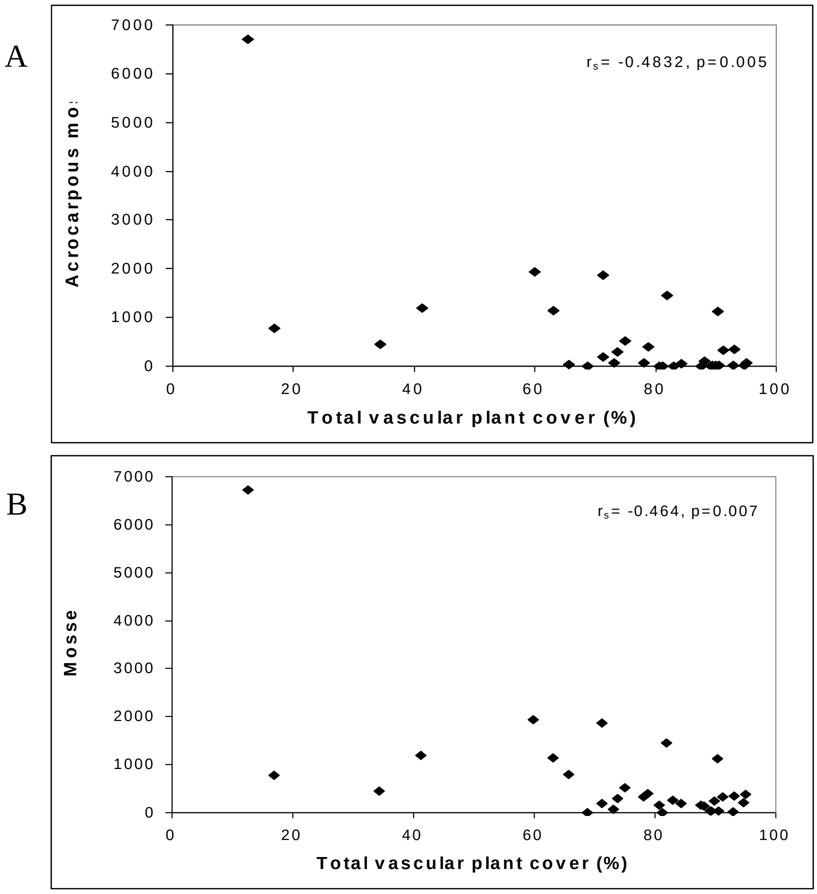


Figure 14: The association between the percentage cover of all vascular plants and the number of growing tips of A) acrocarpous mosses, and B) mosses on the H12a sites



As *Calluna* was the dominant component of the vascular plant canopy, the association between the percentage cover of *Calluna* and bryophytes mirrors that of those for total vascular plant cover, with a statistically significant negative correlation (Figure 15) with the number of stems of *Campylopus introflexus* (p=0.006). When species were grouped together (Figure 16), the percentage cover of *Calluna* had a statistically significant negative correlation with acrocarpous mosses (p=0.011), and all mosses (p=0.013).

Figure 15: The association between the percentage cover of *Calluna* and the number of growing tips of *Campylopus introflexus* on the H12a sites.

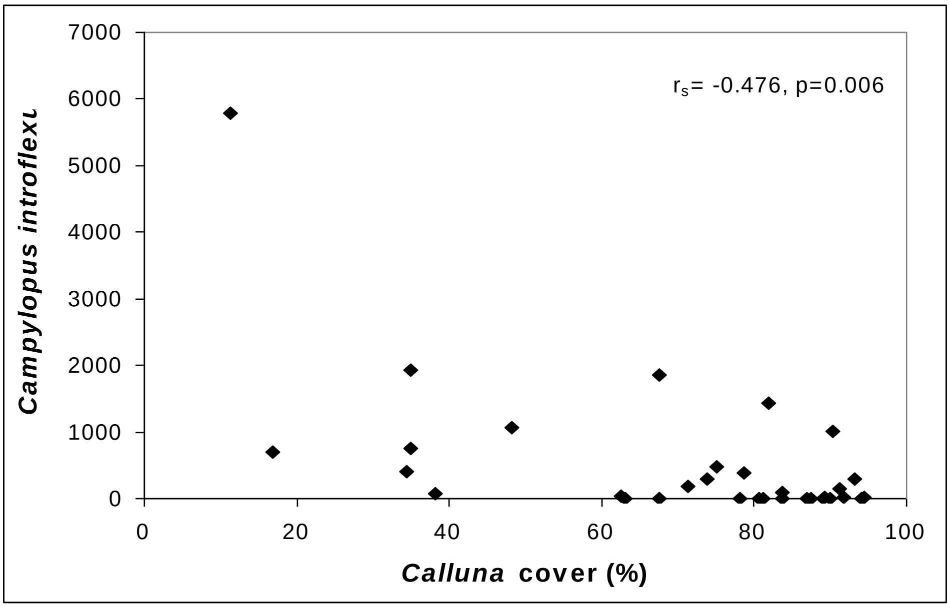
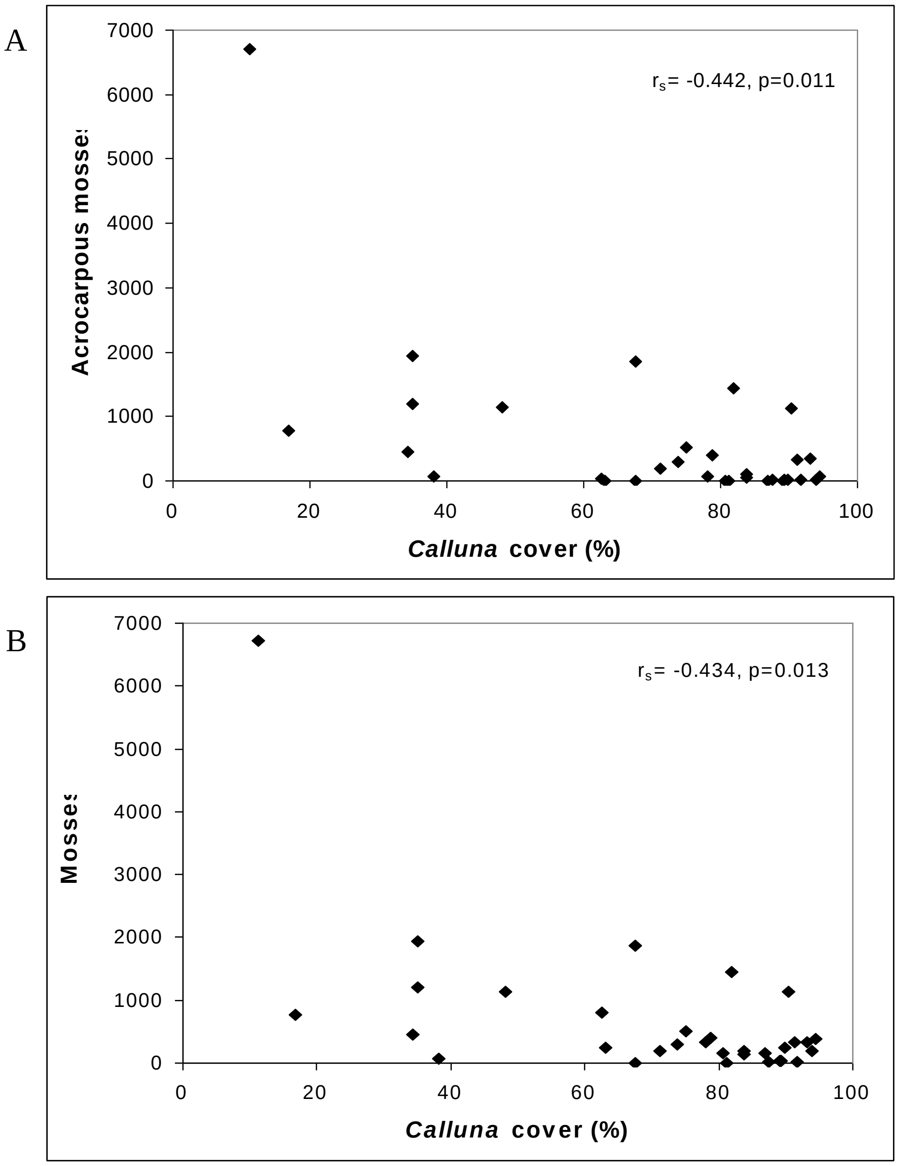


Figure 16: The association between the percentage cover of *Calluna* and the number of growing tips of A) acrocarpous mosses, and B) mosses on the H12a sites



4.3 M16d wet heath

4.3.1 Bryophyte abundance on the M16d moorland

Sphagnum was the most abundant bryophyte genus three years post-burn, with *Odontoshisma sphagni*, and *Campylopus introflexus* also prominent (Table 15). *Sphagnum* persisted throughout the age range, but was more abundant in the younger stands of heather. Species present only in the younger sites included *C. pyriformis*, *Calypogeia fissa*, *Cephalozia connivens*, and *Kurzia pauciflora*. Species restricted to older sites included *Polytrichum commune*, *Pleurozium schreberi*, *Rhytidiadelphus squarrosus*, and *Pseudoscleropodium purum*. *H. jutlandicum* was present throughout the age range of heather, but was most abundant in the older stands.

The mean number of stems recorded in a 10x10 cm quadrat for each age since last burn are given in Table 15, and each stage of heather development in Table 16. Abundance is presented graphically when a statistically significant difference in abundance between age of last burn or stage of heather development was detected, and standard errors are provided on the graphs for these distributions.

The only species to show a statistically significant difference in the number of stems recorded was *O. sphagni*, when the sites were grouped according to stage of heather development ($p=0.048$). The abundance of this species was greatest in the building stage (Figure 17). When species were grouped together (acrocarpous, pleurocarpous, *Sphagnum*, mosses +/- *Sphagnum*, liverworts, and bryophytes +/- *Sphagnum*), there were no statistically significant effect of age or stage of heather growth on the mean number of growing tips recorded in a 10x10 cm area. There was no statistically significant effect of age or stage of heather growth on the number of species recorded.

The number of growing tips of *O. sphagni* showed a statistically significant positive correlation with the number of growing tips of *Sphagnum* species (Figure 18). However, the only section of *Sphagnum* to show a statistically significant positive correlation with the number of growing tips of *O. sphagni* was *Sphagnum* section *Cuspidata* (Figure 19). There is also a statistically significant negative correlation between the number of growing tips of *Sphagnum* species and *Hypnum jutlandicum* (Figure 20).

Sphagnum species were recorded in the greatest number and area cover on the 3 year old sites. The mean number of stems of *C. introflexus* recorded in the 3 year old plots was substantially greater than the number of stems of *H. jutlandicum* (106 and 57 growing tips, respectively). However, due to the branching, creeping, pleurocarpous growth form of *H. jutlandicum* the mean percentage area covered by this species was much greater than that of *C. introflexus* (Figure 21). By 25 years post burn, *C. introflexus* was no longer present, and the number of stems recorded and percentage cover of *Sphagnum* species was less than those of *H. jutlandicum* (Figure 21).

Table 15: The mean number of growing tips recorded in a 10x10 cm area for each species, on each age of burn on the M16d sites. Only the ages 3, 7 and 25 years post burn were represented on all three sites surveyed

	Years since previous burn						
	3 (3 Plots)	**5** (2 Plots)	**7** (4 Plots)	**10** (1 Plot)	**15** (2 Plots)	**20** (2 Plots)	**25** (4 Plots)
Acrocarpous mosses							
Aulacomium palustre	0	22.0	0	0	0	0	3.0
Campylopus flexuosus	6.3	23.5	13.0	0	4.5	0	0
Campylopus introflexus	106.0	70.5	139.0	0	0	1.5	0
Campylopus pyriformis	13.0	0	4.3	0	0	0	0
Dicranum scoparium	9.0	0	4.0	0	5.0	0	3.3
Leucobryum glaucum	3.0	0	98.0	0	22.0	0	0
Polytrichum commune	0	0	0	0	0	0	62.0
Pleurocarpous mosses							
Kindbergia praelonga	0	0	1.3	0	0	41.5	0
Hylocomium splendens	0	0	0	0	0	0	0.5
Hypnum jutlandicum	57.0	34.5	173.3	4.0	132.5	416.0	476.8
Pleurozium schreberi	0	0	0	0	0	0	61.0
Rhytidiadelphus squarrosus	0	0	0	0	0	3.5	0
Pseudoscleropodium purum	0	0	0	0	0	0	0.3
Leafy liverworts							
Calypogeia fissa	9.0	0	46.5	0	0	0	0
Cephalozia connivens	11.7	0	170.5	0	0	0	0
Cephaloziella divaricata	2.3	3.0	2.8	0	0.5	0	0
Gymnocolea inflata	0	0	0	725.0	0	0	0
Kurzia pauciflora	23.7	0	0.3	0	0	0	0
Odontoschisma sphagni	164.3	128.5	306.0	0	0	14.5	22.0
Sphagnum							
section *Sphagnum*	9.0	11.5	100.5	0.0	0.0	3.5	100.5
section *Rigida*	66.0	0.0	6.0	103.0	0.0	2.5	6.0
section *Acutifolia*	15.7	0.0	143.8	0.0	0.0	0.0	143.8
section *Cuspidata*	502.0	463.5	58.8	38.0	0.0	63.5	58.8
section *Subsecunda*	122.7	204.0	0.0	0.0	0.0	0.0	0.0
All *Sphagnum* combined	715.3	679.0	309.0	141.0	0.0	69.5	309.0
Number of species	16	10	18	4	5	8	12

Table 16: The mean number of growing tips recorded in a 10x10 cm area for each species, for each stage of heather growth on the M16d sites

	Stage of heather development			
	Pioneer (3 plots)	**Building** (6 plots)	**Mature** (5 plots)	**Degenerate** (4 plots)
Acrocarpous mosses				
Aulacomium palustre	0	7.3	0	4.0
Campylopus flexuosus	6.3	11.0	1.5	0
Campylopus introflexus	106.0	77.4	0.5	0
Campylopus pyriformis	13.0	2.0	0	0
Dicranum scoparium	9.0	2.3	1.7	2.2
Leucobryum glaucum	3.0	44.0	14.7	0
Polytrichum commune	0	0	0	82.7
Pleurocarpous mosses				
Kindbergia praelonga	0	0.6	13.8	0
Hylocomium splendens	0	0	0	0.3
Hypnum jutlandicum	57.0	112.3	193.8	335.5
Pleurozium schreberi	0	0	0	40.7
Pseudoscleropodium purum	0	0	0	0.2
Rhytidiadelphus squarrosus	0	0	1.2	0
Leafy liverworts				
Calypogeia fissa	9.0	20.7	0	0
Cephalozia connivens	11.7	75.8	0	0
Cephaloziella divaricata	2.3	1.9	0.2	0
Gymnocolea inflata	0	0	120.8	0
Kurzia pauciflora	23.7	0.1	0	0
Odontoschisma sphagni	164.3	380.4	4.8	29.3
Sphagnum				
section *Sphagnum*	9.0	77.8	0.0	154.3
section *Rigida*	66.0	4.0	18.0	0.0
section *Acutifolia*	15.7	117.9	0.0	36.3
section *Cuspidata*	502.0	232.8	6.3	27.3
section *Subsecunda*	122.7	67.7	0.0	4.3
All *Sphagnum* combined	715.3	500.3	46.7	222.3
Number of species	16	22	14	13

Figure 17: The mean number of growing tips recorded in a 10x10 cm area of *Odontoschisma sphagni* for each stage of heather growth on the M16d sites

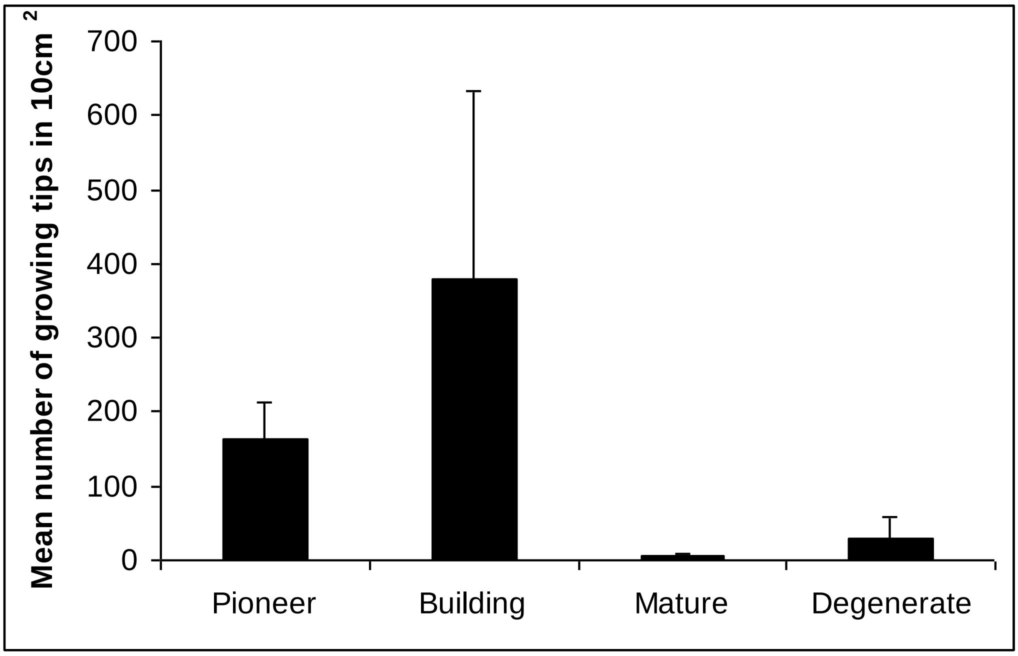


Figure 18: The association between number of growing tips of *Odontoschisma sphagni* and *Sphagnum* species on the M16d sites.

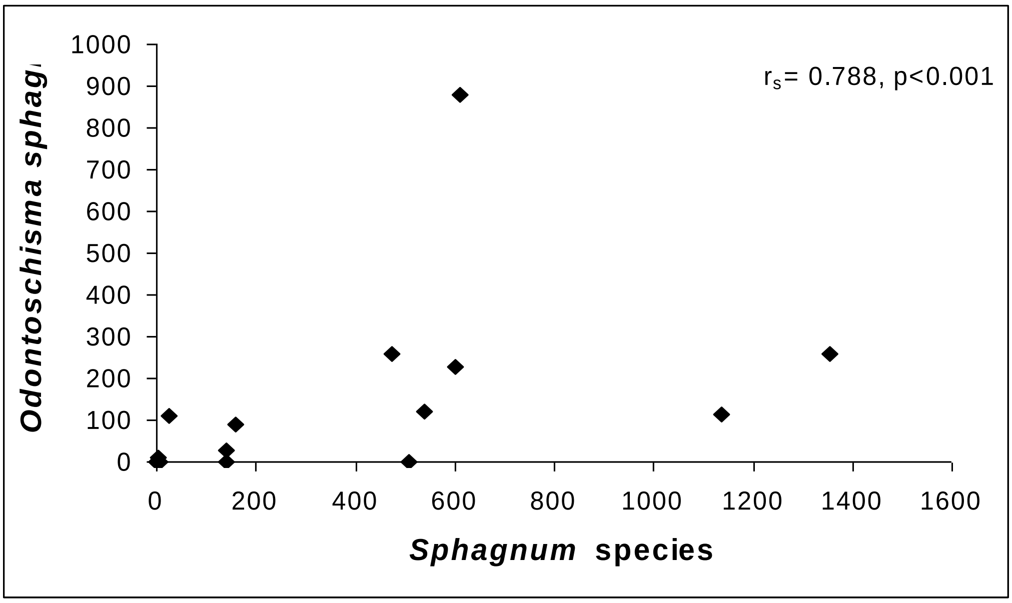


Figure 19: The association between number of growing tips of *Odontoschisma sphagni* and *Sphagnum* section *Cuspidata* on the M16d sites

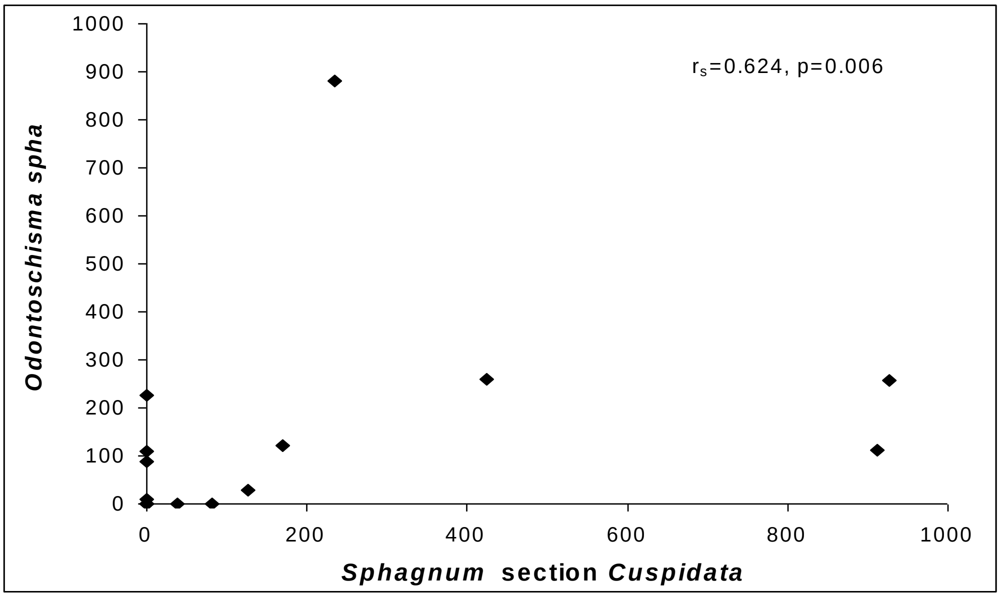


Figure 20: The association between number of growing tips of *Hypnum jutlandicum* and *Sphagnum* species on the M16d sites

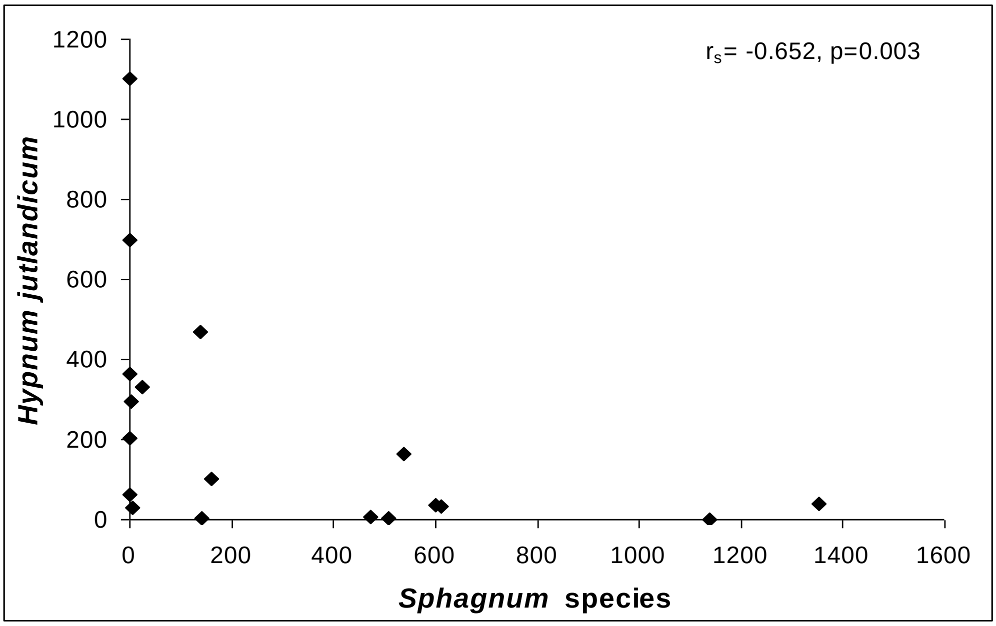
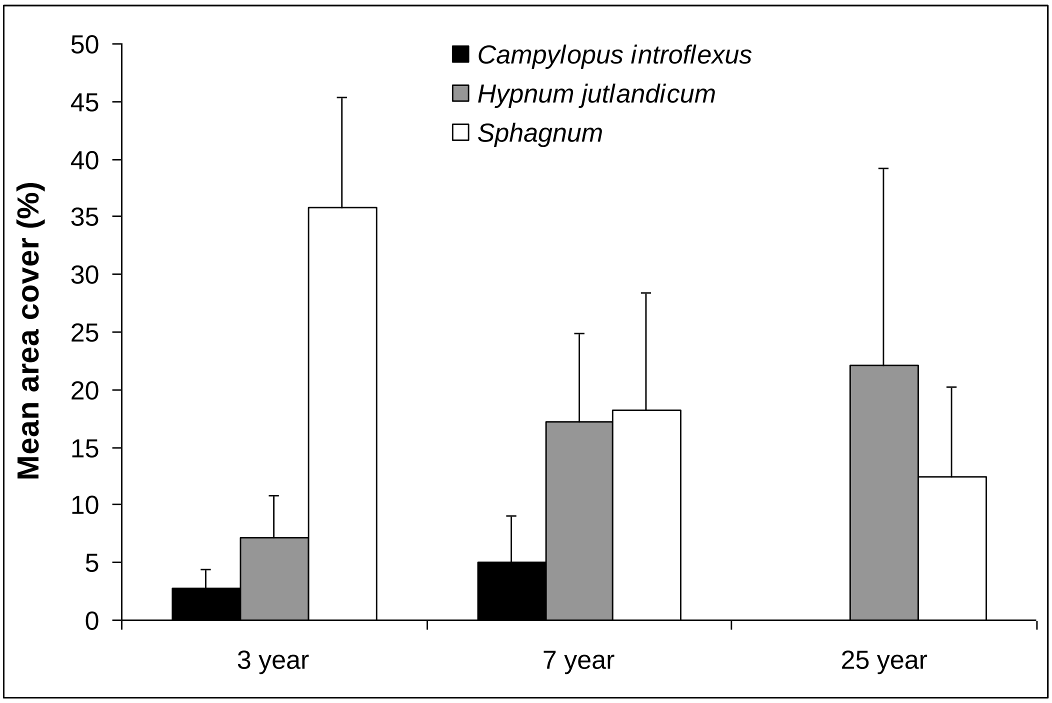


Figure 21: The mean area cover of *Campylopus introflexus*, *Hypnum jutlandicum* and *Sphagnum* species, 3, 7 and 25 years post burn.



The abundance data was used in a principal components analysis (Figure 22). The first two axes account for 17.4% and 15.0% of the variation, with eigenvalues of 4.172 and 3.593 respectively. There are five species groups:

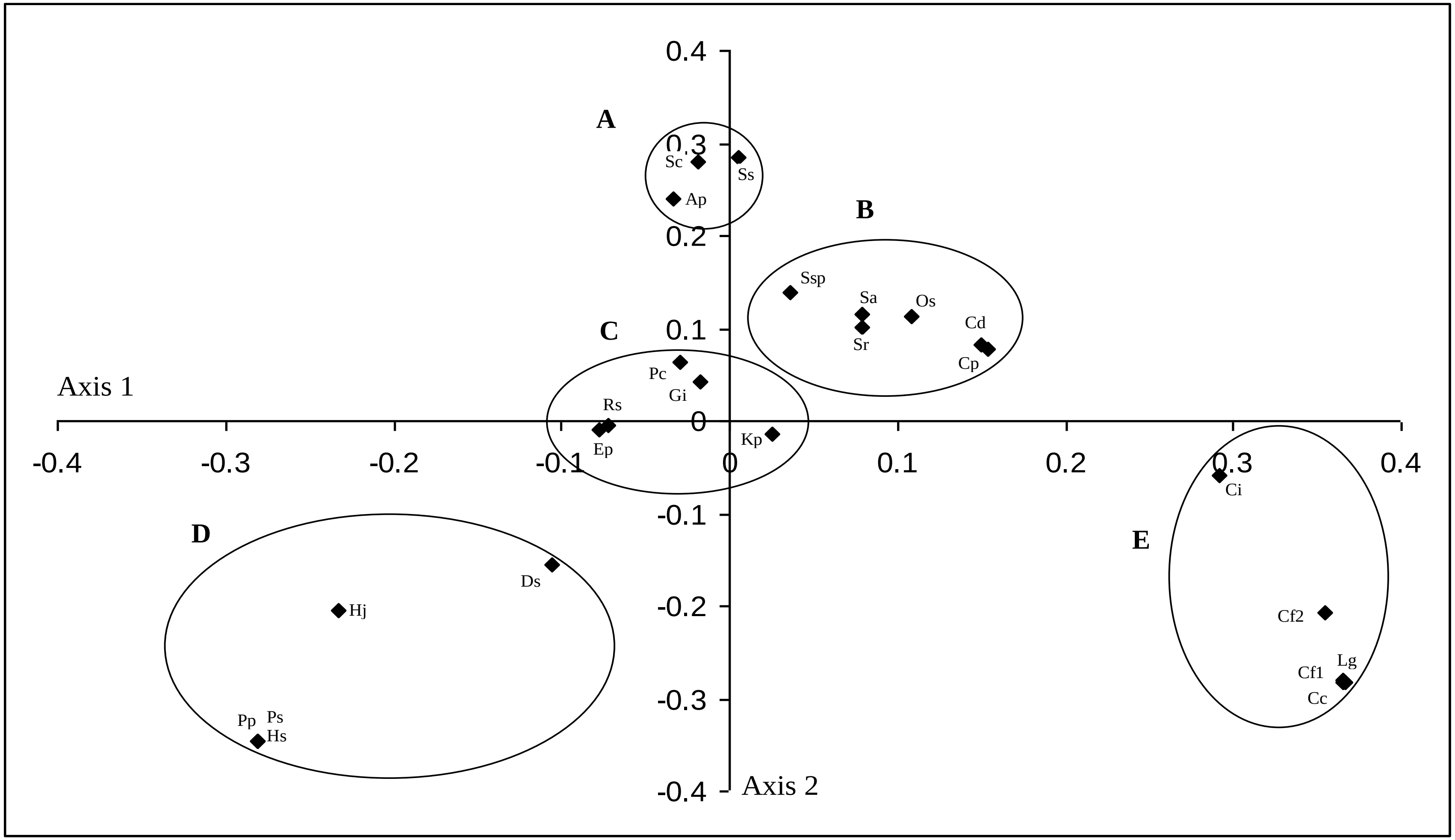
- Group A contains: *Sphagnum* section *Cuspidata* (Sc); *Sphagnum* section *Subsecunda* (Ss), and *Aulacomium palustre* (Ap).
- Group B contains: *Sphagnum* section *Sphagnum* (Ssp); *Sphagnum* section *Aucutifolia* (Sa); *Sphagnum* section *Rigida* (Sr); *Odontoschisma sphagni* (Os); *Cephaloziella divaricata* (Cd), and *Campylopus pyriformis* (Cp1).
- Group E contains: *Campylopus introflexus* (Ci); *Campylopus flexuosus* (Cf2); *Calypogeia fissa* (Cf1); *Leucobryum glaucum* (Lg), and *Cephalozia connivens* (Cc).

Groups A, B and E primarily contain the species of wetter habitats and the younger areas of the M16d sites.

- Group C contains: *Kindbergia praelonga* (*Eurhynchium praelongum*) (Ep); *Rhytidiadelphus squarrosus* (Rs); *Kurzia pauciflora* (Kp); *Polytrichastrum commune* (Pc), and *Gymnocolea inflata* (Gi).
- Group D contains: Hypnum jutlandicum (Hj); Hylocomium splendens (Hs); Pleurozium schreberi (Ps); Pseudoscleropodium purum (Pp), and Dicranum scoparium (Ds).

Groups C and D primarily contain those species more typical of a mature heathland, and are often found on drier sites.

Figure 22: Principle components analysis showing first two principal component axes, and the grouping of species recorded on the M16d sites



4.3.2 Presence and absence of species on the M16d moorland

Overall, the data from the presence and absence survey shows the same trends in species abundance as the stem counts used in the previous section (Table 17). Some species were recorded in one data set and not the other. *H. splendens*, *C. fissa*, *G. inflata* and *K. pauciflora* were recorded in the quadrats, but not on the presence and absence transects. *P. nutans*, *B. rutabulum,* and *P. undulatum* were recorded on the presence and absence transects, but not in the quadrats. In addition, *R. squarrosus* was recorded only on the 20 year old sites during the stem counts. However, on the presence and absence data it was only recorded in the 5 year old sites. *C. connivens* was recorded on the 3 and 7 year old sites during the stem counts, but was only present in the 25 year sites on the presence and absence data. This again demonstrates the patchy nature of bryophyte growth and the value of recording data using both methods.

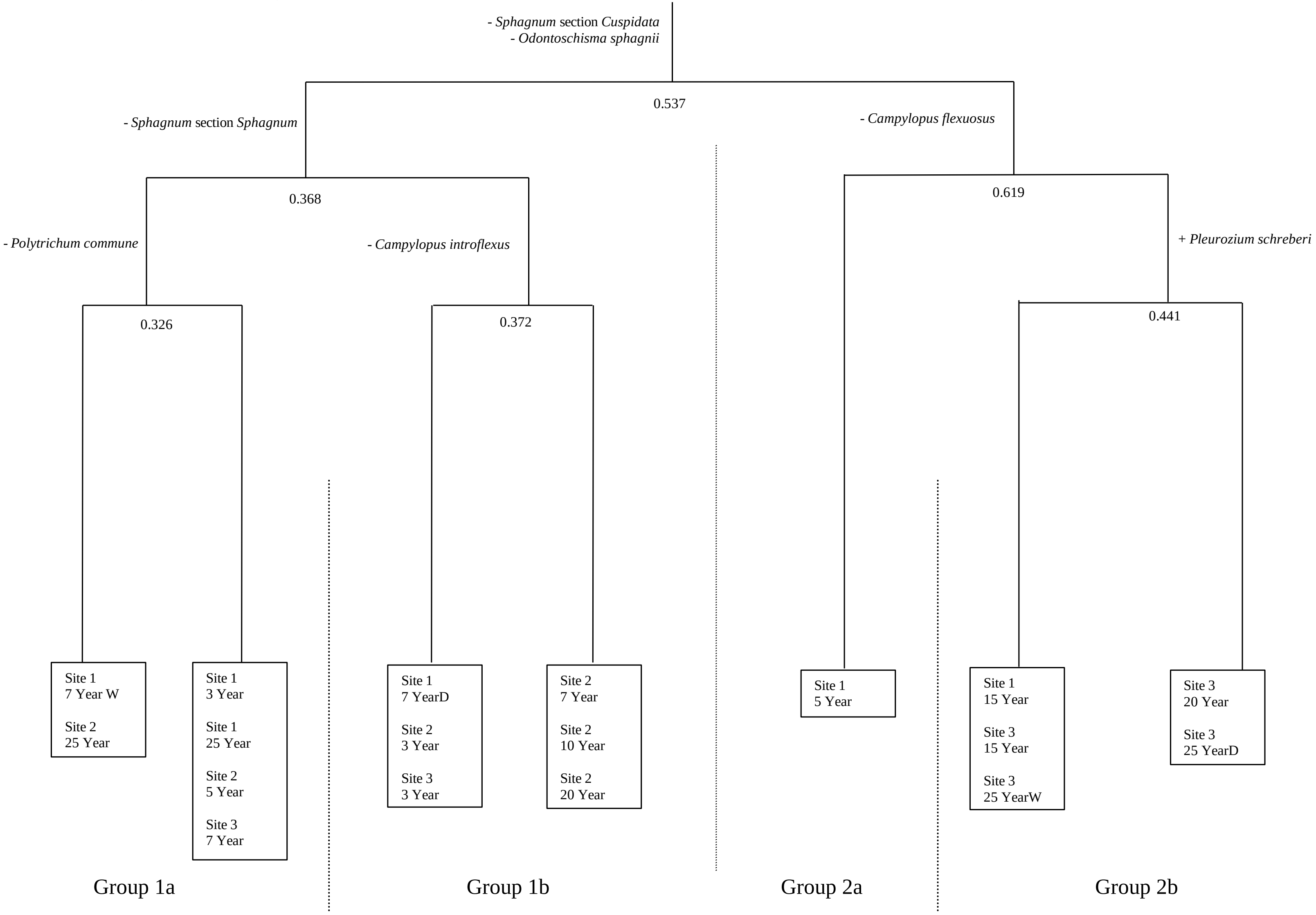
The presence and absence data were used to classify the similarity of sites in relation to species composition and abundance using the TWINSPAN classification program (Hill and Smilauer 2005). The dendrogram produced by TWINSPAN shows two main groups at the first division with an Eigenvalue of 0.537 (Figure 23). The eigenvalue gives an indication as to the degree of separation. The higher the eigenvalue, the bigger the difference between the groups being separated. Group 1 predominantly includes sites that contain *Sphagnum* and are generally younger, and group 2 includes sites without *Sphagnum* that are generally older.

Group 1 can be further divided into two groups, with an eigenvalue of 0.368. The sites in group 1a have a higher abundance of *Sphagnum* than group 1b, and group 1b has a higher abundance of *H. jutlandicum*. Group 2 is also split into two groups, with an eigenvalue of 0.619, with one site being separated from the others, as it is the only site to have *R. squarrosus* and *P. nutans*. Group 2b are the only sites in group 2 to have had either *P. purum* or *B. rutabulum* as part of the bryoflora.

Table 17: Mean number of hits (out of a possible 30) for each species on each age since last burn on the M16d sites. Only 3, 7 and 25 year old stands were represented on all three sites surveyed

	Years since previous burn						
	3 (3 plots)	**5** (2 plots)	**7** (4 plots)	**10** (1 plot)	**15** (2 plots)	**20** (2 plots)	**25** (4 plots)
Acrocarpous mosses							
Aulacomium palustre	0	0	0.33	0	0	0	0
Campylopus flexuosus	0	5.00	0	0	0	0	0
Campylopus introflexus	5.33	3.00	6.67	0	1.50	0	0
Campylopus pyriformis	0.67	0.50	0	1.00	0	0	0
Dicranum scoparium	0.67	0	0.33	0	1.00	0.50	1.50
Leucobryum glaucum	1.00	0	0.67	0	0	0.50	0
Pohlia nutans	0	0.50	0	0	0	0	0
Polytrichum commune	0	0	1.00	0	0	0	2.50
Pleurocarpous mosses							
Brachythecium rutabulum	0	0	0	0	0.50	0	0.25
Kindbergia praelonga	0	1.00	0.33	0	1.00	0	0
Hypnum jutlandicum	7.67	3.50	8.67	4.00	22.50	27.50	18.25
Plagiothecium undulatum	0	0	0	0	0	0.50	0.25
Pleurozium schreberi	0	0	0.33	0	0	0.50	4.25
Rhytidiadelphus squarrosus	0	0.50	0	0	0	0	0
Pseudoscleropodium purum	0	0	0	0	0	0.50	1.75
Leafy liverworts							
Cephalozia connivens	0.33	0	0	0	0	0	0.25
Cephaloziella divaricata	0.67	0	1.33	1.00	0.50	0	0
Odontoschisma sphagni	8.00	1.50	15.67	2.00	0	0.50	0.25
Sphagnum							
section *Sphagnum*	1.33	1.00	9.33	0	0	0	3.75
section *Rigida*	0	0.50	0	2.00	0	1.00	0.25
section *Cuspidata*	18.67	12.00	8.67	1.00	0	1.50	4.00
section *Acutifolia*	1.33	0	5.33	0	0	0	3.50
section *Subsecunda*	5.00	0	1.33	0	0	0	2.50
Any *Sphagnum* species	19.33	12.50	17.00	2.00	0	2.50	9.00
Number of species	13	13	17	7	6	10	16

Figure 23: Dendrogram showing TWINSPAN classification of wet sites on the basis of species presence or absence



4.3.3 Association between bryophytes and vascular plants on the M16d moorland

There was a statistically significant correlation between the height of the vascular plant canopy and the number of stems of *Odontoschisma sphagni* (p=0.001), *Sphagnum* section *Subsecunda* (p=0.008), *Sphagnum* section *Cuspidata* (p=0.002), and *Hypnum jutlandicum* (p=0.012) (Figure 24). When species were grouped together, there was a statistically significant correlation between canopy height and the number of stems of liverworts (p=0.002), pleurocarpous mosses (p=0.012), *Sphagnum* species (p<0.001), and all bryophytes including *Sphagnum* (p=0.025) (Figure 25).

Sphagnum species and *O. sphagni* were recorded in the greatest numbers when the canopy height was below 30 cm. *H. jutlandicum* started to increase in abundance once the canopy height reached approximately 20 cm, with the maximum abundance achieved at a canopy height of approximately 50 cm. The same pattern was seen in the correlations with liverworts and pleurocarpous mosses, as *O. sphagni* and *H. jutlandicum* were the most species in these bryophyte groups, respectively.

When we consider the range of canopy height for each age since last burn (Table 18), a canopy of 20 cm is recorded at 3 to 10 years post burn, and 50 cm at 15 to 25 years post burn. When the median canopy height for each stage of heather development is calculated (Table 19), a canopy height of 20 cm seems to be primarily at the building stage, although a canopy height of 20 cm was recorded in pioneer and mature heather, and 50 cm is achieved at the mature to degenerate stage of heather development.

Table 18: Median height of vascular plant canopy and range for each age since last burn on the M16d sites

Year	Median cm (range)
3	16.5 (11 to 29)
5	25 (9 to 37)
7	23 (11 to 35)
10	36 (5 to 43)
15	48.5 (38 to 58)
20	43.5 (28 to 66)
25	50 (11 to 74)

Table 19: Median height of vascular plant canopy and range for each stage of heather development on the M16d sites

Stage	Median cm (range)
Pioneer	16.5 (11 to 29)
Building	23.5 (9 to 37)
Mature	44 (5 to 66)
Degenerate	50 (11 to 74)

Total vascular plant cover had a statistically significant negative correlation with *Odontoschisma sphagni* (p=0.032), *Sphagnum* section *Subsecunda* (p=0.050) and *Sphagnum* section *Rigida* (p=0.039) (Figure 26). When species were grouped together, total vascular plant cover had a statistically significant negative correlation with liverworts (p=0.013), and all bryophytes including *Sphagnum* (p=0.023) (Figure 27).

Figure 24**: The association between the height of the vascular plant canopy and the number of growing tips of A) *Odontoschisma sphagni*, B) *Hypnum jutlandicum*, C) *Sphagnum* section *Cuspidata* and D) *Sphagnum* section *Subsecunda* on the M16d sites**

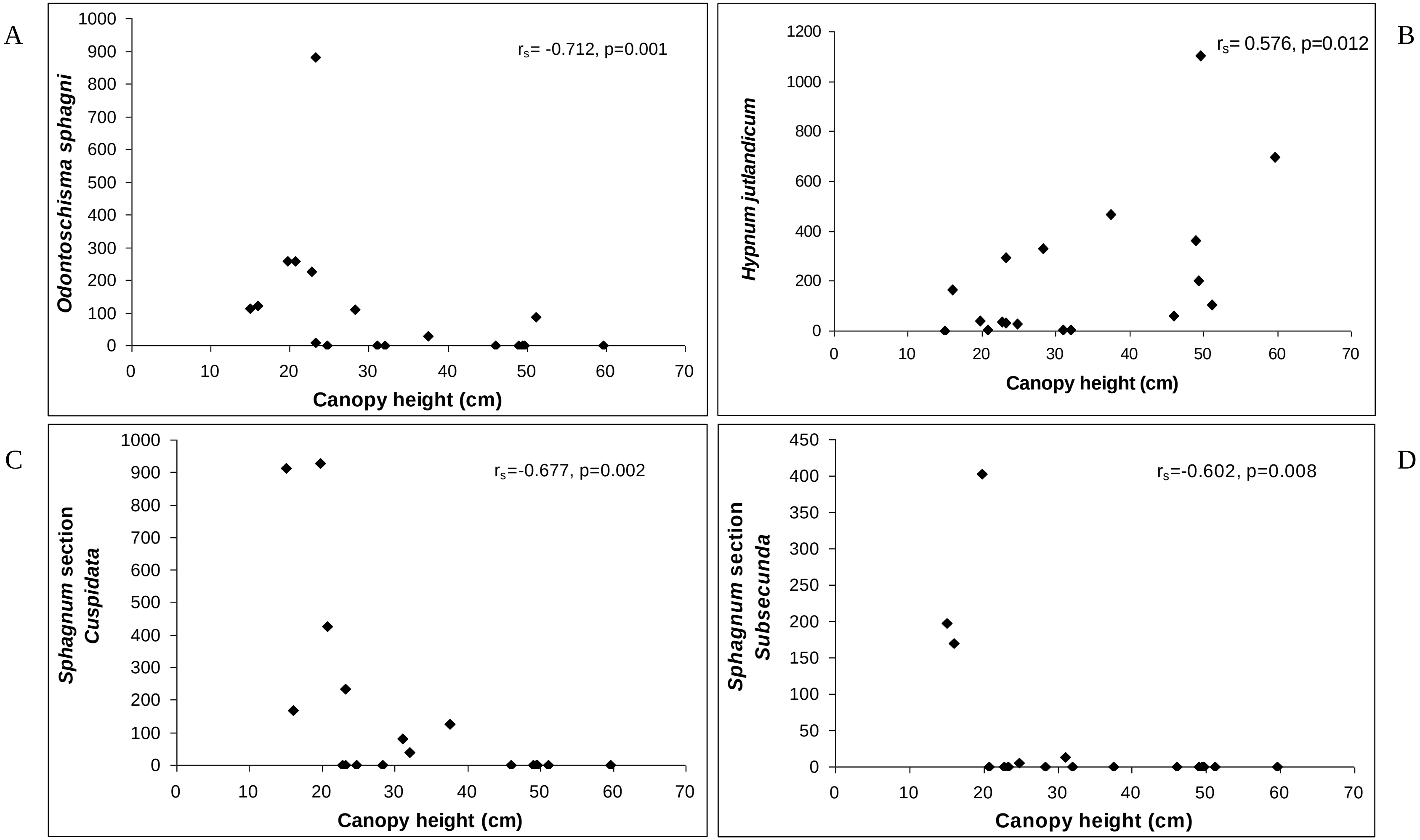


Figure 25: The association between the height of the vascular plant canopy and the number of growing tips of A) pleurocarpous mosses, B) liverworts, C) *Sphagnum* species and D) all bryophytes including *Sphagnum* species on the M16d sites

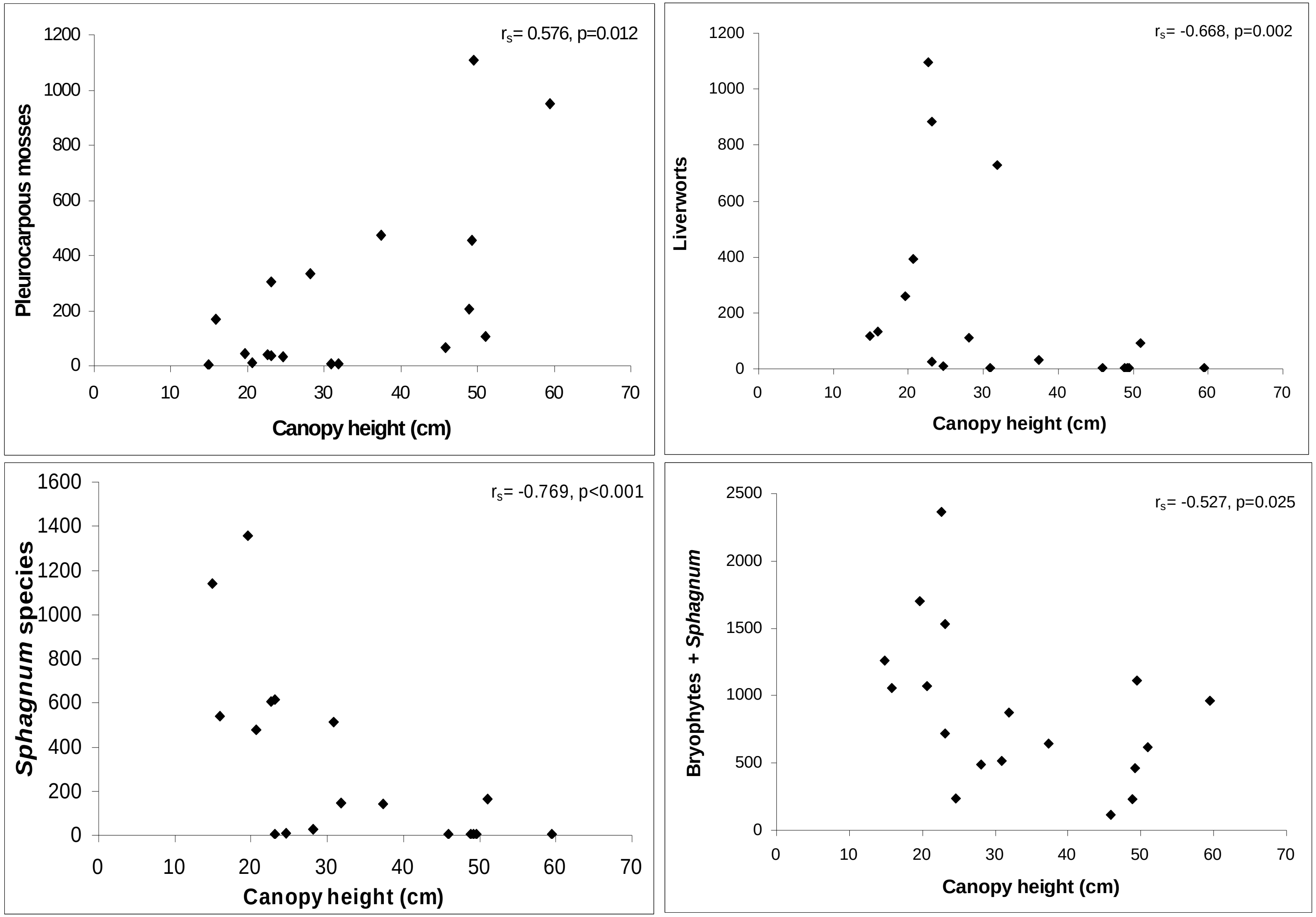


Figure 26: The association between the percentage cover of all vascular plants and the number of growing tips of A) *Odontoschisma sphagni*, B) *Sphagnum* section *Subsecunda* and C) *Sphagnum* section *Rigida* on the M16d sites

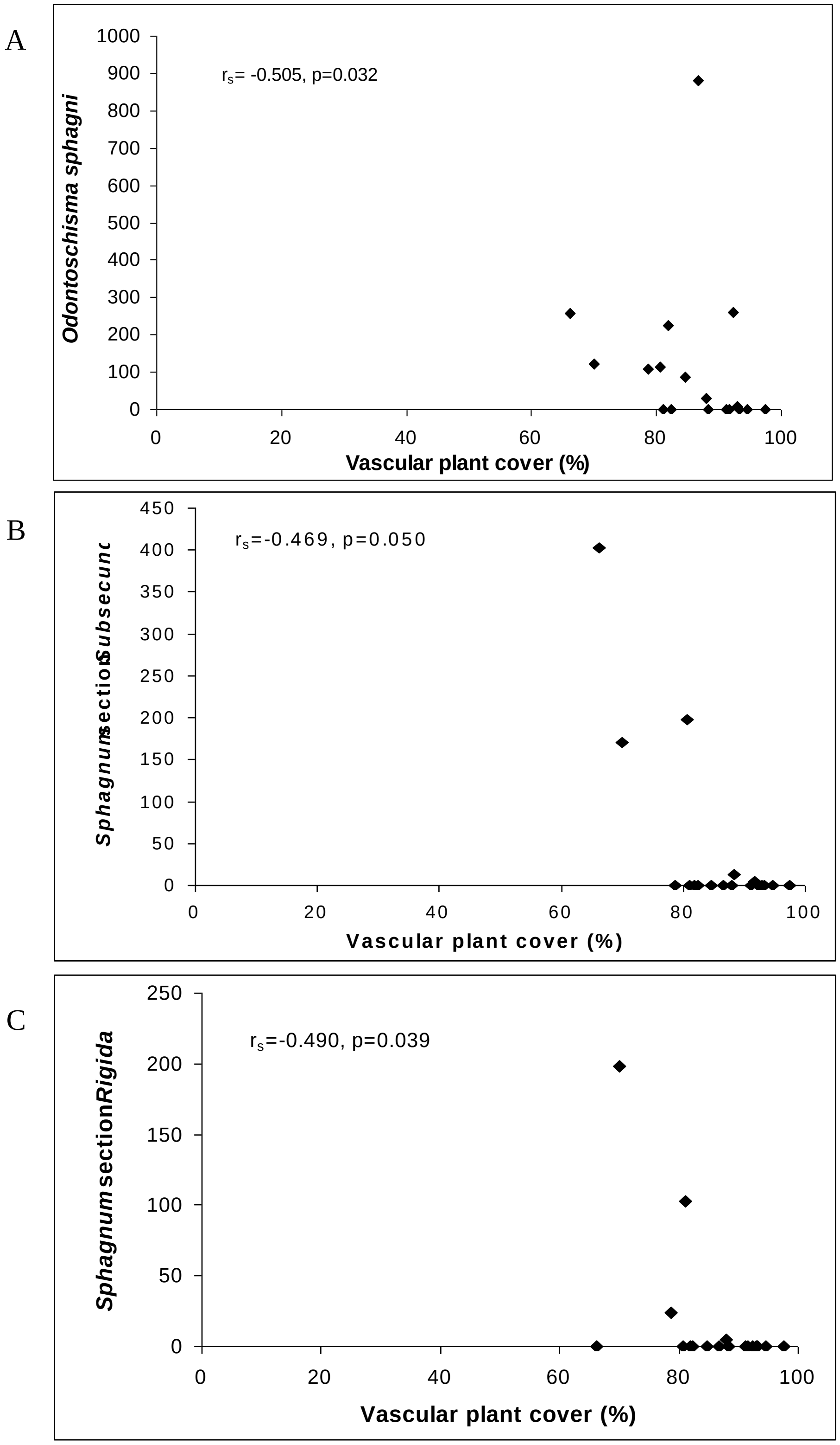
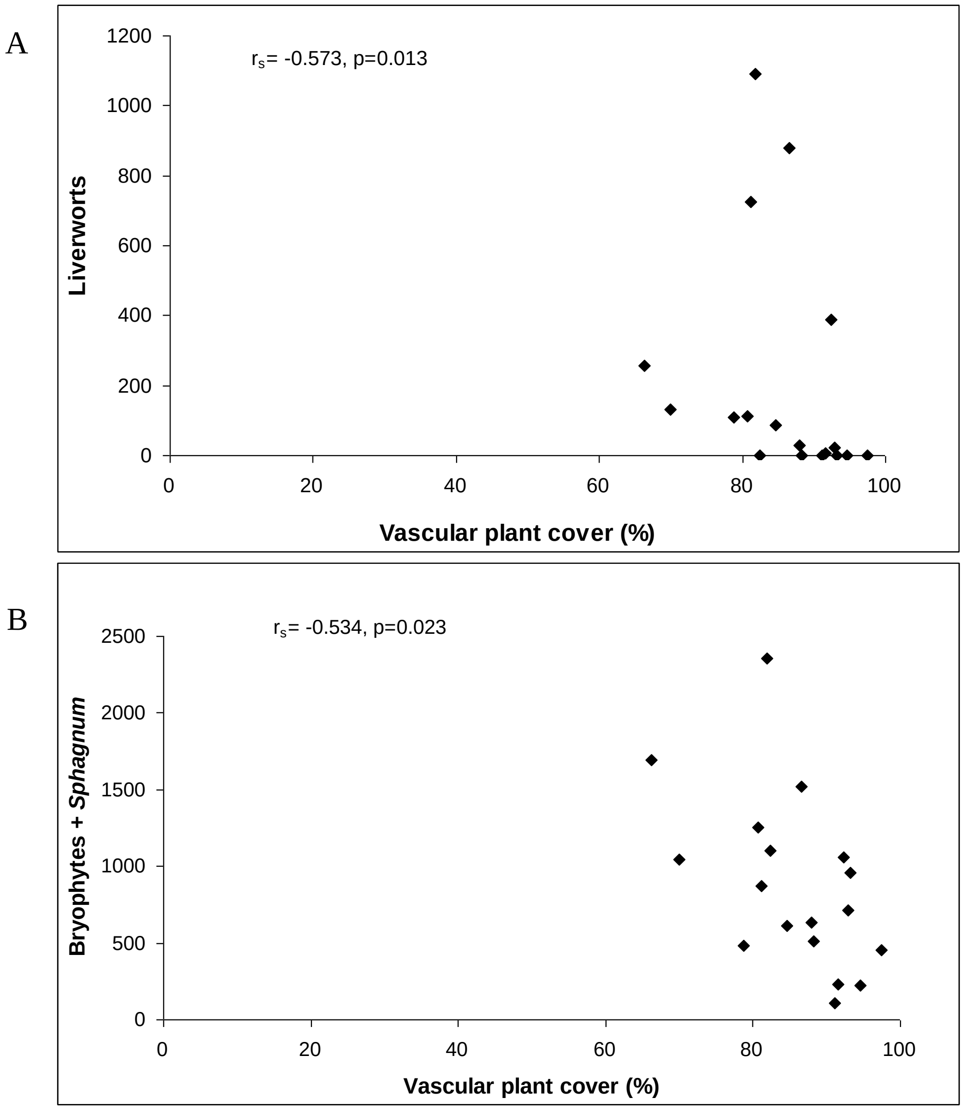


Figure 27: The association between the percentage cover of all vascular plants and the number of growing tips of A) liverworts, and B) all bryophytes including *Sphagnum* species on the M16d sites



There was a statistically significant positive correlation between the percentage cover of *Calluna* and the number of growing tips of *Hypnum jutlandicum* (p=0.014), and a statistically significant negative correlation with *Odontoschisma sphagni* (p=0.009) and *Sphagnum* section *Cuspidata* (p=0.007) (Figure 28). When species were grouped together, there was a statistically significant positive correlation between the percentage cover of *Calluna* and the number of growing tips of pleurocarpous mosses (p=0.014) and a statistically significant negative correlation with liverworts (p=0.003), and all bryophytes including *Sphagnum* (p=0.014) (Figure 29).

There was a statistically significant positive correlation between the percentage cover of grass and the number of growing tips of *Sphagnum* section *Acutifolia* (p=0.001) (Figure 30). When species were grouped together, there was a statistically significant positive correlation between the percentage cover of grass and the number of growing tips of liverworts (p=0.040) (Figure 31).

There was a statistically significant positive correlation between the percentage cover of cottongrass and the number of growing tips of *Odontoschisma sphagni* (p=0.001) and *Sphagnum* section *Cupsidata* (p=0.001) (Figure 32). When species were grouped together, there was a statistically significant negative correlation between the percentage cover of cottongrass and the number of growing tips of liverworts (p=0.004) (Figure 33).

Figure 28: The association between the percentage cover of *Calluna* and the number of growing tips of A) *Hypnum jutlandicum*, B) *Odontoschisma sphagni*, and C) *Sphagnum* section *Cuspidata* on the M16d sites

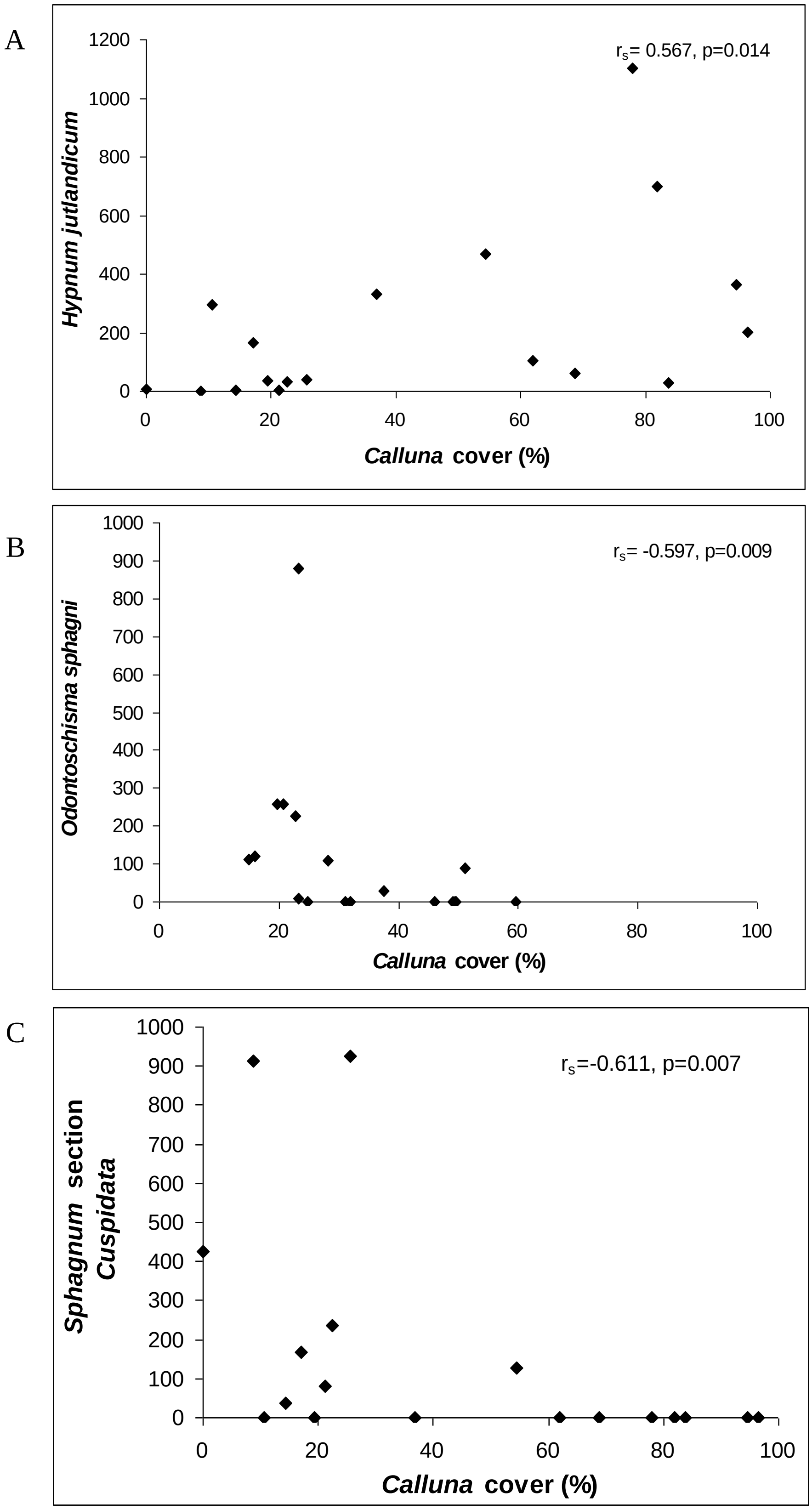


Figure 29: The association between the percentage cover of *Calluna* and the number of growing tips of A) pleurocarpous mosses, B) liverworts, and C) all bryophytes including *Sphagnum* species on the M16d sites

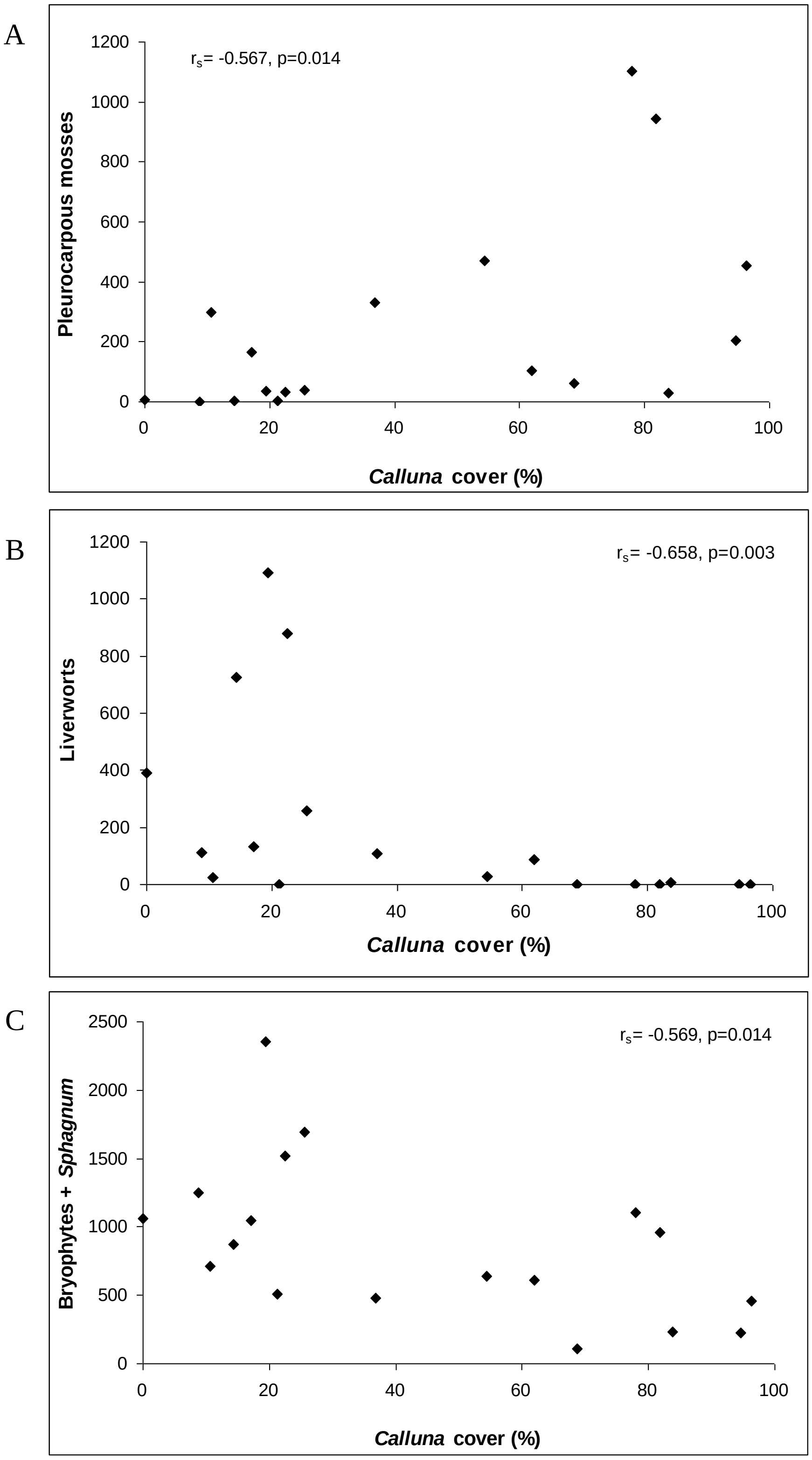


Figure 30: The association between the percentage cover of grass species and the number of growing tips of *Sphagnum* section Acutifolia on the M16d sites

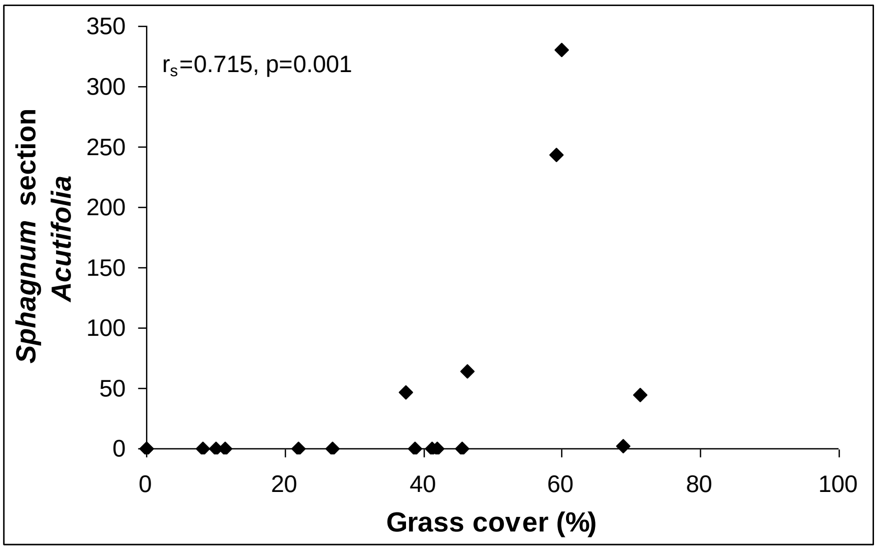


Figure 31: The association between the percentage cover of grass species and the number of growing tips of liverworts on the M16d sites

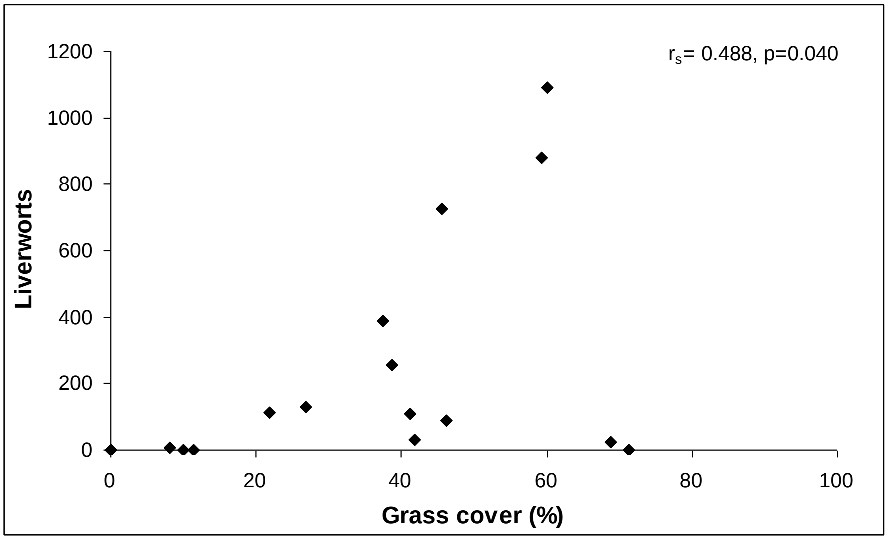


Figure 32: The association between the percentage cover of cottongrass and the number of growing tips of A) *Odontoschisma sphagni*, and B) *Sphagnum* section *Cupsidata* on the M16d sites

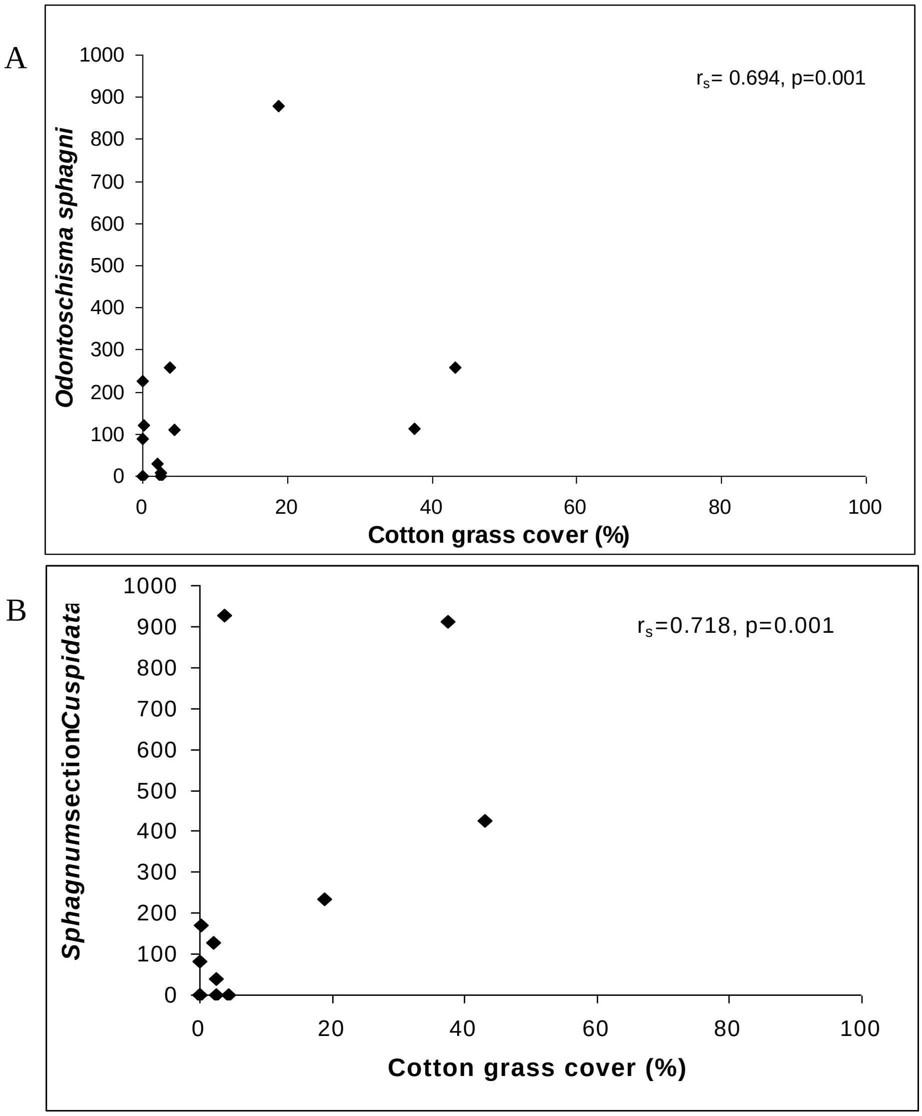
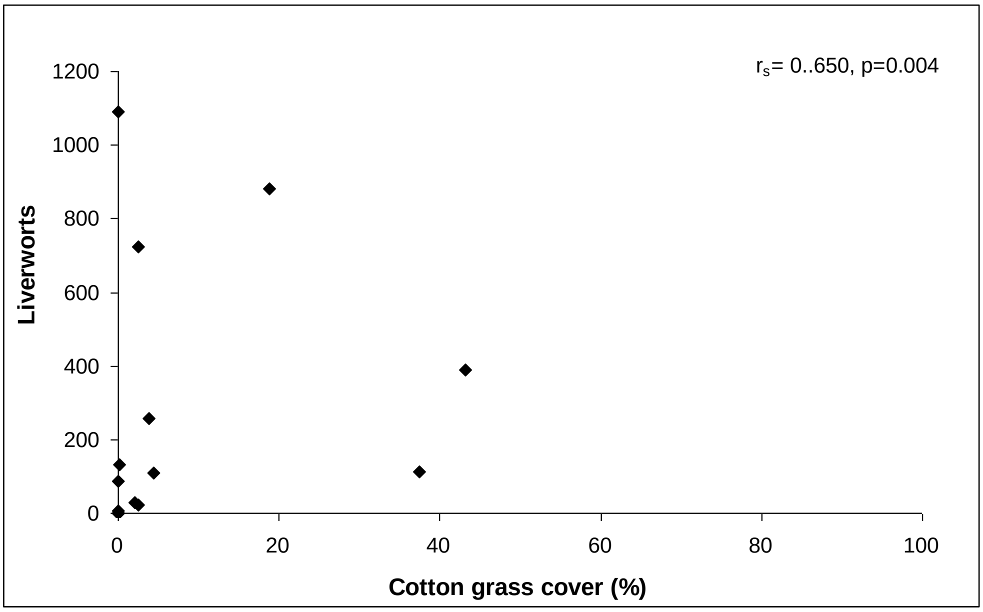


Figure 33: The association between the percentage cover of cottongrass and the number of growing tips of liverworts on the M16d sites



4.4 Comparison of H12a and M16d heathland sites

Several species were recorded on both the H12a and M16d sites. Table 20 gives the National Vegetation Classification (NVC) types in which each species is listed nationally as a component of the bryoflora, and in which of these communities (or subcommunity) the species is deemed to be a constant (Rodwell 1998). Bryophytes may not have been consistently recorded for all NVC field data, therefore a species not recorded for a particular NVC may not indicate that it does not occurr in that community. According to the national NVC community tables, only two of the eight species recorded only on H12a on Spaunton Moor are features of the bryoflora for this NVC type: *B. floerkei* and *L. bidentata*. Not surprisingly, the species characteristic of the pioneer stage of H12a sites on Spaunton Moor are either characteristic of open, exposed areas on drier heathlands (*C. purpureus*, *M. hornum*, *O. lineare* and *P. juniperinum*), or are not stated as being constituents of a heathland or moorland NVC bryoflora, but are characteristic of other open, dry, exposed habitats (*B. capillare*) or colonisers of post-fire habitats (*L. flexifolium*).

Ten of the fifteen species recorded only on the M16d sites on Spaunton Moor are listed in the national NVC community tables as components of the bryoflora for this NVC type, with *C. fissa*, *H. splendens*, *P. purum*, *S. denticulatum* and *S. recurvum* being characteristic of other moorland NVC types.

Of the fifteen species recorded on both the H12a and M16d sites at Spaunton Moor, six are features of the bryoflora of H12 and seven of M16d in the national NVC tables. Of the nine species that were not listed nationally as components of the H12 bryoflora, five were listed in the NVC tables for other heathland NVC types (*C. introflexus*, *C. flexuosus*, *C. divaricata*, *K. praelonga* and *L. glaucum*), three on mire NVC types (*B.*

rutabulum, *C pyriformis* and *P. undulatum*) and one is not listed as a component of a heathland or moorland bryoflora (*P. formosum*). Of the eight species that are not listed in the NVC table as components of the M16 bryoflora, two are listed in the NVC tables as components of other mire sites (*B. rutabulum* and *P. undulatum*), two of heathland sites (*C. introflexus* and *C. divaricata*), three of other heathland and mire sites (*K. praelonga*, *P. commune* and *R. squarrosus*), and one is not listed as a component of a heathland NVC type bryoflora (*P. formosum*).

The presence and absence data was used to classify the similarity of all the sites in relation to species composition and abundance using the TWINSPAN program (Hill and Smilauer 2005). The dendrogram produced by TWINSPAN shows two main groups at the first division with an Eigenvalue of 0.557, with the *0 group being further divided into two groups with an eignevalue of 0.520 (Figure 34).

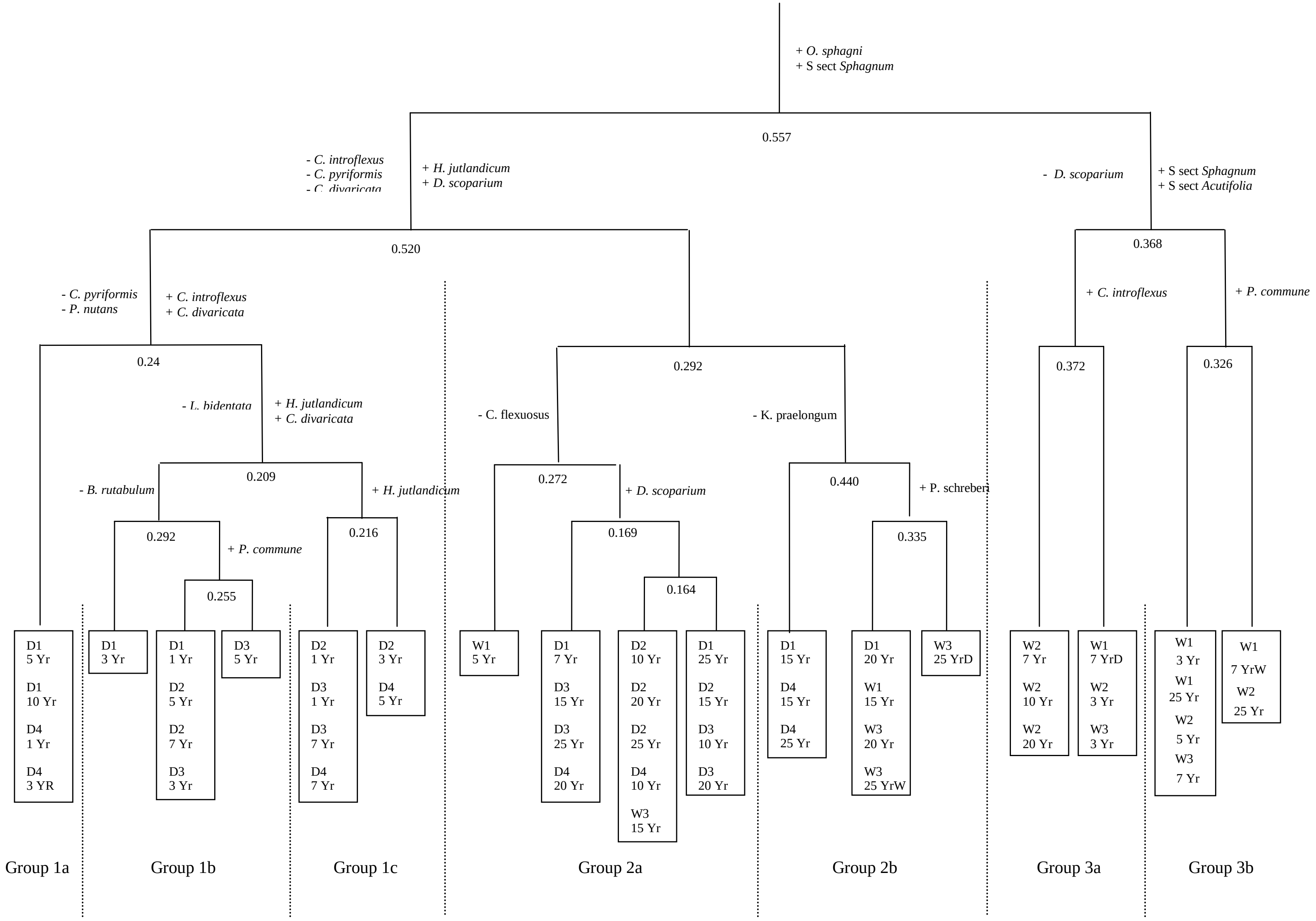
Group 1 predominantly includes H12a sites of seven years and younger, group 2 H12a sites of 10 years and older, along with the sites from M16d that have a higher abundance of *H. jutlandicum* and no *Sphagnum*, and group 3 contains the wet sites that have a high abundance of *Sphagnum*.

Four sites in group 1a are separated early, as these sites have *P. nutans* and *C. purpureus*, and a lower abundance of *C. divaricata* than the other sites in group 1. Group 1b differs from group 1c as they have *L. bidentata*, and less *H. jutlandicum*. Group 2 is split into two main groups, with an eigenvalue of 0.292. Group 2a has *C. introflexus*, *K. praelonga*, *C. divaricata*, and *L. bidentata*, but no *P. undulatum*, whereas group 2b has *P. undulatum*, but no *C. introflexus* or *C. divaricata* and little or no *K. praelonga* or *L. bidentata* as part of the bryoflora. Group 3 is split into two groups with an eigenvalue of 0.368. Group 3a has a much lower abundance of *Sphagnum*, and a higher abundance of *H. jutlandicum* than group 3b.

Table 20: Heathland and moorland NVC types where the species recorded at Spaunton Moor are listed as occurring in the national tables. Note, however, that bryophytes may not have been consistently recorded for all NVC field data. Species in bold are those recorded on Spaunton Moor that are considered to be normal components of that flora. NVC types in bold are those in which the species is considered a constant (or in one of its subcommunities) (Rodwell 1998)

	NVCs where the species a component of the bryoflora
Species recorded on the H12a site at Spaunton moor only	
B. floerkei	M19; M20; M31; H12; H18; H20; H21; H22
B. capillare	-
C. purpureus	H11
L. bidentata	M4; M6; M8; M13; M22; M23; M25; M26; M27; M28; MH4; H11; H12
L. flexifolium	-
M. hornum	M12; H10
O. lineare	M20; H9
P. juniperinum	H1; H2; H3; H4; H8; H11; H16
Species recorded on the M16d site at Spaunton moor only	
A. palustre	M2; M4; **M5**; M6; M7; **M8**; M9; M13; M15; M16; M17; M18; M19; M21; M23; M24; M25; M26; M29
C. fissa	M8; M15; M17; M19; M21; M23; M25; H4; H5
C. connivens	M2; M16; M18; M21
G. inflata	M1; M2; M3; M16; M20; H9
H. splendens	M7; **M8**; M9; M10; M11; **M12**; M15; M17; **M19**; M26; M38; H1; H10; H12; H13; H14; H15; **H16**; **H18**; **H21**; **H22**
K. pauciflora	M14; M16; M17; M18; M19; M20; M21
O. sphagni	M1; M2; M3; M14; M15; M16; M17; **M18**; M19; M21
P. purum	M8; M13; M22; M24; M25; M26; MH1; H4; H8; H11; H12; H16
S. denticulatum	**M1**; M4; M5; M6; M12; **M14**; **M21**; M24; M25; **M29**; M30; **M31**; **M32**; M34; **M35**
S. capillifolium	M6; M7; M12; M15; M16; **M17**; **M19**; M20; M21; M25; H10; H14; H15; H18; **H20**; **H21**; **H22**
S. compactum	M7; M15; **M16**; M17; M19
S. papillosum	M1; M2; M3; M4; M6; **M7**; M8; M14; M15; M16; **M17**; **M18**; M19; M20; **M21**; M25; M29
S. recurvum	M1; **M2**; M3; **M4**; M5; M6; **M7**; M8; M12; M15; M18; M19; **M21**; M25; H10
S. subnitens	M1; M4; M5; M6; **M7**; M8; M9; M10; M11; M12; **M14**; M15; M16; M17; M18; M19; M21; M24; M25; M32; H22
S. tenellum	M2; M14; M15; M16; M17; **M18**; M19; M21; H20; H21
Species recorded on the H12a and M16d sites at Spaunton moor	
B. rutabulum	**M8**; **M13**; M22; **M23**; **M24**; M27
C. flexuosus	M15; M16; M17; M18; M19; **M20**; M21; H2; H3; H4; H6; H8; H9; H10; H13; H14; H15; H18; H20; H21
C. introflexus	H4; H11
C. pyriformis	M16
C. divaricata	H9
D. scoparium	M7; M12; M15; M16; M17; M18; M19; M20; **H1**; H2; **H4**; H6; **H8**; **H9**; H10; **H11**; **H12**; H13; **H14**; H15; **H16**; H17; **H18**; **H19**; **H20**; **H21**; **H22**
H. jutlandicum	M4; M6; M8; M14; M15; **M16**; M17; M18; **M19**; M20; M21; M25; H2; H3; H6; **H12**; H13; **H17**; H19
K. praelonga	M23; M24; M25; M27; M28; H5
L. glaucum	M16; M17; H3; H4
P. undulatum	M9; M22; M26; M27
P. schreberi	M8; M15; M16; M17; **M18**; **M19**; M20; M25; MH1; H4; H8; H10; H11; **H12**; H13; H14; H15; **H16**; **H18**; **H19**; **H20**; **H21**; **H22**
P. nutans	M7; M15; M16; M17; M18; M19; M20; M25; H4; **H9**; H11; H12; H13; H16; H18; H20
P. formosum	-
P. commune	M2; M3; **M4**; M5; M6; **M7**; M8; M12; M15; M17; M18; M19; M20; M21; M23; M25; M29; M31; M32; M35; H10; H12; H13; H16; H18; H19; **H22**
R. squarrosus	M5; M6; M8; M12; M15; M17; M19; M23; M25; M26; M27; M28; M32; M35; H4; H8; H10; H12; H16; **H18**; H19

Figure 34: Dendrogram showing TWINSPAN classification of dry and wet sites on the basis of species presence or absence



5 Discussion

5.1 Key findings

5.1.1 H12a moorland sites on Spaunton Moor

Although the number of species recorded on the H12a sites remained fairly constant across the post-burn age range, the species comprising the bryoflora changed substantially over time. The main pioneer species on the H12a sites was *Campylopus introflexus*. *C. introflexus* is a species introduced from the southern hemisphere that was first recorded in Sussex in 1941 and subsequently spread rapidly throughout the UK (Porley & Hodgetts 2005). This species is a serious conservation concern, as it rapidly colonises areas, particularly those that are subjected to disturbance, and now covers relatively large areas of moorland in the UK. This study indicates that repeated, frequent disturbance as a result of burning, and the lack of surviving patches of pleurocarpous mosses, could promote the spread of *Campylopus introflexus*. This is reflected in the TWINSPAN analysis, where althought the dendrogram generally divides the plots into those younger and older than 10 years post-burn, *Campylopus introflexus* persists in older plots, and desired species characteristic of a mature heathland were absence. The 10-year divide is most likely an indicator to the start of the development of mature heathland on some sites, rather than a widespread recovery of the heathland.

Other species present in the early stages of regeneration were *Cephaloziella divaricata* (usually growing between the stems of *C. introflexus*), *Ceratodon purpureus, Bryum capillare, Campylopus pyriformis, Leptodontium flexifolium, Polytrichum juniperinum* and *Pohlia nutans*. *Campylopus* species have been reported as primary colonisers in three other studies on heathlands (Hobbs & Gimingham 1984; Southorn 1976; Thomas and others 1994). *Pohlia nutans* was the main pioneer species at Skipworth and Allerthorpe Commons (Coppins and Shimwell 1971) and was also recorded in the pioneer community at Rosedale Moor, along with *C. purpureus* and *Polytrichum* species after the fires in 1976 on the North York Moors (Maltby and others 1990). Another species recorded in the pioneer community on Rosedale Moor was *D. heteromalla*, although this species was not recorded on the H12a sites at Spaunton Moor. A coloniser of post-burn sites commonly reported in the studies of bryophyte regeneration described in the literature review, *Funaria hygrometrica*, was not recorded on Spaunton Moor. The lack of *F. hygrometrica* on Spaunton Moor, however, is consistent with other studies conducted on heathlands in the UK (Hobbs & Gimingham 1984; Hobbs & Gimingham 1987; Southorn 1976; Coppins & Shimwell 1971; Maltby and others 1990).

The main species recorded in the older stands of *Calluna* was *Hypnum jutlandicum*. Other species characteristic of older stands included *Lophocolea bidentata*, *Dicranum scoparium*, *Kindbergia praelonga* (*Eurhynchium praelongum*), *Barbilophozia floerkei*, *Plagiothecium undulatum* and *Pleurozium schreberi*. *H. jutlandicum*, *Brachythecium rutabulum* and *L. bidentata* were occasionally recorded on younger sites. When these species were recorded on the younger sites, there tended to be a dense canopy of scorched *Calluna* stems which were not burnt at the very bases, above the surviving patch of bryophyte stems. These dense *Calluna* stems may have afforded the bryophytes some protection from the fire, and indicate a cooler/lower intensity burn. The survival of species from the pre-burn heathland community may be beneficial. Although they are unlikely to survive until the recovery of the canopy in that area, they may be important source populations for adjacent sites that have already been burnt, and where the heather canopy has started to recover, allowing more rapid bryophyte regeneration on these sites. Also, the surviving patches of bryophytes may limit the colonisation of invasive species. In the current study, on the areas where *H. jutlandicum* survived, there was no colonisation by *Campylopus* species, which tends to colonise bare ground, rather than ground occupied by other species (Clement & Touffet 1988).

The characteristics reported of species found solely or primarily on sites of 7 years and younger are given in Tables 21 and 22, and species found solely or primarily on the sites of 15 years and older in Tables 23 and 24. Although all bryophytes are capable of vegetative reproduction, some utilise this method of reproduction more than others. In the tables below, '?' denotes that vegetative reproduction has not been recorded for that species in the description given in the relevant texts, rather than vegetative reproduction not taking place (Watson 1995; Paton 1999; Smith 2004; Porley & Hodgetts 2005). Species found primarily on sites of 7 years or younger are those more commonly found on open, exposed sites, are tolerant of dry or even drought conditions, produce sporophytes at least occasionally, sometimes frequently, and also produce specialist vegetative propagules. The species recorded primarily on sites of 15 years and older, on the other hand, are generally of sheltered or shaded habitats, and although they may be able to tolerate drier conditions, they are more likely to be found in moist or wet habitats. Several of these species rarely produce sporophytes, and most do not produce specialist vegetative propagules, relying on gametophytic fragmentation. The environmental conditions reportedly favoured by all species recorded on the H12a sites are given in Appendix 3, and their reproductive strategies in Appendix 4.

There were three *Campylopus* species recorded on the H12a sites on Spaunton Moor, *Campylopus introflexus*, *C. pyriformis* and *C. flexuosus*. It can be seen from Tables 21 to 24 that *C. introflexus* and *C. pyriformis* are prevalent during the early stages of heather development (7 years and younger) when vascular plant cover is low, and *C. flexuosus* in the later stages (15 years and older) when vascular plant cover is higher. This demonstrates that these species occupy separate niches in this NVC community, with *C. flexuosus* being less tolerant of the exposed conditions post-burn conditions than *C. introflexus* and *C. pyriformis*, requiring increased shade and humidity afforded by the increased canopy cover in the more developed heather stands. Interestingly, *C. introflexus* and *C. pyriformis* demonstrated different reproductive strategies. *C. introflexus* was observed producing large numbers of sporophytes as well as vegetative propagules, whereas *C. pyriformis* was reproducing vegetatively only, with deciduous shoot tips abundant on the surface of the colonies. *C. flexuosus* was also propagating vegetatively, again via deciduous shoot tips, however, they were less abundant on the surface of the colonies than in *C. pyriformis*.

Over time, not only did the components of the bryoflora change, but there was a substantial decrease in the number of bryophyte stems recorded, with approximately 80% fewer growing tips recorded on the 25 year sites than the 1 year sites. This seems a dramatic and significant decrease. However, as the bryoflora changes from small acrocarpous mosses, to branching, creeping pleuorcarpous mosses, the mean percentage of area covered by bryophytes is actually much higher on the 25 year sites than the 1 year sites. This increased cover may be advantageous, as bryophytes hold water, help prevent erosion of the peat, and may even assist the formation of peat by keeping the surface moist and anoxic. In addition, bryophytes, particularly pleurocarpous mosses, absorb nutrients from precipitation, restricting the nutrients available for vascular plants. The retention of nutrients in bryophyte tissue may have a direct effect on the composition and succession of the vascular plant community, and may assist in preventing the invasion of competitive species such as grass and bracken.

Table 21: The reported reproductive strategies, frequency and timing of sporophyte production, and the production of vegetative propagules, of the species recorded primarily on H12a sites of 7 years and younger

Species	**Reproductive strategy**	**Frequency of capsules**	**Timing of capsules**	**Vegetative reproduction**
Species only in sites of 7 years or younger				
C. purpureus	Dioicous	Frequent	Spring/Summer	?
B. capillare	Dioicous	Frequent	Spring/Summer	Rhizoidal gemmae
L. flexifolium	Dioicous	Occasional	Spring	Bulbiferous branches
P. juniperinum	Dioicous	Frequent	Summer	?
Species primarily in sites of 7 years or younger				
C. introflexus	Dioicous	Occasional	Spring	Deciduous leaves/shoots
C. pyriformis	Dioicous	Occasional	Spring	Deciduous leaves/shoots
C. divaricata	Dioicous	Occasional	Winter	Gemmae
P. nutans	Monoicous	Frequent	Spring/Summer	Bulbiferous branches

Table 22: The reported preferences in relation to exposure/shade, moisture and pH of the species recorded primarily on the H12a sites of 7 years and younger

Species	**Exposure/shade gradient**	**Moisture gradient**	**pH preference**
Species only in sites of 7 years or younger			
C. purpureus	Exposed	Dry	Acid - Neutral
B. capillare	Exposed	Drought - Dry	Acid - Basic
L. flexifolium	Exposed - Sheltered	Dry	Acid - Neutral
P. juniperinum	Exposed	Dry	Acid – Mild acid
Species primarily in sites of 7 years or younger			
C. introflexus	Exposed	Dry	Acid – Mild acid
C. pyriformis	Exposed	Dry - Moist	Acid – Mild acid
C. divaricata	Exposed - Shaded	Drought - Moist	Acid - Neutral
P. nutans	Exposed - Shaded	Dry - Wet	Acid – Mild acid

Table 23: The reported reproductive strategies, frequency and timing of sporophyte production, and the production of vegetative propagules, of the species recorded primarily on the H12a sites of 15 years and older

Species	**Reproductive strategy**	**Frequency of capsules**	**Timing of capsules**	**Vegetative reproduction**
Species only in sites of 15 years or older				
B. floerkei	Dioicous	Rare	Summer/Autumn	?
L. glaucum	Dioicous	Rare	Autumn/Winter	Fragmentation
O. lineare	Monoicous	Frequent	Spring/Summer	Protonemal gemmae
P. undulatum	Dioicous	Occasional	Spring/Summer	?
P. schreberi	Dioicous	Rare	?	Fragmentation
M. hornum	Dioicous	Frequent	Spring	?
Species primarily in sites of 15 years or older				
C. flexuosus	Dioicous	Occasional	Spring	Deciduous leaves/shoots
D. scoparium	Dioicous	Occasional	Summer - Winter	?
K. praelonga	Dioicous	Frequent	Winter	?
H. jutlandicum	Dioicous	Frequent	Autumn	?
L. bidentata	Monoicous	Frequent	Winter - Summer	?
R. squarrosus	Dioicous	Rare	Winter	?

Table 24: The reported preferences in relation to exposure/shade, moisture and pH of the species recorded primarily on the H12a sites of 15 years and older

Species	**Exposure/shade gradient**	**Moisture gradient**	**pH gradient**
Species only in sites of 15 years or older			
B. floerkei	Sheltered	Dry - Moist	Acid – Neutral
L. glaucum	Sheltered - Shaded	Dry - Boggy	Acid – Mild acid
O. lineare	Sheltered - Shaded	Dry - Moist	Acid – Neutral
P. undulatum	Shaded	Moist - Wet	Acid – Mild acid
P. schreberi	Sheltered – Deep shade	Drought - Wet	Acid – Mild acid
M. hornum	Sheltered - Shaded	Moist	Acid – Mild acid
Species primarily in sites of 15 years or older			
C. flexuosus	Exposed - Sheltered	Moist	Acid – Mild acid
D. scoparium	Exposed - Sheltered	Moist	Acid – Neutral
K. praelonga	Sheltered – Deep shade	Dry - Moist	Acid – Mild basic
H. jutlandicum	Exposed – Deep shade	Dry - Wet	Acid – Neutral
L. bidentata	Sheltered – Deep shade	Moist - Boggy	Acid – Basic
R. squarrosus	Sheltered –Shaded	Drought - Wet	Acid – Basic

From the distribution of the species across the age range, it can be seen that the reduction in the pioneer species, and the start of the establishment of a bryoflora more characteristic of mature heathland occurs approximately 10 years post-burn on Spaunton Moor. This was confirmed by the classification of the sites by species composition using the TWINSPAN program (Hill & Smilauer 2005). The main pioneer species were recorded in the greatest numbers when the canopy height was below 30 cm, whereas species characteristic of more mature heathland started to increase in abundance once the canopy height reached 30 cm, with *H. jutlandicum* to being recorded in the bryoflora consistently, at a canopy height of over 40 cm. As the median height of the plant canopy reaches 40 cm at approximately 10 years post burn, this also supports the conclusion that a bryoflora more characteristic of a mature heathland starts to recover at this age. The abundance of *H. jutlandicum* begins to decrease once the canopy height reaches approximately 55 cm. Therefore, the ideal height for *H. jutlandicum* growth seems to be between approximately 45 cm and 55 cm, a height range which can be found on sites between 7 and 20 years old. When the range of canopy height for each stage of heather development was considered, a canopy height range of 45 to 55 cm was encompassed in building, mature and degenerate stages of heather development. This would indicate that the height of the canopy is a better indicator of recolonisation and bryoflora composition than either the age or stage of heather development.

When considering a burning rotation, the benefits of having a developed bryoflora containing pleurocarpous mosses in an area to be burnt should be taken in to account. By having a well-developed, primarily pleurocarpous, bryophyte community, the water holding capacity of the bryophytes may keep the bases of the heather stems moist, producing a cooler burn. This in turn may decrease the degree of damage to the peat surface and increase the likelihood of survival of some of the pre-burn bryophyte community. As already mentioned, the survival of species from the pre-burn community may be beneficial as post-fire source populations for adjacent sites, increasing the speed of recovery of the bryoflora, and limiting the colonisation of other, less desirable invasive species, such as *C. introflexus*. By reducing the damage to the peat surface, peat erosion may be decreased.

5.1.2 M16d moorland sites on Spaunton Moor

The species most commonly recorded 3 years post-burn on the M16d moorland were *Sphagnum* species, with *Odontoschisma sphagni* and *Campylopus introflexus* also prominent. *O. sphagni* is known to be closely associated with *Sphagnum* species, usually growing between the *Sphagnum* stems. In the current study, this was also apparent, but this association seemed to be most evident with the *Sphagnum* species from the section *Cuspidata*. In the older stands of heather, the abundance of *Sphagnum* decreased, and that of *Hypnum jutlandicum* increased. As on the H12a sites, there was a fairly constant number of species present throughout the age range. However, on the M16d sites, there was not such a dramatic change in species composition with increasing age. *Sphagnum* species, *O. sphagni* and *H. jutlandicum* were present throughout the age range, although in varying abundances, and many of the other species recorded were patchy in their abundance. Only one species, *O. sphagni*, showed a significant difference in abundance with the stage of heather development. All three *Campylopus* species recorded on the H12a sites were also recorded on the M16d sites. The pioneer species *C. introflexus* and *C. pyriformis* were present in much lower numbers and seemed less able to survive in the older heather stands than they had on the H12a sites. *C. flexuosus* was more common on the younger M16d sites, rather than the older stands as on the H12a sites.

The characteristics reported for the species found solely or primarily on the sites of 7 years and younger are given in Tables 25 and 26, and for species found solely or primarily on the sites of 15 years and older on Tables 27 and 28. Again, '?' denotes that vegetative reproduction has not been recorded for that species in the description given in the relevant texts, rather than vegetative reproduction not taking place (Watson 1995; Paton 1999; Smith 2004; Porley & Hodgetts 2005). It can be seen from these tables that the species found primarily on sites of 7 years or younger are those that are more tolerant of exposed, dry habitats than those of the sites 15 years and older, and produce specialist vegetative propagules, whereas those on the older sites rely on fragmentation for vegetative reproduction. The environmental conditions reportedly favoured by all species recorded on the M16d sites are given in Appendix 3, and their reproductive strategies in Appendix 4.

Table 25: The reported reproductive strategies, frequency and timing of sporophyte production, and the production of vegetative propagules, of the species recorded primarily on the M16d sites of 7 years and younger

Species	Reproductive strategy	Frequency of capsules	Timing of capsules	Vegetative reproduction
Species only in sites of 7 years or younger				
A. palustre	Dioicous	Frequent	Summer	Gemmae (Pseudophilia)
P. nutans	Monoicous	Frequent	Spring/Summer	Bulbiferous branches
S. capillifolium	Monoicous	Frequent	Summer	Innovations
K. pauciflora	Dioicous	Frequent	Summer/Autumn	Underground axes
Species primarily in sites of 7 years or younger				
C. introflexus	Dioicous	Frequent	Spring	Deciduous leaves/shoots
C. pyriformis	Dioicous	Occasional	Spring	Deciduous leaves/shoots
O. sphagni	Dioicous	Rare	Spring/Summer	?
L. glaucum	Dioicous	Rare	Autumn/Winter	Fragmentation
S. papillosum	Dioicous	Occasional	Summer	Innovations
S. tenellum	Dioicous	Frequent	Summer	Innovations
C. connivens	Monoicous	Frequent	Spring	Gemmae (occasional)
C. divaricata	Dioicous	Occasional	Winter	Gemmae
S. denticulatum	Dioicous	Occasional	Summer	Innovations

Table 26: The reported preferences in relation to exposure/shade, moisture and pH of the species recorded primarily on the M16d sites of 7 years and younger

Species	**Exposure/shade gradient**	**Moisture gradient**	**pH gradient**
Species only in sites of 7 years or younger			
A. palustre	Exposed - Shaded	Moist	Acid - Neutral
P. nutans	Exposed - Shaded	Dry - Wet	Acid – Mild acid
S. capillifolium	Exposed - Sheltered	Moist - wet	Acid
K. pauciflora	Shaded	Moist - Boggy	Acid – Mild acid
Species primarily in sites of 7 years or younger			
C. introflexus	Exposed	Dry	Acid – Mild acid
C. pyriformis	Exposed	Dry	Acid – Mild acid
O. sphagni	Sheltered – Deep shade	Moist - Boggy	Acid
L. glaucum	Sheltered - Shaded	Dry - Boggy	Acid – Mild acid
S. papillosum	Exposed - Sheltered	Wet - Submerged	Acid
S. tenellum	Exposed - Shaded	Moist - Boggy	Acid
C. connivens	Shaded	Moist	Acid – Mild acid
C. divaricata	Exposed - Shaded	Drought - Moist	Acid - Neutral
S. denticulatum	Exposed - Shaded	Wet - Submerged	Acid

Table 27: The reported reproductive strategies, frequency and timing of sporophyte production, and the production of vegetative propagules, of the species recorded primarily on the M16d sites of 15 years and older

Species	**Reproductive strategy**	**Frequency of capsules**	**Timing of capsules**	**Vegetative reproduction**
Species only in sites of 15 years or older				
B. rutabulum	Monoicous	Frequent	Autumn - Spring	?
P. undulatum	Dioicous	Frequent	Spring/Summer	?
P. purum	Dioicous	Rare	Autumn/Winter	Fragmentation
Species primarily in sites of 15 years or older				
H. jutlandicum	Dioicous	Occasional	Autumn	?
P. schreberi	Dioicous	Rare	?	Fragmentation
P. commune	Dioicous	Frequent	Summer	?

Table 28: The reported preferences in relation to exposure/shade, moisture and pH of the species recorded primarily on the M16d sites of 15 years and older

Species	**Exposure/shade gradient**	**Moisture gradient**	**pH gradient**
Species only in sites of 15 years or older			
B. rutabulum	Sheltered – Deep shade	Moist	Neutral - Basic
P. undulatum	Shaded	Moist - Wet	Acid – Mild acid
P. purum	Sheltered - Shaded	Moist - Wet	Acid - Basic
Species primarily in sites of 15 years or older			
H. jutlandicum	Exposed - Deep shade	Dry - Wet	Acid - Neutral
P. schreberi	Sheltered - Deep shade	Drought - Wet	Acid – Mild acid
P. commune	Exposed - Shaded	Moist - Boggy	Acid – Mild acid

Unlike in the H12a sites, the decrease in the number of bryophyte stems recorded on the older sites was much less, with approximately 30% fewer growing tips recorded on the 25 year old sites than the 3 year old sites, but again, there was a substantial increase in abundance of *H. jutlandicum*, and therefore the percentage of area covered by this species was much higher on the 25 year sites than the 3 year sites.

Sphagnum species and *O. sphagni* were recorded in the greatest numbers when the canopy height was below 30 cm on the M16d sites, and *H. jutlandicum* started to increase in abundance once the canopy height reached approximately 20cm, with maximum abundance achieved at a canopy height of approximately 50 cm. This was the same canopy height that *H. jutlandicum* was consistently recorded at on the H12a sites, and may reflect the change in species due to both the drying of peat and the increase in vascular plant cover. When considering the range of canopy heights recorded across the ages of heather represented on the M16d sites, a canopy height of 20 cm encompassed in the ranges of sites 3 to 10 years post burn, and a 50 cm canopy height on sites between 15 and 25 years post burn. A canopy height of 20 cm was recorded at all stages of heather development, and 50 cm at the mature and degenerate stages. The height of the canopy where both *Sphagnum* and *H. jutlandicum* are represented ranges from approximately 20 cm to 35 cm, which spans all the ages and stages of heather development when the range of canopy height is taken into consideration. Therefore as with the H12a sites, the height of heather seems to be a better indicator of the composition of the bryoflora than either the age or stage of development of the heather.

A noticeable difference between the M16d and H12a sites not yet mentioned was the classification of the degenerate stage of heather. On the H12a sites, the degenerate stage showed the typical production of gaps and layering of stems. On the M16d sites, however, the characteristics of the degenerate stage was more the death and loss of leaves from the heather, with no apparent gap formation or layering of stems. It could be seen from the median and range of canopy heights recorded that, although there were some areas of low canopy height, the median of the degenerate stages of heather were higher than the mature, and there was an evident skew of the data towards the higher values. On the H12a sites however, the median height of the degenerate heather was lower than that of the mature, and the skew of the data is much less, indicating that the lower canopy heights were more frequently recorded on the degenerate area of the H12a sites than the M16d sites.

5.2 Limitations of the current research

There are inherent problems with this type of study, primarily the identification and controlling for confounding factors. Geographical and environmental factors can impact on the establishment, growth and development of plants, and either mask or enhance the effects of the factor of interest, in this case the burning of heather. To reduce the impact of altitude, aspect, slope, rainfall, soil chemistry and other environmental factors, a block experimental design was used, where surveyed plots were in close proximity to one another. On the smaller scale, edge effects such as, altered light penetration and humidity, were minimised by sampling in the centre of plots, and therefore leaving a buffer zone of at least 2 m between the sampled site and the edge of the vegetation patch. This is particularly important in this type of environment, where there is a mosaic of vegetation development.

Despite these attempts to minimise the effects of these factors, there were other limitations of the research that could not be overcome in this type of study. Firstly, due to the less intensive management of the M16d moorland, there were no areas that were younger than 3 years post-burn. In addition, not all ages post-burn were represented on all the sites surveyed, therefore species may have been under- or over-estimated in the ages with inadequate replication. To account for this, only those ages that were present on all three sites were used in the statistical analyses, which were 3, 7 and 25 years post-burn. This enabled us to gain an insight in to the relationship between age and bryophyte abundance, as the youngest and oldest post-burn ages were represented, with a third intermediate age included.

Secondly, the study was small, with only three replicates on the M16d moorland and four on the H12a heathland. This results in wide standard errors and decreases the power of the statistical analyses. Thus, there may be other statistically significant relationships that were not identified due to lack of statistical power. Also, due to the patchiness of the growth of bryophytes, low levels of replication may under- or over-estimate the abundance of some species. In addition, once sites with a mosaic of differently aged heather were identified, the actual identification of the age of each plot was reliant on the memory of the keeper. It would be expected therefore, that the allocation of age to the younger sites was most accurate, with that of the older sites being close approximations.

Thirdly, only limited information regarding the recent history of burning at the site was known. Factors such as the stage of heather development and environmental factors pre-burn will affect fire intensity, the post-burn conditions, and the rate of regeneration. Several authors have commented on the importance of the stage at which heather is burnt (Mowforth & Sydes 1989; Wood-Gee 1996; Hobbs & Gimingham 1984), and the effect on post-burn species diversity (Hobbs & Gimingham 1984). Others have highlighted the potential difference in regeneration potential after cool and hot burns, with bryophytes typical of more mature heathland surviving cool burns to provide a source population for regeneration, whereas with high intensity burns even pioneer bryophytes are prevented from colonising (Esposito and others 1999; Puche & Gimeno 2000; Schimmel & Granstrom 1996; Southorn 1976; Roze 1993). The repeated burning of heather means that these impacts may be intensified over time, an effect known as catch up burning. We tried to limit the effect of this as much as possible, however, as we had no long-term history of the sites, we were only able to avoid areas of heather known to have been at the degenerate stage pre-burn, with the amount of scorched woody material left after the burn used as an indicator on the younger sites, and the knowledge of the keeper to avoid those areas in the older sites. Therefore, the pre-burn stage of heather may have been at the building or mature stage at the previous burn, which would have an impact on the results, with the regeneration of heather at the sites burnt at the mature stage of heather development, regenerating more slowing than those at the building stage.

In addition, the current study uses the increase in the species *Hypnum jutlandicum* to indicate recovery, particularly on the dry heath sites. However, species diversity is also an important factor when considering recovery of the habitat. Therefore, the increase in the abundance of *Hypnum jutlandicum* does not necessarily indicate a recovery of bryophyte species diversity. However, other species characteristic of a recovered heath were also recorded, and given that the sites in the current study have been subjected to a prolonged period of repeated burning, what could be considered a recovered heathland here may not resemble a more natural, less intensively-managed, moorland.

Lastly, the canopy heights identified as indications of bryophyte recovery are at present only applicable to Spaunton Moor; further research is required to determine whether the canopy heights suggestive of a recovered bryoflora at Spaunton Moor can be extrapolated to other moors.

6 Conclusions

6.1 Implications for management

This study indicates that repeated, frequent burning could promote the spread of *Campylopus introflexus*, particularly on H12a heathland. The 10-year post-burn increase in species characteristic of a mature heathland on H12a heathland is most likely an indicator to the start of the the recovery of the habitat, rather than a widespread recovery of the heathland, as *C. introflexus* persists in older plots and desired species characteristic of a mature heathland were still absence.

This study highlighted the relationship between characteristics of the vascular plant canopy and the recovery of the bryoflora. Bryophyte species tolerate different levels of shade and humidity, and therefore different species will be present depending on the vascular plant cover. Age and the stage of heather development, however, do not seem to be as good indicators of the composition of the bryoflora as canopy height. The association between the presence, and abundance, of species, seems closely related to this variable, and therefore canopy height may be a more reliable indicator as to when the bryoflora has recovered, and may help to inform practice regarding a sustainable burning cycle.

It seems promising that the same canopy height is related to a high abundance of *H. jutlandicum* on both the H12a and M16d sites. However, until this is tested experimentally on other vegetation types, and moorlands in other areas with different environmental conditions, it is premature to apply the results of this study to other areas.

6.2 Recommendations for future research

To obtain an overall understanding of the regeneration of bryophytes across the North York Moors, ideally unburnt areas, of each stage of heather, and of different vegetation types, would be identified and the bryoflora recorded. These areas would then be subjected to controlled hot and cold burns, and permanent quadrats established to allow the bryoflora to be surveyed in successive years. The bryophyte re-establishment could be measured annually, with each plot acting as its own control, as the recolonising community can be compared to the pre-burn community. It is accepted that there may difficulties in securing funding for this type of study due to its long-term nature, resource constraints and the need to burn significant areas of heathland. Therefore, extension of the current experimental design is recommended, preferably on a larger scale, increasing the number of quadrats, over a greater area, in which stem counts can be recorded, to account for the patchy growth of bryophytes.

Post-burn sites where each age of burn being investigated is represented in close proximity to each other need to be identified. Each site can be considered a block and this can be accounted for during the statistical analysis. Ideally, a detailed history of burning rotation should be obtained to establish the impact of catch up burning. Plots for each age of burn need to be large enough to allow sufficient surveying whilst avoiding edge effects. Within each plot, quadrats (either randomly selected or arranged in transects across each plots) should be surveyed, and the number of growing tips and area cover of bryophytes. This report highlighted the importance of recording the characteristics of the vascular plant canopy, therefore it is also recommended that the canopy height and percentage cover of vascular plants should be recorded.

One potential problem with expanding the current experimental design to look at all factors, i.e. the effect of pre-burn stage of heather, vegetation type, and the intensity of the fire, is the availability of suitable sites. It may not be possible to find sufficient sites where all ages of post-burn heather are represented in such close proximity, in all scenarios. If sufficient sites could be identified on each moor, intra-moor, inter-moor, and across moor comparisons and averages could be made.

Once sites have been identified, it is sensible that plots be selected on the time since last burn, therefore the age of heather. However, the reporting of bryophyte recolonisation using age as the only factor may not be the most informative way to present the results. Environmental factors will affect the rate of growth and development of the heather and other plants, therefore, the conditions experienced by bryophytes colonising a particular age will vary across sites. Therefore results should be presented both by age and stage of heather development as in the current report. Correlations between bryophyte recovery and other factors, such as characteristics of the vascular plant canopy, also need to be explored.

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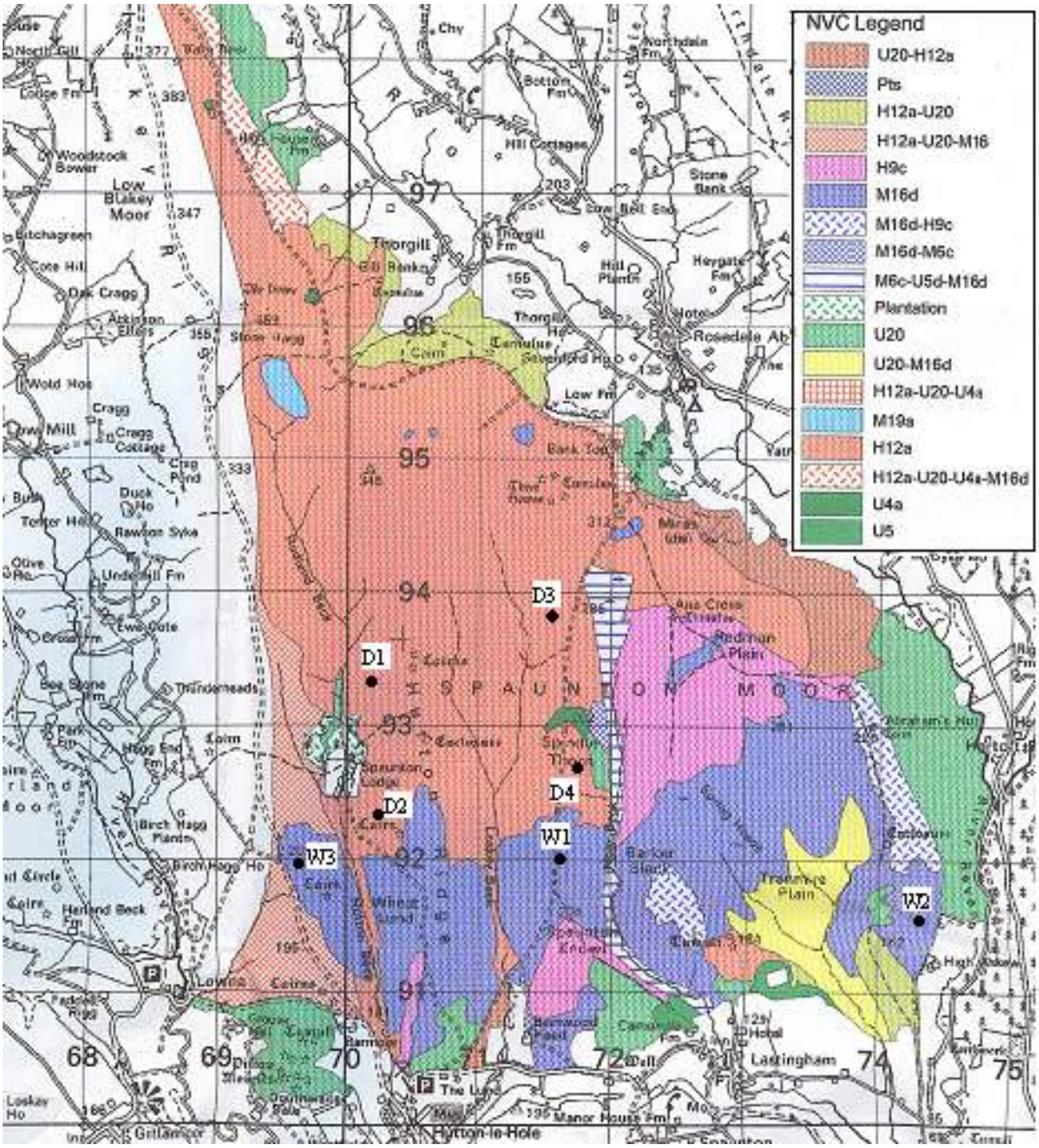
APPENDICES

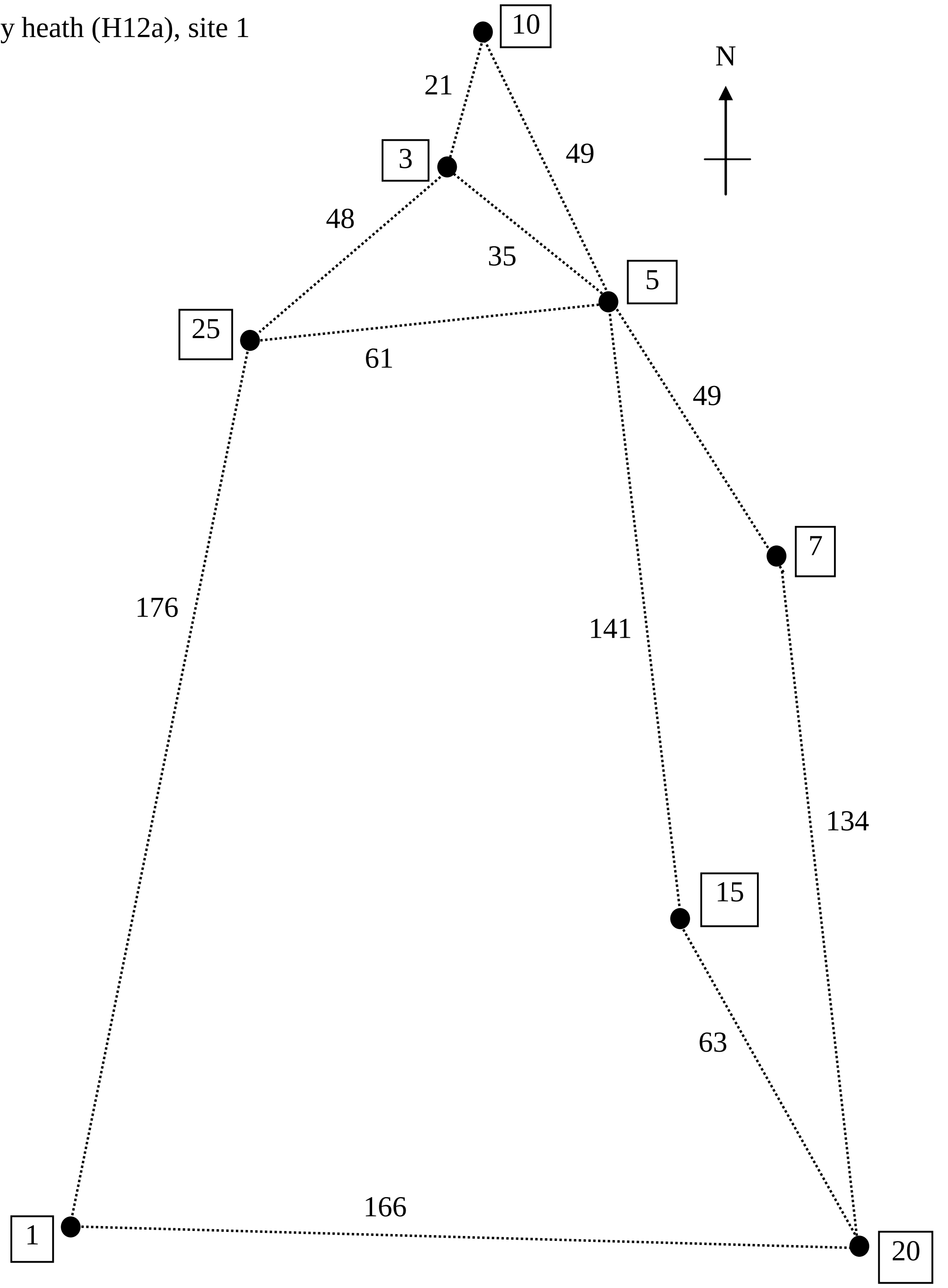
Appendix 1: Location and orientation of plots

The approximate locations of the dry heath (H12a) sites (D1, D2, D3 and D4) and wet heath (M16d) sites (W1, W2, W3) on Spaunton Moor.



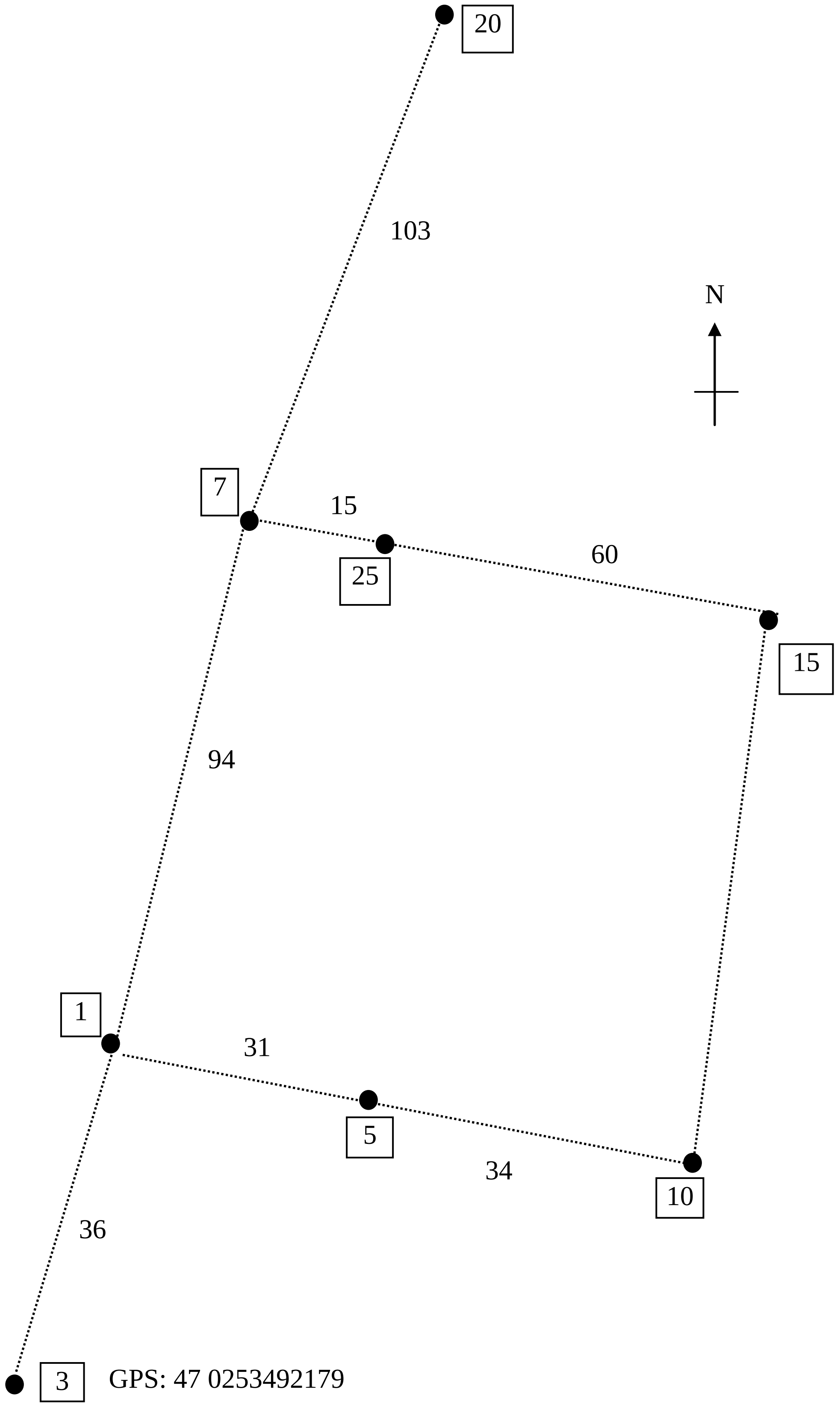
The orientation of plots at each of the sites. The black dots are the central poles, with the number of years since burn indicated. The numbers adjacent to the lines are approximate distances in metres. The GPS reading for one of the central poles is given for each site.

Dry heath (H12a), site 1



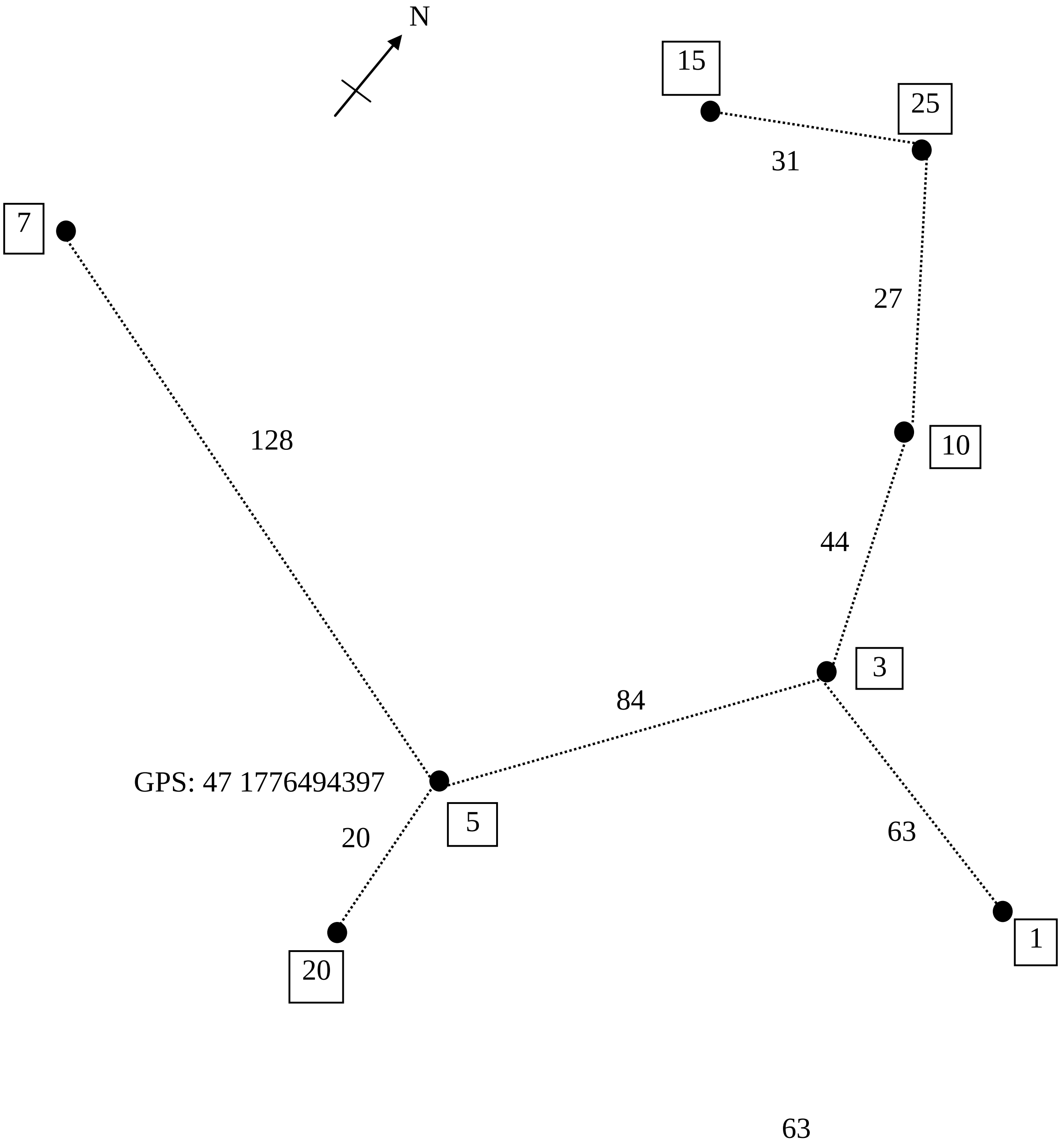
GPS: 47 0486493693

Dry heath (H12a), site 2

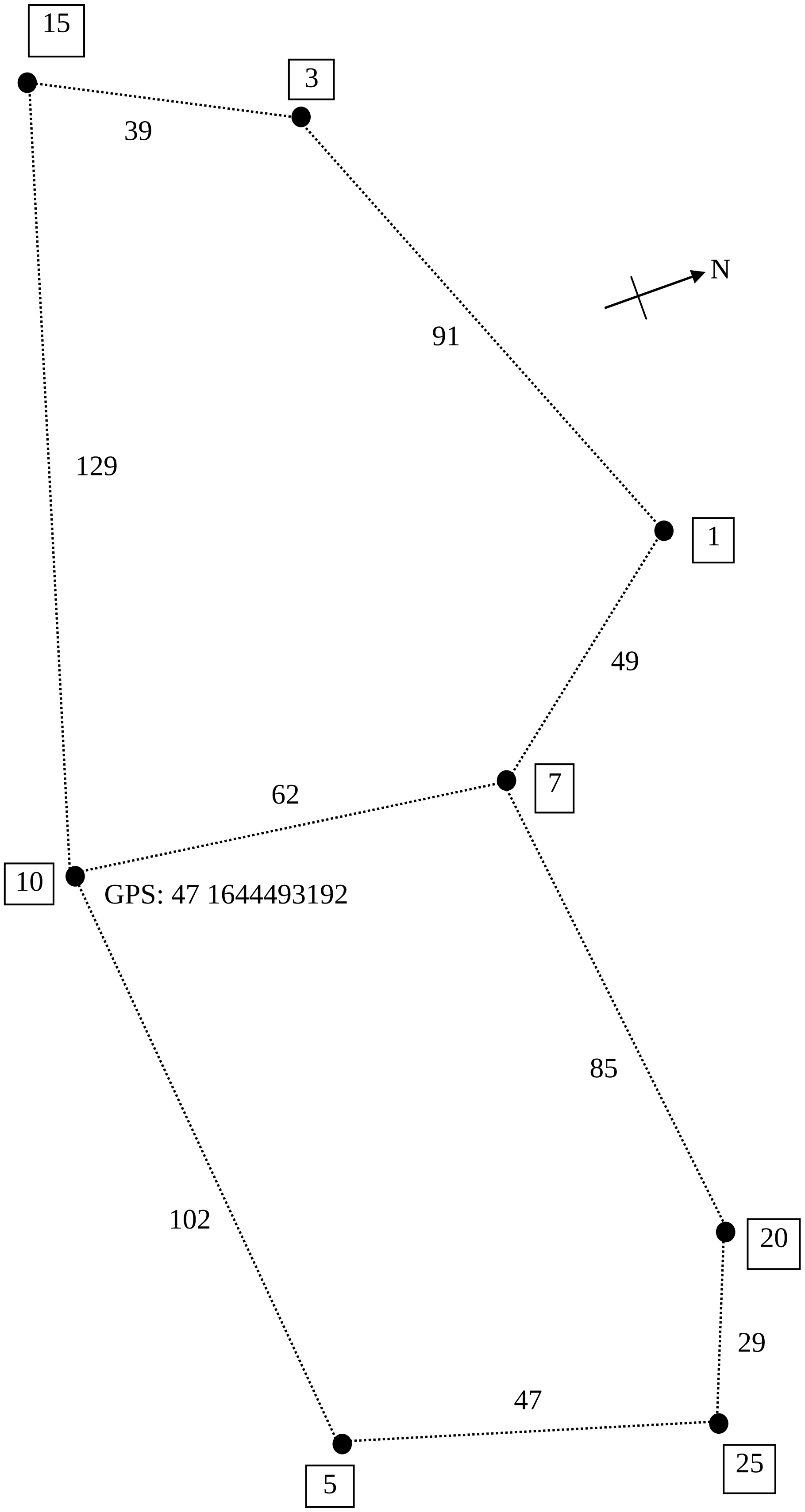


GPS: 47 0253492179

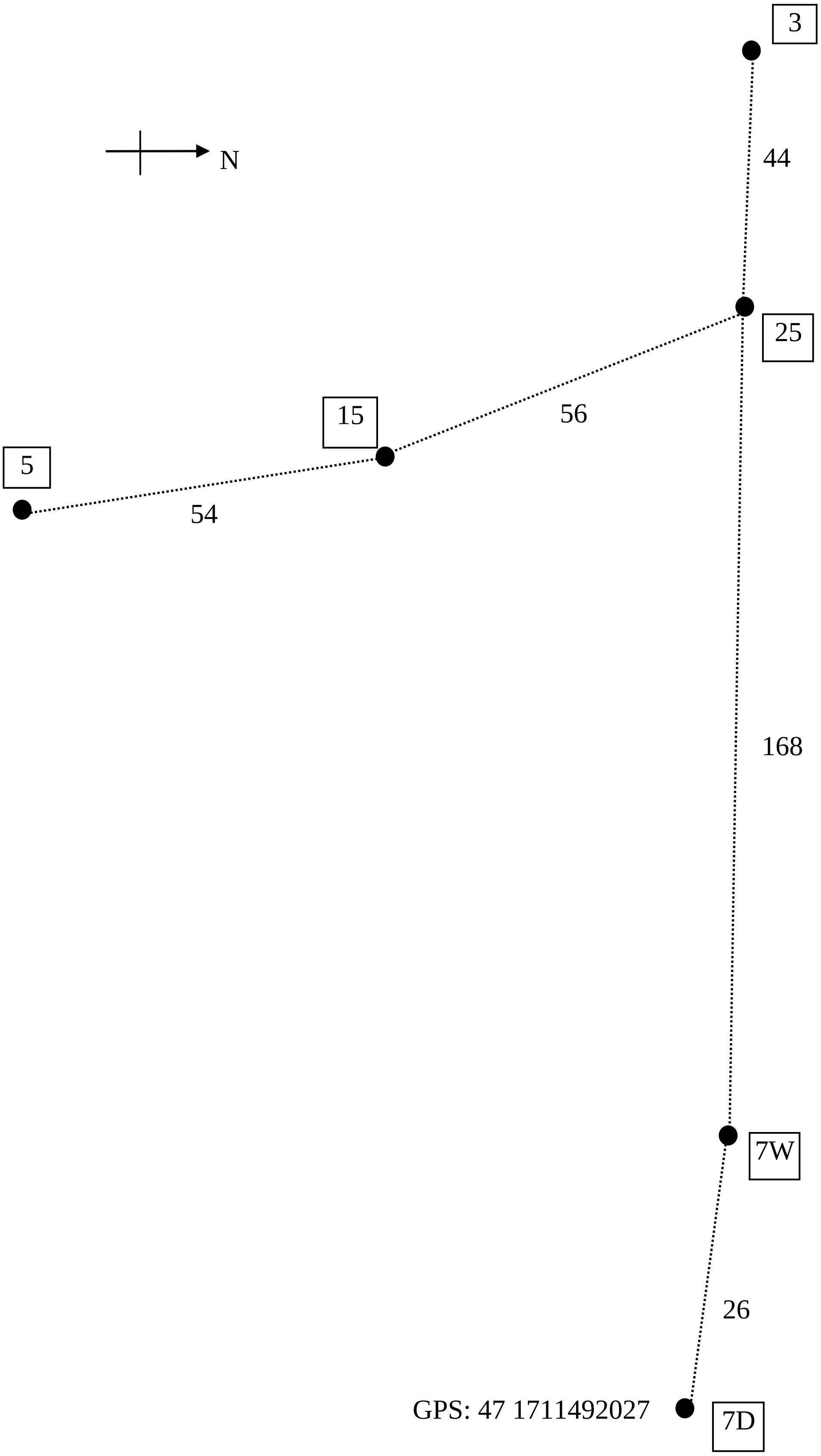
Dry heath (H12a), site 3

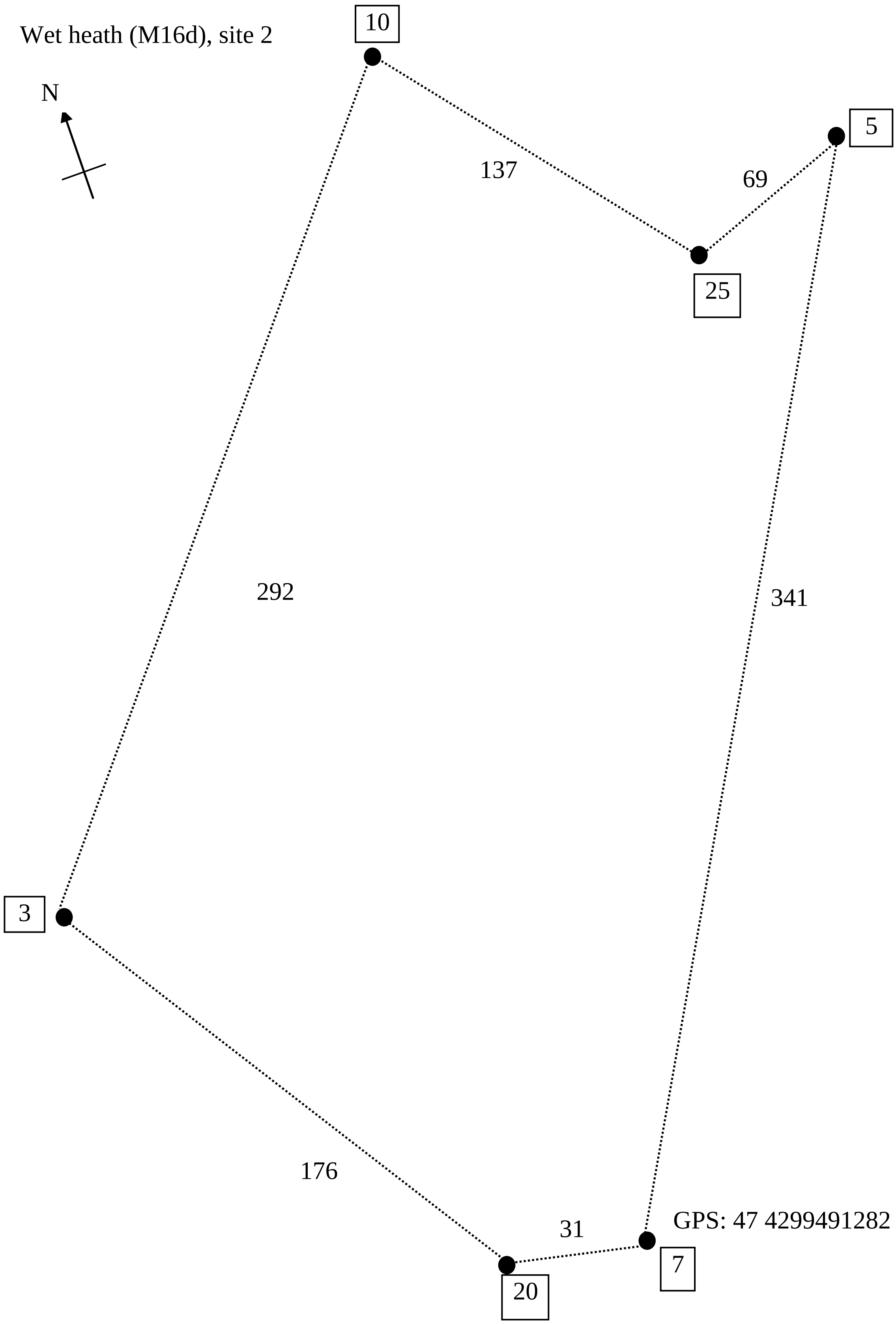


Dry heath (H12a), site 4

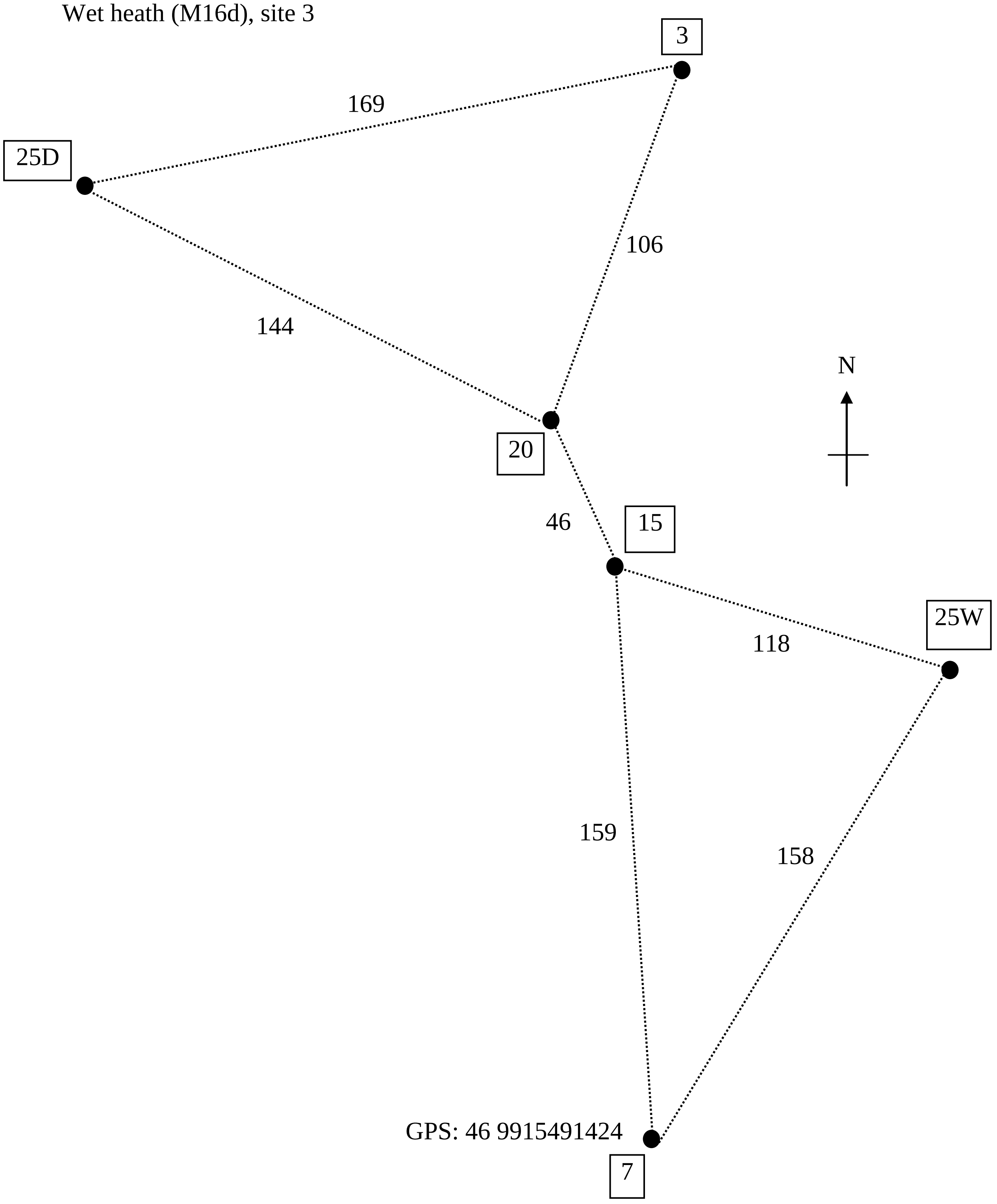


Wet heath (M16d), site 1




Wet heath (M16d), site 2
N
10
5
137
69
25
292
341
3
176
31
GPS: 47 4299491282
7
20

Wet heath (M16d), site 3



Appendix 2: Record sheets

Quadrat data collection sheet.

Heather stage (NB, P, B, M, D)					
Years since burn:		**Direction**		**Distance**	

Species	**No. growing tips**	**Area cover (%)**	**Notes**
Vegetation height (cm)	N/A	N/A	
Calluna	N/A		
Erica	N/A		
Vaccinium	N/A		
Empetrum	N/A		
Grasses	N/A		
C. purpureus			
H. jutlandicum			
D. scoparium			
C. introflexus			
C. pyriformis			
P. schreberi			
L. bidentata			
P. commune			
P. piliferum			
P. alpestre			
P. undulatum			
P. purum			
B. rutabulum			
L. glaucum			
R. squarrosus			
K. praelonga			

Transect data collection sheet.

25 Year	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
H. jutlandicum										
D. scoparium										
C. Introflexus										
C. pyriformis										
B. rutabulum										
K. praelonga										
L. bidentata										
C. divaricata										

25 Year	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
H. jutlandicum										
D. scoparium										
C. Introflexus										
C. pyriformis										
B. rutabulum										
K. praelonga										
L. bidentata										
C. divaricata										

25 Year	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
H. jutlandicum										
D. scoparium										
C. Introflexus										
C. pyriformis										
B. rutabulum										
K. praelonga										
L. bidentata										
C. divaricata										

Appendix 3: Environmental conditions reportedly favoured by the species recorded on the sites at Spaunton Moor

	Drought	Dry	Damp/Moist	Wet	Boggy	Submerged
Sphagnum papillosum				▨	▨	
Sphagnum subnitens				▨	▨	
Sphagnum denticulatum				▨	▨	▨
Aulacomium palustre			▨			
Brachythecium rutabulum			▨			
Campylopus flexuosus			▨			
Campylopus pyriformis			▨			
Cephalozia connivens			▨			
Dicranum scoparium			▨			
Mnium hornum			▨			
Plagiothecium undulatum			▨	▨		
Pseudoscleropodium purum			▨	▨		
Sphagnum capillifolium			▨	▨		
Sphagnum compactum			▨	▨		
Kurzia pauciflora			▨	▨	▨	
Calypogeia fissa			▨	▨	▨	
Lophocolea bidentata			▨	▨	▨	
Odontoschisma sphagni			▨	▨	▨	
Polytrichum commune			▨	▨	▨	
Sphagnum palustre			▨	▨	▨	
Sphagnum recurvum			▨	▨	▨	
Sphagnum tenellum			▨	▨	▨	
Gymnocolea inflata			▨	▨	▨	▨
Campylopus introflexus		▨				
Ceratodon purpureus		▨				
Leptodontium flexifolium		▨				
Polytrichum juniperinum		▨				
Barbilophozia floerkei		▨	▨			
Kindbergia praelonga		▨	▨			
Orthodontium lineare		▨	▨			
Polytrichastrum formosum		▨	▨			
Hylocomium splendens		▨	▨	▨		
Hypnum jutlandicum		▨	▨	▨		
Pohlia nutans		▨	▨	▨		
Leucobryum glaucum		▨	▨	▨	▨	
Bryum capillare	▨	▨				
Cephaloziella divaricata	▨	▨	▨			
Rhytidiadelphus squarrosus	▨	▨	▨	▨		
Pleurozium schreberi	▨	▨	▨	▨		

	Open/Exposed	Sheltered	Shaded	Deep shade
Cephalozia connivens			▨	
Kurzia pauciflora			▨	
Plagiothecium undulatum			▨	
Barbilophozia floerkei		▨		
Calypogeia fissa		▨		
Mnium hornum		▨	▨	
Leucobryum glaucum		▨	▨	
Orthodontium lineare		▨	▨	
Rhytidiadelphus squarrosus		▨	▨	
Pseudoscleropodium purum		▨	▨	
Brachythecium rutabulum		▨	▨	▨
Kindbergia praelonga		▨	▨	▨
Hylocomium splendens		▨	▨	▨
Lophocolea bidentata		▨	▨	▨
Odontoschisma sphagni		▨	▨	▨
Pleurozium schreberi		▨	▨	▨
Bryum capillare	▨			
Campylopus introflexus	▨			
Campylopus pyriformis	▨			
Ceratodon purpureus	▨			
Polytrichum juniperinum	▨			
Campylopus flexuosus	▨	▨		
Dicranum scoparium	▨	▨		
Leptodontium flexifolium	▨	▨		
Sphagnum capillifolium	▨	▨		
Sphagnum palustre	▨	▨		
Sphagnum papillosum	▨	▨		
Aulacomium palustre	▨	▨	▨	
Cephaloziella divaricata	▨	▨	▨	
Gymnocolea inflata	▨	▨	▨	
Pohlia nutans	▨	▨	▨	
Polytrichastrum formosum	▨	▨	▨	
Polytrichum commune	▨	▨	▨	
Sphagnum denticulatum	▨	▨	▨	
Sphagnum compactum	▨	▨	▨	
Sphagnum recurvum	▨	▨	▨	
Sphagnum tenellum	▨	▨	▨	
Sphagnum subnitens	▨	▨	▨	
Hypnum jutlandicum	▨	▨	▨	▨

	Acid	Mild acid	Neutral	Mild basic	Basic
Brachythecium rutabulum			▨	▨	▨
Odontoschisma sphagni	▨				
Sphagnum denticulatum	▨				
Sphagnum capillifolium	▨				
Sphagnum compactum	▨				
Sphagnum papillosum	▨				
Sphagnum tenellum	▨				
Pleurozium schreberi	▨	▨			
Sphagnum subnitens	▨	▨			
Campylopus flexuosus	▨	▨			
Campylopus introflexus	▨	▨			
Campylopus pyriformis	▨	▨			
Cephalozia connivens	▨	▨			
Gymnocolea inflata	▨	▨			
Kurzia pauciflora	▨	▨			
Leucobryum glaucum	▨	▨			
Mnium hornum	▨	▨			
Plagiothecium undulatum	▨	▨			
Pohlia nutans	▨	▨			
Polytrichum commune	▨	▨			
Polytrichum juniperinum	▨	▨			
Barbilophozia floerkei	▨	▨	▨		
Sphagnum palustre	▨	▨	▨		
Sphagnum recurvum	▨	▨	▨		
Aulacomium palustre	▨	▨	▨		
Cephaloziella divaricata	▨	▨	▨		
Ceratodon purpureus	▨	▨	▨		
Dicranum scoparium	▨	▨	▨		
Hylocomium splendens	▨	▨	▨		
Hypnum jutlandicum	▨	▨	▨		
Leptodontium flexifolium	▨	▨	▨		
Orthodontium lineare	▨	▨	▨		
Polytrichastrum formosum	▨	▨	▨		
Calypogeia fissa	▨	▨	▨	▨	
Kindbergia praelonga	▨	▨	▨	▨	
Bryum capillare	▨	▨	▨	▨	▨
Lophocolea bidentata	▨	▨	▨	▨	▨
Rhytidiadelphus squarrosus	▨	▨	▨	▨	▨
Pseudoscleropodium purum	▨	▨	▨	▨	▨

Appendix 4: Reproductive strategies of the species recorded on the sites at Spaunton Moor

		Dioicous	**Monoicous**
Capsule production	**Common/ Frequent/ Often**	*B. capillare* *C. purpureus* *K. praelonga* *K. pauciflora* *M. hornum* *P. formosum* *P. commune* *P. juniperinum* *S. recurvum* *S. tenellum*	*C. connivens* *L. bidentata* *B. rutabulum* *S. subnitens* *P. nutans* *S. compactum* *O. lineare* *S. capillifolium* *C. fissa*
	Frequent where wet/ Occasional elsewhere	*C. introflexus* *D. scoparium* *P. undulatum*	
	Sometimes abundant where dry/Occasional elsewhere	*H. jutlandicum*	
	Occasional	*A. palustre* *C. divaricata* *C. flexuosus* *C. pyriformis* *L. flexifolium* *S. auriculatum* *S. papillosum* *S. palustre*	
	Rare	*B. floerkei* *G. inflata* *O. sphagni* *R. squarrosus* *S purum* *H splendens* *P. schreberi* *L. glaucum*	