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ISBN 82-7126-593-8
ISSN 0332-8554

ABSTRACT

Arnesen, T. 1999. Succession on bonfire sites following burning of management waste in Sølendet Nature Reserve, central Norway. *Gunneria 76*: 1-64.

In Sølendet Nature Reserve in the boreal uplands of central Norway, burning of brash and herbage from clearing and mowing has taken place on 118 bonfire sites since 1978, as part of the management and restoration of outlying haymaking land. In 1982-1997, the revegetation of 36 sites in fen margin, grassland and heathland was investigated using 96 permanent plots. Measurements of pH and mineral content in soil and ash indicated a harsh chemical environment after burning, but conditions ameliorated over time due to leaching. Although the severe conditions seen during the first year after burning seemed to hamper the establishment of new vegetation, the plots were usually covered by early-successional bryophytes within 2-4 years. *Bryum* spp., *Ceratodon purpureus*, *Funaria hygrometrica*, *Leptobryum pyriforme*, *Polytrichum juniperinum* and *Marchantia* spp. were common dominant bryophytes during the early stages of this secondary succession. Recovery of the field layer was a slower process. Anemochorous shrubs (e.g. *Betula pubescens* and *Salix* spp.), the tall graminoid *Deschampsia cespitosa* and rhizomateous species (e.g. *Equisetum palustre*, *Agrostis capillaris* and *Eriophorum angustifolium*) became established early. Although an increase in the occurrence and abundance of common fen and grassland species was recorded, several dominant, early-successional bryophytes and vasculars were stable for many years and seemed to inhibit the expansion of other species.

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CONTENTS

1 INTRODUCTION

In the wake of the protection of cultural landscapes, management is often required to preserve aspects related to the influence of man. The Sølendet Nature Reserve was established in 1974 and comprises fens and grasslands formerly harvested for winter fodder. Scrub and trees have been cleared since 1976 to further restoration and prevent overgrowing (Moen 1990). The management also includes mowing the field layer vegetation with a two-wheeled tractor. In tall, luxuriant vegetation, the herbage has been removed from the area to prevent recycling of nutrients. During 1978-1998, waste from this management (trees, branches and twigs from clearance and herbage from mowing) was burnt on 118 bonfire sites at Sølendet. Seventy of the sites were established during the restoration period of 1979-1983. Altogether, approximately 160 ha of former haymaking land have been restored, including approximately 56 ha cleared of *Betula nana*, juvenile *B. pubescens*, *Juniperus communis* and *Salix* spp. The above-ground standing crop (biomass and litter) of *Betula nana* and *Salix* stands may represent as much as 1-7 tons dry weight per ha (Sonesson et al. 1975, Moen 1990). Large areas of open mire vegetation without trees and shrubs, dominated by graminoids and herbs (non-gramineous vasculars), have a standing crop of about 1 ton dry weight per ha (Moen 1990, 1995). During the last 20 years, a mean area of 20 ha was harvested every year. Ten hectares were raked after mowing. With the addition of some windfall and occasional birch trees felled every year, conservative estimates indicate that at least 350 tons of woody material and 200 tons of hay were burnt from 1978 to 1998. On average, this means that 5-6 tons of waste material were burnt on every bonfire site and more than 25 tons were burnt every year. However, practically all the woody material was burnt before 1983 when most of the clearance was completed. During the restoration period, most bonfire sites were established in early summer. Younger sites were usually established when mowing took place during July or August.

Considerable literature exists on the effects of fire on plants and vegetation and on revegetation after fire, but most of this is related to forest fires, grassland fires, heathland fires and other large-scale fires (Uggla 1958a, b, Kozlowski & Ahlgren 1974, Zackrisson 1977, Hobbs & Gimingham 1984a, b, Trabaud 1987a, Goldammer & Jenkins 1990, Naveh 1990, Legg et al. 1992, Gloaguen 1993, Bond & van Wilgen 1996, Schimmel & Granström 1996, Bleken et al. 1997).

Graff (1935) suggested that small burns resulting from the firing of piled slash offer an opportunity for long-term observations of revegetation in various types of vegetation, but only a few such investigations have been carried out. Prior to Graff's suggestion, Petterson (1931) had examined revegetation on 33 one-year-old recreational camp fire sites in Finland. Southorn (1976, 1977) conducted experiments with bryophyte recolonisation on bonfire sites and after heath fires in England, and Elveland (1978) examined vegetation dynamics on 10 bonfire sites burnt for management purposes in a protected rich fen area in Norrland, Sweden. In 1982-1988, the vegetation of 31 bonfire sites of various age was analysed at Sølendet (Arnesen 1989, 1991).

Graff (1935) found that the bryophyte genera *Bryum*, *Ceratodon*, *Funaria* and *Polytrichum* colonise burnt ground rather quickly after forest fires in the Rocky Mountains. He found that *Marchantia polymorpha* is common on burnt ground in damp localities. *Bryum argenteum*, *Ceratodon purpureus*, *Funaria hygrometrica*, *Polytrichum juniperinum* and *Marchantia polymorpha* have also been found on burnt ground by other authors (Uggla 1958a, b, Ahlgren, C.E. 1974, Brasell & Mattay 1984, Hobbs & Gimingham 1984b, Forgeard 1990, Schimmel & Granström 1996). *Leptobryum pyriforme* occurs frequently in some burnt areas (Buch 1945, Southorn 1976), and also on volcanic ash on Surtsey, Iceland (Fridriksson 1975). *Betula pubescens*, *Epilobium angustifolium*, *Deschampsia cespitosa* and *D. flexuosa* are often observed as the first vascular colonisers after forest fires (Uggla 1958a, b, Schimmel & Granström 1996, Mysterud & Mysterud 1997). Recolonisation seems to take place by means of airborne seeds and spores, surviving subterranean parts and seedlings emerging from the seed bank (Trabaud 1987b, Schimmel & Granström 1996, Mysterud & Mysterud 1997).

On the whole, the same species and mechanisms of establishment are observed on bonfire sites (Petterson 1931, Southorn 1976, Elveland 1978, Arnesen 1991). *Funaria hygrometrica* is usually the first bryophyte species to occur both there and on large-scale burns (Uggla 1958a, b, Brasell & Mattay 1984, Forgeard 1990). Because the area covered by a bonfire site is rather small, invasion of vascular plant species from the surrounding vegetation by runners and rhizomes seems to be important (Elveland 1978, Arnesen 1991).

Burning has some obvious effects on the vegetation through the action of high temperatures and the physical and chemical properties of the post-fire environment. Increased solar radiation (less shading vegetation), increased absorption of heat (dark ash) and increased pH (leaching from ash) are such effects (Smith 1970, Viro 1974, Christensen 1987, Kimmins 1997). Great overall loss of nutrient capital by volatilisation, particularly of N, but also of P and K, and less so of Ca and Mg, has been reported as a result of large-scale fires (Evans & Allen 1971, Raison et al. 1985, Christensen 1987, Kimmins 1997). Burning may also increase post-fire production through leaching of mineral nutrients from the ash, or through changes in soil ion exchange properties or increased mineralisation (Viro 1974, Christensen 1987, Naveh 1990, Kutiel et al. 1990). Allen (1964) found that the potential loss of nutrients decreases because soils, in particular organic and clay soils, have a capacity to retain nutrient ions from the percolating solution of ash minerals in rainwater. A rise in microbial activity following the increase in temperature, pH and available nutrients may also enhance the mineralisation rate (Christensen 1987). Several authors have, however, reported a reduction of microbial activity (Ahlgren, I.F. 1974, Christensen 1987). Christensen (1987) pointed out that fire is a very heterogeneous phenomenon and the variation observed in the effects of fire on nutrient availability reflects the actual range of potential fire effects.

Bonfires usually have more severe effects on soil and vegetation than large-scale fires. Temperature increase in the soil below a bonfire will generally be greater and more prolonged. Uggla (1958b) found that temperature barely increased at depths of 3 cm in moist humus during a light forest fire, and reached 100°C at 3 cm depth in rather dry humus during a more severe fire. Schimmel & Granström (1996) did not find temperatures lethal for plants deeper than 2-3 cm under the burn boundary. Higher temperatures are reported under drier conditions (Ahlgren, I.F. 1974, Wright & Bailey 1982, Whelan 1995). On the other hand, Fenn et al. (1976) found that the temperature increased to more than 399°C at 5.1 cm below the soil surface in a camp fire site on moist loam after desiccation of the soil. The piled ash will also cause larger and more lasting release of mineral ions (Southorn 1976).

For the benefit of the future management of Sølendet, it appeared to be essential to assess the revegetation of the bonfire sites. These sites also offered an opportunity to observe the revegetation of small-scale, well-defined burnt spots in general. Most bonfire site vegetation analyses undertaken in 1982-1989 at Sølendet were one-off studies; re-analysis was seldom performed (Arnesen 1989, 1991). That investigation aimed to provide chronosequences of bonfire sites of various age, but the sequences included sites from several types of vegetation and were not very clear.

The aim of the present investigation was to study the succession taking place over a long period by repeated analyses of the sites. During the last decade, all the sites were re-analysed at least twice, some every year. Four experimental bonfire sites were established during this period, and investigations of the pH development, the biomass production and the seed bank were also carried out at some bonfire localities. The investigations reveal that the post-fire environment of the burnt sites comprises severe conditions with high pH and high mineral content during the first years after burning. Revegetation is a rather slow process, which mainly consists of the invasion, by seeds, spores or rhizomes, of species from the surroundings, dominating early-successional species apparently hampering the establishment of other species. At the end of the investigation period, sites were commonly revegetated, but early-successional species were still dominant on many sites.

Nomenclature follows Lid & Lid (1994) for vascular plants, Frisvoll et al. (1995) for bryophytes and Krog et al. (1994) for lichens.

2 INVESTIGATION AREA

2.1 GEOGRAPHICAL LOCATION, GEOLOGY AND CLIMATE

The Sølendet Nature Reserve near Røros in the county of Sør-Trøndelag, central Norway (Fig. 1), was established in 1974 and covers 306.4 ha. Approximately half the reserve is covered by mires, mainly rich fen, the remainder being open or wooded grassland and heathland. The predominant vegetation is northern boreal plant communities of the alliances *Lactucion alpinae* Nordh. 43 and *Caricion atrofuscae* Nordh. 35. For many centuries up to 1950, the fens and grasslands at Sølendet (200 ha) were scythed to yield winter fodder for livestock. The nature reserve was established to protect the rich flora and vegetation, and to maintain the old haymaking landscape. Since 1976, some 160 ha of former haymaking land have been restored by

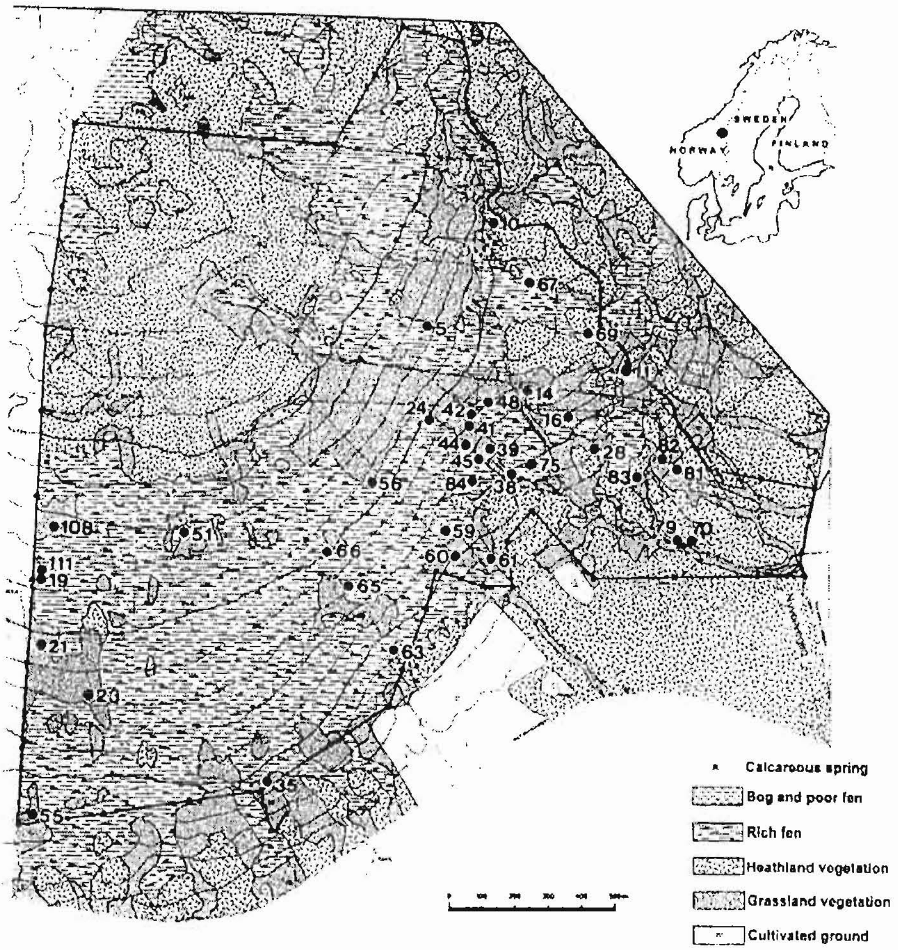

Fig. 1. The vegetation of Sølendet Nature Reserve, with the bonfire localities (dots with numbers).

scrub clearance and regular mowing using a two-wheeled tractor. Stack poles, barns and bothies have been restored.

Sølendet has been an important area for research on the management of outlying land and the public use of a managed nature reserve. Important aspects of this research are summarised by Moen (1990, 1995), Aune et al. (1996) and Arnesen (1999). Moen (1990) describes the area, the vegetation and the management in detail, while a short description of the nature reserve, its history and the research is found in Arnesen & Moen (1997).

Sølendet lies at an altitude of 700 to 800 m, at the transition between the middle boreal and northern boreal vegetation zones, in the slightly oceanic vegetation section (Moen 1998). The ground slopes east, south-east and south. The bedrock of the study area consists of metamorphosed Cambro-Silurian sedimentary rocks, mainly base-rich, grey-green phyllite. The phyllite yields a fine-grained soil and a type of moraine that tends to become waterlogged, thereby giving rise to the development of a substantial layer of peat. More than 50 springs rise in the upper half of the reserve, mostly at 770-780 m a.s.l., feeding the fens with calcareous, mineral-rich water throughout the year.

The climate of the area (Moen 1990, Førland 1993, Aune, B. 1997) is intermediate between subcontinental and suboceanic, with an annual mean precipitation of 600 mm, more than half of this falling as rain during June-September. The annual mean temperature is about +0.6°C. Summers are cool (July mean about +10.5°C) and winters cold (January mean about -9.5°C), and snow covers the ground for 210-220 days in a normal year.

2.2 THE MOWN VEGETATION AND THE BONFIRE LOCALITIES

Most of the mown areas at Sølendet are rich and extremely rich fen (Moen 1990), and burning mostly took place in fen margin localities rather close to the mown areas. These localities comprised vegetation of the alliances *Sphagno-Tomentypnion* Dahl 57 and *Caricion atrofuscae* Nordh. 35. Common dominant species of these communities are *Crepis paludosa*, *Saussurea alpina*, *Succisa pratensis*, *Thalictrum alpinum*, *Carex dioica*, *Molinia caerulea*, *Trichophorum cespitosum*, *Campylium stellatum*, *Sphagnum warnstorfii* and *Tomentypnum nitens*.

Mowing and burning also took place in damp herb-rich grassland of the association *Deschampsio-Salicetum* Nordh. 43 (*Lactucion alpinae* alliance), with dominants such as *Betula pubescens*, *Alchemilla* spp., *Crepis paludosa*, *Geranium sylvaticum*, *Saussurea alpina*, *Thalictrum alpinum*, *Deschampsia cespitosa*, *Campylium stellatum* and *Rhytidiadelphus squarrosus*.

Drier grassland vegetation of the association *Geranietum sylvatici* (Nordh. 43) Dahl 87 (*Lactucion alpinae*) was also mown and subjected to bonfire burning. Common dominants here are *Betula pubescens*, *Alchemilla* spp., *Geranium sylvaticum*, *Solidago virgaurea*, *Viola biflora*, *Agrostis capillaris*, *Anthoxanthum odoratum*, *Deschampsia cespitosa*, *Brachythecium salebrosum* and *Mnium spinosum*.

Although no mowing took place in heathland vegetation, a few bonfires were burnt in such areas. One bonfire site was situated in dry, wiry grass heathland vegetation that belongs to the association *Nardo-Betuletum* Moen 90 in the alliance *Vaccinio-Piceion* Br.-Bl. et al. 39. Common dominants in this vegetation are *Nardus stricta*, *Deschampsia flexuosa*, *Polytrichum juniperinum* and *Pleurozium schreberi*.

3 MATERIALS AND METHODS

3.1 SAMPLING

3.1.1 Bonfire localities, sites and permanent plots

In 1982-1992, 36 localities in homogeneous vegetation comprising 36 bonfire sites (actual burnt spots) of varying age were chosen to study revegetation (Fig. 1). All the localities were situated on slightly sloping ground (1.5-6.0^{g}). Most were inclined towards south-east or south, some towards east or south-west. A total of 96 permanent plots were laid out subjectively on the 36 bonfire sites to observe the revegetation. An additional 13 plots were established in unburnt vegetation at seven localities, either on a site before burning or in the surrounding vegetation uphill or downhill close to a site. The diameters of the burnt sites were 2-4 m, mostly approximately 3 m. Eighteen of the investigated bonfire sites were in rich and extremely rich fen vegetation of the alliances *Sphagno-Tomentypnion* and *Caricion atrofuscae* (Table 1), nine in damp, herb-rich grassland of the *Deschampsio-Salicetum* association, eight in drier grassland vegetation of the *Geranietum sylvatici* association, and one in heathland vegetation of the *Nardo-Betuletum* association.

Table 1. The investigated bonfire sites sorted by vegetation types and syntaxa (associations and alliances; after Moen 1990). Sites in parentheses were sampled for the seed bank investigations only, and no formal analyses of vegetation were made.

Rich fen margin (Caricion atrofuscae Nordh. 35/Sphagno-Tomenthypnion Dahl 57):
Sites 5, 38, 39, 41, 42, 44, 45, 48, 56, 59, 60, 61, 63, 65, 66, 67, 75, 83, (112).

Damp grassland (Deschampsio-Salicetum Nordh. 43, Lactucion alpinae Nordh. 37):
Sites 11, 14, 19, 24, 25, 28, 51, 55, 69, (108).

Dry and mesic grassland (Geranietum sylvatici (Nordh. 43) Dahl 87, Lactucion alpinae):
Sites 10, 16, 21, 23, 35, 79, 81, 82.

Heathland (Nardo-Betuletum Moen 90, Vaccinio-Piceion Br.-Bl. et al. 39):
Site 70.

Three plots were usually established within each bonfire site, one 0.5 x 0.5 m plot at the upper margin (marked U in figures and tables), one 0.5 x 0.5 m plot at the lower margin (L) and one 1 x 1 m plot in the centre (C) of the site. Plots of 0.5 x 0.5 m were laid out on the margin (M) of some sites, and occasionally fewer or more than three plots were laid out. U and M plots showed only minor differences and were treated as belonging to the same category. Figure 2 shows the positions of the plots. From 1982 to 1998, all the plots were re-analysed at least three times, and some, mainly in the centre of sites, were re-analysed almost every year. Twenty-four sites included three types of plots (U/M, C and L) and were re-analysed three times during the investigation period. This material ('the 24-site set') was processed separately. Experimental burning was carried out in four localities (nos. 75, 81, 82, 83) where

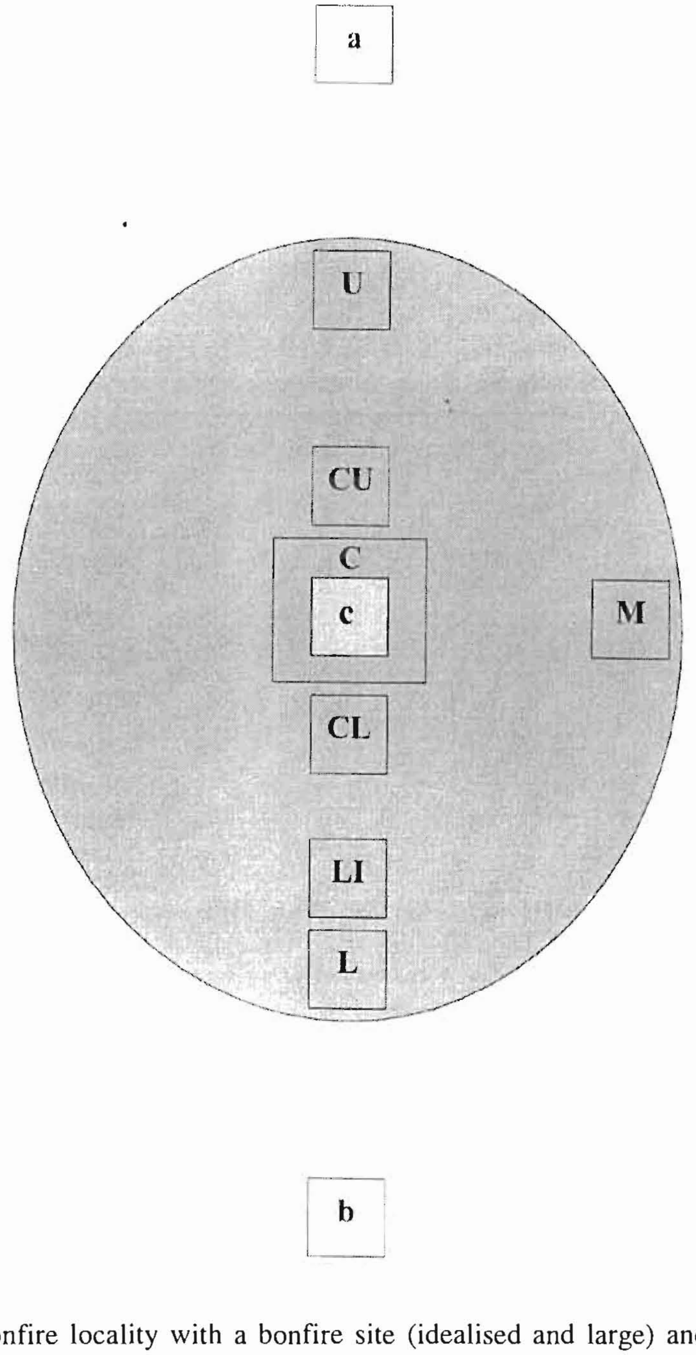

Fig. 2. A bonfire locality with a bonfire site (idealised and large) and the types of plots analysed in this investigation: a: above (uphill from) the site, b: below (downhill from) the site, c: small plot in the centre of the site. a, b and c were plots harvested for measurements of above-ground production. U: upper margin, M: (side) margin, CU: centre upper, C: centre, CL: centre lower, LI: lower inner margin, L: lower margin. C was commonly 1 m^2, the rest 0.25 m^2. Only U, C and L were established on most sites.

vegetation was also analysed before burning. These sites were burnt for 4-5 hours and the material burnt was a mixture of brash (twigs of *Betula*, *Salix* and *Juniperus*) and herbage from grassland and fen. Analyses and re-analyses of 96 plots within the bonfire sites and analyses of 13 plots in unburnt vegetation at the bonfire localities total 346 samples, containing 228 taxa of plants, including lichens.

3.1.2 The cover scale

The cover of shrub layer, field layer, bottom layer, bare ground and species was recorded in a modified version of the Hult-Sernander-Du Rietz scale, also used in previous research at Sølendet (Moen 1990): 1: found within 5 cm of the plot, 2: 0-1%, 3: 1-3.125%, 4: 3.125-6.25%, 5: 6.25-12.5%, 6: 12.5-25%, 7: 25-50%, 8: 50-75%, 9: 75-100%.

3.1.3 Soil: types, nutrients, pH and ground water level

Soil profiles were recorded as peat, brown soil or podsol. Measurements of pH in soil and ash were performed repeatedly during the research period. Soil samples were collected from 5-10 cm beneath the ash or the soil surface on the margin of plots and outside each bonfire site. Soil and ash samples were saturated with de-ionised water and stored overnight before being stirred and the pH measured. In 1992, pH and the total content of P and N and other minerals were analysed in the organic soil and the mineral soil of a 10-year-old and a 1-year-old bonfire site (nos. 25 and 82) at the Norwegian Agricultural Service Laboratory. Ash from these and five other sites of varying age was also analysed. The ground water level was measured in the lower part of sites as the distance (cm) between the water surface in peat pits and the surface of the peat layer. Measurements were carried out in the course of one day after three days without rain at the end of July 1986.

3.1.4 Plant biomass and flowering

The annual biomass (dry weight) of the field layer was measured in the centre of, and 1 m uphill and downhill from, three bonfire sites (nos. 24 and 25 in damp grassland, no. 61 in fen margin). Plots of 0.5 x 0.5 m were harvested. Some species were weighed separately, the rest were sorted by growth form (woody species, graminoids, herbs). The number of flowering shoots was also counted on these three bonfire sites. They were counted as individual shoots when separated below ground level, except for tussock grasses where separation at the shoot base was used as the criterion. The number of flowering shoots of species groups and some selected species is presented.

3.1.5 Seed bank and underground organs

Seed bank samples were collected from two newly established bonfire site localities (not included in the 36 sites analysed for vegetation), one in damp herb-rich grassland vegetation (*Deschampsio-Salicetum*) (no. 108) and one in wetter fen margin (*Crepis paludosa-Molinia caerulea* lawn, *Caricion atrofuscae/Sphagno-Tomentypnion*) (no. 112). The samples were collected from the upper 5-6 cm of the soil, both outside the sites, and in the margin and centre of the sites. Sampling was carried out in autumn 1997, and the upper centimetre of litter/soil at the sampling spots outside the sites and of ash inside the sites was removed before sampling to avoid contamination from surface seeds deposited during the 1997 season. Seed plants therefore mainly emerged from seeds deposited during the years before burning. This implied that the seeds were naturally stratified and had experienced changing temperatures for at least one year. Three 0.5 litre samples were taken in the three positions at the two localities, i.e. a total of 18 samples. These were stored in dark, cool conditions for 5 months (4°C most of the time, and 8°C for the last week). The soil samples were reduced by 50-70% by washing through a coarse (2 mm mesh) and a fine (0.2 mm mesh) sieve. After sieving, they were spread out thinly (approximately 0.5 cm) in plastic trays, which were partly covered with plastic film to avoid rapid drying out. The seeds were germinated under controlled conditions resembling fairly good summer weather at Sølendet (16 hours of light and 16°C, 8 hours of darkness and 5°C, and frequent watering) for 6 weeks. The light source was eight daylight gas tubes of 36 W each. The trays were placed at random in two rows under the light and were shifted one position every second day to neutralise differences in light intensity and temperature. Emerging seedlings were counted and preliminarily identified every day and then replanted in steam-sterilised potting soil for further identification. After 6 weeks, the soil samples were crumbled by hand, redistributed in the trays and allowed to germinate for another 6 weeks under the same conditions. This method is a modification of the procedures described by Milberg (1994) and Thompson et al. (1997). Since no investigation of ungerminated, viable seeds was performed, more seeds may have germinated from the seed bank if proper treatment to break the dormancy had been provided. However, ter Heerdt et al. (1996) have shown that only a few seeds fail to germinate when the present method is used.

Six bonfire sites were examined for surviving rhizomes, corms, etc. Two newly burnt sites (nos. 106 and 107) and four partly revegetated sites (nos. 67 and 69 examined 2-3 years after burning and two older sites, nos. 15 and 27, that had been burnt twice) were investigated (nos. 15, 27, 106 and 107 are not included in the vegetation analyses). Viable subterranean parts were recorded in the newly burnt sites. Shoots of rhizomateous species were excavated from the revegetated sites to determine whether they originated from rhizomes, or were newly established plants. Rhizomes that entered the site from one side and ended inside the site may indicate vegetative expansion after burning. Rhizomes traversing beneath the whole site had probably survived the burning.

3.1.6 Data analysis

The data analysis aimed to investigate major gradients in the species data and trends in the vegetation development after burning. Ordination by Detrended Correspondence Analysis (DCA) using version 3.15 of the CANOCO program (Hill 1979a, ter Braak 1987, Oksanen & Minchin 1997) was performed to achieve this. In the DCA, detrending by 26 segments and non-linear rescaling (4 times) were employed. No downweighting of rare species was applied.

Two-Way Indicator Species Analysis (TWINSPAN; Hill 1979b) was used to achieve a classification of the large quantity of samples. Nine pseudospecies cut levels were used, corresponding to the present cover scale. No weighting or manipulation of indicator potentials were applied. The TWINSPAN clusters are described as vegetation types in a wide sense, named after characteristic species, constants (constancy > 60%), or dominants (cover > 5). Synoptic tables with constancy and characteristic cover of species in TWINSPAN clusters and age groups were constructed using the SAMTAB program (Wilmann 1987, Aune 1998). The calculation of characteristic cover is based only on samples that include the particular species.

Statistical analyses of correlation and differences were performed using statistical techniques from the SPSS for Windows program (SPSS Inc. 1997). T-tests for matched samples were used to compare differences in pH between soil samples taken uphill and downhill from the sites and in the centre of the sites. T-tests were also used to test differences in mineral content in new and old ash. Regression analyses were used with pH development over time and to compare the DCA axis score with site age, sample pH, the number of species found in samples and the ground water level found in sites.

4 RESULTS

4.1 SOIL AND pH

The soil of the 18 localities in rich fen margin was peat or transitional between peat and brown soil. The grassland localities were mainly on brown soil or soil types transitional between brown soil and peat or podsol, while the heathland locality was situated on podsolic soil.

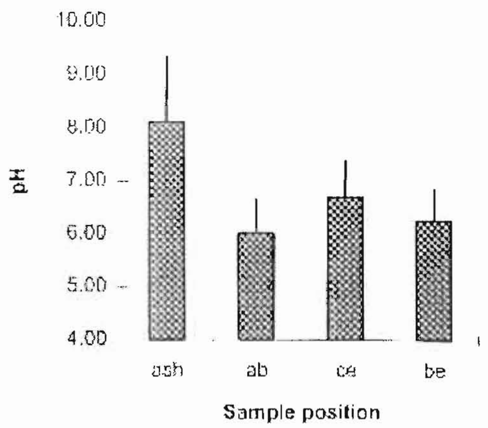

Fig. 3. pH in ash of 17 sites, and in soil above (ab), in the centre (ce) and below (be) the sites. Standard deviation is indicated.

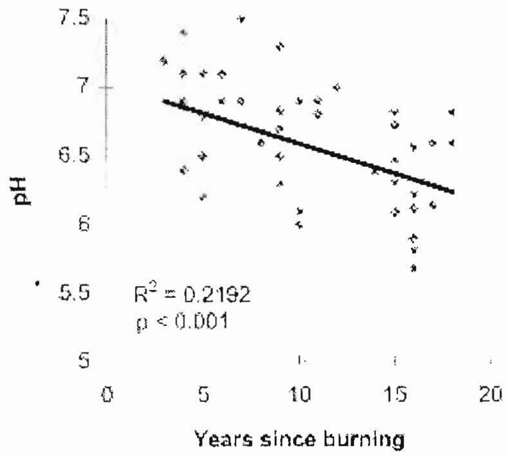

Fig. 4. Regression analysis of the relationship between pH and age (time since burning) in 16 plots where pH was measured three times.

Table 2. pH in the soil/ash of three bonfire localities: above, in the centre and below the sites at three different times after burning.

	Above			Centre			Below		
	1 month	2 months	6-13 years	1 month	2 months	6-13 years	1 month	2 months	6-13 years
81	6,3	6,1	5,9	8,5	8,5	7,5	6,3	6,8	6,2
82	6,1	6,1	6,0	7,2	6,8	5,8	6,0	6,8	6,1
83	6,6	6,3	6,5	7,4	7,0	6,3	6,4	6,7	6,4

The pH in ash from 17 bonfire sites showed a mean value of 8.1 (Fig. 3). T-tests for matched samples showed significant differences between the mean pH in the soil in the centre of sites and below the sites ($t = 2.176$, $p = 0.045$), and between the pH in soil uphill from the sites and in the centre of sites ($t = -3.077$, $p = 0.007$). A significant difference was also found between the unaffected soil above the sites and the soil below the sites ($t = -2.950$, $p = 0.009$). Measurements in three experimental sites indicated that there was an increase in pH downhill from the sites after an interval of time, and that pH was back to normal within 6-13 years (Table 2). The pH in the bonfire sites decreased over time (Fig. 4, Table 3).

Measurements of the mineral content in the soil at the 2-year-old site 82 in mesic grassland and the 11-year-old site 25 in damp grassland, and in ash of varying age, indicated that a substantial amount of mineral matter was added from the ash. High levels of P, K, Mg, Ca, Mn and S were found in the ash (Table 4), and the measurements indicated that the pH and the mineral content decreased over time, but only the decreases in pH and P were statistically significant (Table 5). The ash at sites 61 and 82 was quite high in Zn. At both the 2-year-old and 11-year-old sites, the P level was higher in the soil at the centre of the plot than in unaffected soil above the site. It was also found to be higher downhill from the sites, particularly close to the 2-year-old site. Such differences between unaffected soil and soil within or below the sites were also observed in the content of other mineral elements. Except for

Table 3. The development of pH between age classes for ash and in different positions within the sites. Plot subsets comprise only plots that were subjected to repeated measurements. Since measurements were not made on a regular basis, the subsets vary in the number of plots and year of analysis. n = number of plots, sd = standard deviation.

Age class (yrs.)		0-2		3-7		8-12		13-20	
	n	pH	sd	pH	sd	pH	sd	pH	sd
Ash	4	9,1	0,8	6,6	1,5	-		-	
	3	-		7,3	2,4	6,7	2,1	-	
Upper	22	-		6,4	0,4	6,2	0,3	-	
	4	-		-		6,8	0,9	6,1	0,5
Centre	7	7,1	1,1	6,2	0,9	-		-	
	16	-		6,9	0,4	6,6	0,4	6,3	0,4
	6	-		-		7,1	0,4	6,7	0,5
Lower	23	-		6,8	0,4	6,5	0,3	-	
	4	-		-		7,1	0,6	6,8	0,7

measurements of Ca, Na and Fe, the greatest differences were found at the youngest site.

4.2 PLANT BIOMASS AND FLOWERING

Measurements made in three localities (nos. 24, 25, 61) demonstrated a higher annual field layer biomass 1 m downhill than uphill from the sites, while it was lower in the centre of sites (Table 6). Below sites 24 and 25 in damp grassland, *Crepis paludosa* and *Saussurea alpina* in particular showed increased biomass, flowering and cover. Hardly any other herb species were found immediately downhill from site 25, and the soil at this site was covered with a 10-15 cm thick layer of ash and charcoal. Below site 61 in fen margin, *Succisa pratensis* had higher production, as did several other herbs (e.g. *Bartsia alpina*, *Pedicularis oederi* and *Thalictrum alpinum*) and some graminoids (e.g. *Agrostis capillaris* and *Deschampsia cespitosa*). Graminoid biomass was lower below the grassland sites, and graminoid flowering was reduced below all the sites. *Betula pubescens* and *Salix* spp. were the only field layer species which, due to numerous juvenile plants, increased in production in the centre of the bonfire sites. Scarcely any of these species were found below the sites. The differences between biomass above and below the sites were statistically significant for the sum of *Crepis*, *Saussurea* and *Succisa* ($t = -2.311$, $p = 0.0496$).

Table 4. Comparison of nutrient content and pH in ash and soil in some localites in October 1992. The ash layer in site 82 was 5 cm, and was sampled from the entire depth of the layer. In site 25 the ash layer was 10-15 cm, and was sampled at a depth of 5-10 cm. Samples from organic soil (humus, peat) were taken from 5-15 cm, and samples from mineral soil 40-60 cm below the surface. N.t. = not traceable. Pos. = position on the bonfire site: ab = above, ce = in centre, be = below. P-AL = extraction of P by acetate lactate, Kj-N = Kjeldahl-N.

Loc.	Age yrs.	Sample type	Pos.	pH	P-AL %	Kj-N %	K me/100g	Mg me/100g	Ca me/100g	Na me/100g	Al ppm	Fe ppm	Mn ppm	Zn ppm	S ppm
82	2	Humus	ab	5,9	8,8	0,68	0,87	1,88	33,20	0,14	12,10	5,73	292,00	n.t.	63,20
			ce	6,6	18,0	1,06	0,43	4,43	39,80	0,08	10,10	n.t.	313,00	n.t.	31,20
			be	6,2	12,0	1,11	2,73	4,88	38,70	n.t.	17,70	n.t.	1340,00	8,46	124,00
		Mineral	ab	6,4	1,1	0,05	n.t.	0,11	2,01	n.t.	n.t.	n.t.	6,92	n.t.	n.t.
			ce	6,7	2,3	n.t.	n.t.	0,07	1,29	n.t.	n.t.	n.t.	9,27	n.t.	n.t.
			be	6,4	22,0	n.t.	0,14	0,06	1,12	n.t.	4,92	3,39	2,89	3,09	n.t.
25	11	Peat	ab	5,8	2,6	1,52	0,33	1,16	29,30	0,20	8,51	2,50	99,70	n.t.	63,40
			ce	6,2	23,0	1,21	-	-	-	-	-	-	-	-	-
			be	6,0	3,5	1,09	0,76	1,43	41,00	n.t.	19,10	10,50	193,00	n.t.	108,00
		Mineral	ab	6,5	1,8	n.t.	n.t.	0,19	4,84	n.t.	n.t.	2,62	10,20	n.t.	n.t.
			ce	7,5	6,7	0,05	n.t.	0,33	7,47	n.t.	n.t.	n.t.	12,90	n.t.	n.t.
			be	6,6	3,3	n.t.	n.t.	0,19	3,97	n.t.	n.t.	n.t.	10,20	n.t.	n.t.
3	0	Ash	ce	9,8	350,0	0,39	45,40	42,80	151,00	0,47	29,50	n.t.	82,90	n.t.	562,00
2	0	Ash	ce	9,9	330,0	0,17	16,90	14,40	41,10	0,16	8,56	n.t.	8,86	n.t.	206,00
46	2	Ash	ce	8,7	370,0	0,59	11,50	23,20	147,00	0,37	28,70	n.t.	101,00	n.t.	81,80
82	2	Ash	ce	8,3	167,0	0,20	1,61	10,60	98,10	n.t.	19,80	n.t.	304,00	12,30	47,20
61	10	Ash	ce	7,6	43,0	0,60	1,38	7,11	142,00	0,47	29,50	n.t.	143,00	56,80	42,50
24	11	Ash	ce	7,0	67,0	0,57	0,22	0,64	29,20	n.t.	6,10	n.t.	31,50	n.t.	12,40
25	12	Ash	ce	7,9	132,0	0,34	0,51	4,34	31,80	0,14	6,42	n.t.	29,10	1,88	11,80

Table 5. Mean values of pH and minerals in ash for two age classes. T values are also shown and significance (details in Table 4). Significance: * = 0.05 > p > 0.01.

	Mean		
Age (yrs.)	0-2	10-12	t
pH	9,2	7,5	3,214 *
P-AL	304,25	80,67	3,769 *
Kj-N	0,34	0,50	-1,237
K	18,85	0,70	1,632
Mg	22,75	4,03	2,165
Ca	109,30	67,67	0,957
Na	0,33	0,30	0,189
Al	21,64	14,01	0,879
Mn	124,19	67,87	0,695
S	224,25	22,23	1,449

Table 6. Annual field layer biomass, number of flowering shoots and cover of some species and species groups in 1992. Recordings from three bonfire sites. a = above, in the vegetation 1 m uphill from the bonfire site, c = centre, in the centre of the site and b = below, 1 m downhill from the site.

		Dry biomass in g/m^2			Flowering shoots			Cover		
Species/Sp. group	Site	a	c	b	a	c	b	a	c	b
Crepis paludosa	24	5,4	6,9	47,6	0	1	15	5	5	7
	25	12,7	0,0	170,6	1	0	35	6	2	9
	61	0,0	0,0	5,2	0	0	2	0	0	5
Saussurea alpina	24	0,0	0,0	19,6	0	0	1	0	0	6
	25	7,7	0,0	112,0	0	0	3	4	0	6
	61	1,5	0,0	4,9	0	0	0	2	0	4
Succisa pratensis	24	4,0	0,0	2,7	0	0	0	4	0	4
	25	0,0	0,0	0,0	0	0	0	2	0	0
	61	5,9	4,6	57,2	0	2	4	5	4	8
Other herbs	24	53,7	20,0	44,2	33	12	13	8	5	8
	25	27,4	58,8	0,0	2	30	0	7	7	2
	61	5,2	5,7	60,7	5	20	16	6	6	8
Graminoids	24	147,0	107,1	121,4	49	4	33	8	7	8
	25	209,1	5,6	109,6	126	0	2	8	4	7
	61	68,8	21,2	125,1	159	6	35	8	5	8
Woody species	24	0,1	4,9	0,0	0	0	0	2	4	0
	25	1,5	28,0	0,0	0	0	0	3	8	0
	61	1,8	26,6	0,3	0	0	0	2	6	2
Subtotals	24	210,2	138,9	235,5						
	25	258,4	92,4	392,3						
	61	83,2	67,6	253,3						
Total		551,7	299,0	881,1						

4.3 SEED BANK AND RESPROUTING FROM SUBTERRANEAN PARTS

The soil samples examined for germinating seeds indicated that only a few seeds survive in the upper 5 cm of the soil of a bonfire site (Table 7). While no germinating seeds were found in the centre of the damp grassland site 108, several *Carex* seeds and a few *Alchemilla* seeds germinated in such soil from the fen margin site 112. Even though the margin of both bonfire sites contained more germinating seeds than the centre, substantially more seeds were germinating outside the sites. *Alchemilla glabra* and *Campanula rotundifolia*, and the graminoid *Luzula* spp. germinated quite frequently from the seed bank of the grassland site. *Carex* spp. germinated more abundantly from the seed bank of the fen margin site. This conformed with the species composition found both in the seed bank and in the existing vegetation at the locality, but outside the sites.

Table 7. The number of seedlings that emerged from soil samples at two localities. Samples were taken outside the bonfire site (o), at the margin (m) (20-30 cm into the site) and in the centre (c) of the site. Each number represents the sum of seedlings in 3 soil samples each of 0.5 litre.

		108			112	
Species	o	m	c	o	m	c
Betula pubescens	1	0	0	0	0	0
Alchemilla spp.	50	16	0	20	8	3
Campanula rotundifolia	27	6	0	0	0	0
Cerastium fontanum ssp. vulgare	5	0	0	0	0	0
Myosotis decumbens	1	0	0	0	0	0
Omalotheca norvegica	5	4	0	0	0	0
Potentilla erecta	0	0	0	0	1	0
Agrostis capillaris	2	2	0	3	1	0
Carex spp.	5	3	0	42	36	22
Deshampsia cespitosa	2	1	0	1	1	0
Kobresia simpliciuscula	0	0	0	1	0	0
Luzula spp.	41	26	0	5	0	0
Poa nemoralis	1	0	0	1	0	0
Nardus stricta	1	0	0	1	0	0
Unidentified herbs	20	6	0	9	0	0
Unidentified graminoids	7	5	0	0	0	0
Total	168	69	0	83	47	25

Although cryptogam spores deposited in the soil were not an object of study for the present investigation, and the fine sieve let most spores through, some germinating cryptogams were recorded in the soil samples. Few cryptogam spores were found germinating in soil from within the sites. Some individuals of the fern *Gymnocarpium dryopteris*, and the bryophytes *Amblystegium* sp., *Fissidens adianthioides*, *Rhodobryum roseum* and *Pohlia nutans* were recorded, mostly in margin samples. A larger number of common fen, heathland and grassland species germinated outside the sites; in addition to the species mentioned above, the bryophytes *Campylium stellatum*, *Scorpidium cossonii*, *Lophozia* sp. and *Barbilophozia quadriloba* were recorded.

Several surviving rhizomes of *Equisetum palustre* and *Eriophorum angustifolium* were found 10-30 cm beneath the soil surface at the centre of two newly burnt sites, and these species sprouted in the centre of two 2-3 year-old sites. Viable rhizomes of *Bistorta vivipara*, *Potentilla erecta*, *Succisa pratensis*, *Carex panicea* and *C. rostrata* were found only 5-10 cm below the surface at the margins of the sites. *Carex* spp., *Festuca rubra* and *Hierochloë odorata* seemed to have entered the centre of the 2-3 year-old sites from the margin. At two older sites, *H. odorata* seemed to have survived a second, less intense burning, as shoots were observed close to their centre (75 cm from the margin) the year after burning.

4.4 ORDINATION AND CLASSIFICATION

Eigenvalues and percent variation accounted for in the first four axes were quite low (Table 8). This may reflect the large diversity of the present material and the lack of a single dominant gradient.

Table 8. DCA axis values and length of gradients (in SD) for the treatment of the complete dataset (Figs. 5, 6 and 8).

Axes	1	2	3	4	Total inertia
Eigenvalues	0,335	0,271	0,200	0,145	6,883
Lengths of gradient	3,223	3,478	3,113	2,469	
Variation explained (%)	4,9	3,9	2,9	2,1	

DCA axis 1 has an eigenvalue of 0.34 and accounts for 4.9 of the total variation in the data set. The samples from the heathland site (no. 70) are found at the extreme left (Fig. 5). Species ordination (Fig. 6) indicates that this axis reflects a coenocline from poor heathland, through dry grassland, damp herb-rich grassland and rather dry fen margin to wetter fen margin vegetation. Heathland and dry grassland species such as *Vaccinium* spp., *Deschampsia flexuosa*, *Cladonia* spp., *Achillea millefolium* and *Cerastium fontanum* ssp. *vulgare* obtained low scores along this axis. The grassland and fen margin species *Parnassia palustris*, *Potentilla erecta*, *Saussurea alpina* and *Carex vaginata* got medium scores, and wet fen species such as *Pedicularis palustris*, *Carex rostrata*, *Juncus* spp. and *Pohlia wahlenbergii* obtained high scores. Regression analyses confirmed that this axis was correlated with the depth of the ground water (Fig. 7). Sites on dry podsol and brown soil got low scores, while sites on wet brown soil and peat achieved high scores.

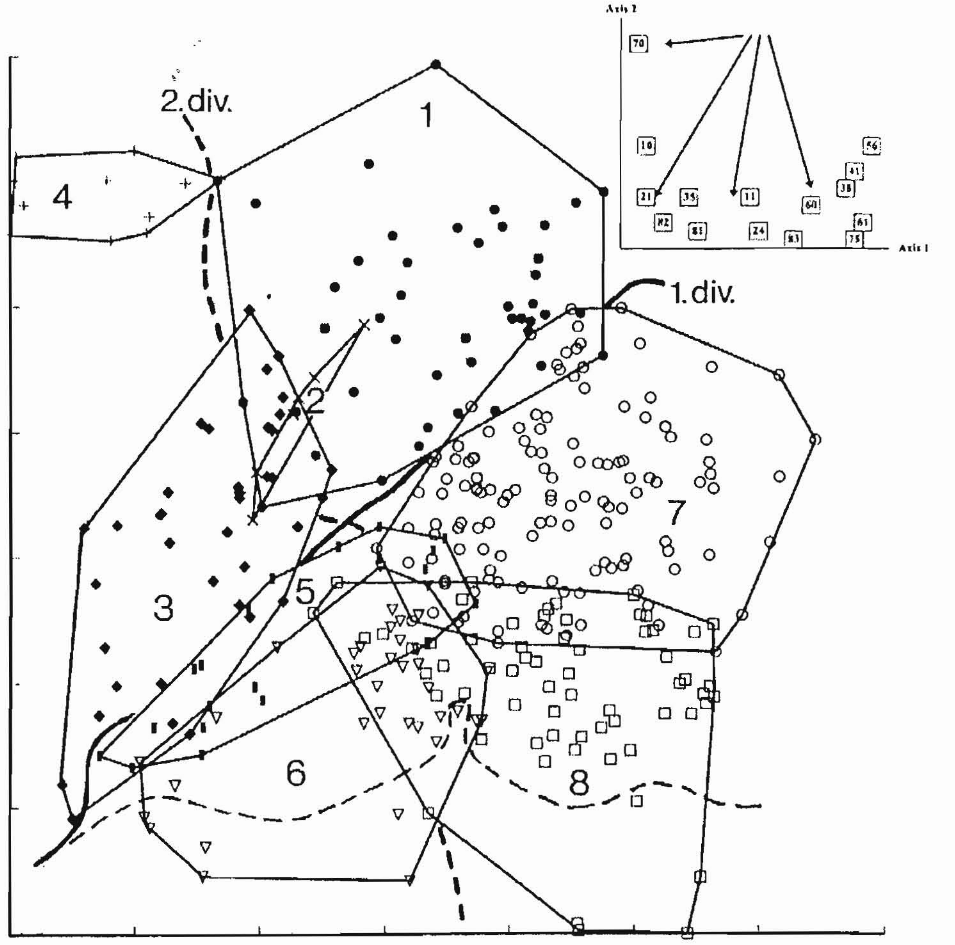

Fig. 5. DCA plot of the entire material (346 samples), axes 1 and 2. For axis values, see Table 8. The first and second divisions in TWINSPAN are indicated. Large numerals refer to TWINSPAN clusters separated on the third level of division. Unburnt plots are found below the thin broken line at the bottom of the diagram. The inset shows the same ordination with arrows that indicate the main directions of the change in plot positions over time, and some characteristic bonfire sites: 70 in heathland, 10 in dry grassland, 35, 81 and 82 in mesic grassland, 11 and 24 in damp grassland, 38, 41, 56, 60, 61, 75 and 83 in fen margin. The sample at the top of the diagram is 75C1, one year after burning and comprising three species (*Betula pubescens*, *Bryum argenteum* and *Ceratodon purpureus*). Cluster 1: ●, cluster 2: X, cluster 3: ◆, cluster 4: +, cluster 5: **I**, cluster 6: ∇, cluster 7: O, cluster 8: □

DCA axis 2 has an eigenvalue of 0.27 and accounts for 3.9% of the variation. In the species ordination (Fig. 6), bryophytes which are commonly found on disturbed ground, such as *Bryum* spp., *Ceratodon purpureus*, *Funaria hygrometrica* and *Pohlia* spp., obtained high scores along this axis. Species occurring in dry habitats with low-growing vegetation (*Vaccinium vitis-idaea*, *Cladonia* spp, *Pleurozium schreberi*), and

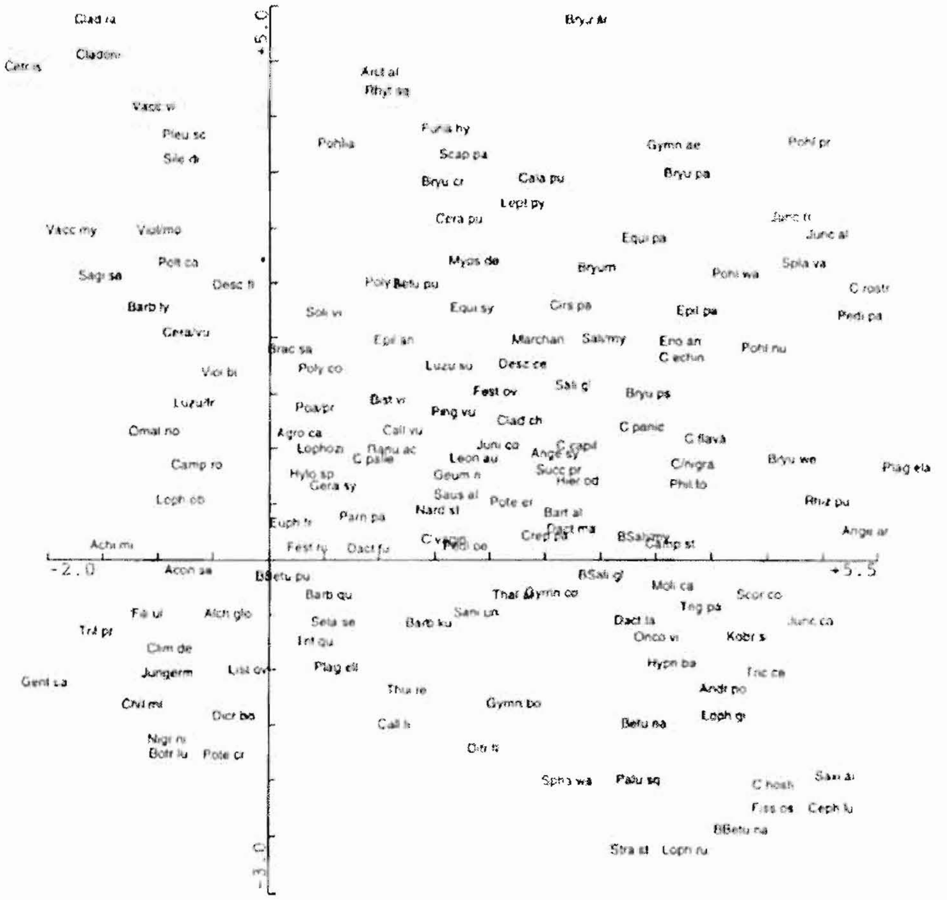

Fig. 6. Species ordination, DCA axes 1 and 2, of the 148 most important species among the 228 species recorded. Abbreviations mostly follow this pattern: the first four letters of the name of the genus followed by the first two letters of the epithet. For Carex, the abbreviations consist of the C of the genus and the first four letters of the epithet. A / shows that this is a subspecies. B before the species abbreviation indicates a shrub layer species.

weakly competitive alpine species which are common in low-growing fen and spring vegetation (*Juncus triglumis*, *J. alpinoarticulatus*, *Pohlia wahlenbergii*), also got high scores. Species that occur mostly in mature vegetation of the northern boreal zone, such as the orchids *Dactylorhiza* spp. and *Gymnadenia conopsea*, achieved low scores along axis 2, as did *Betula* and *Salix* in the shrub layer. This is reflected in the sample ordination as decreasing scores for plots over time (Fig. 8), as samples made a few years after burning very often achieved high scores and samples made after longer periods of revegetation or in unburnt vegetation, achieved low scores. In 79C and 81C, the samples from the first year achieved lower scores than those from later years, but eventually samples moved towards the lower end of the axis. Samples from the unburnt vegetation of sites 75 and 83 obtained the lowest scores on this axis, while those from the newly burnt plots of 75 and 79 and the dry heathland site 70 obtained the highest scores. Regression analyses confirmed that axis 2 was negatively correlated with site age, i.e. the time since burning, and with the number of species recorded in the samples, and positively correlated with pH (Fig. 7).

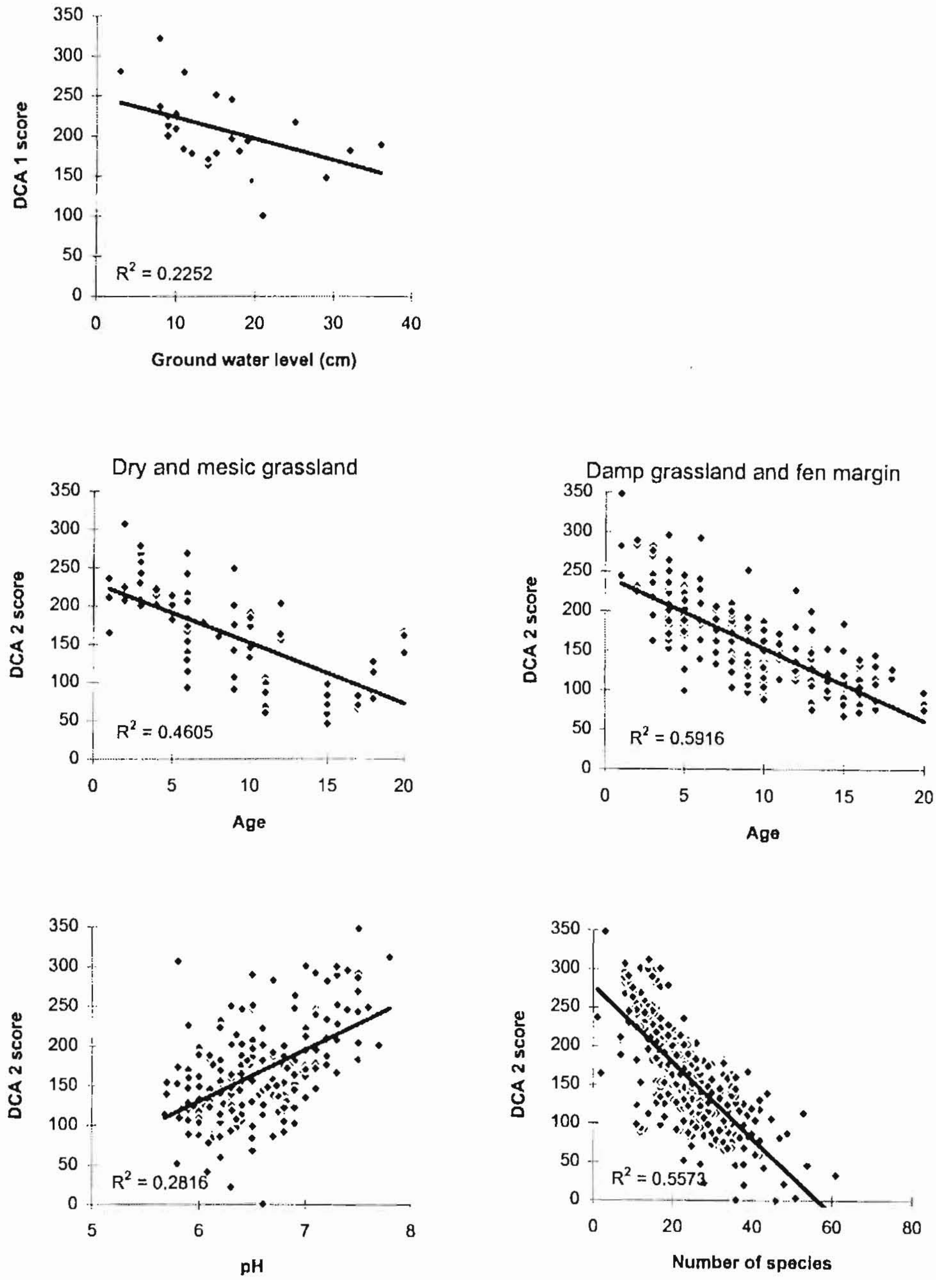

Fig. 7. Regression analyses showing the relationships between ground water level and scores on axis 1, between site age (time since burning) and scores on axis 2, and between measurements of pH and species richness in samples and scores on axis 2. No investigation of the ground water level was accomplished when the level was more than 36 cm below the surface (Arnesen 1989).

DCA axes 3 and 4 have successively lower eigenvalues and explanatory values (Table 8). These axes did not seem to add vital information of ecological relevance, and are not presented here.

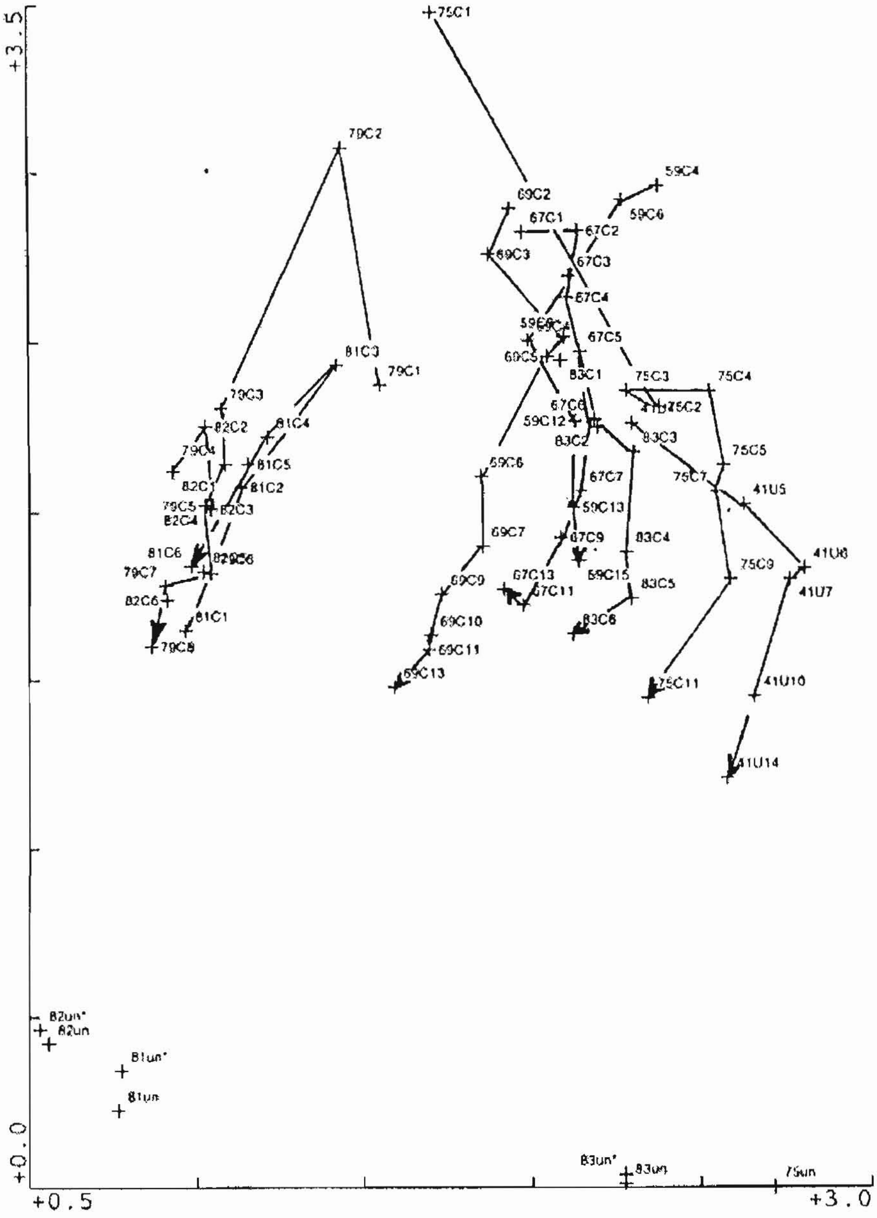

Fig. 8. DCA ordination (extract from the ordination run of the whole material, cf. Fig. 5) of samples from experimental localities 75, 81, 82 and 83 (central plots) and from some plots analysed almost every year for many years (59C, 67C, 69C, 41U). Sample code: plot number, plot position within the site (cf. Fig. 2), years since burning. Un = unburnt (0.25 m^2), un* = unburnt (1 m^2).

The TWINSPAN classification reflected both the main vegetation gradient from dry heathland to wet fen margin and the temporal gradient from young to old sites. The first division classified plots from dry grassland and heathland and samples from young bonfire sites in one group (upper left of DCA plot in Fig. 5), and moister grassland and fen margin samples in the other (lower right). The second division separated young samples in dry grassland and heathland from older ones, on one side of the main division (upper left, Fig. 5). On the other side of the main division (lower right, Fig. 5) grassland samples were separated from fen margin samples. Clusters were delimited at the third level of division (Table 9). Cluster 1 comprises samples from young bonfire sites along the whole of the main vegetation gradient. Indicator and preferential species were early-successional species. Clusters 2, 3 and 4 comprise dry grassland and heathland samples, clusters 5 and 6 mostly moister grassland samples and clusters 7 and 8 mostly fen margin samples. The ecology of the divisions was also reflected in the indicators and preferential species calculated by TWINSPAN (Fig. 9). The temporal gradient may be recognised as an increase in mean bonfire site/plot age from clusters at the upper end of axis 2 to the lower end (Table 10). There was also an increase in the mean number of species per plot in the clusters and a decrease in the mean cluster pH along this gradient. Samples from one plot are often found in different clusters along the time gradient; for instance, 16L whose first sample was in cluster 1, its second and third in cluster 3 and its last in cluster 6, and the samples in 19C which were found in clusters 1, 6 and 7. The unburnt sample, 75un, is found in cluster 8, while the samples from the same locality one and two years after burning (75C1 and 75C2) are found in cluster 1 and those from the following years in 7 (Table 9).

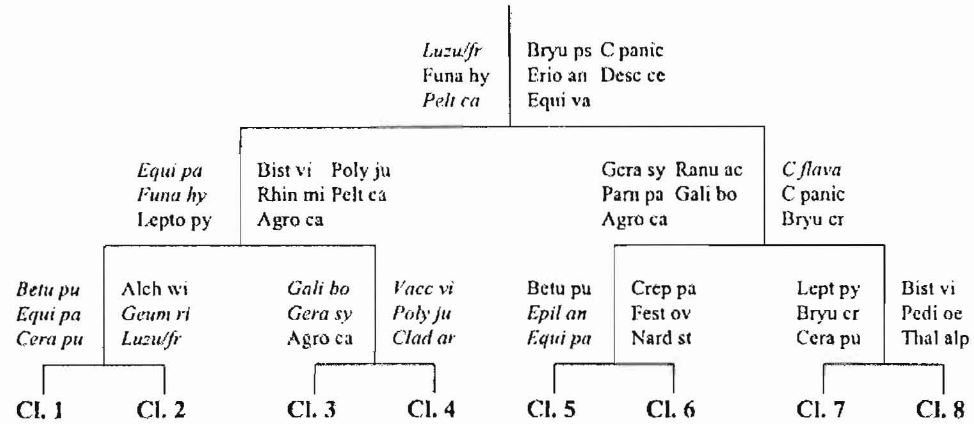

Fig. 9. The TWINSPAN dendrogram. Three levels of division are shown and indicator species and preferential species (italics) for the groups are included. Abbreviations as in Fig. 6.

SPECIES AND VEGETATION CHANGE OVER TIME

The main part of the following description is based on 24 bonfire sites (19 in damp grassland and fen margin and 5 in dry/mesic grassland and heathland), comprising three types of plots (upper margin, centre, lower margin) and re-analysed at quite

Table 9. The TWINSPAN clusters. Sample codes: bonfire site number, position, years since burning (age). Position codes: see Fig. 2. Additional codes: a = above the site, b = below the site, un = unburnt 0.25 m², un* = unburnt 1 m².

Cluster 1 (n = 44, U: 4, C: 32, CU: 2, CL: 3, c: 1, L: 2)
16U3, 16CU3, 16C3, 16CL3, 16L3, 16U6, 16CU6, 16C6, 16CL6, 16C10, 19C3, 25c12, 48C7, 51C6, 55C3, 55L3, 55C7, 59C4, 59C6, 59C9, 59C12, 60CL4, 61U4, 61C4, 63C4, 65C4, 66U4, 67C1, 67C2, 67C3, 67C4, 67C5, 69C2, 69C3, 69C4, 69C5, 70C8, 70C12, 75C1, 75C2, 79C1, 79C2, 82C1, 83C1.

Cluster 2 (n = 6, C: 6)
81C1, 81C2, 81C3, 81C4, 81C5, 81C6.

Cluster 3 (n = 40, U: 10, C: 19, CU: 1, CL: 1, M: 2, L: 7)
10U9, 10C9, 10L9, 10U12, 10C12, 10L12, 10U20, 10C20, 10L20, 16L6, 16U10, 16CU10, 16CL10, 16L10, 16U18, 16C18, 21U6, 21C6, 21L6, 21U11, 21L11, 23U6, 23C6, 23M6, 23U11, 23C11, 23U15, 23C15, 28M6, 79C3, 79C4, 79C5, 79C6, 79C7, 79C8, 82C2, 82C3, 82C4, 82C5, 82C6.

Cluster 4 (n = 10, U: 4, C: 2, L: 4)
70U8, 70L8, 70U11, 70C11, 70L11, 70U12, 70L12, 70U17, 70C17, 70L17.

Cluster 5 (n = 20, U: 6, C: 8, L: 6)
21C11, 21U17, 21C17, 21L17, 35U6, 35C6, 35L6, 35U9, 35C9, 35L9, 35U15, 35C15, 35L15, 51U11, 51C11, 51L11, 51U17, 51C17, 51L17, 55C14.

Cluster 6 (n = 36, U: 5, C: 10, CL: 1, c: 1, M: 3, L: 9, unburnt: 7)
11U9, 11C9, 11L9, 11U13, 11C13, 11L13, 11U20, 11C20, 11L20, 14C12, 14U18, 14C18, 16CL18, 16L18, 19C12, 23M11, 23M15, 24C9, 24L9, 24U13, 24C13, 24L13, 24b10, 24a10, 24c10, 25b12, 28M15, 44C10, 44L10, 44C16, 44L16, 55L7, 81un, 81un*, 82un, 82un*.

Cluster 7 (n = 127, U: 27, C: 58, CU: 2, CL: 2, c: 1, M: 5, LI: 2, L 30)
5U8, 5C8, 5L8, 5U10, 5C10, 5L10, 14U7, 14C7, 14L7, 14U12, 14L12, 19C7, 24U4, 24C4, 24L4, 28C6, 28L6, 28C11, 38U5, 38C5, 38L5, 38C10, 38L10, 39U5, 39C5, 39M5, 39L5, 39C10, 41U4, 41U5, 41M5, 41C5, 41LI5, 41U6, 41U7, 41U10, 41C10, 41LI14, 42C5, 42L5, 42C9, 42L9, 44U5, 44C5, 44L5, 45U5, 45CU5, 45C5, 45L5, 45CU10, 45C10, 48U7, 48L7, 48U12, 48C12, 48L12, 48C16, 51U6, 51L6, 55U3, 56M4, 56C4, 56L4, 56M8, 56C8, 56L8, 56M13, 56C13, 56L13, 59U4, 59L4, 59C13, 59C15, 60U4, 60C4, 60L4, 60U8, 60C8, 60CL8, 60CL15, 61L4, 61U8, 61C8, 61L8, 61C13, 61c10, 63U4, 63L4, 63U8, 63C8, 63L8, 63C13, 63L13, 65U4, 65L4, 65U8, 65C8, 65L8, 65C15, 66C4, 66L4, 66U8, 66C8, 66L8, 66C15, 67C6, 67C7, 67C9, 67C11, 67C13, 69C6, 69C7, 69C9, 69C10, 69C11, 69C13, 75C3, 75C4, 75C5, 75C7, 75C9, 75C11, 83C2, 83C3, 83C4, 83C5, 83C6.

Cluster 8 (n = 63, U: 20, C: 8, CU: 2, M: 5, L: 21, unburnt: 6)
5U17, 5C17, 5L17, 14L18, 16CU18, 24U9, 25a12, 28M11, 28L11, 28C15, 28L15, 38U10, 38U16, 38C16, 38L16, 39U10, 39M10, 39L10, 39U16, 39C16, 39M16, 39L16, 41L5, 41M10, 41LI10, 41L10, 41U14, 41M14, 41C14, 41L14, 42C16, 42L16, 44U10, 44U16, 45U10, 45L10, 45U16, 45CU16, 45C16, 45L16, 48U16, 48L16, 55U7, 59U9, 59L9, 59U13, 59L13, 60L8, 60U15, 60C15, 60L15, 61U13, 61L13, 61b10, 61a10, 63U13, 65U15, 65L15, 66U15, 66L15, 75un, 83un, 83un*.

Table 10 Mean age, number of species and pH in TWINSPAN clusters, with standard deviation. Ground water level measurements were made in 1986 in unburnt vegetation close to the lower margin of the sites (Arnesen 1989). These values were assigned to the latest samples or the unburnt samples from the localities, and mean values are therefore not the mean for plots, but rather the mean for the vegetation of the localities found in the clusters.

	Cl. 1		Cl. 2		Cl. 3		Cl. 4		Cl. 5		Cl. 6		Cl. 7		Cl. 8	
	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd
Age (yrs.)	4,6	2,9	3,5	1,9	9,4	4,9	12,4	3,5	11,0	4,7	13,2	3,8	7,6	3,3	13,5	3,1
Species	12	5	11	5	26	8	16	2	25	6	36	10	22	7	30	8
pH	7,0	0,4	-	-	6,6	0,6	7,2	0,6	6,6	0,3	6,3	0,3	6,5	0,4	6,2	0,4
Gr. water (cm)	-	-	< 36	-	< 36	-	< 36	-	21,0	-	27,0	12,7	12,4	3,7	16,0	9,1

Table 11. The samples from 24 bonfire sites that were re-analysed at least three times, sorted by site age at the time of sampling and by the three plot positions on the site (U = upper margin or side margin, C = centre, L = lower margin, cf. Fig. 2) (24 x 3 x 3 = 216 samples). Sample code: Site number, plot position and age (years since burning).

3-9			8-13			13-20		
U	C	L	U	C	L	U	C	L
Mesic grassland and heathland								
10U9	10C9	10L9	10U12	10C12	10L12	10U20	10C20	10L20
16U3	16C3	16L3	16U10	16C10	16L10	16U18	16C18	16L18
21U6	21C6	21L6	21U11	21C11	21L11	21U17	21C17	21L17
35U6	35C6	35L6	35U9	35C9	35L9	35U15	35C15	35L15
70U8	70C8	70L8	70U12	70C12	70L12	70U17	70C17	70L17
Fen margin and damp grassland								
5U8	5C8	5L8	5U10	5C10	5L10	5U17	5C17	5L17
11U9	11C9	11L9	11U13	11C13	11L13	11U20	11C20	11L20
14U7	14C7	14L7	14U12	14C12	14L12	14U18	14C18	14L18
24U4	24C4	24L4	24U9	24C9	24L9	24U13	24C13	24L13
28M6	28C6	28L6	28M11	28C11	28L11	28M15	28C15	28L15
38U5	38C5	38L5	38U10	38C10	38L10	38U16	38C16	38L16
39U5	39C5	39L5	39U10	39C10	39L10	39U16	39C16	39L16
41U5	41C5	41L5	41U10	41C10	41L10	41U14	41C14	41L14
44U5	44C5	44L5	44U10	44C10	44L10	44U16	44C16	44L16
45U5	45C5	45L5	45U10	45C10	45L10	45U16	45C16	45L16
48U7	48C7	48L7	48U12	48C12	48L12	48U16	48C16	48L16
51U6	51C6	51L6	51U11	51C11	51L11	51U17	51C17	51L17
56M4	56C4	56L4	56M8	56C8	56L8	56M13	56C13	56L13
59U4	59C4	59L4	59U9	59C9	59L9	59U13	59C13	59L13
60U4	60C4	60L4	60U8	60C8	60L8	60U15	60C15	60L15
61U4	61C4	61L4	61U8	61C8	61L8	61U13	61C13	61L13
63U4	63C4	63L4	63U8	63C8	63L8	63U13	63C13	63L13
65U4	65C4	65L4	65U8	65C8	65L8	65U15	65C15	65L15
66U4	66C4	66L4	66U8	66C8	66L8	66U15	66C15	66L15

regular intervals (Tables 11, 12 and 13). Development was also clearly demonstrated in the four experimental sites (Table 14).

The oldest bonfire sites were 20 years old in 1997, but none had fully recovered by that time. Bryophytes were the first to become established on the sites, and only rarely were bare ash and burnt ground still visible after 4-5 years. Occasionally, seed plants of species found in the immediate surroundings occurred during the first year of revegetation, but only rarely did these plants survive to maturity (Table 14). Although few species, except unidentified algae, were observed during the season of burning, *Bryum* spp., *Ceratodon purpureus*, *Funaria hygrometrica*, *Leptobryum pyriforme*, *Polytrichum juniperinum* coll. (including *P. strictum*) and *Marchantia* spp. (*M.*

Table 12. Synoptic table showing constancy and characteristic cover in age-classes. The characteristic cover is mean cover calculated only from samples that include the particular species. The main part of the table, i.e. the last six columns, are based on analyses in 24 bonfire sites comprising 72 plots: 19 sites and 57 plots in fen margin and damp grassland and 5 sites and 15 plots in dry and mesic grassland and in heathland. All these sites included one plot in the upper margin, one in the centre and one in the lower margin and were analysed three times. The first column show species that were recorded in thirteen samples from the centre of newly burnt sites in fen margin and grassland. Species with constancy lower than 18 % and characteristic cover lower than 2 (i.e. lower than 18-2) in all age classes, are excluded. At the end of the table, mean cover in vegetation layers and of ash is included. Cover classes: 1: found within 5 cm of the plot, 2: 0-1%, 3: 1-3.125 %, 4: 3.125-6.25 %, 5: 6.25-12.5 %, 6: 12.5-25 %, 7: 25-50 %, 8: 50-75 %, 9: 75-100 %. Bold type indicates species that become established early and increase in cover quite quickly, italics indicate species from the surroundings that take a long time to become established in the bonfire sites.

	Newly burnt	Fen margin and damp grassland			Dry/mesic grassland and heathland		
Age (years)	0-2	3-9	8-13	13-20	3-9	8-13	13-20
Number of samples	13	57	57	57	15	15	15
Shrub layer							
Betula pubescens	.	.	4-4	16-4	.	13-6	33-7
Salix glauca	.	.	7-4	26-5	.	.	13-1
Salix myrsinifolia coll.	.	.	21-6	49-6	.	7-6	13-3
Field layer							
Woody species							
Betula pubescens	54-3	75-3	70-5	70-5	93-5	100-6	93-4
Empetrum nigrum ssp. hermaphr.	.	4-2	4-2	11-2	.	.	20-2
Salix glauca	.	11-3	46-3	51-4	.	7-3	33-2
Salix myrsinifolia coll.	15-2	68-3	68-4	74-4	33-3	40-2	13-2
Vaccinium vitis-idaea	.	.	.	.	13-4	33-3	33-3
Herbs							
Achillea millefolium	.	.	.	.	13-5	20-5	20-5
Aconitum septentrionale	.	.	.	.	.	20-3	20-2
Alchemilla glabra	.	9-2	9-4	9-4	27-6	27-6	33-6
Alchemilla glomerulans	.	2-6	7-4	7-5	.	27-4	20-3
Angelica sylvestris	8-2	23-2	51-3	63-3	20-5	27-4	40-3
Anthriscus sylvestris	.	.	.	.	13-3	20-3	20-2
Bartsia alpina	.	7-3	26-4	46-3	.	20-1	20-2
Bistorta vivipara	8-2	47-2	75-3	91-4	73-3	80-5	100-5
Campanula rotundifolia	.	2-2	5-2	5-3	20-3	20-3	27-2
Cirsium helenioides	.	.	2-3	2-4	.	7-1	20-2
Crepis paludosa	8-2	21-4	60-4	82-4	.	13-2	20-2
Dactylorhiza fuchsii	.	.	11-2	21-3	.	7-2	33-2
Dactylorhiza maculata	.	2-2	.	19-3	.	.	.
Epilobium angustifolium	15-2	19-3	16-2	19-2	27-4	27-3	33-3
Epilobium palustre	.	14-4	25-5	21-2	.	.	.
Equisetum palustre	62-5	54-6	51-5	56-4	.	.	.

	Newly burnt	Fen margin and damp grassland			Dry/mesic grassland and heathland		
Age (years)	0-2	3-9	8-13	13-20	3-9	8-13	13-20
Equisetum pratense	15-2	7-2	11-4	16-4	20-3	20-3	20-2
Equisetum variegatum	8-2	56-3	70-3	89-3	.	.	.
Euphrasia frigida	15-2	9-3	25-2	39-2	53-3	40-3	47-2
Filipendula ulmaria	.	.	.	.	20-3	27-2	20-5
Galium boreale	15-2	9-4	12-4	16-3	20-6	33-4	40-3
Geranium sylvaticum	38-2	32-3	46-3	51-3	47-3	67-4	80-5
Geum rivale	15-2	25-4	51-5	63-5	20-6	27-5	47-5
Gymnadenia conopsea	.	4-2	7-2	18-2	.	7-2	7-1
Hieracium spp.	8-1	.	7-2	5-2	13-4	7-3	60-3
Leontodon autumnalis	8-1	39-3	56-2	67-2	7-6	27-3	33-3
Melampyrum pratense	.	.	.	7-3	7-2	27-2	20-2
Melampyrum sylvaticum	.	.	5-1	4-5	.	40-4	33-2
Omalotheca norvegica	.	.	2-3	2-2	40-4	60-4	60-3
Parnassia palustris	.	12-3	33-3	51-2	20-4	47-3	53-3
Pedicularis oederi	8-1	9-2	30-3	63-3	.	13-3	20-2
Pinguicula vulgaris	8-2	9-2	23-2	37-4	7-3	33-3	27-3
Potentilla erecta	8-1	26-5	47-4	63-3	13-4	27-3	40-3
Pyrola rotundifolia coll.	.	.	11-3	18-3	7-2	27-2	67-3
Ranunculus acris	.	21-4	40-4	63-4	27-2	47-3	53-3
Rhinanthus minor	8-1	11-3	18-3	19-2	33-3	47-2	33-2
Rubus saxatilis	.	.	.	.	20-4	27-4	27-3
Rumex acetosa	.	5-2	7-3	7-3	20-3	20-5	20-5
Saussurea alpina	15-3	23-4	40-5	49-5	13-4	33-5	47-5
Selaginella selaginoides	.	2-2	14-2	23-2	7-2	20-3	13-4
Solidago virgaurea	.	12-3	19-3	14-2	27-3	60-2	87-3
Succisa pratensis	15-2	39-3	60-4	56-4	7-2	7-1	13-3
Taraxacum spp.	.	.	4-3	.	7-2	20-2	20-2
Thalictrum alpinum	8-1	21-2	42-3	53-3	7-2	7-3	13-2
Tofieldia pusilla	.	.	12-2	25-2	.	.	.
Trientalis europaea	.	7-2	5-3	7-2	20-3	27-2	40-3
Viola biflora	15-2	.	4-2	2-2	.	.	27-2
Graminoids							
Agrostis capillaris	31-2	14-5	26-6	25-4	53-6	80-5	80-5
Anthoxanthum odoratum	.	4-3	19-2	19-2	13-4	40-4	53-3
Carex capillaris	8-2	12-2	30-2	30-2	.	7-2	7-2
Carex dioica	8-2	9-3	30-3	56-3	.	.	.
Carex flava	.	33-5	37-5	35-4	.	.	.
Carex nigra coll.	.	16-6	23-6	21-7	.	.	.
Carex panicea	.	42-5	49-5	70-3	.	.	.
Carex vaginata	.	11-4	19-5	46-4	7-2	7-3	27-3
Deschampsia cespitosa	8-2	81-6	88-6	95-5	67-6	53-6	67-6
Deschampsia flexuosa	8-1	9-2	7-2	7-4	27-2	47-2	47-2
Eriophorum angustifolium	15-2	51-5	54-4	70-3	.	.	.
Festuca ovina	.	40-3	65-4	81-4	27-3	33-3	40-3
Festuca rubra	.	4-2	23-3	26-2	13-3	13-3	53-3
Hierochloë odorata	.	12-5	28-4	35-3	.	.	.
Luzula multiflora ssp. frigida	8-2	2-2	5-2	5-2	27-2	27-3	27-2
Luzula pilosa	.	.	.	.	.	7-4	20-3
Luzula sudetica	.	11-3	30-3	26-2	7-2	13-2	13-2
Molinia caerulea	.	12-5	23-4	33-3	.	.	.

Age (years)	Newly burnt 0-2	Fen margin and damp grassland 3-9	8-13	13-20	Dry/mesic grassland and heathland 3-9	8-13	13-20
Nardus stricta	.	14-3	32-4	42-3	7-4	27-3	27-3
Poa pratensis coll.	.	11-3	14-3	5-2	13-2	27-2	13-2
Bottom layer							
Mosses							
Aulacomnium palustre	.	32-2	44-3	54-5	27-3	33-3	33-2
Brachythecium salebrosum	8-2	2-5	7-3	18-2	27-4	20-4	33-2
Bryum creberrimum	62-3	82-4	58-5	28-4	67-7	67-7	40-5
Bryum pallens	8-3	25-3	11-2	4-2	7-2	.	.
Bryum pseudotriquetrum	38-4	63-4	81-5	93-5	.	.	20-2
Campylium stellatum	8-1	21-3	35-5	56-6	.	.	.
Ceratodon purpureus	85-5	88-6	58-5	26-3	73-5	67-4	33-4
Funaria hygrometrica	69-5	60-4	5-4	.	67-5	20-3	7-2
Hylocomium splendens	.	9-2	9-2	12-4	20-2	13-3	40-2
Leptobryum pyriforme	54-6	89-6	63-4	46-5	73-5	40-5	33-5
Philonotis fontana	.	9-3	12-3	21-3	.	.	.
Pleurozium schreberi	.	5-3	2-2	2-2	27-3	20-2	33-2
Polytrichum commune	.	14-4	16-6	12-5	33-5	13-7	20-6
Polytrichum juniperinum coll.	23-2	21-3	32-4	28-3	53-4	60-5	73-5
Rhizomnium pseudopunctatum	.	4-2	5-2	16-3	.	.	20-2
Sanionia uncinata	.	5-3	14-3	18-3	.	.	.
Splachnum vasculosum	.	19-5	21-4	4-2	.	.	.
Tomentypnum nitens	.	12-3	18-3	30-6	.	13-2	13-2
Liverworts							
Aneura pinguis	.	4-2	16-2	44-3	.	.	13-2
Barbilophozia lycopodioides	.	2-1	2-2	4-2	13-2	20-3	47-4
Chiloscyphus polyanthos	.	2-2	9-2	19-2	.	.	7-2
Marchantia spp.	62-3	95-7	93-8	89-7	53-8	53-8	60-7
Plagiochila porelloides	.	.	.	4-2	.	.	33-2
Lichens							
Cladonia arbuscula	.	.	.	.	13-2	13-2	20-3
Peltigera canina	.	4-4	2-2	7-2	13-4	33-3	40-6
Shrub layer cover	0	0	1	3	0	4	5
Field layer cover	5	7	8	8	7	8	8
Bottom layer cover	7	9	9	8	9	9	8
Ash cover	8	2	.	.	3	.	.

polymorpha and *M. alpestre*) became established quite quickly. *Funaria hygrometrica* was usually the first species observed on the sites, but *Bryum creberrimum*, *Ceratodon purpureus*, *Leptobryum pyriforme* and *Marchantia* spp., in particular, expanded greatly in the course of the first few years. *Marchantia* spp. developed into a compact layer, sometimes as thick as 10 cm, on many sites in damp grassland, and to a large extent in fen margin also. Some of these early-successional bryophytes were dominant on many sites throughout the investigation period. *Marchantia* spp. on damp grassland and fen margin sites, and *Polytrichum juniperinum* coll. on drier sites, were particularly stable, although some decrease in *Marchantia* spp. was observed in the last re-analyses. *Bryum creberrimum*, *Ceratodon purpureus* and *Leptobryum pyriforme* became markedly reduced after their initial expansion, but were still recorded as important species in the last re-analyses. On the other hand, *Funaria*

Table 13. Constancy (%) and characteristic cover (cf. text and Table 12) of some common species in the set of 24 bonfire sites, sorted by age and position on the site (cf. Table 11). U = upper margin and side margin, C = centre, L = lower margin (cf. Fig. 2). I: Species that were more common or abundant in the margin of the sites than in the centre, at least at the time of the first analysis. II: Species that were more common in the centre of sites and species that showed no evident differences in distribution within the sites. Cover classes: 1: found within 5 cm of the plot, 2: 0-1%, 3: 1-3.125%, 4: 3.125-6.25%, 5: 6.25-12.5%, 6: 12.5-25%, 7: 25-50%, 8: 50-75%, 9: 75-100%.

Age (years)		3-9			8-13			13-20	
Position	U	C	L	U	C	L	U	C	L
Number of plots	24	24	24	24	24	24	24	24	24
I									
Alchemilla glabra	13-3	8-2	17-6	17-4	8-3	13-7	17-5	17-2	8-7
Bartsia alpina	4-2	.	13-3	25-3	17-3	33-4	58-3	29-3	33-3
Campanula rotundifolia	13-3	.	4-2	17-3	.	8-3	13-2	8-2	8-3
Equisetum variegatum	50-3	25-3	58-3	50-3	63-3	54-3	71-3	79-4	63-3
Galium boreale	25-5	4-4	4-3	25-5	8-2	17-2	29-3	13-2	21-3
Parnassia palustris	17-3	4-2	21-3	33-3	38-3	38-3	50-3	54-2	50-3
Potentilla erecta	21-5	8-3	42-5	50-3	21-3	58-4	67-3	46-2	63-4
Saussurea alpina	29-4	8-3	25-5	38-5	21-4	58-6	46-5	33-2	67-5
Selaginella selaginoides	4-2	.	4-2	29-2	.	17-2	42-2	.	21-3
Succisa pratensis	38-3	21-2	38-4	38-4	46-3	63-4	54-4	33-3	54-5
Thalictrum alpinum	25-2	.	29-2	50-3	4-2	50-3	71-3	4-2	58-3
Agrostis capillaris	17-6	25-4	25-5	33-5	38-4	42-6	29-4	29-5	50-5
Carex capillaris	8-2	4-2	17-2	33-2	17-2	25-2	25-2	29-2	21-2
Carex flava	38-5	17-3	25-4	46-5	17-3	25-4	50-5	21-2	13-4
Carex panicea	42-5	4-2	54-5	54-5	8-4	54-5	63-4	46-3	58-3
Carex vaginata	13-3	.	17-5	25-4	.	25-5	50-3	29-3	46-5
Molinia caerulea	8-4	.	21-5	21-3	.	33-5	29-2	4-2	46-3
Aulacomnium palustre	42-2	21-2	29-3	54-3	29-3	42-3	63-4	50-4	38-5
Bryum pseudotriquetrum	50-5	50-3	50-4	67-6	63-4	63-5	83-5	75-5	75-5
Campylium stellatum	29-3	13-2	8-3	46-5	8-3	29-3	63-6	25-5	46-5
Ceratodon purpureus	92-6	79-4	83-6	67-5	63-4	50-4	29-3	42-4	13-4
Hylocomium splendens	8-2	8-2	17-2	13-3	.	17-2	17-2	8-2	29-4
Polytrichum commune	33-5	13-2	8-3	25-7	13-3	8-2	21-6	13-2	8-3
Polytrichum juniperinum coll.	62-4	25-2	17-3	67-5	37-3	17-3	58-4	33-2	21-4
Sanionia uncinata	4-2	.	8-3	21-2	.	13-4	25-3	4-2	13-4
Splachnum vasculosum	21-3	4-3	21-6	21-2	13-2	17-6	4-2	.	4-2
Tomentypnum nitens	17-3	.	13-3	17-3	13-2	21-2	21-6	29-6	29-5
II									
Betula pubescens	88-4	71-4	79-4	83-5	79-5	67-5	75-5	79-5	71-4
Salix glauca	8-3	13-2	4-5	42-3	46-3	25-4	46-4	54-4	42-3
Salix myrsinites coll.	63-3	67-3	54-3	83-4	67-4	38-4	63-4	63-5	58-4
Epilobium angustifolium	13-3	33-4	17-3	17-2	29-3	8-3	13-2	46-2	8-2
Equisetum palustre	46-5	42-7	42-6	38-4	42-5	42-4	46-3	46-5	42-4
Solidago virgaurea	13-3	21-2	13-3	25-3	38-2	21-3	21-3	42-2	25-2
Deschampsia cespitosa	71-5	92-6	71-5	79-6	96-6	67-5	88-5	96-5	83-5
Bryum creberrimum	88-5	75-5	75-5	71-6	63-6	46-6	29-5	38-5	25-3
Funaria hygrometrica	54-3	79-5	50-3	.	25-3	4-2	.	4-2	.
Leptobryum pyriforme	83-6	92-6	83-5	46-4	83-5	46-3	17-4	79-5	33-4
Marchantia spp.	83-7	83-8	92-7	75-7	92-8	88-8	75-6	88-7	88-8

Tabel 14. Vegetation development in centre plots (0.25 m²) in 4 experimental bonfire localities; 75 and 83 in fen margin, 81 and 82 in grassland. Sample code: Un = unburnt, digit = number of years since burning. Cover classes: 1: found within 5 cm of the plot, 2: 0-1%, 3: 1-3.125 %, 4: 3.125-6.25 %, 5: 6.25-12.5%, 6: 12.5-25%, 7: 25-50%, 8: 50-75%, 9: 75-100%.

	75									83						
Sample	un	1	2	3	4	5	7	9	11	un	1	2	3	4	5	6
Shrub layer cover	4															
Field layer cover	8	2	2	3	6	7	8	8	8	8	6	7	7	8	8	8
Bottom layer cover	9	2	5	7	9	9	9	9	9	9	3	7	9	9	9	9
Litter cover	7		2	3	2	5	7	7	7	7	2	4	4	5	5	5
Bare soil/ash cover		9	9	7	4	3					9	6	2	2		
Shrub layer height (cm)	50															
Field layer height (cm)	20	1	2	5	7	20	20	17	15	20	10	10	12	13	15	15
Shrub layer																
Betula nana	4															
Field layer																
Woody species																
Andromeda polifolia	4															
Betula nana	6									5						
Betula pubescens		2			2	2	2	2	5		2	2	3	4	4	6
Juniperus communis	4															
Salix glauca														2	2	2
Salix myrsinifolia coll.			1	1	1	1	1	1	1				2	2	2	2
Vaccinium uliginosum	4															
Herbs																
Alchemilla glabra																
Alchemilla glomerulans																
Alchemilla wichurae																
Angelica sylvestris	1							2	2	2		2	2	2	2	2
Antennaria dioica	4															
Bartsia alpina	1									3						
Bistorta vivipara	4						2	2	2	2						
Campanula rotundifolia																
Cerastium fontanum ssp. vulgare																
Crepis paludosa	1									2		2	2	3	4	5
	75									83						

	81							82						
Sample	un	1	2	3	4	5	6	un	1	2	3	4	5	6
Shrub layer cover														
Field layer cover	7	2	3	3	4	5	6	·8	2	4	6	7	7	8
Bottom layer cover	8		6	9	9	9	9	8	4	9	9	9	9	9
Litter cover	7	2			3	3	3	7				5	6	6
Bare soil/ash cover		9	8	2	3	2			9	3	2	2		
Shrub layer height (cm)														
Field layer height (cm)	15	1	3	2	2	4	10	20	2	3	4	3	4	5
Shrub layer														
Betula nana														
Field layer														
Woody species														
Andromeda polifolia														
Betula nana														
Betula pubescens	2								2	3	6	6	7	8
Juniperus communis														
Salix glauca														
Salix myrsinifolia coll.														
Vaccinium uliginosum														
Herbs														
Alchemilla glabra											2	2	2	2
Alchemilla glomerulans								4						
Alchemilla wichurae		2	3	2	2	2	2							
Angelica sylvestris													2	2
Antennaria dioica								2						
Bartsia alpina								2						
Bistorta vivipara	3		2	2	2	3	3	4				2	3	3
Campanula rotundifolia	3							2						
Cerastium fontanum ssp. vulgare					2	2	2						1	2
Crepis paludosa								3						
	8î							82						

Sample	un	1	2	3	4	5	7	9	11	un	1	2	3	4	5	6	un	1	2	3	4	5	6	un	1	2	3	4	5	6
Epilobium angustifolium																									1	2	2	1	2	1
Epilobium palustre				1	2	1	2	2	2																					
Equisetum arvense																												2	2	2
Equisetum palustre			1	2	2	2	2	2	2	2	6	7	7	7	7	6														
Equisetum pratense																									1	2	2	2	2	2
Equisetum scirpoides	4				2	2	2	4	4																					
Equisetum variegatum	4													2	2	2														
Euphrasia frigida																	2							2	1	2	2	2	3	2
Galium boreale										2							3							3	2	2	3	3	3	3
Geranium sylvaticum	4									4		2	2	2	2	2	6	1	1	1	2	2	2	6	1	1	2	2	2	2
Geum rivale																		1	2	2	2	2	2	2			2	2	2	2
Gymnadenia conopsea	4																													
Leontodon autumnalis	4															1	2		1	1	1									
Parnassia palustris										2				2	2	2	2							2						2
Pedicularis oederi	4						1	1	2	2									1	1	1	1	1							
Pinguicula vulgaris	4			2	2	2	2	3	3			2	2	2	2	2														
Potentilla erecta	4							2	2	2														5						2
Potrentilla crantzii																	4													
Pyrola rotundifolia ssp. norvegica																	3													
Ranunculus acris	4			2													3					2	2	2			2	2	3	2
Rhinanthus minor																	2						2	2		1	2	2	2	2
Saussurea alpina	4									3							4							3						
Saxifraga aizoides	4																													
Selaginella selaginoides	4									3							4							2						
Solidago virgaurea																	2													2
Succisa pratensis	6		1	2		2	2	2	2	4	2						3							2						
Taraxacum spp.																														1
Thalictrum alpinum	7		1	2	2	2	2	2	2	4							5							2						
Tofieldia pusilla	4							2	2	2																				
Triglochin palustris	4																													
Viola biflora																								2	2	2	2	2	2	2
Graminoids																														
Agrostis capillaris																	4							4	1	1	2	2	2	2
Anthoxanthum odoratum									2					2	3	5	2							2						
Carex capillaris	5		2	2	2	3	2	2	3								2				2	2	2							
Carex dioica	4		2					2	2	4																				
Carex lasiocarpa										2		1	2	3	3	4														
Carex panicea	6			1	2	3	3	5	7	3			2	2	3	3	2													
Carex vaginata										4						2	3							3				1	2	2
					75								83							81							82			

Sample	un	1	2	3	4	5	7	9	11	un	1	2	3	4	5	6	un	1	2	3	4	5	6	un	1	2	3	4	5	6
Deschampsia cespitosa	4			3	6	7	6	5	4					1	1	2	3	2						2						2
Deschampsia flexuosa																	2				2	2		2						
Eriophorum angustifolium								1	2	3		1	2	3	3	3											2	2	2	2
Festuca ovina	4				1	2	5	6	6	2							3													
Festuca rubra																	2				1	3	5	2						2
Juncus alpinoarticulatus					2	4	5	4	2																					
Juncus castaneus	4																													
Juncus triglumis				3	3	4	3	3	2																					
Kobresia simpliciuscula	4																													
Luzula multiflora ssp. frigida																1	2		2	2	2	2	2	2			2	2	2	2
Molinia caerulea	6																													
Nardus stricta	4							1	1								2				1	1	1	2						
Poa alpina			1														2				2	2	2							
Trichophorum cespitosum	6																													
Bottom layer																														
Mosses																														
Aulacomnium palustre					1	1	1	2	2	2			2	2	2	2												2	2	
Bryum argenteum		2	2	2																										
Bryum creberrimum				3	5	8	6	5	2		3	5	4	4	2	2				2	2	4	4		2	3	3	5	6	5
Bryum pallens			3	4	5	4	5	3	3																					
Bryum pseudotriquetrum	4		2	2	2	3	5	6	7	2	2	6	6	7	7	7	2			2				4						
Campylium stellatum	8		1	2	2	2	2	3	2	2				2	2		3							2						
Ceratodon purpureus		2	2	3	4	5	4	5	3		2	4	3	3	3	2			2	2					5	9	8	8	8	7
Climacium dendroides																	2							4						
Dicranum bonjeanii																	6							2						
Ditrichum flexicaule	4																2													
Fissidens adianthoides	4																													
Fissidens osmundoides	4																													
Funaria hygrometrica			2	5	3														4	6	6	7	5		3	2	3	3		
Hylocomiastrum pyrenaicum																								5						
Hylocomium splendens																	6			2				3						
Hypnum bantriensis	4																													
Leptobryum pyriforme			3	5	8	4	7	6	2		2	6	9	6	4	4				8	9	8	7			2	6	6	6	3
Paludella squarrosa										4																				
Philonotis fontana						2	3	2	2	2						1														
Plagiomnium ellipticum										2							2							5						
Polytrichum juniperinum coll.			2	2	2	3	2	2	2							1										2	2	4	4	6
Rhizomnium pseudopunctatum									2															2						
Sanionia uncinata																	5												2	
					75								83							81							82			

Sample	un	1	2	3	4	5	7	9	11	un	1	2	3	4	5	6	un	1	2	3	4	5	6	un	1	2	3	4	5	6
Scorpidium scorpioides	5																													
Sphagnum warnstorfii										9																				
Straminergon stramineum										2																				
Thuidium recognitum										2							2													
Tomentypnum nitens	4									4						1														
Tortella tortuosa	5				2	2																								
Liverworts																														
Aneura pinguis									2	2																				
Barbilophozia lycopodioides																	2							5						
Barbilophozia quadriloba	4								2								3													
Cephalozia lunulifolia	4																													
Gymnocolea borealis	4																2													
Lophozia gillmani	4																													
Marchantia spp.					2	2	2	2	2		2	3	5	6	7	6			5	6	6	7	7		2	2	2	4	4	4
Plagiochila porelloides																	2							2						
Lichens																														
Peltigera canina																												2	3	3
Total number of taxa	54	3	15	21	26	25	27	32	38	36	9	13	16	22	22	27	48	4	10	16	17	17	19	43	13	15	20	25	27	31

Additional species (with only one occurrence and cover < 3). Species, year and cover:

Site 75: Empetrum nigrum ssp. hermaphroditum 11: 2, Dactylorhiza lapponica un: 1, D. maculata un: 1, Erigeron boreale un: 1, Listera ovata un: 1, Omalotheca norvegica 3: 1, Carex hostiana un: 1, Bryum sp. 4: 2, Dicranum scoparium 11: 2, Pohlia wahlenbergii 4: 2, Polytricum commune 7: 2.

Site 83: Eriophorum latifolium un: 2, Brachythecium salebrosum 1: 2, Chiloscyphus polyanthos un: 2, Lophozia rutheana un: 2.

Site 81: Achillea millefolium 6: 2, Botrychium lunaria un: 2. Myosotis decumbens 3: 2, Phleum alpinum 6: 1, Brachythecium turgidum un: 2, Calliergonella lindbergii un: 2, Rhytidiadelphus squarrosus 3: 2, Barbilophozia bantriensis un: 2, Jungermannia sp. un: 2, Tritomaria quinquedentata un: 2.

Site 82: Filipendula ulmaria un: 2, Hieracium spp.: un: 2, Pyrola minor un: 2, Trientalis europaea un: 2, Mnium stellare un: 2, Rhodobryum roseum un: 2.

hygrometrica quickly became reduced and the latest observation registered it in one heathland plot after 17 years. Except for *Polytrichum juniperinum* coll. and *Marchantia* spp., the early bottom layer species were most frequent and abundant in the centre of the sites when the last re-analyses took place. The number of bryophyte species increased notably over time, particularly during the first years (Table 15). Eleven bryophyte species were found in a set of 13 samples from centre plots on 1-2 year-old sites, and in the 24-site set the number of bryophyte species increased from 44 recorded at 3-9 years of age to 59 on the same sites after 13-20 years. The number of species found in centre plots was lower than in margin plots up to the time of the last re-analysis. *Brachythecium salebrosum*, *Pleurozium schreberi* and *Polytrichum commune* became established quite early in dry grassland, as did *Aulacomnium palustre*, *Bryum pseudotriquetrum*, *Campylium stellatum* and *Splachnum vasculosum* in fen margin and damp grassland. *Aulacomnium palustre*, *Bryum pseudotriquetrum*, *Campylium stellatum* increased substantially over time, while *Polytrichum commune* was quite stable and *Splachnum vasculosum* soon decreased. Common fen and grassland bryophytes such as *Philonotis fontana*, *Rhizomnium pseudopunctatum*, *Sanionia uncinata*, *Scorpidium cossonii*, *Tomentypnum nitens*, *Aneura pinguis* and *Chiloscyphus polyanthos* became established later and increased more slowly. They commonly expanded from the margins of the sites. Towards the end of the investigation period, a decrease in the mean bottom layer cover was observed (Table 12).

Table 15. The number of species found in the centre plots of 13 newly burnt sites and in the set comprising 24 sites which were re-analysed three times (cf. Table 11) in three age classes and sorted by position on the sites (U: upper margin, C: centre, L: lower margin, cf. Fig. 2).

	1-2	3-9				8-13				13-20			
	Tot.	Tot.	U	C	L	Tot.	U	C	L	Tot.	U	C	L
Woody sp.	2	11	11	5	7	12	11	7	7	12	11	8	8
Herbs	22	51	41	37	42	64	58	49	57	68	56	58	59
Graminoids	10	34	27	20	30	37	33	26	31	36	32	29	28
Bryophytes	11	44	37	23	30	46	39	25	33	59	47	42	40
Lichens	0	4	4	0	2	3	3	2	2	7	6	5	3
Total	45	144	120	85	111	162	144	109	130	182	152	142	138

Betula pubescens and *Deschampsia cespitosa* were among the first vascular plant species in most sites and occurred in more than 75% of the plots 3-9 years after burning. *Bistorta vivipara* was found on more than half the sites of this age, most commonly in grassland. *Salix myrsinites* coll. and *Equisetum palustre* were found in more than half of the 3-9 year-old fen margin and damp grassland sites. After their initial increase during the first two years, the juvenile populations of *Betula pubescens* and *Salix myrsinites* coll. thinned out and increased very little in frequency. The remaining individuals, in particular of *Salix*, often grew vigorously, increased substantially in cover, and eventually reached shrub layer height. *Bistorta vivipara* increased both in frequency and cover, while *Equisetum palustre* decreased. Several other species soon became established and were found in more than one-fifth of the plots. In grassland, and to some extent in fen margin, this included *Angelica sylvestris*, *Epilobium angustifolium*, *Geranium sylvaticum*, *Geum rivale*, *Ranunculus acris*, *Saussurea alpina* and *Agrostis capillaris*, while *Succisa pratensis*, *Equisetum variegatum*, *Carex flava*, *C. panicea* and *Eriophorum angustifolium* mainly occurred on fen margin sites. *Leontodon autumnalis* and *Potentilla erecta* became established early in both damp grassland and fen margin sites. Most of these species increased in frequency over time, but only *Geranium sylvaticum*, *Geum rivale*, *Saussurea alpina* and *Succisa pratensis* increased in cover as well. After the first 3-9 years, *Leontodon autumnalis*, *Potentilla erecta* and *Eriophorum angustifolium* decreased in cover. *Equisetum variegatum*, *Potentilla erecta*, *Saussurea alpina*, *Succisa pratensis* and the *Carex* spp. became established mainly in the margins of the sites, as did several species that occurred later, such as *Alchemilla glabra*, *Galium boreale*, *Selaginella selaginoides* and *Thalictrum alpinum*. Orchids such as *Dactylorhiza* spp. and *Gymnadenia conopsea* arrived late at the sites and were still rare after 13-20 years. Some species were reduced in cover and frequency towards the end of the investigation period. This happened on several sites with species such as *Epilobium palustre*, *Equisetum palustre*, *Agrostis capillaris* and *Deschampsia cespitosa* (Tables 12, 13 and 14). In the 24-site set, the total number of herb species found in the plots increased from 51 in the 3-9 year-old sites to 68 in the oldest sites (Table 15), but there was only a slight increase in the number of graminoid species. Fig. 10 shows the development of species richness over time.

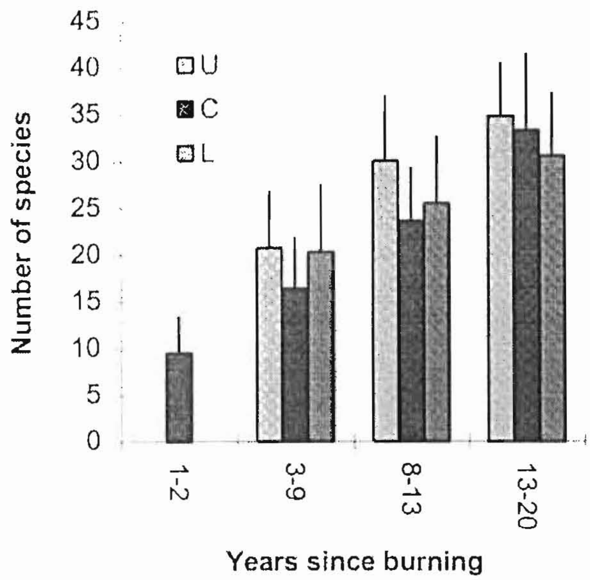

Fig. 10. The mean number of species in upper margin plots (U), central plots (C) and lower margin plots (L) over time. The class of 1 to 2 year-old bonfire sites is only represented by 13 central plots. The rest of the diagram is made from countings on 24 sites where U, C and L plots were re-analysed three times. Standard deviation is indicated.

The plots on site margins contained the largest number of species throughout the investigation period, but towards the end there was a great increase in the number of herbs and bryophytes in the centre plots. Very often, the first species that arrived were dominant in the plots even after 13-20 years. On most sites, the field layer was usually quite revegetated by 1997, but several early-successional species, such as *Betula pubescens*, *Equisetum palustre* and *Deschampsia cespitosa*, were still abundant. The classical fireweed *Epilobium angustifolium* never became dominant, although it occurred quite frequently. Plants were mostly small and no flowers were observed until the end of the research period.

4.5.1 Experimental burning

The four experimental bonfire sites, two in fen margin (75 and 83) and two in grassland (81 and 82), yielded detailed documentation of development after burning (Table 14). Very few species became established during the first year after burning. Some seedlings of late-successional species (*Alchemilla wichurae*, *Geranium sylvaticum*, *Geum rivale*) occurred on site 81 during the first year. The bottom layer cover of the experimental sites recovered within 2-4 years (Fig. 11), but comprised mainly early-successional species. Only a few of the original species became re-established during that time, and species richness increased more slowly than cover. Four to seven years were needed to restore the field layer cover, but here as well, species composition was very different from that found before burning. Although species richness was 40-75% of the original after 6-7 years, only 19-36% of the original species were re-established at that time. *Angelica sylvestris*, *Bistorta vivipara*, *Equisetum* spp., *Geranium sylvaticum*, *Ranunculus acris* and *Carex panicea* were among the original species that re-established on some of the sites within 6-7 years. Very few of the original bryophytes re-established within that time and only *Bryum pseudotriquetrum* approached, and in a few cases even exceeded, its original abundance. More than half of the species that were found were new species in the

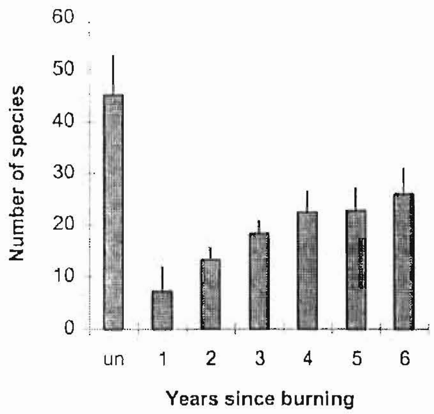

Fig. 11. The development of species richness and field and bottom layer cover in four experimental localities (75, 81, 82, 83) over time. The mean cover is calculated from the means of the cover classes. Standard deviation is indicated. Un = unburnt.

plots, such as *Betula pubescens*, *Salix* spp., *Epilobium* spp., *Cerastium fontanum* ssp. *vulgare*, *Eriophorum angustifolium* and the early-successional bryophytes. An interesting effect of burning was observed on site 75, where bryophytes failed to colonise the upper margin. After 3-4 years, vasculars such as *Betula nana* and *Carex* spp. resprouted from subterranean shoots, but the bottom layer remained very sparse up to 1997, comprising charred litter with a few bryophyte shoots. This was also observed on several other sites not included in the present material.

4.5.2 The bonfire locality vegetation

Six TWINSPAN clusters (Figs. 5 and 9, Tables 9, 10 and 16) included samples from several bonfire sites with a species composition that resembled one another, and could be treated as vegetation types. Two clusters (nos. 2 and 4) included only a few samples from one site each. The following description provides a survey of the bonfire locality vegetation types. Clusters 6 and 8 contain some samples from unburnt vegetation, the other clusters contain only samples from bonfire sites. The number of samples/sites included in each type is given after the cluster name.

TWINSPAN cluster 1, the *Funaria hygrometrica-Leptobryum pyriforme* type (44/19)
The samples in cluster 1 were mainly from centre plots on young sites in grassland and fen margin. They were rather poor in species and comprised much bare ground and ash. The vegetation was dominated by early-successional bryophyte species such as *Funaria hygrometrica* and *Leptobryum pyriforme*. *Bryum creberrimum* and *Marchantia* spp. were also common and abundant. Only these and *Betula pubescens* in the field layer were constant species. *Equisetum palustre* was also an important species in the field layer, its greatest cover values being found in samples in this vegetation type. *Salix myrsinites* coll., *Bistorta vivipara*, *Agrostis capillaris* and *Deschampsia cespitosa* were also quite common. The samples from older sites that were found in this cluster were either heathland (no. 70) or dry grassland (no. 16), or from sites with large amounts of ash (nos. 25 and 59). Only a sparse field layer (on sites 70 and 16 below 20%) was recorded in the centre of these sites, or they were still dominated by the early-successional species.

TWINSPAN cluster 2 (6/1)
This cluster comprised all post-fire samples from site 81. The vegetation of the locality was species-rich, rather dry grassland, and common species were *Geranium sylvaticum*, *Potentilla crantzii*, *Thalictrum alpinum*, *Agrostis capillaris*, *Dicranum bonjeanii* and *Hylocomium splendens* (Table 14). However, none of the post-fire samples from the site was older than 6 years and bonfire vegetation was dominated by early-successional bryophytes. The site also contained some of the species from unburnt vegetation, such as *Campanula rotundifolia*, *Geranium sylvaticum* and *Rhinanthus minor*. This cluster has much in common with clusters 1 and 3.

TWINSPAN cluster 3, the *Rhinanthus minor-Agrostis capillaris-Polytrichum juniperinum* type (40/7)

Table 16. Synoptic table showing constancy (%) and characteristic cover (cf. text and Table 12) in TWINSPAN clusters. Only species occurring with constancy > 10% in at least one of clusters 1, 3, 5, 6, 7 or 8 (clusters that include samples from several sites) or > 50% in at least one of clusters 2 or 4 (that include samples from one site only) are listed. Cover classes: 1: found within 5 cm of the plot, 2: 0-1%, 3: 1-3.125%, 4: 3.125-6.25%, 5: 6.25-12.5%, 6: 12.5-25%, 7: 25-50%, 8: 50-75%, 9: 75-100%.

Cluster no.	1	2	3	4	5	6	7	8
Number of samples	44	6	40	10	20	36	127	63
Shrub layer								
Betula pubescens	.	.	3-5	.	30-7	.	3-5	13-4
Salix glauca	.	.	.	.	10-1	14-5	4-4	17-5
Salix myrsinifolia coll.	.	.	.	.	20-6	28-6	9-7	44-6
Field layer								
Woody species								
Betula pubescens	84-5	.	100-6	100-2	90-5	53-4	80-4	59-4
Salix glauca	7-3	.	23-3	.	10-2	31-4	33-4	49-4
Salix myrsinifolia coll.	50-2	.	30-3	.	25-4	53-4	76-4	73-5
Sorbus aucuparia	11-2	.	15-2	.	.	6-2	7-2	8-2
Vaccinium vitis-idaea	2-2	.	15-2	100-4	.	6-3	1-2	3-5
Herbs								
Achillea millefolium	2-2	17-2	25-6	.	20-4	11-3	.	.
Aconitum septentrionale	.	.	.	.	30-2	.	.	.
Alchemilla glabra	7-4	.	23-2	.	50-7	17-4	4-2	10-5
Alchemilla glomerulans	.	.	8-6	.	30-3	25-5	3-5	6-3
Alchemilla wichurae		100-2				3-2		
Angelica sylvestris	11-2	.	18-2	.	75-4	42-2	37-3	56-3
Anthriscus sylvestris	.	.	.	.	40-3	.	.	.
Bartsia alpina	7-2	.	15-2	.	.	31-3	25-3	48-3
Bistorta vivipara	34-3	83-3	93-5	60-3	85-3	94-4	54-3	94-3
Campanula rotundifolia	7-3	.	35-3	.	.	14-3	1-2	6-3
Cerastium fontanum ssp. vulg	2-3	50-2	28-3	.	10-2	8-2	2-3	.
Cirsium helenoides	.	.	13-4	.	20-2	3-2	.	3-4
Crepis paludosa	7-2	.	8-2	.	55-3	83-5	36-3	73-4
Dactylorhiza fuchsii	.	.	8-2	.	25-2	31-3	2-2	10-2
Dactylorhiza lapponica	.	.	.	.	.	.	1-2	16-2
Dactylorhiza maculata	.	.	.	.	.	11-2	2-3	11-3
Epilobium angustifolium	14-3	.	23-2	.	60-4	17-2	17-2	10-2
Epilobium palustre	11-3	.	.	.	25-2	11-2	24-4	24-4
Equisetum palustre	48-6	.	18-3	.	35-7	39-3	55-5	43-3
Equisetum pratense	2-1	.	13-2	.	45-3	36-4	3-4	6-3
Equisetum scirpoides	2-5	.	.	.	.	.	12-6	10-6
Equsetum sylvaticum	5-4	.	.	.	20-2	6-3	7-4	8-2
Equisetum variegatum	18-3	.	.	.	15-3	56-3	74-4	65-3
Euphrasia frigida	9-2	.	63-3	.	25-2	75-3	7-2	30-2
Filipendula ulmaria	.	.	15-3	.	30-4	14-3	.	2-2
Galium boreale	11-2	.	53-4	.	40-4	58-3	4-4	13-3
Geranium sylvaticum	16-3	100-2	90-4	.	90-5	97-4	31-2	35-3
Geum rivale	9-4	100-2	25-3	.	85-6	53-4	30-4	51-4
Gymnadenia conopsea	2-2	.	5-2	.	.	19-2	9-2	24-3

Cluster no.	1	2	3	4	5	6	7	8
Number of samples	44	6	40	10	20	36	127	63
Hieracium spp.	2-1	.	10-2	.	40-3	17-2	5-2	6-2
Leontodon autumnalis	9-2	50-1	33-4	10-2	30-2	72-3	43-3	52-2
Melampyrum pratense	2-2	.	13-2	.	10-3	14-3	2-5	3-3
Melalampyrum sylvaticum	.	.	5-3	.	45-3	3-2	3-2	2-6
Omalotheca norvegica	2-2	.	58-4	.	40-4	14-3	2-2	.
Parnassia palustris	11-2	.	43-3	.	75-4	83-3	20-3	32-2
Pedicularis oederi	5-2	83-1	28-3	.	10-2	44-3	25-2	65-3
Pinguicula vulgaris	2-3	.	25-3	.	.	22-3	26-2	40-4
Polygonatum verticillatum	.	.	5-3	.	15-3	.	.	.
Potentilla erecta	7-2	.	55-3	.	20-4	50-5	35-3	68-4
Pyrola minor	.	.	13-2	.	.	8-4	2-3	6-2
Pyrola rotundifolia coll.	.	.	38-3	.	30-3	28-3	2-3	16-3
Ranunculus acris	5-2	33-2	53-3	30-2	75-5	92-4	29-3	40-3
Rhinanthus minor	5-2	17-2	78-3	10-2	35-3	56-3	9-3	13-2
Rubus saxatilis	2-2	.	3-2	.	45-4	.	.	.
Rumex acetosa	.	.	28-4	.	30-3	31-2	.	.
Saussurea alpina	20-4	.	38-5	.	45-6	78-5	33-5	54-5
Selaginella selaginoides	2-2	.	28-2	.	5-2	25-3	6-2	30-3
Solidago virgaurea	9-2	.	50-3	60-3	45-3	25-3	20-2	13-3
Succisa pratensis	20-3	.	28-3	.	.	47-4	57-3	71-5
Taraxacum spp.	5-3	.	15-2	20-2	30-2	6-2	2-2	2-1
Thalictrum alpinum	7-2	.	15-3	.	5-2	44-4	25-2	71-4
Tofieldia pusilla	9-2	.	.	.	.	.	16-2	25-3
Trientalis europaea	.	.	35-3	70-3	5-3	19-2	2-3	6-3
Trifolium repens	.	.	.	.	.	22-7	.	.
Viola biflora	5-2	.	23-2	.	10-2	8-2	1-2	5-2
Graminoids								
Agrostis capillaris	25-3	.	100-6	.	65-5	69-5	10-4	24-5
Anthoxanthum odoratum	2-2	.	38-4	.	20-3	56-2	15-3	14-3
Calamagrostis purpurea	11-7	.	.	.	40-3	.	6-7	.
Carex capillaris	11-2	50-2	8-2	.	.	22-2	25-2	43-3
Carex dioica	2-2	.	.	.	5-2	8-2	20-2	62-3
Carex flava	.	.	.	.	.	17-4	28-5	54-5
Carex lasiocarpa	9-2	.	.	.	.	6-2	17-5	8-4
Carex nigra coll.	.	.	.	.	5-2	31-6	9-6	24-7
Carex panicea	5-3	.	3-3	.	.	17-4	57-5	87-5
Carex vaginata	5-2	.	35-2	.	15-3	50-4	19-4	33-4
Deschampsia cespitosa	45-5	17-2	40-6	.	95-6	97-5	88-6	89-5
Deschampsia flexuosa	16-2	33-2	30-3	70-2	20-2	33-2	5-4	5-2
Eriophorum angustifolium	2-2	.	10-2	.	25-3	42-3	61-4	59-3
Eriophorum vaginatum	.	.	3-2	.	.	.	6-5	13-3
Festuca ovina	32-2	.	50-3	10-1	10-2	81-3	59-4	79-4
Festuca rubra	2-1	50-4	30-5	.	30-3	67-3	9-3	17-2
Hierochloë odorata	2-4	.	.	.	15-3	56-4	9-5	22-3
Juncus alpinoarticulatus	.	.	.	.	.	.	12-4	3-4
Juncus triglumis	.	.	.	.	.	.	14-3	2-2
Luzula multiflora ssp. frigida	.	83-2	50-3	.	.	25-2	2-2	3-2
Luzula sudetica	7-2	.	25-2	.	20-2	39-2	17-2	17-3
Molinia caerulea	.	.	.	.	.	14-4	15-4	51-4
Nardus stricta	7-3	50-1	45-3	.	.	53-3	20-3	49-4
Phleum alpinum	2-2	17-1	33-3	.	30-3	28-2	2-5	2-2

Cluster no.	1	2	3	4	5	6	7	8
Number of samples	44	6	40	10	20	36	127	63
Poa alpina	2-1	50-2	10-2	.	.	8-3	2-2	.
Poa pratensis coll.	2-2	.	13-2	30-2	25-3	33-3	4-2	3-2
Trichophorum cespitosum	.	.	.	.	.	.	2-1	19-4
Bottom layer								
Mosses								
Aulacomnium palustre	14-2	.	28-2	80-3	25-6	53-4	39-2	54-4
Brachythecium salebrosum	9-2	.	23-4	.	25-2	8-2	4-4	8-2
Brachythecium turgidum	.	.	.	.	.	17-3	3-2	2-2
Bryum creberrimum	89-5	67-3	70-5	100-8	15-3	8-3	83-5	29-3
Bryum pallens	11-2	.	3-2	.	.	6-2	20-3	2-2
Bryum pseudotriquetrum	20-2	17-2	.	.	45-4	89-4	74-5	87-5
Campylium stellatum	7-3	.	3-2	.	10-2	36-3	28-3	63-6
Ceratodon purpureus	82-5	33-2	70-7	100-5	20-3	22-4	75-5	29-3
Climacium dendroides	.	.	5-2	.	5-2	17-3	.	2-1
Dicranum bonjeanii	.	.	.	.	.	11-5	.	2-3
Fissidens adianthoides	.	.	.	.	.	8-2	5-2	19-3
Funaria hygrometrica	93-5	83-6	48-5	50-3	.	.	29-4	.
Hylocomium splendens	9-2	17-2	28-3	40-2	5-2	39-4	9-2	6-4
Leptobryum pyriforme	91-7	67-8	60-5	50-4	45-3	31-3	90-6	29-4
Mnium stellare	.	.	.	.	10-2	6-2	2-4	2-5
Philonotis fontana	.	.	.	.	.	.	13-3	29-3
Plagiomnium ellipticum	.	.	.	.	.	28-5	.	3-2
Plagiochila porelloides	.	.	15-5	.	10-2	22-3	1-2	6-3
Pleurozium schreberi	5-2	.	8-3	100-2	.	6-3	3-2	2-4
Polytrichum commune	.	.	23-6	20-1	.	8-6	9-3	17-5
Polytrichum juniperinum coll.	11-5	.	65-4	80-5	55-3	36-3	29-3	40-4
Rhizomnium pseudopunctatum	.	.	3-2	.	25-2	31-3	2-2	3-2
Sanionia uncinata	.	.	5-2	.	.	19-4	6-3	14-3
Scorpidium cossonii	.	.	.	.	.	.	6-2	21-3
Sphagnum warnstorfii	.	.	.	.	.	14-5	.	3-9
Splachnum vasculosum	2-2	.	.	.	.	.	20-4	.
Tomentypnum nitens	7-2	.	15-2	40-2	5-3	19-3	17-3	37-5
Tritomaria quinquedentata	.	.	.	.	.	14-3	.	3-3
Liverworts								
Aneura pinguis	2-2	.	20-3	.	.	42-2	7-3	40-3
Barbilophozia lycopodioides	5-2	.	23-4	90-2	.	19-5	1-2	5-2
Barbilophozia quadriloba	2-2	.	5-4	.	.	25-3	2-2	11-3
Marchantia spp.	80-6	83-6	48-7	.	100-8	78-8	97-7	78-7
Scapania irrigua	.	.	.	.	.	11-2	2-2	6-2
Lichens								
Cladonia arbuscula	2-2	.	.	90-3	.	.	.	.
Peltigera canina	.	.	53-5	80-5	.	22-4	6-2	6-3

The samples in cluster 3 were mostly from sites of medium or high age. The vegetation type comprised a lot of heathland and dry and mesic grassland species. *Rhinanthus minor* and *Agrostis capillaris* occurred frequently, and *A. capillaris* was also a dominant in many samples. *Betula pubescens* and *Bistorta vivipara* occurred in almost every sample, and *Euphrasia frigida* and *Geranium sylvaticum* were also constants. *Campanula rotundifolia*, *Galium boreale*, *Omalotheca norvegica*, *Potentilla erecta*, *Solidago virgaurea* and *Luzula multiflora* ssp. *frigida* were quite common in this type. In the bottom layer, *Polytrichum juniperinum* coll. was a characteristic species, but all the other early-successional species occurred frequently and with high cover values. The lichen *Peltigera canina* was typically found in this type.

TWINSPAN cluster 4 (10/1)
Cluster 4 included 10 of 12 samples from site 70, the only bonfire locality in pure heathland vegetation. This heathland vegetation type is poor in species and dominated by wiry grasses (e.g. *Deschampsia flexuosa*, *Festuca ovina* and *Nardus stricta*), *Vaccinium* spp. and lichens. The first and the third samples taken in the centre plot of this site were classified in cluster 1, which had much in common with this cluster. The bonfire samples were completely dominated by early-successional bryophytes, but also comprised a few individuals of, for instance, *Vaccinium vitis-idaea*, *Bistorta vivipara*, *Solidago virgaurea* and *Deschampsia flexuosa*.

TWINSPAN cluster 5, the *Angelica sylvestris-Geum rivale-Marchantia* type (20/4)
This rather small cluster was dominated by damp and mesic grassland species like *Angelica sylvestris*, *Geum rivale*, *Parnassia palustris* and *Deschampsia cespitosa*. *Alchemilla glabra*, *Crepis paludosa*, *Epilobium angustifolium* and *Geranium sylvaticum* were also common in the field layer. *Equisetum palustre* occurred in more than one-third of the samples and often had high cover values. Just as in cluster 3, *Betula pubescens* and *Bistorta vivipara* occurred in most samples. Both *Betula pubescens* and *Salix* spp. had grown to shrub size in this vegetation. The only species that were constant and dominant in the bottom layer were the *Marchantia* species, but *Bryum pseudotriquetrum*, *Leptobryum pyriforme* and *Polytrichum juniperinum* coll. were also quite common.

TWINSPAN cluster 6, the *Crepis paludosa-Festuca rubra-Bryum pseudotriquetrum* type (36/12)
Cluster 6 comprised samples from sites of medium or high age, or from unburnt vegetation. Nearly all species found in cluster 5 also occurred in this type. Samples were rich in grassland and fen margin species, such as *Crepis paludosa*, *Geranium sylvaticum*, *Leontodon autumnalis*, *Parnassia palustris*, *Saussurea alpina*, *Agrostis capillaris*, *Deschampsia cespitosa* and *Festuca rubra*. All these species were also found in cluster 5, but *Crepis paludosa*, *Leontodon autumnalis*, *Saussurea alpina* and *Festuca rubra* were much more common in cluster 6. *Equisetum palustre* occurred quite frequently in this type, but had less cover than in cluster 5. *Betula pubescens* was less abundant, but still quite common, while *Bistorta vivipara* was recorded in most samples. In the bottom layer, *Bryum pseudotriquetrum* and *Marchantia* spp. were the only constants, but *Aulacomnium palustre*, *Campylium stellatum*, *Hylocomium splendens*, *Leptobryum pyriforme* and *Rhizomnium pseudopunctatum* also occurred quite frequently. Most of the early-successional bryophyte species had lower constancy and/or cover in this cluster than in cluster 5. A number of damp grassland and fen species that were rarely found in cluster 5 were quite common in cluster 6, such as *Gymnadenia conopsea*, *Pinguicula vulgaris*, *Succisa pratensis*,

Carex flava, *Thalictrum alpinum*, *Plagiomnium ellipticum* and *Aneura pinguis*. The heathland and grassland species *Nardus stricta* was also quite frequent in this type.

TWINSPAN cluster 7, the *Equisetum variegatum-Eriophorum angustifolium-Marchantia* type (127/25)
Fen margin species were the most important species in this vegetation type, but it also comprised species common in damp grassland. *Equisetum palustre*, *Equisetum variegatum*, *Succisa pratensis*, *Carex panicea* and *Eriophorum angustifolium* were common in the field layer. *Betula pubescens* and *Salix myrsinites* were found in most samples, while *Bistorta vivipara* was less common in this type. The early-successional bryophytes were dominant in the bottom layer, particularly *Marchantia* spp., but *Aulacomnium palustre*, *Bryum pseudotriquetrum* and *Campylium stellatum* were also common.

TWINSPAN cluster 8, the *Thalictrum alpinum-Carex panicea-Campylium stellatum* type (63/23)
The samples found in this cluster were mostly from margin plots on old bonfire sites or from unburnt vegetation. They included most of the fen margin and damp grassland species found in cluster 7, but the importance of the various species differed between the two clusters. Field layer species such as *Crepis paludosa*, *Pedicularis oederi*, *Succisa pratensis*, *Thalictrum alpinum*, *Carex capillaris*, *C. panicea* and *Nardus stricta* had higher cover and constancy values in this cluster, and *Betula pubescens* and *Salix* spp. often reached shrub size in the plots. In the bottom layer, the early-successional species were lower in cover and constancy, whereas for instance *Aulacomnium palustre*, *Campylium stellatum* and *Aneura pinguis* were more abundant.

A significant increase in the mean number of species in the samples was observed from the *Funaria hygrometrica-Leptobryum pyriforme* type (cluster 1) to all other types that comprised samples from more than one bonfire site (Table 10). There was also a significant increase from the *Angelica sylvestris-Geum rivale-Marchantia* type (cluster 5) to the *Crepis paludosa-Festuca rubra-Bryum pseudotriquetrum* type (cluster 6); and from the *Equisetum variegatum-Eriophorum angustifolium-Marchantia* type (cluster 7) to the *Thalictrum alpinum-Carex panicea-Campylium stellatum* type (cluster 8).

5 DISCUSSION

5.1 GENERAL

The severe effect of burning destroyed most of the vegetation on the bonfire sites, but some rhizomes and seeds survived and organic soil remained. The revegetation of the bonfire sites was therefore a secondary succession that took place on charred organic soil or soil covered by ash or charcoal. During the research period from 1982 to 1997, the vegetation cover on the bonfire sites at Sølendet recovered substantially. Although the extent of the recovery varied, only a few sites that were more than 5 years old, contained patches of bare ash. The number of species recorded in the plots also increased over time, but the increase in species richness was slower than the increase in cover. Species that invaded the sites shortly after burning were often still dominant at the end of the research period, and the bonfire site vegetation was clearly different from the unburnt vegetation. Del Moral (1993) found that species richness increased more quickly than cover on nutrient-poor volcanic substrates from the Mount St Helens eruption, and regarded this as an indication of severe growing conditions. Following a period of amelioration, nutritional conditions on bonfire sites seemed to offer good growing conditions for the early-successional species.

Analyses of soil pH and mineral content indicated that the bonfire sites provided a harsh environment during the first years after burning, with high pH and high levels of mineral salts. The increase of pH was probably caused by the release of alkalis (e.g. K, Na) and alkaline earth metals (e.g. Ca, Mg) from the ash (Viro 1974, Raison 1979). A bonfire site offers a more severe soil chemistry than a normal forest fire due to the accumulation of large amounts of ash from the burning of organic material brought to the site from the surroundings (Southorn 1976, Elveland 1978). The amount of waste burnt in each site varied considerably. To some extent, this was indicated by the thickness of the ash layer (Arnesen 1989), but ash and charcoal were sometimes removed from the sites (Moen 1990) or washed away by surface water. No exact data exist on the amount of material burnt, or the duration of the burning, except for the four experimental sites. Comparisons therefore had to be made without any clear knowledge of the intensity of the burning.

Although both loss and addition of nutrients are frequently reported from forest fires (Viro 1974, Christensen 1987, Naveh 1990), the accumulated ash on bonfire sites will supply the vegetation with leaching minerals for several years. Charcoal may also be an important source of N for plants (Zackrisson et al. 1996). The increase in pH and nutrient content downhill from the sites, recorded in the present investigation, indicated leaching from the ash. This agrees with observations from forest fire areas (Lewis 1974, Boerner & Forman 1982, Hegna 1986). The leaching probably also explains the increased production observed downhill from the sites, although Christensen (1987) hypothesised that such an increase could be due to a reduction in some allelochemical constituent released from plant roots. This is probably not an important factor below bonfire sites. Some reduction in such substances may have occurred since vegetation is killed at the sites, but there was still undamaged vegetation above the sites. At Sølendet, annual above-ground biomass below bonfire sites increased by 12-50% in damp grassland and 300% in a fen margin locality, and this brought the production almost up to a level usually found in highly productive tall-herb grasslands (Aune et al. 1996).

Cyanobacteria are common pioneers on burnt and other types of disturbed ground (Ahlgren, I.F. 1974, Abou El-Kheir et al. 1988), and unidentified algae, probably both cyanobacteria and green algae, were the only organisms observed on the bonfire sites shortly after burning. Very few species of higher plants became established on the fresh ash during the season when burning took place. Southorn (1977) showed that even the germination of spores of the common burnt-ground species *Funaria hygrometrica* were hampered by fresh bonfire ash, probably due to elevated concentrations of ammonium ions. Thomas et al. (1994) found that growth was suppressed on newly charred peat after a heathland fire, although the ash seemed to be a favourable growth medium, and that an amelioration of chemical conditions was needed before bryophytes became established. Measurements of bonfire ash and soil at Sølendet showed a reduction of pH and a depletion of mineral content over time. This was also observed after forest fires (Viro 1974, Christensen 1987, Klingsheim & Wielgolaski 1997). Subsequently, during the next growth season, several plant species became established on the bonfire sites.

5.2 BOTTOM LAYER DEVELOPMENT

At the onset of the succession, bryophyte species invaded the sites and quite quickly covered much of the ash. *Bryum creberrimum, Ceratodon purpureus, Funaria hygrometrica, Leptobryum pyriforme, Polytrichum juniperinum* coll. and *Marchantia* spp. became dominant on the bonfire sites at Sølendet. Except for the less frequently occurring *Bryum creberrimum*, these species are cosmopolites that very often occur on newly burnt and other types of disturbed ground all over the world, but only rarely in closed vegetation (Ahlgren, C.E. 1974, Southorn 1976, Brasell & Mattay 1984, Schimmel & Granström 1996). Southorn (1976) found that several bonfire site bryophytes are promoted by disturbed ground in general, but *Funaria hygrometrica* seems to be promoted by ash (Southorn 1976, 1977, Duncan & Dalton 1982). According to these authors, high concentrations of Ca, K, N (nitrate) and P (phosphate) are advantageous to *F. hygrometrica*, and the species seems to have a pH optimum of 7-8 (cf. Brown 1982). This coincides quite well with the chemistry of the bonfire site ash and soil observed in the present study during the first few years after burning. Duncan & Dalton (1982) also found that germination of *Ceratodon purpureus* and *Marchantia berteroana* spores was promoted by ash, and that the rapid development of protonemata and gametophytes may be of great importance for the success of the colonising bryophyte species. Brown (1982) found no unambiguous evidence that fire-site bryophytes were promoted by the specific nutrient environment. He put forward the alternative hypothesis that the initial chemical regime is inhibitory to higher plants than bryophytes, thereby contributing to the success of the latter. The research on bonfire sites at Sølendet did not provide evidence for either of these hypotheses, but the early occurrence of *Funaria hygrometrica*, later followed by other bonfire species, may indicate a difference in tolerance to fresh ash. The failure of bryophytes to become established on charred surfaces on the margin of some sites may be due to leaching of toxic substances from the partially destroyed organic matter (Brown 1982, Thomas et al. 1994).

Although the large amounts of ash and charcoal that commonly accumulate on bonfire sites make leaching less of a problem than the nutrient losses seen after forest fires, the establishment and growth of bryophytes early in the succession may also preserve some of the nutrients which would otherwise have leached out. Furthermore, several bryophytes such as *Ceratodon purpureus, Funaria hygrometrica* and *Polytrichum commune* are able to associate with N-fixing cyanobacteria (cf. Brown 1982), and increased levels of N are reported beneath moss turf on burnt sites (de Las Heras et al. 1996).

At Sølendet, *Polytrichum juniperinum* coll. and *Marchantia* spp. were the only bonfire species that commonly occurred on unburnt ground (Moen 1990), but both were much more abundant on bonfire sites. All the early-successional bryophytes frequently produced sporophytes and *Funaria hygrometrica*, *Leptobryum pyriforme* and *Marchantia* spp. are able to produce gemmae, although this seems to be less common in *Funaria hygrometrica* (Nyholm 1989). *Leptobryum pyriforme* often accompanies *Funaria hygrometrica* on burnt ground (Nyholm 1989), and Bopp (1976) found that *Leptobryum pyriforme* promotes the creation of buds in *Funaria hygrometrica*. *Polytrichum juniperinum* coll. has been reported to re-establish from surviving rhizoids after fire (Uggla 1958a, Brown 1982). This may account for some of the establishment on the bonfire sites. As this is not an important species in fen vegetation at Sølendet (Moen 1990), its common occurrence on bonfire sites on fen margins indicates that it also emerged from spores. No early-successional species emerged from the soil samples. Although the investigation primarily aimed at looking for viable seeds of higher plants, this may indicate that the establishment of colonising bryophytes was mainly from airborne spores or from gemmae, not from the spore bank. Further investigations are needed to determine the extent of different modes of establishment.

An establishment of the coprophilous species *Splachnum vasculosum* occurred quite early on eight sites on moist ground, although no excrements were found. *S. vasculosum* is fairly common on reindeer and elk dung at Sølendet, and spores are mostly dispersed by flies (Cameron & Wyatt 1986). The flies are attracted by dung-like volatiles from the sporophytes (Pyysalo et al. 1983), and *Splachnum* spp. seem to be mainly restricted to open, neutral substrates (Cameron & Wyatt 1989). Such ground occurs on many sites after burning, and the N-rich leachates from the ash may also have created a suitable substrate for the species over a longer period of time. The mineral content depletion and the growth of taller species eventually changed this situation, and after 13-20 years *S. vasculosum* was only found on a few bonfire sites. Flies are everywhere, but the occurrence of *S. vasculosum* on as many as eight bonfire sites nonetheless seemed to be more than one might expect from chance visits by flies carrying *Splachnum* spores. Winter et al. (1980) found that a number of insects are able to utilise the nutrient-rich substrate on burnt ground, among them the *Sciaridae* family. These gnats and closely related species of the *Mycetophilidae* family commonly occur on decaying fungus and vegetable matter, possibly also dung (Richards & Davies 1977), and may visit *Splachnum* sporophytes as well. *Scatophaga* spp. (dung flies s. str.), and other species that most commonly visit *Splachnum*, may also find the nutrient-rich, warm, substrate on bonfire sites attractive.

Funaria hygrometrica disappeared even earlier than *Splachnum vasculosum*, and was extinct on most sites after 3-9 years. As with *S. vasculosum*, this may partly be a result of less favourable pH and nutrient status, or the growth of other, usually larger species. The reduction seemed to happen faster on moist sites than on drier sites. An investigation of the structure of the bryophyte layer revealed that dead *Funaria* shoots on moist sites were very often found beneath lush stands of *Marchantia polymorpha* and *Leptobryum pyriforme* (Arnesen 1991). The compact mats of these species effectively hindered any secondary establishment of *Funaria* spores. The re-establishment of *Funaria hygrometrica* on some of the drier sites was observed in drought-induced openings occurring in the bottom layer.

Polytrichum juniperinum coll. usually increases on burnt ground after some years (Uggla 1958a, Watson 1967), and this also occurred on the drier bonfire sites at Sølendet. Apart from this, all the early-successional species declined as time passed, and common species from the immediate surroundings became established and increased in number and cover. The early colonisers, in particular rather stable species such as *Marchantia polymorpha* and *Leptobryum pyriforme* on moist sites and *Bryum creberrimum* and *Polytrichum juniperinum* coll. on drier sites, may have inhibited the establishment of other species for a long time simply by covering the ground. Several authors (Drury & Nisbet 1973, Connell & Slatyer 1977) have previously noted such inhibition. This aspect may in part explain the slow recovery of the original dominance and species composition. Several of the species that became established after some time were initially observed on margins. Some of them (e.g. *Aulacomnium palustre*, *Campylium stellatum*, *Hylocomium splendens* and *Pleurozium schreberi*) are rarely fertile, but are able to disperse as fragments (Elveland 1978, Tyler 1984). *Bryum pseudotriquetrum* is a common species on disturbed ground in fens (Tyler 1984), and frequently became dominant on moist bonfire sites at Sølendet.

Most of the bryophyte species that colonised the sites early in the succession were fugitives or colonists, according to the revised life-strategy system of During (1992). *Funaria hygrometrica* is a typical fugitive; an ephemeral species with numerous, very small spores and a high reproductive effort. Such species commonly occur in habitats that are unpredictable and last only for a short time. However, the sites provided suitable conditions for these species for several years. *Bryum creberrimum*, *Ceratodon purpureus*, *Leptobryum pyriforme* and *Marchantia polymorpha* are colonists s. str. They have somewhat longer life spans, numerous small spores, and the last two species frequently produce gemmae. Such species are common during the early stages of secondary successions and occupy open, potentially productive habitats that last for some years and then disappear. Many of the early-successional species on the bonfire sites were still dominant after 13-20 years, and it is too early to draw final conclusions regarding their longevity. However, most species (except *M. polymorpha*) were reduced and even disappeared from some plots after a few years. It appears that During's strategy fits well for the description of the mode of reproductive effort and establishment, but is perhaps less appropriate for describing the longevity of the species and populations on these sites.

Splachnum vasculosum is an example of the short-lived shuttle strategy. Its spores are small, but are dispersed in clumps by flies. Members of this group usually produce few, but large, spores and have a rather short life span and a moderate reproductive effort. Such species are adapted to microhabitats that predictably disappear and re-appear within the same community, such as dung. Bonfire sites are evidently not a predictable habitat in fens, but seemed to be a suitable alternative for *Splachnum vasculosum*.

The species occurring later in the succession, and also some of the early species, displayed a perennial stayer strategy. Such species commonly occur in more predictable habitats, such as stable fen, grassland and heathland vegetation, are long-lived and have many small spores, but generally a low reproductive effort. The early arriver *Polytrichum juniperinum* coll. can probably be classified as a stress-tolerant perennial with high drought tolerance, although the rather frequent occurrence of sporophytes may assign it to the colonists s. str. *Bryum pseudotriquetrum* demonstrated a competitive perennial strategy, with vigorous growth, often covering extensive areas of the moist sites after some years. *Campylium stellatum*, *Hylocomium splendens* and *Pleurozium schreberi* may also be classified as competitive perennials with rather high growth rates. *Aulacomnium palustre*, *Sanionia uncinata*, *Tomentypnum nitens*, *Aneura pinguis* and *Chiloscyphus polyanthos* may be assigned to the stress-tolerant perennials. However, our knowledge of the reproductive effort, longevity and growth rates of most bryophyte species is rather scanty, and this makes the classification somewhat ambiguous (During 1992).

5.3 FIELD AND SHRUB LAYER DEVELOPMENT

Vasculars that became established early were mostly common species from the unburnt vegetation, mainly *Betula pubescens, Salix* spp., *Equisetum palustre* and *Deschampsia cespitosa*. These species also quickly became much more abundant on the bonfire sites than in the immediate surroundings (Moen 1990). *Betula pubescens* and *Salix* spp. are anemochores and entered the sites by means of wind-dispersed seeds. According to Sarvas (1948) and Hester et al. (1991), up to 2000-3000 seeds of *Betula pubescens* can often be found per m² in a birch forest, i.e. potentially approximately 20,000 seeds on each bonfire site. Sarvas (1948) found a maximum of more than 50,000 seeds per m² during a good year. Investigations of the seed bank of two bonfire sites did not reveal germination of surviving seeds of *B. pubescens* and *Salix* spp. Both these and *Deschampsia cespitosa* have often been classified as transient species in the seed bank, although greater longevity has been observed (cf. Thompson et al. 1997). Two *Deschampsia cespitosa* individuals germinated in soil samples taken in the site margins. *D. cespitosa* is a tall grass that seemed to enter the sites mainly by seeds or whole fertile shoots falling into the sites.

Equisetum palustre has deep rhizomes (Metsävaino 1931), and finds of viable underground parts on bonfire sites clearly indicated establishment by means of sprouting from such rhizomes. However, the species is wind-dispersed and may have entered sites by air also. *E. palustre* is regarded as a common colonist of disturbed habitats, both by vegetative spread and occasionally by the establishment of large populations of gametophytes on bare, moist ground (Grime et al. 1988). Rapidly developing geophytes were also found to be important during the first years after heathland fires (Mallik & Gimingham 1983).

Epilobium angustifolium occurs here and there in dry areas (roadsides and other anthropogenous vegetation) on unburnt ground at Sølendet (Moen 1990). It occurred quite frequently on bonfire sites, but with low cover values. *E. angustifolium* is regarded as an early coloniser of burnt ground by means of wind-dispersed seeds

(Grime et al. 1988), and Elveland (1978) also found it to be common on bonfire sites. Uggla (1958a) and Sunding (1981) claimed that *E. angustifolium* often survives forest fires and resprouts from subterranean parts, but the small, flowerless individuals found on bonfire sites at Sølendet indicated establishment by seeds dispersed from the nearest roadsides and margins of cultivated ground, usually more than 200 m away. Furthermore, fen margin may be too moist for extensive growth of this species.

The first stages of revegetation, comprising bryophytes and vasculars with an ability to colonise by widely dispersed spores and seeds or vigorous vegetative expansion, were followed by the establishment of species from the immediate surroundings, demonstrating lower reproductive effort or less efficient dispersal. These species mostly entered the sites from the margin by seeds dispersed from fertile shoots just outside the sites or rhizomes that grew into the sites. Even though only a few species were found to become established from rhizomes, further investigations would probably have revealed that more species emerged from surviving subterranean parts. Rhizomatous species, such as *Achillea millefolium*, *Bartsia alpina*, *Campanula rotundifolia*, *Saussurea alpina* and *Geranium sylvaticum*, may well have survived burning on the margin of a site to give rise to new fertile plants further on the site, and subsequently to a secondary spread by seeds. Investigations showed that some species on the margins of the sites, for instance *Alchemilla glabra*, *Campanula rotundifolia*, *Carex* spp. and *Luzula* spp., might have germinated from the seed bank as well. On the moist sites, some seeds even survived and germinated from the seed bank samples taken in the centre of the site. Soil moisture probably restrained the temperature increase below the evaporation zone (Fenn et al. 1976). Several authors have found indications that *Campanula rotundifolia* and the probable species of *Carex* and *Luzula* (e.g. *Carex nigra*, *C. pallescens*, *Luzula multiflora* coll., *L. pilosa*) belong to the persistent seed bank (cf. Thompson et al. 1997). *Alchemilla* spp. have only been found a few times and these records mainly show that these are transient seed bank species, although Milberg (1994) found that *Alchemilla* spp. were long-term persistent species in the seed banks of Swedish grasslands.

Orchids depend on mycorrhiza, at least for germination and growth of seed plants, but often also for further development. Fires are reported to reduce the mycorrhiza in soil (Klopatek et al. 1988, Wicklow-Howard 1989), although reactions to fire seem to be variable (Mysterud & Mysterud 1997). The substantial disturbance caused by bonfires and the possible effects on mycorrhiza may in part explain the fact that the orchids became established late in the succession, mostly after more than 13 years.

The vigorous growth of *Salix myrsinifolia* coll. and *S. glauca* on many fen margin sites and of *Betula pubescens* on some grassland sites gave rise to scrub in vegetation that was otherwise mown. This only happened on sites where permanent plots were established. Sites that were not followed up by research were mown or used for further burning. The establishment of scrub will presumably reduce the growth of herbs, graminoids and bryophytes on the sites. Since a shrub layer developed quite late in the investigation period, further investigations are needed to determine the significance of this for the reduction observed in the cover of the bottom layer and of some vascular species, and also for the reduction in the number of species found in some plots during the last re-analysis.

According to Grime (1987), different plant strategies will predominate at different stages during a secondary succession. Ruderals will dominate first, followed by competitors which will eventually be followed by stress tolerators. Ruderals (R) are very short-lived species that have potentially high relative growth rates and quickly capture resources from disturbed and unpredictable habitats diverting them into flowers and seeds. Competitors (C) are long-lived or relatively short-lived species with high growth rates and the ability to quickly withdraw resources from rather stable and productive environments. Resources are commonly diverted to storage organs. Stress tolerators (S) are long-lived species with a low growth rate, delayed reproduction and a capacity to occupy stable, but hostile, habitats with low productivity and to capture and retain scarce resources.

The vascular plant species that dominated early in the succession on bonfire sites showed a variety of strategies. *Betula pubescens* has an intermediate strategy between competitor and stress-tolerant competitor and this probably also applies to *Salix* spp., but juveniles of these species seem to have strong elements of ruderal strategy. The strategy of *Deschampsia cespitosa* is intermediate between a stress tolerator and a CSR strategist (CSR is intermediate between all three strategies), and *Equisetum palustre* is intermediate between competitive-ruderal and CSR. No typical ruderal was found, but some subdominant species showed strong elements of ruderal strategy, for instance *Leontodon autumnalis*, *Rhinanthus minor* and *Taraxacum* spp. The early-successional bryophytes seemed to demonstrate a more pronounced ruderal strategy than any of the vasculars. The species that invaded the sites later in the succession mostly showed a diversity of intermediate strategies between the competitive and the stress-tolerant strategy. The only typical competitor observed was *Epilobium angustifolium*, but it played only a minor role in the competition for resources on these sites. Several stress tolerators occurred, such as *Campanula rotundifolia*, *Dactylorhiza maculata*, *Solidago virgaurea*, *Succisa pratensis*, *Carex panicea*, *Eriophorum angustifolium*, *Luzula* spp. and *Nardus stricta*.

For vasculars, it seems reasonable to suggest that the rather stochastic nature of establishment, i.e. modes of dispersal, proximity of seed sources, climate and germination success, severity of heat and soil chemistry, that affects survival of seeds and underground organs, visits by animals and insects, etc. were of great importance for the colonisation of the bonfire sites. The floristic composition established immediately after the fire was of great importance for the subsequent development, as Hobbs & Gimingham (1984b) also found after heathland fires in Scotland.

Vegetative expansion from rhizomes and dispersal of seeds from the margin seemed to be the dominating modes of establishment, although long-distance dispersal by wind was quite important early in the succession (Arnesen 1991). Vegetative expansion is a regenerative strategy that commonly occurs in competitive and stress-tolerant species, while regeneration with widely dispersed seeds is found in the whole range of plant strategies. Apparently, and in spite of the stochastic processes mentioned above, better knowledge of the severity of the fire, the conductivity of the soil, the size of the ash deposits and the autecology of species would make it possible to predict development in more detail. The general patterns found in the present research may still prove useful. However, regenerative strategies seemed more appropriate for predicting the development than the complex, established plant strategies.

5.4 THE VEGETATION

The early-successional species were major constituents of the *Funaria hygrometrica-Leptobryum pyriforme* vegetation type of TWINSPAN cluster 1, and this vegetation represented the onset of the succession. At Sølendet, it occurs only on bonfire sites. Samples from the centre plots of some rather old sites in heathland (70C8, 70C12) and dry grassland (16C10) were also found in this cluster, thus demonstrating the slow recovery of these vegetation types.

In fen margin, vegetation developed to the *Equisetum variegatum-Eriophorum angustifolium-Marchantia* type (cluster 7), comprising both early-successional species and later establishers, and subsequently to the *Thalictrum alpinum-Carex panicea-Campylium stellatum* type (cluster 8). Both are rather similar to the rich fen margin *Campylium* communities described by Moen (1990), mainly the *Molinia caerulea-Succisa pratensis-Campylium stellatum* type. However, the species composition and the fact that many early-successional species were still dominant clearly showed that the vegetation was nowhere near being fully recovered. Several species commonly found in unburnt fen margin vegetation of this type, such as *Dactylorhiza lapponica*, *Carex atrofusca*, *C. dioica* and *Kobresia simpliciuscula*, were still rather rare in the bonfire vegetation after approximately 13 years (the mean age of bonfire sites in cluster 8).

The sequences were not so evident in the grassland clusters. Samples from the same plot occurred in clusters 1 and 5 on only two occasions, and in clusters 1 and 6 on five occasions. Clusters 5 and 6 had no plots in common. This indicated a rather indistinct sequence from the *Funaria hygrometrica-Leptobryum pyriforme* vegetation type (cluster 1) to the *Angelica sylvestris-Geum rivale-Marchantia* type (cluster 5), and a somewhat clearer sequence from cluster 1 to the *Crepis paludosa-Festuca rubra-Bryum pseudotriquetrum* type (cluster 6). A possible explanation for these vague connections may be that only a few analyses from sites of low age exist for grassland vegetation. Clusters 5 and 6 were also quite heterogeneous, comprising a variety of both grassland and fen margin species, and covering approximately 1.5 SD even though they contained few samples. Both clusters seemed to have much in common with the open grassland vegetation found in the *Betula pubescens-Crepis paludosa-Campylium stellatum* type of Moen (1990), but here, too, the bonfire vegetation still included several early-successional species with quite high abundance, while the dominants of Moen's type, such as *Crepis paludosa*, *Alchemilla* spp., *Geranium sylvaticum* and *Thalictrum alpinum*, were less abundant.

Clusters 1 and 3 had seven plots in common (i.e. samples taken from one plot occurred in both clusters on seven occasions), all of them from two sites (16 and 79). This implies a sequence from the *Funaria hygrometrica-Leptobryum pyriforme* vegetation type (cluster 1) to the *Rhinanthus minor-Agrostis capillaris-Polytrichum juniperinum* type (cluster 3), but several sites have all their samples, regardless of age, within cluster 3. The vegetation in cluster 3 resembles the *Achillea millefolium-Tortula ruralis* type of open grassland and the *Betula pubescens-Agrostis capillaris-Succisa pratensis* type of wooded grassland described by Moen (1990), both comprising a number of heathland species such as *Vaccinium* spp., *Melampyrum pratense*, *Hylocomium splendens* and *Pleurozium schreberi.* Some dominants in Moen's types, for instance *Achillea millefolium* in the open grassland type and *Betula pubescens*, *Agrostis capillaris* and *Deschampsia cespitosa* in the wooded type, were also dominants in the bonfire vegetation. *Thalictrum alpinum* in the open grassland type and *Geranium sylvaticum* and *Potentilla erecta* in the wooded type were still less abundant on the bonfire sites than in adjacent unburnt vegetation.

A sequence from cluster 1 to the heathland cluster 4 (comprising most of the samples from site 70) may also be perceived, as two of the first three samples from site 70 were found in cluster 1. Several heathland species had low cover values in the later samples in cluster 4. The plots from site 70 found in cluster 1 were the oldest (8 and 12 years) in that cluster, but they were still dominated by early-successional species. This indicated the slow process of revegetation in heathland vegetation.

Both TWINSPAN and DCA axis 1 separated the samples quite well along the main ecological gradient related to moisture. The age of the bonfire sites found within different TWINSPAN clusters, and the development in pH and the number of species seen in the sequences of clusters, mostly coincided with a decrease in the score on axis 2 in DCA. The over-representation of samples from centre plots in cluster 1, and the corresponding over-representation of samples from margin plots and unburnt vegetation in clusters 6 and 8, also supported this interpretation, since margin plots were usually revegetated much earlier than centre plots. The correlation between DCA axis 1 and the ground water level would probably have been even stronger if levels from the dry grassland samples had been included, and the correlation between DCA axis 2 and age, would also have been strengthened if a "succession age" for the unburnt samples could have been calculated.

The somewhat unusual increase in score over time, seen for instance in plots 79C and 81C, may be explained by the early occurrence of seed plants of some late-successional species with low scores on axis 2 (e.g. in 81C: *Alchemilla wichurae*, *Geranium sylvaticum*, *Geum rivale*) before any of the early-successional species had become important. Age, pH and the number of species were correlated with axis 2. Early-successional species were ordinated with high scores, and late-successional species with low scores on axis 2. All in all, DCA and TWINSPAN seemed to give a fairly consistent picture of the ecological variation and successions.

5.5 CONCLUSIONS

The oldest bonfire sites were still clearly distinguishable from the surrounding vegetation despite up to 20 years of revegetation. The bottom layer recovered quite quickly, but recovery of the field and shrub layers was a slower process, although the species composition of both the bottom and the field layers still differed greatly from the surroundings. Early-successional species were still dominant on many sites and appeared to inhibit the re-establishment of the natural vegetation found in these outlying lands. Further investigation should be undertaken to follow up the development in a selection of sites. The lack of information on the severity of the burning calls for controlled burning on experimental sites. This would also enable the existing vegetation to be analysed before it is burned and the establishment of unburnt reference plots at the time of burning.

Recreational bonfires are not allowed within the nature reserve, but the bonfire sites linked with the management also cause undesirable disturbance. They cover nearly 0.1 ha, and visitors to the reserve will inevitably pass some of them. During the 1990's, efforts have been made to arrange for farmers to collect herbage. During the last five years, some of the herbage has also been composted. However, these measures increase the demand for transport, which may also cause problems in the nature reserve. It seems clear that for many years to come burning will still be necessary in the central parts of the reserve, where mowing takes place far from the nearest roads. The slow recovery demonstrated during the investigation period clearly calls for some caution when deciding where to burn the waste. Bonfire sites near public nature trails, particularly in heathland and dry grassland which show the slowest recovery, should be avoided. Existing sites should be used rather than establishing new ones whenever this can be done without increasing transport.

5.6 ACKNOWLEDGEMENTS

I sincerely thank Professor Asbjørn Moen for his support and help during this project. He lit the fire that made me burn for bonfire vegetation. Thanks are also due to Egil Ingvar Aune, Hans Stenøien, Sigurd Mjøen Såstad and Dag-Inge Øien for valuable discussions and help. Advice from Renée M. Bekker, Groningen on the treatment of seed bank samples was greatly appreciated. I thank Chris McLees and Richard Binns for correcting my English and Eli Fremstad for useful comments. The work was funded by the Museum of Natural History and Archaeology at the Norwegian University of Science and Technology, Sør-Trøndelag College and the Norwegian Research Council.

6 SUMMARY

Succession on bonfire sites following burning of management waste in Sølendet Nature Reserve, central Norway.

As part of the management and restoration of the haymaking lands, brash and herbage derived from clearance work and mowing have been burned at 118 bonfire sites in the Sølendet Nature Reserve since 1978. In 1982-1997, the revegetation of 36 sites in fen margin, grassland and heathland was investigated by repeated analyses in 96 permanent plots. The pH and mineral content in ash and in soil within and outside sites were measured. The biomass within and outside the sites was also measured, and investigations of the seed bank were carried out. Ordination by Detrended Correspondence Analysis (DCA) using version 3.15 of the CANOCO program (Hill 1979a, ter Braak 1987, Oksanen & Minchin 1997) was performed. Two-Way Indicator Species Analysis (TWINSPAN; Hill 1979b) was used to classify the large number of samples (346). The TWINSPAN clusters were described as vegetation types in a wide sense, named after characteristic species, constants or dominants. Synoptic tables with constancy and the characteristic cover of species in TWINSPAN clusters and age groups were constructed using the SAMTAB program (Wilmann 1987, Aune 1998). Statistical analyses of differences and correlations were performed using statistical techniques (t-tests and regression analyses) from the SPSS for Windows program (SPSS Inc. 1997). This aimed to compare differences in pH in soil between plots and over time, to test differences in the mean number of seedlings and the mineral content in new and old ash. These statistics were also used to compare DCA axis scores with records of site age, sample pH, the number of species found in samples and the ground water level found in sites.

The main findings are:

1. A harsh chemical environment with elevated pH and a high content of minerals in soil and ash was recorded after burning, but conditions ameliorated over time due to leaching.

2. The severe conditions observed during the first year after burning seemed to impede the establishment of new vegetation, but the plots were usually covered by early-successional bryophytes (*Bryum* spp., *Ceratodon purpureus*, *Funaria hygrometrica*, *Leptobryum pyriforme*, *Polytrichum juniperinum* and *Marchantia* spp.) within 2-4 years.

3. Recovery of the field layer was a slower process, particularly in dry grassland and heathland. Anemochorous shrubs such as *Betula pubescens* and *Salix* spp., the tall graminoid *Deschampsia cespitosa* and rhizomateous species such as *Equisetum palustre*, *Agrostis capillaris* and *Eriophorum angustifolium* became established quite early.

4. The seed bank seemed to be of minor importance for the establishment of species, but some species (e.g. *Equisetum palustre* and *Hierochloë odorata*) were able to survive with rhizomes.

5. Although a substantial increase in the occurrence and abundance of common fen and grassland species was recorded, several dominant, early-successional bryophytes and vasculars were stable for many years and seemed to inhibit the expansion of other species.

6. An increase in biomass was observed downhill from the sites, probably caused by leachates released from the ash.

7. Management waste should be burnt on existing bonfire sites, and burning should not occur in heathland and dry grassland vegetation near the public trails.

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