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Recovery of Danish coastal dune vegetation after a wildfire

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Abstract. The initial recovery of vegetation after a wildfire in a coastal dune area in NW Jutland, Denmark, was studied over a 5-yr period by means of permanent plots representing various dune communities along a topographical gradient.

The impact of the fire varied with the position of the plots. Fens and south-facing dunes were little affected while dune heath plots were severely affected including loss of the O-horizon. Post-fire conditions included presence of remaining soil organic matter, a soil seed bank and surviving belowground plant parts. The soil surface remained stable during the study period.

The initial five years of recovery comprised of an initial three-year recruitment phase during which cover and number of species increased and the quantitative species composition changed markedly, followed by two years of a declining rate of change.

38 species of vascular plants were recorded, 35 are regular components in dune, dune heath and heath fen and were recruited from the seed bank, from locally dispersed seeds and/or by sprouting from surviving vegetative parts. The remaining three species were 'aliens', dispersed from sources outside the area. Crustose lichens had an important role in the initial recovery by stabilizing the surface and probably inhibiting seed germination, whereas mosses mostly had a subordinate role.

The seral position of the plots, as well as the expected time needed for full recovery of pre-fire vegetation, vary with topography and initial soil conditions. Five years after the fire the fen and the south-facing dune probably need less than a decade for full recovery. The remaining plots are judged to be relatively early seral; their full recovery into mature dry or moist dune heath vegetation and O-horizon is expected to need several centuries.

Keywords: Coastal heath; Crustose lichen; Fire; Permanent plot; Recovery time; Soil seed bank; Species recruitment; Transect.

Nomenclature: Hansen (1981) for vascular plants; Andersen et al. (1976) for mosses; Santesson (1993) for lichens.

Introduction

The effect of fire on ecosystems and ecosystem dynamics is a field of research which is receiving increasing attention (e.g. Zackrisson 1977; Goldammer & Jenkins 1990; Naveh 1990; Glenn-Lewin & van der Maarel 1992; Tybirk et al. 2000). Very little information is available about the effects of fire in coastal dune systems, in spite of fire being a potential risk in this type of landscape due to the, often intensive, recreational use (van der Maarel & Usher 1997; van der Zande 1989; Jensen 1998). Information on recovery of dune heaths, which constitute the innermost, most stabilized part of the dune system can be obtained from studies on fire in inland heathlands (e.g. Hansen 1964, 1976; Gimingham 1972; Gill & Groves 1981; Hobbs & Gimingham 1984a, b; Prentice et al. 1987).

The dunes along the west coast of Jutland constitute an important part of the coastal dune landscapes in NW Europe (Doody 1991; Brandt & Christensen 1994). In one of the major localities in this dune complex, the Hansted Reserve in NW Jutland, a wildfire caused by lightning occurred in August 1992 which provided an opportunity to study the effects of a dune fire and the subsequent vegetation dynamics. The damage to the plant cover was severe. The area was left black and most of the soil organic O-horizon had disappeared, exposing the dune sand below a layer of ashes. Only a few living plants were found, sprouting from belowground parts. Close examination revealed a large spatial variation in the intensity of the fire, owing to spatial variation in topography.

Since December 1992, recovery of the vegetation has been studied in permanent plots (Alstrup & Vestergaard 1996). The aim of the present paper is to give an indication of the direction of post-fire recovery, based on data from initial vegetation development in selected plots. It is the intention to present and discuss the material in more detail after re-analysis of all plots in 2002.

Site and Methods

The Hansted Reserve (Fig. 1) includes 3399 ha of sand dunes, dry and moist dune heath, oligotrophic dune slacks and dune lakes on a former sea bottom. For a general description of the vegetation see Nielsen & Jensen (1963). The reserve has been selected as a Natura 2000 locality. On the 11th and 12th of August 1992, after an unusually hot and dry summer period (Table 1), an area of ca. 175 ha was burnt. The fire started at a point a few hundred metres from the coastline, spread in a ca. 400 m wide belt about 3.5 km towards the east-northeast and stopped when it reached an area of moist meadows. The study is based on 18 burnt plots of 7.5 m × 1.5 m, representing the topographical (and hence the vegetation) variation in the burnt area. The plots were marked by red iron corner-sticks. As the exact composition of the pre-fire vegetation of the burnt plots was not known, it was not possible to establish corresponding unburnt control plots. Five unburnt plots which, based on topography, were judged to correspond to the pre-fire state of five of the burnt plots were selected outside the burnt area to allow estimation of the loss of organic matter and nutrients during the fire.

This paper examines vegetation development until 1997 in five burnt plots (A-E) which were judged to represent the major heath and dune communities characteristic of the reserve. Plots A-D were established along an altitudinal gradient from the bank of a dune lake (plot A) to moist (plot B) and dry (plot C) dune heath and a south-facing dune slope (plot D). Plot E was established on the north-facing slope of the dune of plot D. The public were excluded from this part of the burnt area. Summer weather conditions from 1993 to 1997 did not differ too much from the long-term means, except for the summer of 1996 which was cool and dry (Table 1).

Field methods

At the start of the research (December 1992), the post-fire conditions of the plots were recorded and pre-fire vegetation estimated from plant remains and by comparison with vegetation of nearby unburnt areas with similar topography (Table 2).

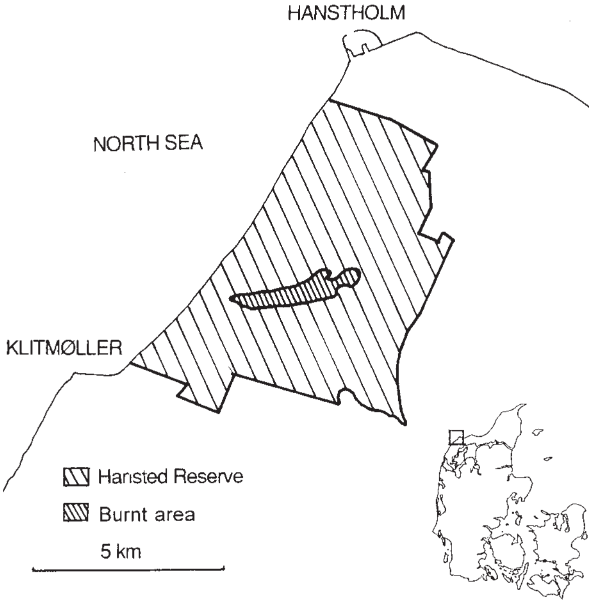

Fig. 1. Location of the study area along the coast of NW Jutland, Denmark (shown to the right).

The vegetation of the plots was studied in December 1992, May 1993, September 1993, July 1994, August 1995, August 1996 and August 1997. Each plot was divided into five subplots measuring 1.5 m × 1.5 m. In the subplots, % cover of all species of vascular plants, mosses and lichens was estimated and mean values for each plot calculated. In 1995 and 1996, lichens were recorded in June and September respectively. For each plot, soil samples were taken with an auger at 0 - 5 cm and 5 - 10 cm depth at eight fixed positions just outside the plot. The samples from each depth were pooled. In December 1992 25 cm × 25 cm samples for determination of the viable soil seed bank were taken at depths of 0 - 2.5 cm and 2.5 - 5.0 cm just outside each plot. During the study period, possible changes in the level of the soil surface due to erosion or sand drift were estimated at each sampling date by measuring the above-ground height of the iron plot markers.

Table 1. Air temperature (mean value for June and July) and precipitation (June plus July) for northwest Jutland 1990-1997. Data from the Danish Meteorological Institute.

	1990	1991	1992	1993	1994	1995	1996	1997	Mean 1982-1996	Mean 1961-1990
Air temperature (°C)	14.8	14.6	16.7	13.4	15.8	15.4	13.3	16.4	14.9	-
Precipitation (mm)	113	105	33	114	81	74	39	134	-	119

Table 2. Characteristics of the plots. Soil profiles: O = organic matter, Ah = Near surface with humified organic matter, C = parent material.

	Estimated pre-fire vegetation	Post-fire characteristics	Post-fire soil profile
Plot A	Wet *Myrica gale*-*Molinia caerulea* fen	Peat superficially burnt *Myrica* and *Molinia* black, partly living; Scattered green shoots	Ashes: few mm O: sandy peat: 15 cm C: sand
Plot B	Moist dune heath with *Salix repens*	Surface black and firm. Charred branch remains; Scattered green shoots; Fungus *Anthracobia*	Ashes: few mm Ah: 3 cm (1 cm charred) C: sand
Plot C	Dry *Empetrum nigrum* dune heath with *Ammophila arenaria* and *Salix repens*	Surface black and firm; Charred remains of dwarf bushes; Scattered green shoots.	Ashes: few mm Ah: 2 cm (1 cm charred) C: sand
Plot D	South-facing fixed, acid dune with *Ammophila arenaria*, rich in lichens	Lightly burnt; Numerous green shoots; Dead lichens	Ah: 2 cm C: light-brown sand
Plot E	North-facing dune heath, rich in lichens	Surface black. Charred remains of dwarf bushes; Scattered green shoots; Charred (dead?) lichens	Ashes: few mm Ah: 3 cm (1 cm charred) C: sand

Laboratory methods

The soil samples were analysed for actual moisture content (% of dry weight) and bulk density (g/cm^3). After drying to constant weight at 60 °C the samples were ground and sieved through a 2 mm mesh then analysed for organic matter content (loss on ignition on heating to 550 °C for 6 hours), pH and specific conductivity (microS) of water extracts (dry soil: demineralized water = 1 : 2.5).

The seed bank samples were stored at 5 °C in plastic bags until the beginning of January 1993 when living, vegetative plant parts were removed before the samples were homogenized. Subsamples (ca. 15% by volume) were spread evenly across germination boxes in layers (ca. 0.75 cm) on top of sterilized soil. The boxes were placed at 24 °C in a greenhouse in the Botanical Garden, University of Copenhagen, and watered regularly. The boxes were later moved outside. Seeds germinating between January and September 1993 were identified to species and counted.

For each plot and sampling date, the total number of vascular plant species as well as the total cover of vascular plants, mosses and lichens were recorded. Differences in the quantitative composition of vascular plants between the years were expressed by the weighted Sørensen similarity index (Sørensen 1948;, van Tongeren 1987) using cover percentage as the quantitative parameter. To detect the spatial and temporal variation in the quantitative composition of vascular plant species of the plots the data were subjected to Detrended Correspondence Analysis (DCA), using the program PC-ORD (McCune & Mefford 1995). The seed bank data were expressed in the number of germinated seeds per species per m^2 for the depths 0 - 2.5, 2.5 - 5 and 0 - 5 cm.

Results

The topographical gradient

In the DCA-ordination (Fig. 2) the plots are distributed along the first axis (eigenvalue 0.97). With respect to the eigenvalues of the second and third axes, 0.29 and 0.09 respectively, the first axis clearly explains most of the floristic variation between the plots.

The variation along the first DCA-axis reflects the topographical position of the plots, which is again reflected in a soil gradient, composed of significantly intercorrelated ($p < 0.05$) values of moisture, dry bulk density, organic matter and specific conductivity at soil depths 0 - 5 cm and 5 - 10 cm and by a weaker pH-gradient (Table 3).

The main factor determining the soil gradient seems to be drainage. In plot A the soil is wet with ground water at the soil surface in winter and ca. 20 - 30 cm below the soil surface in summer. In plot B the top soil is better drained (Table 3). In plots C and D the soil is dry, but plot E is slightly more moist (probably due to lower evapotranspiration).

Based on the observed changes in organic matter stocks after fire the topographical gradient also reflects a gradient in the intensity of the fire. Plots A and D were lightly burnt due to high water content and low amount of combustible biomass respectively (cf. Hobbs & Gimingham 1984a). Plots B and C were severely burnt, causing complete loss of the O-horizon. Plot E appeared to have been somewhat less severely burnt.

The recordings of the soil surface in relation to the permanent plot markers gave no indication of any significant erosion, sand drift or accumulation during the study period.

Changes in species composition of the plots

Details in the changes in vascular species composition of the plots from winter 1992 until 1997 are given in Table 4. Because the effect of the fire is superimposed on a normal winter/spring pattern in the analyses from December 1992 and May 1993, the situation in September 1993 was chosen as the starting point for the description of the development of post-fire vegetation. The total cover of vascular plants from 1993 to 1997 is shown in Fig. 3.

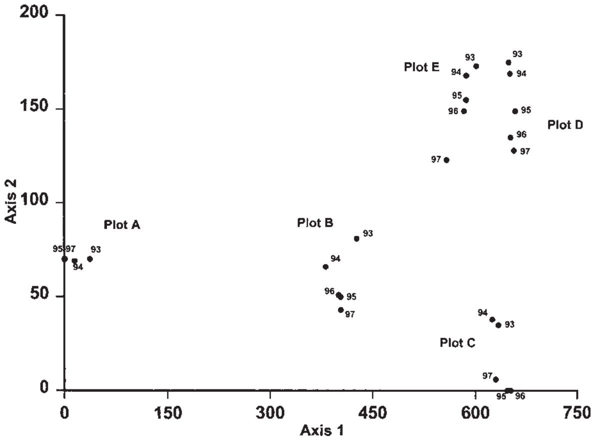

Fig. 2. DCA ordination of the plots, 1993-1997. Note the different axis scales. Eigenvalues: axis 1 = 0.9685, axis 2 = 0.2891.

Between 10 and 20 species of vascular plants were recorded in the plots. Most of the cover values recorded during the study period were below 1% and only five species (*Myrica gale, Potentilla erecta, Ammophila arenaria, Molinia caerulea* and *Salix repens*) reached a cover value of more than 10% in any plot.

In plot A, the majority of the species are typical oligotrophic fen species. In 1993, the total cover was 26%, mainly due to *Potentilla erecta, Myrica gale, Molinia caerulea* and *Carex nigra*. From 1993 to 1997 the total cover gradually increased to 108%, mainly due to an increase in *M. gale* and *M. caerulea.*

In plot B, the majority of the species are typical of

Table 3. Soil characteristics of the plots in September 1993.

	Soil depth	Plot A	Plot B	Plot C	Plot D	Plot E
Soil moisture, % dry weight	0 - 5 cm	161.5	9.1	2.3	0.3	5.2
	5 - 10 cm	66.7	7.7	1.1	0.4	2.8
Dry bulk density, g/cm	0 - 5 cm	0.30	0.92	1.13	1.53	1.22
	5 - 10 cm	0.75	1.41	1.59	1.66	1.59
Organic matter, % dry weight	0 - 5 cm	28.1	7.4	2.6	1.5	3.4
	5 - 10 cm	6.0	2.4	0.5	0.4	0.5
pH	0 - 5 cm	3.7	3.7	4.2	4.5	3.9
	5 - 10 cm	3.9	3.9	4.2	4.4	4.2
Specific conductivity, μS	0 - 5 cm	1278	258	133	56	127
	5 - 10 cm	325	103	54	38	50

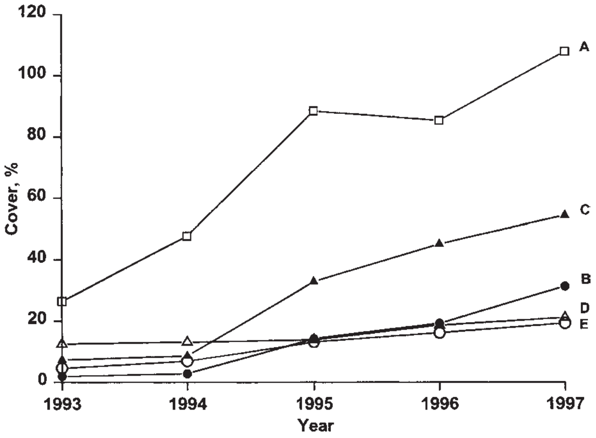

Fig. 3. Total cover of vascular plants in plots A-E, 1993-1997.

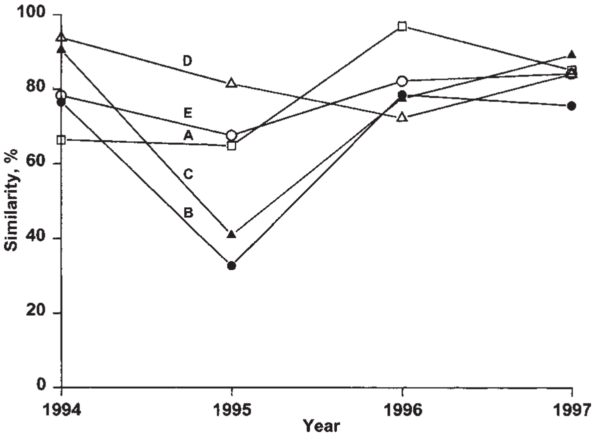

Fig. 4. Weighted similarity in species composition between successive years for plots A-E.

relatively dry, sandy, oligotrophic soils. In 1993 the total cover was 2%, mainly made up by shoots of *Salix repens* sprouting from surviving vegetative parts. From 1993 to 1997, the cover gradually increased to 31%, mainly due to an increase in *S. repens* and, from 1995, in *Calluna vulgaris* (flowering from 1996).

In plot C, the majority of the species are typical of fixed, acid dune or dune heath. In 1993 the total cover was 7%, mainly of *Ammophila arenaria* sprouting from surviving below-ground parts. From 1993 to 1997 the cover gradually increased to 55%, mainly due to an increase in biomass of *A. arenaria*, but also in *Deschampsia flexuosa* and *Calluna vulgaris* (flowering from 1996).

In plot D, all species recorded are typically dry dune species. In 1993 the total cover was 13%, mainly *Carex arenaria* and *Ammophila arenaria*. From 1993 to 1997 the cover gradually increased to 21%, mainly due to an increase in biomass of *A. arenaria* and *Corynephorus canescens* and also of *Deschampsia flexuosa*, while *C. arenaria* gradually declined.

In plot E, all species are typically fixed, acid dune or dune heath species. In 1993, the total cover was 5%, mainly *Deschampsia flexuosa, Carex arenaria* and *Corynephorus canescens*. From 1993 to 1997, the cover gradually increased to 19%, mainly due to an increase in biomass of *D. flexuosa, C. canescens* and *Calluna vulgaris*.

The change in vascular plant species composition from 1993 to 1997 in terms of (dis)similarity between successive years is shown in Fig. 4. In most plots, the largest change took place between 1994 and 1995, i.e. between the second and the third year after the fire. The changes in species composition were also reflected in the DCA-diagram (Fig. 2) by a relatively large spatial distance between the position of '1994' and '1995' within most plots.

Changes in species richness

In the two most heavily burnt and initially 'barest' plots (B and C), the number of vascular plant species increased markedly from 1993 to 1995 (Fig. 5), mainly due to germination of seeds from the seed bank or seeds coming from outside the burnt area. Another relatively marked change in species number occurred in the fen plot (A) between 1993 and 1995. In 1997, the number of species varied between eight in the south-facing dune plot (D) and 16 in plot B, where only four species were recorded in 1993.

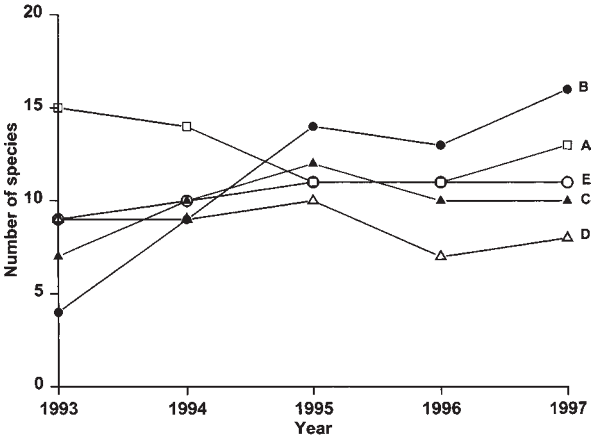

Fig. 5. Number of vascular plant species in plots A-E, 1993-1997.

Table 4. Change in species composition of the plots from 1992 to 1997. The figures indicate % cover of green biomass of vascular plants according to the following scale: 1: < 1%, 2: 1%, 3: 2 - 4%, 4: 5 - 9%, 5: 10 - 19%, 6: 20 - 29%, 7: 30 - 39%, 8: 40 - 49%, 9: 50 - 74%, 10: ≥ 75%.

Plot A	Dec92	May93	Sep93	Jul94	Aug95	Aug96	Aug97
Myrica gale	1	2	3	6	9	9	10
Potentilla erecta	2	2	5	5	4	4	4
Molinia caerulea		3	3	3	4	4	5
Salix repens		1	1	1	1	1	
Vaccinium uliginosum		1	1	1	1	1	1
Chamaenerion angustifolium		1	1	1			
Calluna vulgaris			1	1		1	1
Erica tetralix			2	2	3	3	3
Carex arenaria			1				
Carex panicea			1	1			
Carex nigra			3	3	4	4	3
Salix aurita			1	1	1	1	
Juncus articulatus			1	1	1	1	1
Juncus squarrosus			1				
Jasione montana			1				
Viola palustris				1	1		1
Dryopteris cristata				1			
Senecio sylvaticus					1		1
Hydrocotyle vulgare						1	1
Eriophorum angustifolium						1	1

Plot B	Dec92	May93	Sep93	Jul94	Aug95	Aug96	Aug97
Carex arenaria	1	1	1	1	1	1	1
Genista anglica		1	1	1	2	3	3
Salix repens		1	2	2	4	5	5
Vaccinium uliginosum			1	1	1	1	1
Chamaenerion angustifolium				1	1	1	1
Senecio sylvaticus				1	1		
Molinia caerulea				1	1	1	1
Carex pilulifera				1	1	2	2
Erica tetralix				1	1	1	2
Calluna vulgaris					3	3	4
Hypochoeris radicata					1	1	1
Luzula multiflora					1	1	1
Jasione montana					1		1
Polygala vulgaris					1		
Empetrum nigrum						1	1
Corynephorus canescens						1	1
Aira praecox							1
Deschampsia flexuosa							1

Plot C	Dec92	May93	Sep93	Jul94	Aug95	Aug96	Aug97
Ammophila arenaria	1	1	3	3	6	7	7
Carex arenaria	1	1	2	2	3	2	2
Salix repens	1	1	1	1	3	2	3
Hieracium umbellatum	1	1	1	1	1	1	1
Deschampsia flexuosa		1	1	1	2	3	3
Lotus corniculatus			1	1	3	3	3
Polypodium vulgare			1				
Empetrum nigrum				1			
Calluna vulgaris				1	1	3	4
Hypochoeris radicata				1	1	1	2
Jasione montana				1	1	1	2
Corynephorus canescens					1	1	1
Holcus lanatus					1		
Senecio sylvaticus					1		

Table 4. *(cont.)*

Plot D	Dec92	May93	Sep93	Jul94	Aug95	Aug96	Aug97
Carex arenaria	3	3	4	4	3	3	3
Ammophila arenaria	1	1	3	3	3	4	4
Hypochoeris radicata	2	2	2	2	2	1	1
Corynephorus canescens	1	1	1	1	2	3	4
Viola canina	1	1	1	1	1	1	1
Hieracium umbellatum	1	1	1	1	1		
Jasione montana	1	1	1	1	1	1	2
Deschampsia flexuosa		1	2	2	2	2	3
Festuca rubra		1	1	1	1		
Teesdalia nudicaulis		1			1		1
Plot E	Dec92	May93	Sep93	Jul94	Aug95	Aug96	Aug97
Carex arenaria	1	1	2	2	2	2	2
Ammophila arenaria	1	1	1	1	1	1	1
Deschampsia flexuosa	1	1	2	3	3	3	4
Polypodium vulgare	1		1	1	1	1	1
Jasione montana	1	1	1	1	1	1	1
Corynephorus canescens		1	1	1	3	3	3
Genista anglica		1	1	1	1	1	1
Calluna vulgaris			1	1	3	3	4
Luzula multiflora			1	1	1	1	1
Empetrum nigrum				1	1	1	1
Hypochoeris radicata					1	1	1

Initial soil seed bank

A total of 11 species were recorded in the seed bank four months after the fire (Table 5). All species were typical dune, dune heath and heath fen species. The two most common species in the seed bank, *Erica tetralix* and *Calluna vulgaris*, which made up 80% of the total number of seeds were each recorded in four plots. The remaining species were found in 1-3 plots.

Most seeds were found in plots A and B. The seed bank in plot A comprised of six species, of which *Dryopteris filix-mas* was not observed in the vegetation during the study period. The most abundant seeds were *E. tetralix*. In plot B, five species were found of which *Juncus squarrosus* was not recorded in the vegetation. High seed numbers were found for *C. vulgaris* and *E. tetralix*. In plots C, D and E the number of seeds was lower; in plot C, only *C. vulgaris* was found. In plot D, five species were found, of which *C. vulgaris* and *E. tetralix* were not observed in the vegetation during the study period. The seed bank of plot E included four species of which *E. tetralix* was not observed in the vegetation.

Role of various groups of species

38 species of vascular plants were recorded in the plots during the study period. The majority (35) of the species are regular components of dune, dune heath and heath fen vegetation inside the reserve. These species include three scrub species, five heathland chamaephytes, 13 perennial graminoids, 11 perennial dicots and ferns and three annuals. The following species were particularly indicative of the future vegetation development in one or more plots: the scrub species *Salix repens* and *Myrica gale*, the heathland chamaephytes *Calluna vulgaris*, *Erica tetralix*, *Empetrum nigrum* and *Genista anglica*, the perennial graminoids *Ammophila arenaria*, *Corynephorus canescens*, *Deschampsia flexuosa*, *Molinia caerulea* and *Carex arenaria* and the annual *Jasione montana*.

The remaining three species, *Senecio sylvaticus*, *Chamaenerion angustifolium* and *Holcus lanatus*, are more typically found in woodland clearings or meadows than in mature dune and heath vegetation. As these species were not recorded in the seed bank of the burnt soils, their occurrence is ascribed to seeds dispersed from sources outside the reserve. They were, however, recorded ephemerally in the three lower-lying plots only, and always low in cover (< 0.5%). Other 'alien' species recorded in the burnt area (but not in the plots) during the first years were *Sonchus asper*,

Table 5. Soil seed bank. Number of germinated seeds/spores per m^2 at a depth of 0 - 5 cm.

Plot	A	B	C	D	E
Potentilla erecta	8746				
Jasione montana				853	107
Corynephorus canescens				213	
Molinia caerulea	2453				
Carex arenaria	107			1920	320
Juncus squarrosus	107	107			
Genista anglica		107			
Calluna vulgaris		13973	9706	213	5440
Erica tetralix	13333	18347		640	427
Dryopteris filix-mas	213				
Luzula multiflora		320			
Total	24959	32854	9706	3839	6294

S. oleraceus, *Senecio vulgaris*, *S. vernalis*, *Cirsium arvense*, *C. vulgare* and *Epilobium hirsutum* (Alstrup & Vestergaard 1996).

In the fen and south-facing dune plots, lichens had a very subordinate role during the study period (Fig. 6A). In the other, more heavily burnt plots, the importance of lichens gradually increased. The dominant species was *Placynthiella icmalea* which, particularly from 1995 onwards, colonized the black, firm fire crust found during the first years. In the north-facing dune plot (E) a rich lichen flora (*Cladina*) was recorded in 1996 and 1997. Mosses had a subordinate role in all plots except B (Fig. 6B). The most important species were *Ceratodon purpureus* on humic soil and *Polytrichum juniperinum* on more sandy soil. Between 1994 and 1995 plot B in particular was invaded by *C. purpureus*, giving those parts of the plot not covered by vascular plants a bright brown-yellow hue.

Discussion

Vegetation recovery: Post-fire conditions

The post-fire conditions were characterized by the presence of remaining soil organic matter as well as by viable seeds and living vegetative remains of the pre-fire vegetation. The post-fire conditions after the Hansted fire differ from those left after other types of vegetation destruction in dunes, e.g. blowouts (Carter 1988). However, along the topographical gradient studied, a considerable variation in post-fire conditions exists caused by variation in the pre-fire conditions and hence in the intensity of the fire.

The actual amount of soil organic matter left in the plots is shown in Table 1. As no exact data exist on the pre-fire soil and vegetation of the plots, the amount of organic matter lost during the fire has to be estimated

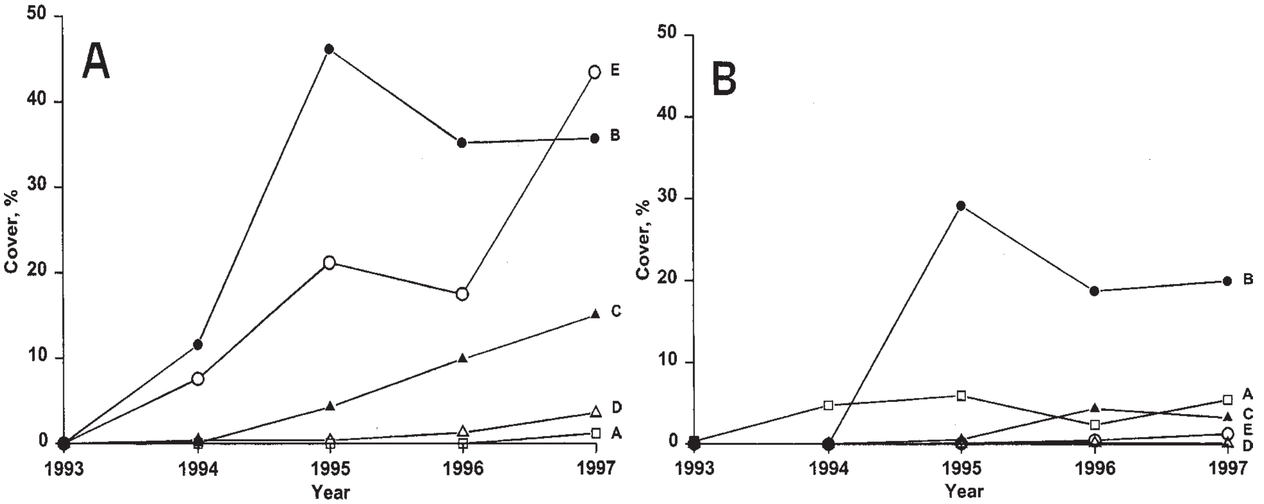

Fig. 6. Total cover of lichens (**A**) and mosses (**B**) in plots A-E, 1993-1997.

by comparison of the burnt area with unburnt nearby areas of similar topography and hydrology. On this basis, estimates of soil organic matter loss from dry and moist dune heath, corresponding to plots B, C and E, were 55-60% (Vestergaard & Alstrup 1996). This loss reduces the capacity of the soil to absorb and release nutrients as well as it reduces its moisture retention.

In areas of heath fen (plot A), the loss of organic matter was much less (ca. 10%). For the south-facing dune, no local data exist which would allow a direct estimation of the loss. The soil profile and the content of soil organic matter found in plot D, however, does not differ substantially from natural dune profiles published by James & Wharfe (1989) and Vestergaard (1991), indicating little fire loss from this plot.

A considerable part of the pre-fire seed bank could have been lost during the fire by burning of the upper organic soil layer in which a large number of seeds are expected to be present (Chippindale & Milton 1934; Legg et al. 1992) or by killing of the seeds by excessive heating of the uppermost layer of non-burnt soil. However, after the Hansted fire the seed bank was apparently not seriously damaged, since no unambiguous reduction in the seed bank was detected when the burnt plots were compared to reference plots (Alstrup & Vestergaard 1996). Furthermore, the number of viable seeds found in the burnt area has to be considered as a minimum value, since an unknown number of seeds may not have germinated under the treatment of the soil samples (Fenner 1985).

Another potential biotic factor in the post-fire recruitment of plants is that of resprouting from surviving plant parts. Such plant parts were found at the soil surface or in the topsoil of all plots.

As an additional factor influencing the initial recovery of the vegetation post-fire modification of the soil surface due to erosion and sand drift has to be considered (Jungerius & Dekker 1990; Diaz-Fierros et al. 1990). This is especially important during the first autumn and winter after the fire when large areas of burnt dune heath were left bare; such modifications could have been expected due to rain and strong winds. However, only very local and small-scale effects have actually been observed. This high degree of stability may partly be caused by the firm fire crust, which seems to be very resistant to erosion by wind. Later, these crusts were largely invaded by lichens, especially *Placynthiella icmalea*, further stabilizing the soil surface (cf. Legg et al. 1992).

Unusual weather conditions during the study period may also have influenced the recovery. Such conditions were, however, not indicated by meteorological data.

Processes during the initial development

The initial recruitment and establishment phases during which species immigrated or were recruited from local sources was short (1993-1995). In 1996 and 1997 new establishment of species had virtually stopped in most plots, and as significant exclusions of species did not take place either, the stock of species available for subsequent development seems to have stabilized.

Immigrating ‘alien’ species, dispersed from adjacent woodlands (mostly coniferous plantations), meadows and arable land, played a minor role during initial post-fire development. The ‘alien’ species observed are common species with a large potential for wind or epizoic dispersal (Andersen 1993). Their lack of success in establishing in the burnt area may be ascribed to the acid and unproductive environment (Grime 1979).

Establishment of immigrating species may also be prevented by lack of open patches due to the high cover of species already present (cf. Connell & Slatyer 1977; Grime 1979). This is probably the case in the fen plot due to high cover of *Myrica gale* and *Molinia caerulea.* In other plots vascular plant cover in most years was less than 50% leaving a lot of free space for plant establishment. In the most heavily burnt plots, however, the lichen *Placynthiella icmalea* colonized the fire crust extensively from 1995 and may have prevented immigrating seeds from germinating. Legg et al. (1992) found that a film of crustose lichens + algae over exposed organic soil after a severe fire reduced germination of *Calluna vulgaris* by ca. 40%. *P. icmalea* is known elsewhere as a primary colonizer, e.g. in heathlands after burning (Purvis et al. 1992).

The majority of the species present in the plots after the fire originate from local sources, from seeds present in the seed bank, plants in nearby unburnt areas of similar vegetation or from surviving perennial plant remains (observed for *Ammophila arenaria*, *Carex arenaria*, *Deschampsia flexuosa*, *Salix repens*, *Myrica gale*, *Molinia caerulea* and others). The ability of heath plants to survive fire has been widely studied (e.g. Hansen 1964, 1976; Gimingham 1972; Mallik & Gimingham 1985). The dominance of local species agrees well with observations by Trabaud & Lepart (1980) and Trabaud (1990) after fires in Mediterranean garrigue vegetation.

A short initial recruitment phase was also found in post-fire succession in heathland in Brittany (Gloaguen 1990; Clement & Touffet 1990). Here, mosses were much more important as primary colonizers than at Hansted, while lichens had a subordinate role. At both localities, *Ceratodon purpureus* was among the early colonizers due to its wide diaspore dispersion (Clement & Touffet 1990).

Seral relationships

The actual relative seral positions of the plots vary with the initial post-fire soil conditions and hence with topography. According to common practice in vegetation dynamics (e.g. Glenn-Lewin & van der Maarel 1992; Miles & Walton 1993) post-fire recovery after the fire at Hansted should be characterized as secondary succession. This may be the case for the severely burnt plots. For the least severely burnt plots, however, the early recovery seems very similar to early post-fire development of Mediterranean garrigue described by Trabaud & Lepart (1980). They argue that the early recovery should not be seen as succession (in the general sense of the word, with substitution of a community by another one), but rather as a progressive reappearance of the species belonging to the original community.

The communities least affected by the fire, i.e. the fen and the south-facing dune, already seem to represent near-mature stages not far (probably less than 10 years) from the pre-fire vegetation. The fen plot (*Myrica gale-Molinia caerulea*) and the south-facing dune plot (*Corynephorus canescens-Ammophila arenaria*) are similar to mature heath fen vegetation and fixed, acid dune vegetation ('grey dune') as described by Påhlsson (1994). The presence of *Calluna vulgaris* in the seed bank of the south-facing dune may point towards dry dune heath as a potential outcome of long-term development of this plot.

For the more severely fire-affected north-facing dune plot, future development is less predictable. One possible direction is towards fixed, acid dune with *Corynephorus canescens*. The increase in lichens supports this view (cf. Påhlsson 1994). Another possible direction is towards dry dune heath which is supported by the gradual increase in *Calluna vulgaris* and *Deschampsia flexuosa* and the presence of *Empetrum nigrum*.

The most severely burnt plots still seem to be in an early seral position, and their future development is uncertain. In plot B, the most likely mature type of vegetation seems to be a moist dune heath with *Calluna vulgaris*, *Erica tetralix* and *Salix repens*. The most significant development in plot C has been the increase in *Ammophila arenaria*, favoured by a combination of free space and a below-ground system surviving the fire. Due to the lack of supplies of fresh sand, however, *A. arenaria* is expected to weaken during the coming years (van der Putten 1989, 1993) and to be gradually replaced by *Calluna vulgaris* and *Deschampsia flexuosa*. The mature type of vegetation in this plot may, therefore, be a dry dune heath with scattered *A. arenaria* (cf. Påhlsson 1994).

Estimation of the recovery time after fire may be useful in the management of nature types for conservation. In a nature conservation perspective, the dune heaths on acid sand along the west coast of Jutland are important and have been selected by the European Union as a high priority type of nature on a European level. Therefore, knowledge of the time needed for development into mature dune heath, which is tentatively predicted for several of the plots studied here, is relevant. As no exact information of the development on the coastal dune heath of Jutland has been published, estimation of the time needed has to be based on experience from inland heaths (Hansen 1964; Böcher 1970; Prentice et al. 1987; Degn 1997). It is estimated that at the burnt plots, the development of a closed cover of dwarf shrubs, but without an O-horizon, will take about a decade. Based on the increase of *Calluna vulgaris* during the study period, this species is initially expected to dominate the heath. Later *Empetrum nigrum* is expected, at least on dry sand, to gradually replace *C. vulgaris* due to its prostrate growth form. This allows individuals to compete more effectively for the restricted growing space than individuals of *C. vulgaris* (Prentice et al. 1987). The competition between the two species is, however, long-term as described by Tybirk & Hansen (1999) who estimated that *E. nigrum* may need ca. 80 yr to replace *C. vulgaris*.

The O-horizon associated with mature dwarf shrub heath will probably require much more time to develop. According to Olsson (1974) a ranker soil with an O-horizon on sand, with a vegetation similar to the dry dune heath at Hansted, will take up to 200 yr to develop.

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