Loss of organic matter and nutrients from a coastal dune heath in northwest Denmark caused by fire

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Abstract. The loss of organic matter and nutrients due to a natural fire in a Danish coastal dune heath system (175 ha) was studied for three heath types: dry *Empetrum nigrum* heath, moist *E. nigrum-Vaccinium uliginosum* heath, and wet *Erica tetralix-Molinia coerulea* heath. The highest loss of organic matter, as well as N, P and K, was found in the moist heath (67 %, 68 %, 20 % and 25 % respectively). The lowest loss was found in the wet heath (35 %, 28 %, 14 %, and 11 % respectively). The loss in the dry heath was intermediate. For the burnt heath in total, loss of organic matter, N, P and K of about 13000, 192, 10 and 6 tons respectively, was estimated. Processes of nutrient loss by fire and regeneration of nutrients are discussed.

Keywords: Empetrum nigrum; Erica tetralix; Regeneration.

Introduction

The effects of fire on the nutrient status of NW European inland heaths, dominated by *Calluna*, has been the subject of thorough studies (e.g. Allen 1964; Hansen 1969; Allen et al. 1969; Evans & Allen 1971; reviews by Gimingham 1972; Gill & Groves 1981; Gimingham 1981; Riis-Nielsen et al. 1991) because of the considerable interest in the use of fire in the management of heathlands. A consequence of fire management is loss of nutrients. Losses of ca. 60 - 68 % of C, 68 - 76 % of N and 50 - 56 % of S by burning of *Calluna* have been reported by Allen (1964), and Evans & Allen (1971) found losses of other elements of between 10 and 20 %.

Coastal dune heaths seem to be far more stable than inland heaths. The natural succession in dune heath is very slow (Christensen 1989) and in Denmark dune heath may be considered as a climax community (Riis-Nielsen et al. 1991) \tilde{N} nowadays, however, dune heath is threathened by spread of the alien *Pinus mugo*. Therefore, management by fire to maintain dune heath vegetation seems less relevant when compared to inland heaths and to our knowledge no studies of the effect of fire have been published from NW European coastal dune heaths.

Along the west coast of Jutland in Denmark, dune

heath on acid sand dominated by *Empetrum nigrum* is an important element in the landward part of the dune complex. In one of the major dune heath localities, the Hansted Reserve in NW Jutland, lightning caused a fire in 1992. Since December 1992 the effects of that fire and the subsequent revegetation have been studied (Alstrup & Vestergaard 1996). In the present paper we present some data on loss of nutrients and organic matter during the fire and the post-fire period.

Site and Methods

The Hansted reserve (Fig. 1) includes 3399 ha of sand dunes, dry and moist dune heath, oligotrophic fens and dune lakes on a former sea-bottom, which has been above sea level since the Stone Age. For a general description of the vegetation see Nielsen & Jensen (1963).

On August 11 and 12, 1992, an area of ca. 175 ha was burnt. The fire started at a point a few hundred metres from the coastline and spread in a ca. 400 m wide belt about 3.5 km towards the east-northeast. The fire stopped when it reached an area of moist meadows.

An investigation into the effects of the fire and subsequent revegetation processes was initiated in December 1992. The study was mainly based on 23 permanent plots of 7.5m \times 1.5m, 18 of which were established within the burnt area and five reference plots in unburnt vegetation. Each plot was subdivided into five subplots of 1.5m \times 1.5m.

Here we present data on losses of organic matter, N, P and K obtained from six plots, representing burntunburnt pairs of plots from three types of vegetation:

1. Dry dune heath, dominated by *Empetrum nigrum* and mosses. The soil was mor humus, 3 - 4 cm deep, with an average organic content of 60 % (n=5).

2. Moist dune heath, dominated by *Empetrum nigrum*, *Vaccinium uliginosum* and mosses on somewhat thicker, mor humus, ca. 5 cm deep, with an average organic content of 81 % (n=5).

3. Wet heath, dominated by *Erica tetralix* and *Molinia coerulea* on a peaty soil, ca. 7 cm deep, with an average

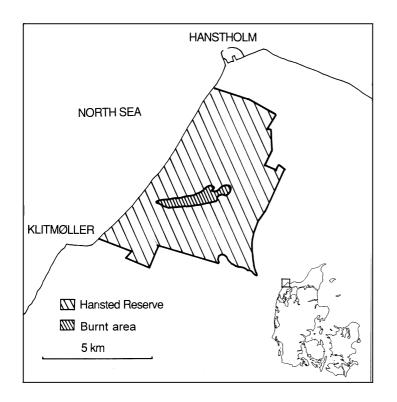


Fig. 1. Location of study area.

organic matter content of 55 % (n=5).

At the time of the fire, soil and vegetation were very dry after a hot and rainless summer, and the intensity of the fire was high. So, in the dry and moist heath plots the above-ground vegetation and the mor layer were fully burned, leaving scattered charred plant remnants on a hard fire crust. In the wet heath, above-ground biomass was severely damaged, leaving dead stems of *Myrica* gale and dead and living bases of tufts of *Molinia coerulea* and *Carex nigra*. The peat was partly burned.

Based on the presence of plant remnants in the burnt plots after the fire, as well as on topographical position, we selected the unburnt reference plots outside the burnt area, so that they showed maximal similarity to the respective burnt plots and had not been downwind of the fire, i. e. they were not likely to have received significant amounts of airborne ash during the fire. The species composition of the unburnt plots is shown in Table 1.

Field sampling: In May 1993 outside each burnt and unburnt subplot (n=30) we defined a 0.1 m⁻² sampling circle. From the unburnt sampling circles we sampled the above-ground biomass including standing litter and the mor humus/peat layer in total. From the burnt dry and moist heath sampling circles we sampled charred plant remnants. From the burnt wet heath sampling circles we sampled the partly burnt plant material, including peat and tufts of *Molinia*. Two 15-cm deep cores of subsoil were taken from each circle in each treatment using a brass auger with a diameter of 4.5 cm.

Laboratory analysis

All samples were dried at 60 °C. For each sampling circle total above-ground dead and living organic material and subsamples of the organic soil layer were comminuted and homogenized by means of a grinding mill, and the organic content of the mor humus/peat and subsoil samples was determined as loss on ignition at 550 °C for 6h. Dry weight of above-ground biomass, of charred remnants of plant, and of organic matter in mor humus/peat and subsoil was expressed in g/m².

Nutrients

For each sampling circle, the content of N, P and K was determined in above-ground biomass plus litter, in charred plant remnants, in the mor humus/peat layer and in the subsoil. For K and P, 3 g of sample was digested in 50 ml 1N HNO₃ (8h; low temperature) and measured using a Tecator Aquatec 5400 Spectrophotometer. For N, the Dumas Method (Leco FP-428) was used. The results were expressed in g/m^2 as mean values of duplicate samples.

The significance of the difference in total and in subsoil organic content, N, P and K, between the burnt and unburnt plot of each heath type was assessed by a *t*-test (n=5) or, in case of unequal variances, by a Mann-Whitney U-test (Fowler & Cohen 1990).

Table 1. Species composition and plant coverage (%) of unburnt plots. Cover data are means of five $1.5 \text{ m} \times 1.5 \text{ m}$ subplots.

	Dry heath	Moist heath	Wet heath
Empetrum nigrum	55	65	
Ammophila arenaria	1		
Plantago maritima	< 1		
Rosa pimpinellifolia	<1		
Salix repens	<1		
Carex arenaria	1	1	<1
Vaccinium uliginosum		20	<1
Genista anglica		<1	<1
Erica tetralix		<1	20
Carex nigra		<1	<1
Molinia coerulea			12
Narthecium ossifragum			5
Myrica gale			4
Potentilla erecta			<1
Juncus squarrosus			<1
Gentiana pneumonanthe			<1
Sieglingia decumbens			<1
Carex panicea			<1
Mosses	85	75	3
Lichens	5	3	4

Results

Organic matter and N, P and K in unburnt dune heath

In the unburnt plots we found between 11677 and 14398 g/m² of organic matter, between 17 and 26 % of this being above-ground biomass plus litter (Table 2). The total amount of nitrogen ranged between 206 and 243 g/m² with 13 - 21 % present in the above-ground biomass plus litter (Table 3). We found 18.7 to 20.4 g/m² of phosphorus, of which only 4 to 6 % was found in the above-ground biomass plus litter (Table 4). Total K

in the plots varied between 26.7 and 35.8 g/m², of which 11 - 14 % was present in the above-ground biomass plus litter (Table 5).

Loss of organic matter by the fire

The total amount of organic matter decreased significantly in all heath types after burning (Fig. 2), with the largest losses of 8583 and 9576 g/m² in the dry and moist heaths, respectively. In both these heath types the losses correspond to about 66 % of the total plant plus soil organic matter (Table 2). In the wet heath the loss was smaller, about 4059 g/m², corresponding to 34.8 % of the total plant biomass plus soil organic matter. In the subsoil alone, i.e. the soil below the organic soil layer, the amounts of organic matter changed much less and declined significantly only in the dry heath (Fig. 2).

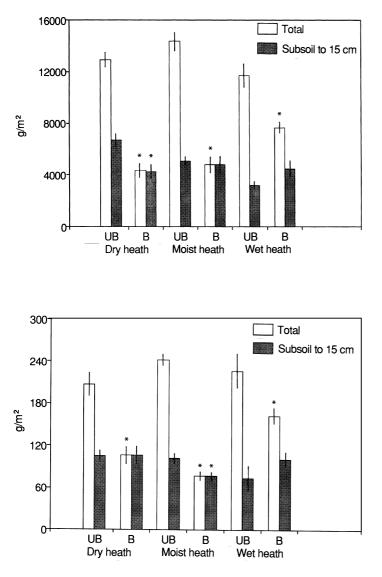
Loss of N, P and K by the fire

The total amount of N decreased significantly in all three heath types (Fig. 3). The loss amounts to 63 - 166 g/m², corresponding to 27.9 - 68.3 % (Table 3). Losses of total P and K were much lower than of N and only significant in dry and moist heath (Figs. 4 and 5). Of P the loss amounts to 2.7 - 4.0 g/m², corresponding to 14.4-19.6% (Table 4). Of K the loss amounts to 3.0-9.1 g/m², corresponding to 11.3-25.4% (Table 5). In all three nutrients the highest and lowest total loss was found in the moist heath and wet heath, respectively, with the dry heath being intermediate.

The nutrient losses found were mostly due to the burning of the above-ground biomass plus litter and of the organic soil layer. In the subsoil alone, the changes in N, P and K were small and mostly insignificant (Figs. 3-5).

	Dry heath		Moist heath		Wet heath	
	UB	В	UB	В	UB	В
Above-ground biomass	2238 ±529		2487 ±339		3052 ±1303	
Tufts + peat, partly burnt						3167 ±1303
Charred remnants		93 ±59		21 ±19		
Organic soil layer	4002 ± 1375		6487 ±1726		5437 ±1551	
Subsoil to 15 cm	6678 ±1134	4242 ±1113	5064 ±591	$4803\pm\!\!305$	$3188\pm\!\!440$	4451 ±1371
Total	12918 ± 1220	4335 ±1156	14398 ± 1503	4822 ±1305	11677 ±1976	7618 ±794
Fire loss		8583		9576		4059
Fire loss (%)		66.4		66.5		34.8

Table 2. Distribution of organic matter (g/m^2) in burnt (B) and unburnt (UB) dune heath vegetation. Means and standard deviations of five replicate samples are given.



Discussion

Organic matter and N, P and K in unburnt vegetation and soil

The contents of organic matter and N, P and K per unit area in the unburnt dune heath at Hansted were similar to those reported from heath vegetation elsewhere. For instance, the amount of above-ground biomass plus litter corresponds well with figures of 2000-2500 g/m² reported for mature *Calluna* heath in Britain by Chapman et al. (1975), but are slightly higher than the amounts reported by Tyler et al. (1973) from coastal *Calluna* and *Erica* heaths in south Sweden. The total amount of organic matter, including the soil organic matter is, however, somewhat lower than on these heaths due to higher content of organic matter in the soil of the Swedish systems.

Fig. 2. Content of organic matter (g/m^2) of unburnt (UB) and burnt (B) dune heath. Total: Above-ground parts + organic soil layer + subsoil to 15 cm. Mean and standard deviation of five replicate samples. *: Fire loss significant (*t*-test or *U*-test; *P*< 0.05).

Fig. 3. Content of total N (g/m^2) of unburnt and burnt dune heath. For explanation: see Fig. 2.

The content of N and P in the above-ground bio-mass plus litter at Hansted is similar to values reported by Robertson & Davies (1965) from a Scottish heath, burned more than 15 years earlier (25 g N/m² and 1.1 g P/m²) whereas the pool of K is somewhat lower (5.9 g/m² in the Scottish heath). But both K and P are higher than in the Swedish systems studied by Tyler et al. (1973). The soil content of N is somewhat lower than, and K and P similar to, the contents found in the Scottish heaths.

Loss of organic matter, N, P and K due to the fire

A prerequisite for the validity of the estimated losses due to the fire in the present study is that vegetation and soil of burnt plots before the fire were similar to those of the unburnt plots with which a comparison was made. Although we can not guarantee an exact similarity, our selection of the reference plots was done in such a way

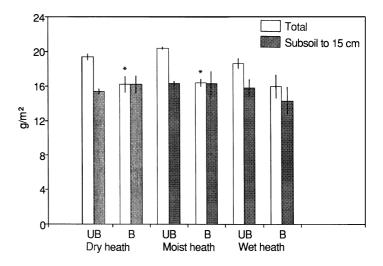


Fig. 4. Content of total P (g/m^2) of unburnt and burnt dune heath. For explanation: see Fig. 2.

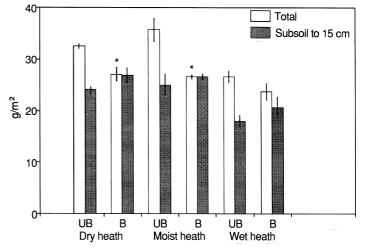


Fig. 5. Content of total K (g/m^2) of unburnt and burnt dune heath. For explanation: see Fig. 2.

that the reference heath should have been as similar as possible to the burnt heath. A potential source of error, not possible to quantify, however, is the possible redistribution of elements during the fire. So, a local loss may have been trapped elsewhere within the burned area or in the unburnt surroundings.

The total loss of organic matter per unit area was a little higher in absolute amounts in the moist than in the dry *Empetrum* heath, but they were similar in relative amounts, and agree well with the loss of 60-68% of C, reported by Allen (1964) for burnt *Calluna*. The dry conditions at the time of the fire caused an almost total loss of above-ground biomass, litter and mor humus. The amount of mor humus lost in the moist heath was larger than in the dry heath because of the deeper mor horizon there.

In the wet *Erica-Molinia* heath, less organic matter was burned, probably due to more moist conditions. The

groundwater level was closer to the surface, reducing the intensity of the fire and the temperature. Some tussocks of *Molinia* survived the fire and resprouted shortly after. The resistance of densely tufted plants, such as *Molinia*, to fire is probably due to oxygen being excluded from the inner part of the tufts, preventing burning (Daubenmire 1968). Additionally, due to the inner part of the tussocks being wet, the temperature was probably kept low enough during the fire to prevent damage to the meristems.

In the period between the fire and the sampling some decomposition took place as indicated by an abundance of fungi, especially of the genus *Anthracobia*, in December 1992. Also, a thin layer of algae was formed in many places, and some vascular plants had also started to grow. It is not possible to estimate the amount of decomposition and growth during this period, but the net change in organic matter is probably negligible.

	Dry heath		Moist heath		Wet heath	
	UB	В	UB	В	UB	В
Above-ground biomass	27±5		32±8		47±7	
Tufts + peat, partly burnt						62 ±25
Charred remnants		<1		<1		
Organic soil layer	74 ±26		108 ± 20		105 ±30	
Subsoil to 15 cm	105 ± 18	106 ±29	103 ±17	77 ±13	74 ±41	101 ±23
Total	206 ± 36	106 ±29	243 ±19	77 ±13	226 ±56	163 ±25
Fire loss	-	100	-	166	-	63
Fire loss (%)	-	48.5		68.3		27.9

Table 3. Distribution of total N (g/m^2) in burnt (B) and unburnt (UB) dune heath vegetation. Means and standard deviations of five replicate samples are given.

Table 4. Distribution of total $P(g/m^2)$ in burnt (B) and unburnt (UB) dune heath vegetation. Means and standard deviations of five replicate samples are given.

	Dry heath		Moist heath		Wet heath	
	UB	В	UB	В	UB	В
Above-ground biomass	1.2 ±0.3		1.1 ±0.3		0.8 ± 0.2	
Tufts + peat, partly burnt						1.8 ± 0.5
Charred remnants		< 0.1		< 0.1		
Organic soil layer	2.8 ± 0.7		3.0 ± 0.7		2.1 ±0.7	
Subsoil to 15 cm	15.4 ±0.6	16.2 ±2.0	16.3 ±0.6	16.4 ±2.9	15.8 ±1.7	14.3 ±3.2
Total	19.4 ±0.7	16.2 ±2.0	20.4 ±0.9	16.4 ±2.9	18.7 ±1.4	16.0 ±2.9
Fire loss		3.2		4.0		2.7
Fire loss (%)		16.5		19.6		14.4

Table 5. Distribution of total K (g/m^2) in burnt (B) and unburnt (UB) dune heath vegetation. Means and standard deviations of five replicate samples are given.

	Dry heath		Moist heath		Wet heath	
	UB	В	UB	В	UB	В
Above-ground biomass	3.8 ±1.2		4.1 ±0.7		3.7 ±0.5	
Tufts + peat, partly burnt						3.0 ± 1.0
Charred remnants		< 0.1		< 0.1		
Organic soil layer	$4.8\pm\!\!1.6$		6.8 ± 1.4		5.0 ± 1.1	
Subsoil to 15 cm	24.1 ±1.3	26.9 ±2.9	24.9 ±3.9	26.7 ±0.9	17.9 ±2.5	$20.6\pm\!\!3.9$
Total	32.7 ± 1.2	26.9 ±2.9	35.8 ±4.8	26.6 ±0.9	26.7 ±2.6	23.6 ± 3.7
Fire loss		5.8		9.1		3.0
Fire loss (%)		17.7		25.4		11.3

The loss of N, P and K, absolutely as well as in %, decreased in the same order as the loss in organic matter: moist heath > dry heath > wet heath. The absolute and relative losses of the three elements decreased in the following order: N > K > P. This order of loss corre-

sponds with previous observations by Allen (1964) for a fire in a peat ecosystem at Moor House, even though the losses in K and P in the present study was considerably larger than those found by Allen. The order of loss also corresponds with reported losses by Evans & Allen

(1971) after controlled experimental burning of Calluna.

The loss of N, P and K could largely be ascribed to burning of the above-ground biomass plus litter and the mor humus/peat layer, while the loss from the mineral subsoil was mostly insignificant.

A possible analytical source of error, according to Emmer & Verstraten (1993), relates to the digestion method used; this has not been considered in the evaluation of the present results. This source of error may be relevant in the comparison of the heath types, due to the difference between the organic content of their respective organic soil layer (see above), but probably not in the comparison of the burnt and unburnt subsoils, which were very similar in organic content (range 1.4-3.7%).

Processes in nutrient loss

During a heath fire nutrients may be lost by volatilization and transport of ash by the smoke. After the fire further losses may occur through erosion or leaching (Gimingham 1981; Groves 1981; Riis-Nielsen et al. 1991). According to Evans & Allen (1971) the loss by volatilization in a heath fire is positively correlated to the temperature of the fire. The temperature reached at the Hansted fire is not known, but the strong effect of the fire on the vegetation and organic soil layer as well as scattered occurrence over the burnt area of calcite boulders, blasted by the fire, indicate that the temperature was high. Therefore, the main part of the nutrients lost is probably accounted for by volatilization.

Observations in the field showed that some of the nutrients were lost or redistributed by erosion. On slopes ash was washed downwards and accumulated at footslopes. On uneven, exposed ground ash was removed by wind and accumulated on lee sides.

The amount of the nutrients lost by leaching during the period between the fire in August 1992 and the sampling date in May 1993 is not known. According to Allen et al. (1969) leaching is largely prevented by a surface organic layer, even of a thickness of only 1 cm. In the dry and moist heath studied here the mor humus layer was completely burned, but the content of organic matter left in the subsoil (about 3%) probably reduced leaching to some extent. Some nutrients may also have been fixed in the hard fire crust formed on the surface.

Loss and regeneration of organic matter and nutrients in the burnt dune heath

The total area of the burnt dune heath at Hansted amounts to 175 ha. From field inspections and air photographs taken before the fire, it was estimated, that the three investigated heath types occupied the burnt area in about equal proportions. Even recognizing the simple sampling regime of this study, a multiplication of the total area burnt by the average loss of organic matter, N, P and K from the three heath types may give a rough estimate of the magnitude of the total loss from the burnt heath. Based on this calculation roughly 13000 tons of organic matter (about 6500 tons of C) was lost, together with 192 tons of N, 10 tons of K, and 6 tons of P.

For the revegetation of the burnt area and re-establishment of the former dune heath vegetation and soil, nutrient loss of such magnitude may be expected to have serious consequences. Among the processes in rebuilding of the stock of nutrients dry and wet atmospheric deposition as well as N-fixation are likely (Gimingham 1972). Hovmand et al. (1994) reported on the wet and dry atmospheric deposition in a mixed forest-arable land system in northwest Jutland during the years 1985-92 and found an average total deposition of 20 kgáha^Dáyi^{D1} of N and 5 kgáha^{D1}áyi^{D1} of K. From an input of this magnitude alone it will take about 50 years to replace N loss in dry heath, 83 years in moist heath and 32 years in wet heath. Replacement of K will take 12 years in dry heath, 18 years in moist heath and six years in wet heath. For P a total atmospheric deposition in Denmark and surrounding waters of about 0.12 kgáha^{D1}áyi^{D1}has been estimated (Hovmand et al. 1993). From this input it will take about 276 years to replace P in dry heath, 333 years in moist heath and 225 years in wet heath.

In this estimate of regeneration time gain by N-fixation as well as loss by leaching has not been considered. Input by N-fixation particularly by symbiotic microorganisms, will probably play a significant role (cf. Larcher 1975). Occurrence since 1993 over the burnt dry and moist heath of *Fabaceae* (*Genista anglica, Lotus corniculatus* etc.), well equipped with root nodules indicate, that symbiotic N-fixation has started. Neither has a possible gain from weathering of the exposed mineral soil been considered. Through extraction with HNO₃ only part of the total P and K stocks are extracted. Besides quartz, the dune sand of Jutland contains amounts of felspar (Warming 1907), from which K will be freed by weathering and taken up by the plants.

Concluding remarks

The data presented in this study are based on a limited sampling regime. Possible spatial variation within each heath type and possible redistribution of elements during and after the fire has not been taken into account, and, most importantly, we have no exact data on the situation before the fire. In our opinion, however, the data presented leave little doubt about the magnitude of the fire loss of organic matter and nutrients, nor about the long-lasting consequences of uncontrolled fire for the nutrient status of the burnt dune area.

The actual consequences of the nutrient loss for the revegetation of the dune heath at Hansted will be studied in years to come. By summer 1995 the burned wet heath already appeared almost as luxuriant as in the unburnt area. So, in the wet heath there seem to be enough nutrients left for vegetation to develop. The moist and the dry heath were far behind in 1995. This may however, be additionally explained by the severe destruction of vegetation and seed bank during the fire.

In a nature conservation management context the results of the study point at the importance of carrying out burning treatment in heathland within controlled frames. It is especially important to choose the optimal combination of wind, dry above-ground biomass and moist ground, so as to avoid burning of the mor humus layer and thereby retaining sufficient amounts of nutrients (as well as living seeds and below-ground plant parts) to ensure a fast recovery of the vegetation.

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References

- Allen, S.E. 1964. Chemical aspects of heather burning. J. Appl. Ecol. 1: 347-367.
- Allen, S.E., Evans, C.C. & Grimshaw, H.M. 1969. The distribution of mineral nutrients in soil after heather burning. *Oikos* 20: 16-25.
- Alstrup, V. & Vestergaard, P. 1996. Branden i Hansted-Reservatet i August 1992. Naturoverv@gningsrapport. Milj¿- og Energiministeriet, Skov- og Naturstyrelsen. K¿benhavn.
- Chapman, S.B., Hibble, J. & Rafarel, C.R. 1975. Net aerial production by *Calluna vulgaris* on lowland heath in Britain. *J. Ecol.* 63: 233-258.
- Christensen, S.N. 1989. Floristic and vegetational changes in a permanent plot in a Danish coastal dune heath. *Ann. Bot. Fenn.* 26: 389-397.
- Daubenmire, R. 1968. Ecology of fire in grass-lands. In: Cragg, J.B. (ed.) Adv. Ecol. Res. 5: 209-266.
- Emmer, I.M. & Verstraten, J.M. 1993. Applicability of HNO₃-H₂O₂ digestion for elemental analysis of organic matter in mor humus forms. *Z. Pflanzenernaehr. Bodenkd.* 156: 507-514.
- Evans, C.C. & Allen, S.E. 1971. Nutrient loss in smoke

produced during heather burning. Oikos 22: 149-154.

- Fowler, J. & Cohen, L. 1990. *Practical statistics for field biology*. John Wiley & Sons. Chichester.
- Gill, A.M. & Groves, R.H. 1981. Fire rŽgimes in heathlands and their plant-ecological effects. In: Specht, R.L. (ed.) *Heathlands and related shrublands. Ecosystems of the World 9B*, pp. 61- 84. Elsevier, Amsterdam.
- Gimingham, C.H. 1972. *Ecology of Heathlands*. Chapman and Hall, London.
- Gimingham, C.H. 1981. Conservation: European heathlands. In: Specht, R.L. (ed.) *Heathlands and related shrublands*. *Ecosystems of the World 9B*, pp. 249-259. Elsevier, Amsterdam.
- Groves, R.H. 1981. Nutrient cycling in heathland. In: Specht, R.L. (ed.) *Heathlands and related shrublands. Ecosystems of the World 9B*, pp. 151-163. Elsevier, Amsterdam.
- Hansen, K. 1969. Edaphic conditions of Danish heath vegetation and the response to burning-off. *Bot. Tidsskr.* 64: 121-140.
- Hovmand, M.F., Grundahl, L., Runge, E.H., Kemp, K. & Aistrup, W. 1993. *Atmosfærisk deposition af kvælstof og fosfor*. Vandmilj¿planens OvervŒgningsprogram 1992. Faglig rapport fra DMU, no. 91. Danmarks Milj¿unders¿gelser, Roskilde.
- Hovmand, M.F., Andersen, H.V., Bille-Hansen, J. & Ro-Poulsen, H. 1994. Atmosfærens stoftilførsel til danske skovøkosystemer. Faglig rapport fra DMU, no. 98. Danmarks Milj¿unders¿gelser, Roskilde.
- Larcher, W. 1975. *Physiological plant ecology*. Springer-Verlag, Berlin, Heidelberg, New York.
- Nielsen, H. & Jensen, J. 1963. Hansted-Reservatet. Dan. Naturfredningsfor. Årsskr. 1963: 43-49.
- Riis-Nielsen, T., S¿chting, U., Johansson, M. & Nielsen, P. 1991. Hedeplejebogen, de danske heders historie, pleje og udforskning. Milj¿ministeriet, K¿benhavn.
- Robertson, R.A. & Davies, G.E. 1965. Quantities of plant nutrients in heather ecosystems. J. Appl. Ecol. 2: 211-220.
- Tyler, G., Gullstrand, C., Holmquist, K.-•. & Kjellstrand, A.-M. 1973. Primary production and distribution of organic matter and metal elements in two heath ecosystems. *J. Ecol.* 61: 251-268.
- Warming, E. 1907. Dansk Plantevækst. 2. Klitterne. Gyldendalske Boghandel, Nordisk Forlag, K¿benhavn, Kristiania.

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