**Modern pollen-vegetation relationships in traditionally mown and unmanaged boreal rich-fen communities in central Norway**

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Keywords:

Plant-pollen relationship, pollen representation, pollen surface samples, rich fen, boreal vegetation zone Norway, haymaking

# Abstract

Knowledge of the relationship between vegetation and modern pollen deposition is necessary to improve the interpretation of fossil pollen samples. We compared the cover of plant species and the modern pollen deposition in surface moss samples in 49 plots in rich-fen vegetation from the boreal vegetation zone in Norway in two areas (one oceanic and one more continental). These rich fens were used for traditional hay cutting until ca. 1950. Three management regimes are used: 1) biennial mowing2) quadrennial mowing and 3) unmown. The unmown areas were traditional hay fens, with no management since the 1950s. Of the 89 plant taxa and corresponding 65 taxa of pollen and spores, 29 and 22, respectively, were sufficiently represented in both vegetation and as pollen, to allow direct comparisons of the two data sets. Most of the plant and pollen taxa were found in the plots from both study areas and in plots with different mowing frequency. Therefore, quantitative differences in vegetation cover and pollen percentages were the main focus in this investigation of plant-pollen relationships in mown and unmown vegetation. The relative difference in plant cover was largest between biennially and unmown plots. 12 species showed a significant positive correlation with difference in plant cover between mown and unmown areas (p<0.05; Wilcoxon signed rank test), most pronounced for *Molinia caerulea* (most common in unmown plots), and *Carex dioica* and *Thalictrum alpinum* (most common in mown plots). A significant positive plant-pollen correlation (Spearman rank-correlation) was found for 10 pollen taxa. *Thalictrum alpinum* is a very good pollen indicator, and Cyperaceae, *Eriophorum*-type and *Pedicularis*-type are good pollen indicators of mowing. Poaceae/*Molinia caerulea* and *Succisa pratensis* are negatively correlated with mowing. The impact of mowing on species composition was similar in both study areas. Mown and unmown areas were differentiated in the vegetation data and could be identified by modern pollen data. These results will improve the interpretation of past land-use practices using pollen analysis of rich-fen vegetation.

# 1. Introduction

All over northern Europe fens have, for centuries, been important for production of hay for winter fodder. The fertile infields were often of limited extent, so the outfields were of great importance for haymaking, grazing and summer farming (e.g. Ellenberg, 1988; Hjelle et al., 2012; Solem et al., 2012). This long-term regular harvesting has influenced the fens, turning large areas into open semi-natural landscapes. The traditional use of the fens ceased many decades ago in most countries in western and central Europe, including southern Fennoscandia. In parts of central boreal Norway the traditional use of fens, including our study areas, lasted until the 1950s (Moen, 1990; Tretvik and Krogstad, 1999).

Cultural landscapes leave contemporaneous traces in the form of pollen assemblages in accumulating deposits. Pollen analysis is thus a widely used approach for reconstructing the history of past cultural practices and landscapes (e.g. Berglund, 1991). Investigations of the modern local plant-pollen relationship in areas with documented land-use regimes are a basis for reconstructing these practices back in time. The taphonomy of pollen in modern moss samples is comparable to pollen analytical data from peat cores. Pollen assemblages from vegetation dominated by dwarf-shrubs, graminoids or herbs reflect local sources of non-tree pollen (NAP) and thus small-scale vegetation variations (Hjelle, 1999a; Bunting 2003; Bunting and Hjelle, 2010; Pardoe, 1996). The relationship between number of deposited pollen grains and the corresponding plant cover is complex (e.g. Sugita, 1994), and the pollen taphonomy must be taken into account when interpreting pollen assemblages (e.g. Fægri and Iversen, 1989).

Mowing leads to disturbance and changes in available resources and competition between species (Crawley, 1997; Grime, 2001). Species resilient to mowing will be favoured and plants with low and rosette growth forms, with meristems close to the ground or clonal growth, are tolerant to mowing (Klimešová et al., 2008). In addition, stress-tolerant species are less affected by mowing (Grime, 2001; Øien & Moen, 2001). Thus mowing affects the composition of vegetation and species abundance. For example the plant cover of *Thalictrum alpinum* and several *Carex* and *Eriophorum* species increases with mowing in boreal fens (Moen, 1995).

In order to reconstruct past vegetation communities from pollen data the relationship between the vegetation community and the pollen produced and deposited within it must be known. If good pollen–plant relationships exist and the plant community is reflecting a type of land use today, pollen types/species may be identified as indicator taxa for that land-use (cf. Behre 1981). The present study aims to produce indicator taxa for mown fens which may be of international value when interpreting pollen diagrams. Also the whole pollen assemblage may be used in a comparative approach (Birks and Birks, 1980) to aid in the identification of past vegetation communities or land-use practices. The results from the present study will be combined with plant-pollen data from mown and grazed vegetation types in Western Norway (Hjelle, 1999a) to form a larger data set. This data will aid the interpretation of possible land-use practices (e.g. Gaillard et al., 1994; Hjelle, 1999b) for pollen diagrams from the rich fens in Tågdalen and Sølendet. The data set should also be useful as part of future pollen–plant databases, e.g. the European Pollen Database (http://www.europeanpollendatabase.net/index.php).

The aim of the present study is to assess the modern pollen–plant relationships in rich fens in two study areas. The areas are situated at the transition between the middle and northern boreal vegetation zones, but in different vegetation sections (regional differences oceanity–continentality, Moen 1999). Both study areas were used for traditional haymaking until ca. 1950. Regular mowing (with a scythe) of permanent plots was reintroduced in early 1970s and they have been mown regularly for nearly 40 years. The plant communities vary between the study areas, but with the same dominant species, where the impact of mowing on different species is similar (Moen et al., 2012). Further, differences between mowing regimes and unmown areas facilitate various species, giving mainly quantitative differences in plant cover (Moen et al., 2012). We study the correlation between the plants growing in fen vegetation and pollen deposited on a local scale. Three hypotheses are thus put forward: 1) There is a close connection between the taxa in fen vegetation and local pollen deposition, 2) There are small differences in local pollen–plant relationships between the two studied rich fens (regional differences), and 3) Differences between mown and unmown vegetationcan be detected from the contemporary pollen assemblages. The modern plant–pollen relationship in fens will provide a basis for interpretations of palaeoecological investigations of past land-use in the study areas.

# 2. Study areas and plant communities

The two study areas (Fig. 1) are both situated at the transition between the middle boreal and northern boreal vegetation zones of central Norway (Moen, 1999). Tågdalen is an oceanic inner-fjord area nature reserve and Sølendet is a continental nature reserve. Tågdalen is part of the markedly oceanic vegetation section while Sølendet is situated on the transition between the indifferent and slightly continental vegetation sections (sensu Moen, 1999). The 20 localities with 49 study plots presented in this paper were established as permanent plots 40 years ago, and vegetation and plant populations dynamics are described in a number of papers (e.g. Moen, 1990, 1995, 2000; Aune et al., 1996; Moen et al., 1999, 2012, 2015; Øien and Moen, 2001; Sletvold et al., 2010; Lyngstad et al., 2016). 10 localities are situated along a line over a distance of 940 m in Tågdalen (Fig. 2a). In Sølendet the 10 localities are situated in an area of just below 1 km2 (Fig. 2b).

The duration of the growing season is similar in both areas, from the end of May until the first part of September. Tågdalen has an oceanic climate with high annual precipitation and a thick, long-lasting snow cover, while Sølendet has a more continental climate with less precipitation and cold winters (Table 1). The distance between the study areas is 145 km. In both areas calcareous Cambro-Silurian bedrock (Sigmond et al., 1984) is overlaid with base-rich till (Follestad, 1995).

The dominant rich-fen vegetation at Tågdalen and Sølendet forms a mosaic with birch woodland (*Betula* *pubescens*). Sloping fens (slope >3°) cover large areas. At Tågdalen the slopes are between 3 and 12° and at Sølendet 3 to 5°. The depth of the underlying peat layer exceeds 50 cm at Tågdalen, and 20 cm at Sølendet. The study areas have the same historical land-use, where the traditional hay cutting declined during the 1930s, and ended in the 1950s. Experimental scything (hereafter called mowing) of permanent plots started in 1973 and was carried out in August, allowing flowering, seed production and dispersal to take place for important species. The localities were established in homogenous fen areas, and the studied plots have been mown regularly biennially or quadrennially since 1970s, or they have been left unmown for ca. 60 years. The hay crop of the studied communities was estimated to about 110 g/m2 and 140 g/m2 (dry matter) in plots mown biennially and quadrennially, respectively (Moen, 1990; Moen et al., 2015; Lyngstad et al., 2016). Biennial mowing represents the traditional practice, where the harvest output was maximized in relation to labour invested. Quadrennial mowing is a possible equivalent to the mowing frequency during periods of extensive mowing, and during the period when hay-cutting was declining.

The terminology of mires follows the Fennoscandia tradition in mire ecology (*sensu* Sjörs, 1948), separating units related to the main local vegetation gradients. Rich fens are peat-forming mire sites with characteristic vegetation dominated by brown mosses (e.g. *Campylium stellatum*), and with base-rich water (pH above 6). Lawn communities of extremely rich fen vegetation (Sjörs, 1948; Moen et al., 2012; Jiménez-Alfaro et al., 2013) cover the study localities. Phytosociological analyses of the permanent study plots were included in multivariate analyses of 134 rich fen plots from the two study areas (Moen et al., 2012; the plots in this paper mainly belong to their communities II – IV). In the phytosociological classification system (e.g. Dierssen, 1982; Rybniček, 1985), the studied mires belong to the alliances Caricion davalianae Klinka 1934 at Tågdalen, and at Sølendet Caricion atrofuscae Nordh. 1936. The mean number of species in plots with an area of 12.5 m2 ranged between 30 and 37 (Table 2 and Supplementary A in Moen et al., 2012). The most common vascular plant species in both areas are *Andromeda polifolia*, *Dactylorhiza* spp., *Equisetum palustre*, *Euphrasia wettsteinii*, *Parnassia palustris*, *Pinguicula vulgaris*, *Potentilla erecta, Selaginella selaginoides, Succisa pratensis, Thalictrum alpinum, Tofieldia pusilla, Carex dioca, C. flava, C. hostiana, C. lasiocarpa, C. panicea, C. rostrata, Eriophorum angustifolium, E. latifolium, Molinia caerulea* and *Trichophorum cespitosum*. The bottom layer was dominated by *Campylium stellatum*, with *Aneura pinguis, Barbilophozia rutheana, Fissidens adianthoides, Gymnocolea borealis* and *Scorpidium cossonii* occurring in all or a large majority of the plots*.* At Tågdalen the western/lowland species *Drosera longifolia, Narthecium ossifragum* and *Schoenus ferrugineus* were present in some plots. At Sølendet a number of alpine/inland species were present, the most common being *Pedicularis oederi, Saxifraga aizoides* and *Kobresia simpliciuscula.*

# 3. Material and methods

## 3.1. Research design and vegetation plots

Ten localities with permanent experimental plots with and without mowing within each study area in similar vegetation units of rich fens were chosen for the present research design (Fig. 3). Each locality consisted of two or more permanent plots of 2.5×5 m (total 49 plots). The field work for this study was carried out in 2008. Inside each permanent plot one sample plot of 1×1 m was placed in the centre, thus reducing potential edge effects. The minimum distance from a sample plot to an area with different management regime was 0.75 m. The minimum distance between the border of two sample plots was 1.5 m. Initial studies of different sizes of sample plots (from 0.25 m2 to 4 m2) revealed that intermediate-sized plots of 1 m2 were representative of the plant composition of the stand (e.g. Mueller-Dombois and Ellenberg, 1974).

Three management regimes have been maintained since the 1970s: 1) biennial mowing, 2) quadrennial mowing and 3) unmown since 1950s (Fig. 3). Management regimes 1) and 3) were present in all investigated localities. Six localities at Tågdalen and three localities at Sølendet included management regime 2). For management regime 1) mowing was done one year prior to investigation of plant cover and sampling; for management regime 2) mowing was done three years prior to investigation. The intensive mowing practice 1) represents the traditional mowing, and 2) reflects extensive mowing.

Plant nomenclature follows Lid and Lid (2005) for vascular plants and Frisvoll et al. (1995) for mosses (Table 2). The species cover was visually recorded using the following cover classes [percent range of cover – cover class mean]: 1 [1-2 plants – 0,25%], 2 [0-1% – 0,5%], 3 [1-2,5% – 1,75%], 4 [2,5-5% – 3,75%], 5 [5-10% – 7,5%], 6 [10-20% – 15%], 7 [20-30% – 25%], 8 [30-40% – 35%] and so on up to 14. For each taxon the mean plant cover from each management regime was calculated from the average of cover class means from all plots of similar management regime (Table 3). Species recorded in the vegetation are equivalent to the taxa included in “local terrestrial pollen” (see 3.3).

## 3.2. Surface pollen sampling

Moss polsters were collected from the sample plots as traps for pollen deposition (e.g. Hicks, 1977; Hjelle, 1998). Each moss sample consisted of five merged sub-samples, one from the centre of the plot and four in each direction out from the centre and half way to the sample plot border (Fig. 3). The result, a minimum distance of 1 m between a pollen sub-sample and different land-use, reduces the risk of strong plot-edge effects. If moss was absent, sampling was done as close as possible to these points. The modern analogue to a fossil sample from a peat core is a single moss sample, but collecting several sub-samples reduce the potential effect of outliers and of micro-scale differences in pollen content in moss polsters from neighbouring samples (Pardoe, 1996; Hicks, 2001). Moss samples were collected in late July 2008. The moss sample consisted of the whole moss turf from the top down to the soil surface. Thus several years of pollen deposition were probably included in the sample (e.g. Mulder and Janssen, 1999; Pardoe et al., 2010), integrating observed year to year fluctuations in fertility and pollen production (Hicks, 2001; Nielsen et al., 2010). Such samples are comparable to the vegetation community when single-year effects can be evened out, as well as to a peat pollen sample reflecting several years. By far the most frequently sampled moss in all localities was *Campylium stellatum*. Among other common species were *Scorpidium cossonii, Scorpidium scorpioides, Drepanocladus* spp. *and Sphagnum* spp.

## 3.3. Pollen processing and analysis

Moss samples were thoroughly rinsed through 450 µm sieves to remove the moss. Pollen preparation of the material passing through the sieve followed standard methods, with KOH and acetolysis (Fægri and Iversen, 1989), but without hydrofluoric acid treatment because the minerogenic content was negligible in all samples. The residue was mounted in glycerol for pollen counting. At least 500 terrestrial-plant pollen (range 563-1349) including more than 100 local terrestrial pollen (range 164-724) were counted per sample. Taxa were identified to the lowest possible taxonomic level by the use of keys (Moe, 1974; Fægri and Iversen, 1989; Moore et al., 1991; Beug, 2004) and the modern pollen reference collection at the University of Bergen. Pollen data-analysis was made using TILIA (Grimm, 1990). When possible, Cyperaceae pollen was identified to *Dulichium*-type, representing *Carex* spp., and *Eriophorum*-type pollen (sensu Fægri and Iversen, 1989).

The percentage calculation sum is the sum of local terrestrial pollen (∑ LP). The pollen calculation sum for other pollen and microfossils is ∑P+X, where X is the microfossil in question. Local terrestrial pollen and spores represent pollen and spores from taxa belonging to the studied rich fen vegetation (e.g. Janssen, 1966). In this sense extra-local taxa are only or mainly recorded as growing on nearby mineral soil, such as Ericaceae, *Calluna vulgaris*, *Juniperus communis*, *Salix* spp. and *Betula* spp., which occur at low abundances or are absent in the fen plots (Moen et al., 2012). Pollen from *Betula* spp. is mainly a part of the regional pollen deposition, along with pollen from species not represented in the fen localities, like *Pinus sylvestris*. As the yearly moss growth rates may vary between and within moss taxa, as well as with mowing (Moen, 1995), the pollen trapping ability and concentration values will not be directly comparable between samples. Therefore percentages based on the sum of local pollen were used. The use of local terrestrial pollen as the calculation basis will minimize the problems of absolute variations in extra-local and regional pollen related to percentage calculations. Such variations are not related to the vegetation on the fen nor the local mowing.

## 3.4. Data analyses

In the data analysis comparing vegetation and pollen data, only the local terrestrial taxa are included. A comparison of species occurrences and pollen data requires comparable taxonomic groups. Therefore, the plant species were grouped according to the pollen taxa that represent them. Analyses of some species were carried out for both single plant species and for the corresponding palynological taxonomic groups, see Table 2.

### 3.4.1. Gradients in the data - ordination

Principal components analyses (PCA) implemented in CANOCO for Windows 4.5 (ter Braak and Šmilauer, 2002) was used to ordinate the 49 vegetation plots according to the pollen taxa they contained. Species centring with square-root transformed data was used. Species scores were divided by their standard deviation to obtain inter-species correlations. Pollen percentages (square-root transformed) from the same plots and taxa and the three management regimes were added as passive samples and environmental variables, respectively, and projected on the ordination diagram. The results were drawn using Canodraw for Windows 4.5 (Fig. 4a and b).

### 3.4.2. Paired comparisons from mown and unmown vegetation

A paired test was carried out comparing the vegetation composition in pairs of mown-unmown plots within each locality. The Wilcoxon signed rank test was used for the nonparametric data to identify taxa with a statistically significant difference in mean percentage plant cover between land-use regimes. It was run in R version 2.11.1 (R Development Core Team, 2010). An exact Wilcoxon signed-rank test was chosen as the grouped data-set has a potential for ties for the pairs. The data from Tågdalen and Sølendet were analysed jointly providing a maximum of 20 pairs. Three sets of tests were run: 1) plots from biennially mown and unmanaged plots, 2) Plots mown biennially and quadrennially, 3) Plots mown quadrennially and unmown plots. Taxa with plant cover registrations in ≥6 plots were included.

### 3.4.3. Analyses of differences in species plant cover between management regimes

The indices of difference (ID), equation (1), show whether and how often each taxon increases, displays no change, or decreases in cover from the unmown to the mown pairs of plots:

(nA(1)+nB(0)+nC(-1)) (nA+nB+nC)-1 ⇨ (nA-nC) (nA+nB+nC)-1 (1)

Where nA is the number of pairs of plots where each taxon has larger vegetation cover in the mown plot than in the unmown plot, nB is the number of pairs of plots with no difference, and nC displays the number of pairs of plots where the taxa has lower vegetation cover in the mown plot than in the unmown plot.

### 3.4.4. Correlation between vegetation and pollen data

To investigate whether plant cover is correlated with the corresponding pollen percentages in the surface samples, the nonparametric Spearman rank-correlation coefficient, ρ (rho) (e.g. Webb et al., 1978), was used to measure statistical dependence between pollen percentages and plant cover for taxa in all plots for the three management regimes. The test was carried out in R version 2.11.1 (R Development Core Team, 2010), examining the absolute percentage differences of paired plots. The statistical significance level was set to 0.05. The data-set of 49 plots from both Tågdalen and Sølendet was used. The correlation test was run for only one study area when plant cover or pollen was absent from the other area. The tests were run for all taxa recorded in ≥6 pairs of plots in each paired comparison.

### 3.4.5. Indices of pollen association and representation

Based on presence/absence data of vegetation and pollen from all investigated plots, calculations of indices of association with coincidence (A), over-representation (O) and under-representation (U) (Davis, 1984; Hjelle, 1997; Bunting, 2003; Mazier et al., 2006) were made for each taxon. The definitions of the three indices are:

A = B0 (P0 + P1 + B0)-1; O = P0 (P0 +B0)-1; U = P1 (P1 + B0)-1 (2)

where B0 is the number of plots where the pollen or spore type and the associated taxon is present, P0 represents the number of plots where the pollen or spore type is recorded but this taxon is not present in the vegetation, and P1 is the number of plots where the pollen or spore type is absent in the surface sample but the taxon is present in the vegetation. Based on the indices, taxa were grouped into associations: strongly associated types (SAT, A> 0.65), associated types (AT, A between 0.65 and 0.5), weakly associated types, (WAT, A<0.5, positive O and U), over-represented type (ORT, A<0.5, U=0), under-represented type (URT, A<0.5, O=0) and unassociated type (UT, A=0, positive O and U).

# 4. Results

89 plant species (77 vascular plant species and 12 moss species) were recorded from Tågdalen and Sølendet. Taxa present in both the vegetation data-set and the pollen and spore analyses wereconsidered (Table 2). Thus 57 vascular plant taxa were represented in the pollen assemblages and grouped into 26 pollen taxa (Table 2).

Taxa only recorded in the vegetation, like *Dactylorhiza* spp., *Equisetum* spp. and most moss species, and taxa only identified in the pollen record, e.g. several tree species, were excluded.

## 4.1. Vegetation data

The most frequent species in both study areas were: *Trichophorum cespitosum* ssp*. cespitosum,* *Thalictrum alpinum*, *Molinia caerulea, Potentilla erecta,* *Eriophorum latifolium, Carex flava, C. panicea, C. rostrata* and *Succissa pratensis* (Table 3)*.* *Molinia caerulea, Thalictrum alpinum*, *Eriophorum latifolium, Betula nana* and several *Carex* taxa displayed a large difference in plant cover between biennually mown and unmown plots (Table 3).

Twelve plant taxa had significantly different cover values in biennially mown and unmown plots (Table 4 a). Highest cover values in biennially mown plots were found for: four *Carex* species, *Thalictrum alpinum, Pinguicula vulgaris, Eriophorum latifolium*, *E. angustifolium* and *Pedicularis palustris.* *Molinia caerulea* was much more abundant in unmown plots, and this was the only plant taxon displaying a difference in plant cover between all the management regimes. *Betula nana* and *Succisa pratensis* were more abundant in unmown plots than in biennially mown plots. Combining the plant taxa into pollen groups resulted in *Dulichium*-type (i.e. *Carex* spp.) displaying a difference in vegetation cover between all management regimes, whereas *Eriophorum*, Cyperaceae and Poaceae only displayed a difference between the two mown and the unmown plots (Table 4 b). The difference in plant cover in biennially mown and unmown plots represented the main variation in plant cover in fen vegetation (Table 4 a), most pronounced for *Molinia caerulea, Carex dioica* and *Thalictrum alpinum*.

## 4.2. Ordination of vegetation and pollen data

The first two axes of the PCA-ordination of the 49 plots (Fig. 4) had eigenvalues of 0.25 and 0.23 respectively. The other axes had eigenvalues lower than 0.10 (not shown). The vegetation samples representing different mowing frequencies were spread along the whole range of the first axis (Fig. 4a), but were separated on the second axis, reflected in both the dispersal of samples and the mean scores for the environmental variables. On axis 2 the variable representing biennial mowing had a high negative mean score, while quadrennial mowing had a small negative mean score and unmown had a high positive mean score. The majority of pollen samples (passive data) had low scores on both axes. The pollen samples showed a similar pattern as the vegetation samples, where the pollen samples from the unmown plots to a large extent are separated from the plots with the two mowing frequencies, most pronounced for unmown and biennially mown plots.

*Pedicularis*-type had a negative score on the first axis of the PCA ordination of plant taxa (as pollen taxa groups, Fig. 4b) whereas *Potentilla erecta*, *Rhinanthus*-type and *Succisa pratensis* hadhigh scores. *Dulichium*-type, *Thalictrum*, Cyperaceae and *Eriophorum* had lowest scores on the second axis whereas Poaceae had the highest score followed by *Sphagnum*.

## 4.3. Pollen data in relation to management regimes

Of the 65 palynological taxa found at Tågdalen and Sølendet, only 26 pollen and spore taxa represented the investigated, contemporary vegetation (Table 2). Pollen taxa present in >4 plots are displayed in Table 5.

At Tågdalen *Thalictrum* and *Eriophorum*-type pollen had their largest pollen percentages in mown plots, especially seen for *Thalictrum* in biennially mown plots in Tågdalen. Poaceae and *Potentilla*-type had largest pollen percentages in unmown plots. *Dulichium*-type pollen had largest pollen percentages in unmown plots, but in Tågdalen the differences are small. Cyperaceae had generally small relative changes to no differences between management regimes, and the standard error is large. *Succisa pratensis* had also small to no differences between management regimes in Tågdalen, where at Sølendet the largest pollen percentages were registered in unmown plots. *Pedicularis*-type pollen had a general low pollen presence. The *Pedicularis*-type pollen percentages were slightly higher in biennially mown than in unmown plots in Sølendet, and where absent in unmown plots in Tågdalen.

From Sølendet only three plots represent quadrennially mown fen, giving a potential for uncertainties regarding the result. In Sølendet the pollen data does not always follow the trend from Tågdalen, as for *Thalictrum* and Poaceae.

## 4.4. Pollen-vegetation relationships

Spearman rank-correlation coefficients relating plant cover to pollen percentages are presented in Table 6, along with the indices of association and association types which reflect relationships between presence/absence of plants and their pollen. As *Molinia* *caerulea* formed the majority of the Poaceae plant cover (Table 3), both *M.* *caerulea* and Poaceae plant cover were individually correlated to the Poaceae pollen data. *Eriophorum*-type pollen was compared to both *Eriophorum* spp. and *Eriophorum*-type vegetation.

Most of the strongly associated plant-pollen types (SAT) and the associated plant-pollen type (AT) had a statistically positive correlation between plant cover and pollen percentages (Table 6). These were Rosaceae, *Potentilla*–type, *Pedicularis*, *Thalictrum*/*Thalictrum alpinum*, *Selaginella selaginoides*, *Eriophorum*-type/*Eriophorum* spp., Poaceae/*Molinia caerulea* and Cyperaceae. *Succisa pratensis* and *Menyanthes trifoliata* had significant plant-pollen correlations, but had weak associations with their corresponding pollen types as they displayed a trend towards pollen under-representation.

The remaining taxa in Table 6 did not have a significant relationship between the vegetation cover and pollen percentages. However, common species in the vegetation, such as Poaceae, *Eriophorum* spp. and *Carex* spp., were also common in the pollen assemblages, reflected in a strong association. Underrepresented taxa were insect pollinated species which were poorly presented in the pollen assemblages, but they were present in the vegetation when present as pollen, e.g. *Drosera rotundifolia*-type, *Bistorta vivipara*-type and *Saxifraga oppositifolia*-type.

# 5. Discussion

Rich fen vegetation is widely distributed in Europe. Vegetation plots from our two study areas are included in a European study, and are classified as boreal fens (Jiménez-Alfaro et al., 2013, cluster 3a). The relationships between vegetation and pollen assemblages in our two fen areas add to the database of surface-pollen samples from a variety of vegetation types and land-use regimes (e.g. Gaillard et al., 1994; Hjelle, 1999a; Mazier et al., 2006; Ejarque et al., 2011; Waller et al., 2017). These data contribute to modern-pollen studies and long-term investigations. However, there are few studies that consider rich fens. An exception is the nemoral rich fens of Waller et al. (2005, 2017) which include a number of species in common with our studied fens; e.g. *Potentilla erecta*, *Carex nigra*, *C. panicea*, *C. rostrata* and *Molinia caerulea*. These are among the most common species in our two study areas as well as in the two study areas in southern and eastern England. The annually cut “Sedge fen” included in Waller et al. (2017) has many features in common with our fens, and represent a community with close relationship between vegetation and local pollen deposition.

Comparable to our study, Waller et al. (2017) found that nemoral rich fen vegetation subject to different types of management, including different cutting regimes, produce distinctive pollen signatures. Their study area is in nemoral vegetation zone, with somewhat different plant communities and species, compared to our boreal rich sloping fens. Also, de Klerk et al. (2017), in arctic fens, state that pollen deposition reflects vegetation, and that regional pollen deposition relate to different biogeographical regions.

## 5.1. Plant cover and pollen deposition

The pollen recovery from moss samples is a measure of plant representation based on fertility and pollen production, and not only plant cover. However, there is a close connection between plant cover, plant biomass and flowering of a large number of species, as shown in the long-term population and vegetation studies in the two study areas (Moen, 1990, 1995; Aune et al., 1996; Lyngstad et al., 2016). Mowing leads to a reduction in above ground biomass and plant cover and a reduction in flowering for several tall-growing species, e.g. *Molinia* *caerulea* and shrubs (Table 3). A number of low growing species, with most of the above-ground biomass close to the surface (not reached by the scythe) increased in biomass, cover and flowering, e.g. *Thalictrum alpinum* and *Carex dioica*. Thus pollen recovery is regarded an approximation of plant cover of a taxon.

There can be a large variation in annual flowering, pollen production and pollen deposition between years (e.g. Hicks, 2001; Hättestrand et al., 2008), and several years of pollen deposition should be sampled (Pardoe et al., 2010). Although moss samples may contain only one or two years of pollen deposition (Räsänen et al., 2004), it is generally assumed that moss polsters contain several years of pollen deposition (Bunting et al., 2013). The annual pollen productivity for species of boreal trees such as *Pinus*, *Betula,* and *Picea* has been found to be related to summer temperature of the year prior to pollen emission (Autio and Hicks, 2004). Our moss samples were gathered in late July 2008. The meteorological stations in the two study areas recorded summer temperatures close to the 30-year normal for the summers 2007 and 2008 (Lyngstad et al., 2016). Both 2007 and 2008 were normal/good flowering years for most of the studied species; e.g. for *Eriophorum latifolium* (Lyngstad et al., 2016), indicating that even if only a few years are represented in the moss samples, the pollen data are probably representative.

The investigated plots are designed for vegetation studies (e.g. Lyngstad et al., 2016), where different management regimes (and collected moss polsters) are very close, but still there were differences between pollen assemblages taken 1-4 m apart. The differences in pollen percentages corresponded well with the vegetation from different management regimes, indicating that a substantial part of pollen was derived locally and that rich fens are suitable for local-scale plant-pollen studies. Comparable studies have also demonstrated a strong correspondence between local vegetation and pollen assemblages for herbs and dwarf-shrubs (e.g. Pardoe, 1996; Hjelle, 1999a; Waller et al., 2017) and a relevant pollen source area (*sensu* Sugita, 1994) of only a few meters is found within mire communities (Bunting 2003; Bunting and Hjelle, 2010).

## 5.2. Identification of management regimes by modern pollen assemblages

Most plant species occurred in both study areas, and in plots with different mowing regimes. Those with high cover in all plots were *Trichophorum cespitosum, Thalictrum alpinum* and *Molinia caerulea*. Six other vascular plant species occurred in at least 80% of the plots: *Carex dioica, C. panicea, Eriophorum angustifolium, E. latifolium, Potentilla erecta* and *Selaginella selaginoides*. Many bryophytes occurred in the plots, e.g. the dominant and constant rich-fen species *Campylium stellatum* and *Scorpidium cossonii* (Moen et al., 2012). Several rare species distinguish between the fens of the two areas, leading to the classification of the oceanic and the more continental fens in different alliances in the phytosociological system (Moen et al., 2012). All of these species had low pollen percentages, and they are not included in this discussion.

The differences in plant cover and pollen assemblages between the management regimes were mainly quantitative. Earlier studies from these localities have shown that the variation in vegetation cover of plots from similar land-use between localities can be larger than between plots from different management regimes within the same locality, and that permanent plots with different management regimes inside each locality belong to the same plant community/vegetation cluster (Moen et al., 2012; Lyngstad et al., 2016). The differences between vegetation plots from different managemental regimes were more pronounced than the differences between pollen samples from these regimes (Fig. 4a)*.* Generally, the plant compositions in plots mown biennially and quadrennially were more similar than to unmown vegetation (Fig. 4a and b), whereas this to a lesser degree was found for pollen data (Fig. 4a). Similar results for plant cover were found in the same areas (e.g. Aune et al., 1996), as well as for plant and pollen data from other studies of mown vegetation (e.g. Hjelle, 1999a).

Palynological studies of rich fens have received little attention in comparison to lakes and raised bogs (Waller et al., 2017). Our results are a contribution to knowledge established in earlier studies from fen vegetation (e.g. de Klerk et al., 2017; Waller et al., 2017) demonstrating that fen vegetation produce distinctive pollen signatures with indicator taxa and should be used also for palaeoecological studies.

To detect past types of land use and changes in land use by pollen analysis, taxa that show responses to land use regimes, in the present case mowing, and have pollen deposition that correlate with plant cover, must be identified. Here five groups of pollen taxa with different potential for land-use reconstruction were identified (Table 7).

### 5.2.1. Very good and good pollen indicators for managemental regimes

In rich fens *Thalictrum* is sensitive to land-use changes, and the contemporary pollen percentages correlate with the local plant cover. *Thalictrum alpinum* occurred in all plots, with highest cover in biennially mown plots compared with unmown plots (Fig. 4b), absolutely (Table 3) and relatively (Table 4a). This is in accordance with previous studies from Sølendet, which also report increased biomass, cover and flowering with mowing frequency (Moen, 1995; Aune et al., 1996). A difference in cover of *T. alpinum* between biennially and quadrennially mown plots is not clear from this study. Its growing point is at the soil surface and is little affected by mowing, so it becomes more abundant in mown fens where competition is reduced. The effect of competition was demonstrated by Klanderud and Totland (2005), who removed neighbouring vegetation in an alpine community and found increases in the number and cover of leaves and reduction in the length of the flowering stems of *T. alpinum.* However, *T. alpinum* is also present in grazed communitites in outfields, as in Budalen, located between our two study areas (Austrheim et al. 1999), and without comparing mown and grazed communities one cannot exclude *Thalictrum* as indicator of more than one land-use practice. The strong association of the presence of both plant and pollen and absence of pollen when plants are lacking, indicates a limited pollen-dispersal distance from these plots with a minimum distance of 1 m. *T.* *alpinum* is wind dispersed, but dispersal can be limited by the short flower stems. This means that *Thalictrum* pollen is a good indicator of local plant presence, and an increase in plant cover can indicate land use like mowing (Table 7). Increased percentages of *Thalictrum* pollen in peat profiles have been used as an indicator of mowing in vegetation history studies of rich fens in boreal areas of central Norway (Gunnarsdóttir, 1999; Solem et al., 2012).

The interpretation of the pollen representation of Cyperaceae undiff. is more challenging. The family is generally well adapted to mowing, although with variations and opposite trends for single species, as for *Carex* species (Table 4 a) (e.g. Moen, 1990, 1995). Both mowing regimes differed from unmown plots in total Cyperaceae plant-cover percentages, but the differences between mowing intensities could not be detected in modern pollen samples. The differences in the Cyperaceae pollen percentages between management regimes are small. The strong plant-pollen correspondence from these closely situated plots suggests a limited dispersal distance for Cyperaceae, which was reported by Bunting and Hjelle (2010) to be between 1.5 and 3.5 m. The present investigation has shown the value of separating *Dulichium*-type pollen, which in our area consists of *Carex* spp., from Cyperaceae undiff. pollen.

*Eriophorum*-type pollen includes three *Eriophorum* species and two *Trichophorum* species. *Eriophorum* spp. and *Trichophorum* spp. (included in Cyperaceae) were most abundant in vegetation mown biennially (Fig. 4b). *E. angustifolium,* *E. vaginatum* and the more widespread species *E. latifolium,* were well adapted to mowing, which also promoted increased flowering according to Moen (1990, 1995), Aune et al. (1996) and Lyngstad et al. (2016). *Trichophorum cespitosum* ssp. *cespitosum*, the dominant species in the rich fens, was indifferent to mowing, as found in earlier studies (e.g. Moen, 1995; Aune et al., 1996) and the difference between management regimes was relatively small.

There was a positive plant-pollen correlation between *Eriophorum*-type pollen and total *Eriophorum* species, but not for the pollen type and all five individual species. Most of the pollen type might be from *Eriophorum* if *Trichophorum* pollen deposition was reflecting the small variation in *Trichophorum* vegetation cover. The difference in *Eriophorum* spp. plant cover between the two mowing regimes and unmown plots could be detected from pollen analysis, as found from other studies (Hjelle, 1998), indicating that *Eriophorum*-type pollen should be separated from Cyperaceae undiff. if possible to increase its value in the interpretation of past communities.

*Molinia caerulea* is the most abundant grass in the plots but the pollen taxon Poaceae can also include *Deschampsia cespitosa, Festuca ovina* and *Nardus stricta*. *M. caerulea* is clearly most abundant and very fertile in unmown plots (Moen, 1990, 1995; Aune et al., 1996). The plant cover of *M. caerulea* decreased with the intensity of mowing, whereas the cover of Poaceae only differed clearly between the mowing regimes and unmown plots (Table 3 and 4). The main reason for the decrease of *M. caerulea* in mown fens is the exposure of the elongation zone to the mower (scythe), strongly reducing the plants. Under moist conditions grazing also reduces plant cover of *M. caerulea* (Hume et al., 1999). In boreal shrub-dominated plant communities and in areas with mowing every 5-10 years (Aune et al., 1996) and in temperate tall-growing fen communities (Rowell et al., 1985) *M. caerulea* increases in biomass and cover with mowing. On the generally nutrient-poor boreal fens *M. caerulea* suffers from the removal of reserves by intensive cutting during a short growing season (Øien and Moen, 2001). In more fertile localities, strong competitors like shrubs and tall herbs are removed by mowing. In such areas, and under mowing with higher stubble, the *Molinia* tussocks can develop. In addition, the fertility of *M. caerulea* is reduced in mown plots on boreal rich fens (Moen, 1995). The modern Poaceae pollen percentages correlated with the plant cover of *Molinia*, but not with all Poaceae species (Table 6). This indicates that most of the Poaceae pollen originated from *M. caerulea*. *Molinia caerulea*/Poaceae displays a difference in plant cover and pollen percentages between areas mown biennially and quadrennially from Tågdalen, whereas the data from quadrennially mown areas in Sølendet are few and difficult to interpret. Overall, mowing of the rich fens results in a reduction of Poaceae plants and pollen and an increase of Cyperaceae plants and pollen. This is in accordance with investigated fen communities in UK where Cyperaceae (including *Carex nigra*, *C. panicea* and *C. rostrata*) have high values in intensively managed communities and decrease with longer cutting rotation when Poaceae (including *Molinia*) increases (Waller et al., 2017). The results from fens seem therefore to contrast to pollen assemblages from dry meadows dominated by high Poaceae pollen values and relatively low values of Cyperaceae (Hjelle, 1999a).

*Succisa pratensis* was present throughout the rich fens, with its largest cover in unmown plots, as reported in Moen (1995) (Fig. 4b, Table 3 and 4). In other communities a decrease in competition following mowing allows an increase in plant cover of *S. pratensis* (Moen 1995). However, with relatively little competition in the boreal rich-fens the effect of reduced biomass had an important impact on this species. In mesic to dry grasslands *S. pratensis* increase in cover with grazing (Herben et al., 2006), making both vegetation type and type of land use important for *S. pratensis* plant cover. The cover of *S. pratensis* in the plots was low and the differences between management regimes were small. It is insect-pollinated and has a limited dispersal distance (Hjelle, 1997, 1998), reflected also in this study by a strong plant-pollen relationship, but with a tendency of being under-represented. This makes the species suited for interpretation of local vegetation, but less important for differentiating the investigated management regimes in the present study.

*Pedicularis*-type pollen included *Pedicularis palustris* and *P. sylvatica* at Tågdalen and mainly *P. palustris* and *P. oederi*, in addition to the rare *P. sceptrum-carolinum* at Sølendet (Moen, 1990, 2000). The pollen percentages of *Pedicularis*-type related well to the cover for *Pedicularis* spp., possibly because *P. palustris* is the main pollen source as well as the main plant in the studied vegetation. As an associated type *Pedicularis* species were common, but not dominant in either vegetation or in pollen deposits. Both *Pedicularis* spp. and *P. palustris* had greatest cover in mown plots, with a trend to greater abundance in quadrennially mown plots. Only biennially mown and unmown plots displayed a difference even if the percent values are small. Earlier studies (e.g. Moen, 1995) confirm this, along with increased flowering frequency in mown plots. *Pedicularis* has a very low pollen representation, so even small differences in pollen percentages may represent substantial differences in number of plants between plots. *P. palustris* is a biennial species mainly occurring in mud bottoms and carpets with a scattered field layer, i.e. localities with low competition. *P. oederi*, a common species in lawns and open fen margins at Sølendet (Moen, 1990) occurred in only 11 of 49 plots. This species shows reduced plant biomass and lower flowering frequency in response to mowing, especially intensive mowing, and is also reduced by abandonment during succession. The pollen data showed a correlation with plant cover, in contrast to the usually rare occurrence of *Pedicularis* in pollen diagrams. Bunting (2003) found no association between plant and pollen in surface studies of heathland communities in UK. Our results indicate that *P. palustris* has a larger potential of being recorded than the other species, which may indicate that *Pedicularis* may be regarded as an indicator of mown fens.

There are short distances between areas of different land-use in the investigated plots. The strong plant-pollen relationship and strong association of presence indicate a local pollen source area of approximately 1 to a few meters for taxa defined as very good and good pollen indicators for managemental regimes.

### 5.2.2. Potential pollen and spore indicators for managemental regimes

Within the homogenous rich-fen community a wide distribution of both plants and pollen gave a high probability of association for many taxa (cf. Hjelle, 1997; Mazier et al., 2006). However, for several of these taxa there was no identified plant response to different managemental regimes. From other studies *Potentilla erecta* displays larger cover and increased flowering in unmanaged plots compared to mown fens (Moen, 1995; Aune et al., 1996). A reduction in plant cover of *P. erecta* has been documentet from grazed vegetation on moist soil (Hulme et al., 1999). With the high cover, the relatively coarse resolution for abundant taxa in the chosen cover scale (e.g. Bunting and Hjelle, 2010), and substantial variations between and within managemental regimes, potential vegetation trends were not identified in the present study (Fig. 4b). Rosaceae undifferentiated pollen correlated with *P. erecta,* its only species in the vegetation, thus Rosaceae pollen was interpreted to mainly representing *P. erecta*. With a good plant-pollen correlation *P. erecta* reflects local vegetation, it is a good indicator of grazing (e.g. Hjelle, 1999; Mazier et al., 2006) and can, in the present study, represent a pollen indicator type of open vegetation more than mowing. High moisture levels might limit the plant cover of *P. erecta* on these rich fens, playing a more important role in plant distribution than land use.

*Selaginella selaginoides* is known to be favoured in mown fens (Moen, 1995; Aune et al., 1996). In the studied fens the spore recovery was a good indicator of its plant presence, but no statistical relationship between plant cover and management regime has been identified. With low percentages on the investigated fens, any trends have been difficult to decipher. There was a tendency of increased plant presence with mowing from pairwise comparisons (Table 3 and 4), even if the general tendency in the plots is a slight decrease with mowing (Fig. 4b). If its land-use response is identified from further studies, *S. selaginoides* could be an indicator-type of mowing.

### 5.2.3. Pollen types reflecting unidentified factors or not reflecting plant cover

*Menyanthes trifoliata* was rare but still demonstrated a positive plant-pollen correlation on these rich fens. Its main distribution on the fens was outside the investigated localities, in the wettest places in the fens and in small lakes (Moen et al., 2012). However, in lawn and carpet communities, the cover of *Menyanthes* increases and flowering decreases with mowing (Moen et al. unpublished data).

Two sub-groups of pollen types not reflecting plant cover were identified:

a) Mowing regime affected the species cover, but there was no significant plant-pollen correlation. The strong association between plant and pollen was due to their large abundance. *Carex* species display a variety of plant responses to mowing regarding biomass, cover and fertility (Moen, 1995). Several *Carex* species and the genus as a whole were most abundant in mown plots (Fig. 4b; Moen, 1990; Aune et al., 1996). The low taxonomic precision of *Dulichium*-type pollen and variations in pollen production within the genus (Randall et al., 1986; Hjelle, 1998) were probable reasons for a lack of plant-pollen correlation. *Dulichium*-type pollen has a potential in palaeoreconstruction if the plant-pollen relationship can be interpreted locally. *Betula* species as a whole*,* and the main species *B. nana* and *B. pubescens* were mainly found in relation to succession on the fen, along the margins and as surrounding vegetation (e.g. Moen, 1990). The over-represented and variable pollen recovery from *Betula* was probably from the extra-local and the regional vegetation. Thus *Betula* pollen has limitations in reconstructing local vegetation, but an increase in pollen may indicate fen succession and increased tree cover on extra-local and regional scales. The cover of *Drosera* spp. at Tågdalen and *Pinguicula vulgaris* at Sølendet increased with mowing, as shown by Moen (1995). As entomophilous and cleistogamous species, respectively, their strongly under-represented and unassociated pollen document the presence of the plant, but they are not suitable to represent variation in the vegetation.

b) The second sub-group includes taxa with no identified plant response to different land-use and no plant-pollen correlation on the rich fens (Table 7). These were rare in this vegetation type, but could be common in nearby herb and heather woodland (Moen, 1900, 2000). The pollen might mainly be extra-local. These taxa are of limited value in local land-use reconstructions in such boreal fens, but can be valuable in reconstructions of extra-local vegetation, succession and fen dynamics.

Changes in climate and fen characteristics might change the effect mowing plays on single taxa through time as well as geographically. Still, the ecological effect of mowing will be similar for many taxa under various conditions, and thus comparable between regions (e.g. Hjelle, 1999a).

# 6. Conclusion

The differences in plant cover between mown and unmanaged plant communities on the boreal rich-fens were mainly quantitative, where the same taxa are present in the vegetation in mown and unmown fens, but in varying amounts (Table 3). For several taxa managemental regimes explained a substantial part of the plant-cover variation on the boreal rich-fens. The relative changes of several taxa in the vegetation rather than the presence or absence of any single pollen-indicator taxon indicate land-use changes on these fens.

A correlation between the plant cover of taxa constituting the majority of the vegetation on the rich fen and their contemporary, deposited pollen on a local scale was documented. The short distances between different managemental regimes in this study indicate a local pollen source area from 1 and up to a few meters for important taxa in the mown fens, like *Thalictrum alpinum*, Cyperaceae and *Succisa pratensis*. Thus, presences of their pollen in peat samples can generally be assumed to reflect presence in the vegetation.

Modern pollen assemblages, with correlation to plant cover, display a difference in pollen percentage between biennially mown and unmown vegetation. Further, several taxa have a potential for indicating mowing quadrennially, even if the two mowing regimes are not clearly separated in the present study. A modern pollen assemblage indicating mowing on these rich fens has high percentages of *Thalictrum*, *Eriophorum*-type and Cyperaceae undiff. pollen. *Pedicularis* pollen percentages are generally higher than in unmown vegetation, and Poaceae (*Molinia caerulea*) and *Succisa* *pratensis* pollen percentages are lower than in unmown vegetation. *Potentilla*-type and Rosaceae, pollen together representing *Potentilla erecta*, decrease with mowing of the fens, whereas an increase in *Selaginella selaginoides* spores potentially indicates mowing. In combination, these changes in pollen percentages from such species can be considered a fingerprint for mowing regimes on rich fens. In other vegetation types and under different land use, some of these species would display a different combination of increase and decrease in plant cover and pollen deposition.

This study emphasises the importance of identification of pollen to as low a taxonomic level as possible. The separation of *Eriophorum*- and *Dulichium*-type (i.e. *Carex* spp.) pollen from Cyperaceae undiff. is essential as the two former, partly in different ways, are important taxa in identifying land-use regimes.

This study has shown a close connection between taxa in fen vegetation and the local pollen deposition in the two contrasting climate regimes (oceanic and continental) of the middle and northern boreal vegetation zones, confirming hypothesis 1. Boreal rich-fens in the two areas have the same dominant species and the same species producing the majority of the pollen, supporting hypothesis 2. The difference between mown and unmown vegetation can be detected from the contemporary pollen assemblages, particularly between biennial mown and unmown vegetation, supporting hypothesis 3. In this study *Molinia caerulea*/Poaceae display a difference in plant cover and pollen percentages between areas mown biennially and quadrennially. This difference between biennially and quadrennially mown areas was not identified for most taxa, and should be further investigated. The results from the present paper contribute to a better understanding of vegetation-pollen relationships on rich fens and separation of mown and unmown fens, based on pollen assemblages. Our findings will aid in the interpretation of fossil pollen assemblages in terms of local land use on fens in the boreal zone.

**Acknowledgements**

We are grateful to John Birks for valuable comments on the research design and to Anders Lyngstad for help during field work, and Dag-Inge Øien for peparing the maps from Tågdalen and Sølendet. The manuscript was improved by the valuable suggestions and comments from two anonymous referees. This study has received financial support from The Olaf Grolle Olsen and Miranda Bødtker legacy and A. Heiberg and H.B. Fasmers fund, both at the University of Bergen. This study was part of a PhD project at the Department of Biology, University of Bergen.

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Figure legends

Fig. 1. The location of the two study areas, Tågdalen in the inner fjord area and the inland area Sølendet. Vegetation sections in central Norway after Moen (1999).

Fig. 2. The location of investigated localities in a) Tågdalen Nature Reserve and b) Sølendet Nature Reserve. The reserves are marked with black solid borders. Numbering of the plots follows the permanent plots in long-term studies from the reserves (Moen, 1990, 2000).

Fig. 3. Schematic presentation of a typical locality with permanent plots, investigated plots of 1 m2 for the present study and collection points for moss samples. A= mown biennially, C= mown quadrennially and B= unmown.

Fig. 4. PCA showing a) vegetation samples, pollen samples and environmental variables. Pollen samples and environmental variables are treated as passive samples and variables respectively. Veg. = vegetation samples, Pollen = pollen samples, 2nd = mown biennially, 4th = mown quadrennially. Grey triangles = environmental variables, three mowing regimes, b) plant species grouped into pollen taxa according to Table 2, based on 26 plots from Tågdalen and 23 plots from Sølendet. Pollen types close to the center are not shown to increase readability. Abbreviations: t = type, *Menyanthes tri* = *Menyanthes trifoliata*, *Saxifraga opp = Saxifraga oppositifolia*.



Fig. 1.



Fig. 2a.

**Table 1**

Characteristics of the two study areas. Climatic data from Norwegian Meteorological Institute (see Lyngstad et al., 2016, including Supplementary Material) for the study areas at Tågdalen nature reserve and Sølendet nature reserve. Vegetation zones and sections after Moen (1999).

|  |  |  |
| --- | --- | --- |
|  | **Tågdalen** | **Sølendet** |
| Latitude (N)  | 63°03’ | 62°40’ |
| Longitude (E) | 9°05’ | 11°50’ |
| Altitude (m a.s.l.) | 440-460 | 715-785 |
| Mean annual precipitation (mm) | 1583 | 637 |
| Mean annual temperature (°C) | 3.0 | 0.6 |
| Mean July temperature (°C) | 11.2 | 10.5 |
| Mean January temperature (°C) | - 2.7 | - 9.5 |
| Vegetation zone | middle/ northern boreal | middle/ northern boreal |
| Vegetation section | markedly oceanic (O2) | indifferent (OC)/slightly oceanic (O1) |

**Table 2**

The 26 pollen and spore taxa with their corresponding 57 plant species present in the studied localities. Only taxa registered in both vegetation and pollen samples are included. T = pollen or plant only present in Tågdalen; S = pollen or plant only present in Sølendet. Nomenclature for pollen taxa follows Fægri and Iversen (1989), plant taxa follow Frisvoll et al. (1995) and Lid and Lid (2005).

|  |  |
| --- | --- |
| **Pollen/spore taxa**  | **Plant species in the vegetation plots**  |
| *Anemone* | *Anemone nemorosa***T** |
| Asteraceae Cichorioideae | *Crepis paludosaS, Leontodon autumnalis***S** |
| *Betula* | *Betula nana, Betula nana* x *pubescens, Betula pubescens* |
| *Bistorta vivipara*-type | *Bistorta vivipara* |
| *Calluna vulgaris* | *Calluna vulgaris***S** |
| Cyperaceae | *Carex* spp.*, Eleocharis quinqueflora, Eriophorum* spp.*, Kobresia simpliciuscula***S***, Schoenus ferrugineus***T***, Trichophorum* spp., |
| *Drosera rotundifolia*-type**T** | *Drosera longifolia***T** *,Drosera rotundifolia,*  |
| *Dulichium*-type | *Carex capillaris, Carex chordorrhiza***T***, Carex dioica, Carex echinata, Carex flava, Carex flava* x *hostiana***S***, Carex hostiana, Carex lasiocarpa, Carex limosa***T***,Carex nigra, Carex panicea, Carex pauciflora***T***, Carex rostrata, Carex vaginata***S** |
| Ericaceae | *Andromeda polifolia, Calluna vulgaris***S***, Erica tetralix***T***, Vaccinium uliginosum* ssp. *uliginosum* |
| *Eriophorum*-type | *Eriophorum angustifolium, Eriophorum latifolium, Eriophorum vaginatum***S**, *Trichophorum alpinum, Trichophorum cespitosum* ssp. *cespitosum* |
| *Galium*-type**T** | *Galium boreale* |
| *Juniperus communis* | *Juniperus communis* |
| *Menyanthes trifoliata***T** | *Menyanthes trifoliata***T** |
| *Pedicularis*-type | *Pedicularis oederi***S***, Pedicularis palustris*  |
| *Pinguicula*-type**S** | *Pinguicula vulgaris***S** |
| Poaceae | *Deschampsia cespitosa***S***, Festuca ovina***S***, Festuca vivipara***T***, Molinia caerulea, Nardus stricta* |
| *Potentilla*-type | *Potentilla erecta* |
| *Rhinanthus*-type**S** | *Bartsia alpina***S***, Euphrasia wettsteinii* |
| Rosaceae  | *Potentilla erecta* |
| *Salix***S** | *Salix glauca***S** |
| *Saxifraga oppositifolia*-type | *Saxifraga aizoides***S** |
| *Selaginella selaginoides* | *Selaginella selaginoides* |
| *Solidago*-type | *Solidago virgaurea***S** |
| *Sphagnum* | *Sphagnum warnstorfii, Sphagnum* Section *Subsecunda* |
| *Succisa pratensis*  | *Succisa pratensis*  |
| *Thalictrum* | *Thalictrum alpinum* |

**Table 3**

Number of plots with plant recorded (n), mean plant cover in vegetation plots based on 26 plots from Tågdalen (T) and 23 from Sølendet (S), and differences in cover between plots mown biennially (M2) and unmovn (U). T = only from Tågdalen; S = only from Sølendet; – = not present. The difference in % values displays absolute differences on a % scale between plots mown biennially and unmown plots.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Plant taxa**  | **n** | **T, mean %** | **S, mean %** | **Difference in % values M2 – U (T & S)** |
| *Bartsia alpina* | 29 | 2.5 | 0.5 | **-**1.6 |
| *Betula nana* | 16 | 0.01 | 2.9 | **-**5.7 |
| *Bistorta vivipara* | 19 | 0.1 | 0.6 | **-**0.5 |
| *Carex capillaris* | 20 | 0.7 | 0.8 | 0.3 |
| *Carex dioica* | 40 | 2.2 | 1.1 | 2.2 |
| *Carex echinata* | 9 | 0.7 | 0.01 | 2.1 |
| *Carex flava* | 35 | 2.6 | 6.1 | 5.9 |
| *Carex hostiana* | 22 | 4.3 | 0.01 | 4.9 |
| *Carex limosa***T** | 25 | 2.8 | – | 2.4 |
| *Carex nigra* | 11 | 0.02 | 1.8 | 2.1 |
| *Carex panicea* | 48 | 2.2 | 4.0 | 1.2 |
| *Carex rostrata* | 30 | 3.1 | 2.3 | 4.8 |
| *Drosera longifolia***T** | 13 | 2.0 | – | 4.0 |
| *Eriophorum angustifolium* | 43 | 0.7 | 0.8 | 0.9 |
| *Eriophorum latifolium* | 44 | 7.8 | 6.4 | 5.7 |
| *Eriophorum vaginatum***S** | 10 | – | 0.3 | **-**0.5 |
| *Euphrasia wettsteinii* | 25 | 0.8 | 1.4 | 0.0 |
| *Festuca ovina***S** | 12 | – | 0.7 | **-**0.7 |
| *Menyanthes trifoliata* | 9 | 0.4 | 1.6 | **-**5.4 |
| *Molinia caerulea* | 49 | 8.3 | 7.4 | **-**13.6 |
| *Pedicularis oederi***S** | 11 | – | 0.5 | **-**0.3 |
| *Pedicularis palustris* | 26 | 0.2 | 3.0 | 3.1 |
| *Pinguicula vulgaris* | 13 | 1.7 | 0.9 | 2.6 |
| *Potentilla erecta* | 44 | 9.2 | 5.2 | 0.4 |
| *Selaginella selaginoides* | 43 | 1.5 | 1.9 | 0.2 |
| *Succisa pratensis* | 32 | 3.5 | 1.6 | **-**1.9 |
| *Thalictrum alpinum* | 49 | 10.8 | 13.9 | 10.6 |
| *Trichophorum alpinum* | 22 | 1.7 | 0.1 | **-**0.4 |
| *Trichophorum cespitosum ssp. cespitosum* | 49 | 18.4 | 14.5 | **-**1.9 |

**Table 4**

Results (p-values) from paired comparisons of differences in a) mean percentage cover of plant taxa and b) sum of mean percentage cover of pollen taxa between management regimes in Tågdalen and Sølendet using the Wilcoxon signed rank test. The test was run for plots mown biennially and unmown plots (M2 & U), plots mown biennially and quadrennially (M2 & M4), and plots mown quadrennially and unmown plots (M4 & U). Numbers in bold display values statistically significant at a 0.05**-**level. **--** = not enough plots to compute the test. The rightmost column displays indices of difference (ID), range +1.0 to **-**1.0, between plots mown biennially and unmown (M2 & U). Positive values refer to taxa with an increase in plant cover with mowing, negative values vice versa.

|  |  |  |
| --- | --- | --- |
|  | **p-values** | **ID** |
| **a) Plant taxa**  | **M2 & U** | **M2 & M4** | **M4 & U** | **M2 & U** |
| *Molinia caerulea* | **<0.0001** | **0.047** | **0.010** | **-**0.95 |
| *Carex dioica* | **<0.0001** | 0.25 | 0.22 | 0.89 |
| *Thalictrum alpinum* | **<0.0001** | 0.50 | 0.06 | 0.90 |
| *Pinguicula vulgaris* | **0.001** | **0.031** | 0.38 | 0.65 |
| *Carex hostiana* | **0.002** | 0.50 | 0.06 | 1.00 |
| *Carex flava* | **0.002** | >0.99 | 0.13 | 0.60 |
| *Eriophorum latifolium* | **0.003** | 0.50 | 0.06 | 0.72 |
| *Eriophorum angustifolium* | **0.012** | 0.06 | 0.13 | 0.44 |
| *Pedicularis palustris* | **0.017** | >0.99 | 0.50 | 0.58 |
| *Betula nana* | **0.027** | **--** | **--** | **-**0.60 |
| *Succisa pratensis* | **0.036** | >0.99 | >0.99 | **-**0.38 |
| *Carex limosa***T** | **0.047** | >0.99 | 0.38 | 0.60 |
| *Carex echinata* | 0.06 | **--** | **--** | 0.83 |
| *Drosera longifolia***T** | 0.06 | >0.99 | 0.25 | 0.83 |
| *Bartsia alpina* | 0.18 | 0.63 | 0.25 | **-**0.40 |
| *Carex nigra* | 0.19 | **--** | **--** | 0.50 |
| *Eriophorum vaginatum***S** | 0.22 | **--** | **--** | **-**0.57 |
| *Carex panicea* | 0.23 | 0.25 | 0.25 | 0.40 |
| *Bistorta vivipara* | 0.27 | **--** | 0.38 | **-**0.40 |
| *Carex rostrata* | 0.31 | 0.06 | >0.99 | 0.25 |
| *Trichophorum alpinum* | 0.34 | 0.31 | 0.63 | **-**0.29 |
| *Festuca ovina***S** | 0.38 | **--** | **--** | **-**0.29 |
| *Trichophorum cespitosum ssp. cespitosum* | 0.44 | 0.38 | 0.50 | **-**0.15 |
| *Menyanthes trifoliata* | 0.50 | 0.75 | 0.88 | **-**0.25 |
| *Carex capillaris* | 0.67 | **--** | **--** | 0.10 |
| *Euphrasia wettsteinii* | 0.70 | **--** | **--** | **-**0.07 |
| *Selaginella selaginoides* | 0.72 | 0.06 | 0.25 | 0.05 |
| *Potentilla erecta* | 0.87 | 0.13 | 0.31 | 0.11 |
| *Pedicularis oederi***S** | 0.94 | **--** | **--** | **-**0.17 |
|  |  |  |  |  |
| **b) Plant taxa in pollen taxa group** |  |  |  |  |
| *Dulichium-type* | **<0.0001** | **0.047** | **0.039** | 1.00 |
| Cyperaceae | **<0.0001** | 0.06 | **0.012** | 1.00 |
| Poaceae | **<0.0001** | 0.09 | **0.008** | **-**0.95 |
| *Eriophorum* spp. | **0.002** | 0.14 | **0.039** | 0.60 |
| *Betula* | **0.002** | **--** | 0.38 | **-**0.69 |
| *Pedicularis*-type | **0.023** | >0.99 | 0.13 | 0.38 |
| *Drosera*.T | **0.031** | 0.38 | 0.25 | 0.75 |
| *Eriophorum*-type (incl. *Trichophorum)*  | **0.040** | 0.77 | 0.35 | 0.30 |

**Table 5**

Mean pollen percentages of local terrestrial pollen and spores from the two study areas, Tågdalen and Sølendet, for each land-use regime. SE= standard error; n= number of samples. \* displays pollen taxa included in the local terrestrial pollen sum. Cyperaceae includes *Dulichium*-type and *Eriophorum*-type, Ericaceae includes *Calluna vulgaris*, Rosaceae includes *Potentilla*-type. *Menyanthes trifoliata***,** Ericaceae, *Drosera rotundifolia*-type, *Saxifraga oppositifolia*-type and *Galium*-type from Tågdalen and *Anemone, Saxifraga oppositifolia*-type, *Bistorta vivipara*-type, *Pinguicula*-type and *Rhinanthus*-type from Sølendet, were found in few plots and with low percentages and are not included.

|  |  |  |  |
| --- | --- | --- | --- |
|  | Mown biennially | Mown quadrennially | Unmown |
| **Pollen/spore taxa** | **n (of 10)** | **Mean %**  | **SE** | **n (of 6)** | **Mean %** | **SE** | **n (of 10)** | **Mean %** | **SE** |
| **Tågdalen** |  |  |  |  |  |  |  |  |  |
| Cyperaceae  | 10 | **80.0** | 1.8 | 6 | **78.2** | 3.2 | 10 | **80.8** | 1.4 |
| *Betula* | 10 | **32.7** | 1.9 | 6 | **29.7** | 3.5 | 10 | **29.1** | 1.3 |
| *Dulichium*-type\* | 10 | **25.5** | 1.3 | 6 | **25.2** | 1.6 | 10 | **26.7** | 2.4 |
| *Eriophorum*-type\* | 10 | **16.2** | 0.6 | 6 | **16.1** | 2.3 | 10 | **9.0** | 1.3 |
| *Selaginella selaginoides* | 10 | **15.1** | 1.5 | 6 | **11.0** | 2.2 | 10 | **17.4** | 3.7 |
| Poaceae\* | 10 | **7.8** | 0.5 | 6 | **9.3** | 1.2 | 10 | **9.4** | 0.7 |
| *Thalictrum\** | 10 | **4.8** | 1.0 | 6 | **5.9** | 1.6 | 10 | **3.2** | 0.6 |
| Rosaceae | 9 | **2.4** | 0.5 | 6 | **2.6** | 0.4 | 10 | **2.9** | 0.3 |
| *Potentilla*-type\* | 8 | **1.4** | 0.3 | 5 | **2.0** | 0.3 | 10 | **2.5** | 0.3 |
| *Juniperus communis* | 9 | **0.9** | 0.2 | 4 | **0.5** | 0.2 | 9 | **0.7** | 0.1 |
| *Sphagnum* | 7 | **0.6** | 0.2 | 5 | **0.6** | 0.1 | 7 | **0.6** | 0.2 |
| *Solidago*-type\* | 3 | **0.4** | 0.2 | 1 | **0.1** | 0.1 | 3 | **0.1** | 0.05 |
| *Succisa pratensis\** | 5 | **0.2** | 0.07 | 1 | **0.2** | 0.1 | 3 | **0.2** | 0.1 |
| *Anemone\** | 4 | **0.2** | 0.08 | 1 | **0.06** | 0.04 | 4 | **0.2** | 0.07 |
| *Pedicularis*-type\* | 3 | **0.2** | 0.09 | 3 | **0.3** | 0.1 | 0 | **0** | 0 |
| *Menyanthes trifoliata***T** \* | 1 | **0.1** | 0.03 | 1 | **0.08** | 0.05 | 2 | **0.05** | 0.03 |
| **Sølendet** |  |  |  |  |  |  |  |  |  |
| Cyperaceae  | 10 | **78.5** | 4.1 | 3 | **90.4** | 2.2 | 10 | **83.7** | 2.8 |
| *Betula* | 10 | **32.4** | 3.0 | 3 | **18.2** | 2.6 | 10 | **30.2** | 2.9 |
| *Eriophorum*-type\* | 10 | **28.9** | 2.2 | 3 | **35.9** | 1.9 | 10 | **14.9** | 1.1 |
| *Selaginella selaginoides* | 10 | **19.2** | 3.1 | 3 | **9.6** | 1.2 | 10 | **11.3** | 1.8 |
| *Dulichium*-type \* | 10 | **18.4** | 1.2 | 3 | **21.6** | 2.4 | 10 | **24.4** | 1.2 |
| *Thalictrum*\* | 10 | **12.6** | 3.9 | 3 | **5.4** | 2.6 | 10 | **3.9** | 1.1 |
| Poaceae\* | 10 | **4.6** | 0.6 | 3 | **2.7** | 0.5 | 10 | **7.2** | 1.3 |
| *Juniperus communis* | 8 | **1.0** | 0.2 | 3 | **0.5** | 0.1 | 8 | **0.6** | 0.1 |
| *Pedicularis*-type\* | 7 | **0.6** | 0.1 | 2 | **0.6** | 0.3 | 7 | **0.4** | 0.1 |
| Asteraceae CichorioideaeS\* | 9 | **0.5** | 0.1 | 1 | **0.1** | 0.1 | 5 | **0.5** | 0.2 |
| *Sphagnum* | 6 | **0.4** | 0.1 | 3 | **0.7** | 0.2 | 10 | **0.5** | 0.1 |
| Ericaceae | 5 | **0.3** | 0.1 | 1 | **0.2** | 0.2 | 6 | **0.3** | 0.1 |
| *Calluna vulgaris* | 5 | **0.3** | 0.1 | 1 | **0.2** | 0.2 | 4 | **0.2** | 0.1 |
| *Salix*S | 6 | **0.3** | 0.1 | 2 | **0.3** | 0.1 | 7 | **0.4** | 0.1 |
| Rosaceae | 8 | **1.0** | 0.2 | 0 | **0** | 0 | 9 | **2.1** | 0.5 |
| *Potentilla*-type\* | 7 | **0.7** | 0.2 | 0 | **0** | 0 | 9 | **2.0** | 0.5 |
| *Solidago*-type\* | 4 | **0.2** | 0.1 | 0 | **0** | 0 | 4 | **0.3** | 0.1 |
| *Succisa pratensis*\* | 4 | **0.2** | 0.1 | 0 | **0** | 0 | 2 | **0.6** | 0.3 |
|  |

**Table 6**

Correlation between plant cover (transformed to pollen taxa) percentages and pollen percentages, and indices of association (A, U, O) based on presence/absence data. Abbreviations: T = test only from Tågdalen; S = only from Sølendet; ρ(rho) = Spearman rank**-**correlation coefficient. Correlation coefficient significant at p<0.05 in bold. The indices of association were classified into SAT = strongly associated types, AT = associated types, WAT = weakly associated types, ORT = over**-**represented type, URT = under-represented type and UT = unassociated type. See section 3.4.5. for further description. *Anemone* (WAT), *Calluna vulgaris* (ORT), *Juniperus communis* (WAT), *Salix* (UT) and *Solidago***-**type (WAT) were present in too few plots with plant or pollen to conduct the test.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Pollen taxon** | **ρ** | **A** | **U** | **O** | **Association** |
| Rosaceae  | **0.47** | 0.83 | 0.11 | 0.07 | SAT |
| *Potentilla*-type | **0.44** | 0.8 | 0.16 | 0.05 | SAT |
| *Pedicularis*-type | **0.43** | 0.59 | 0.34 | 0.14 | AT |
| *Succisa pratensis*  | **0.43** | 0.38 | 0.59 | 0.13 | WAT |
| *Thalictrum* | **0.35** | 1 | 0 | 0 | SAT |
| *Menyanthes trifoliata* | **0.31** | 0.25 | 0.67 | 0.5 | WAT |
| *Selaginella selaginoides* | **0.30** | 0.88 | 0 | 0.12 | SAT |
| *Eriophorum*/*Eriophorum spp.* | **0.25** | 0.98 | 0 | 0.02 | SAT |
| Poaceae/*Molinia caerulea* | **0.25** | 1 | 0 | 0 | SAT |
| Cyperaceae | **0.24** | 1 | 0 | 0 | SAT |
| *Drosera rotundifolia*-type**T** | 0.21 | 0.06 | 0.94 | 0 | URT |
| Poaceae | 0.20 | 1 | 0 | 0 | SAT |
| Asteraceae Cichorioideae **S** | 0.18 | 0.19 | 0.25 | 0.8 | WAT |
| *Bistorta vivipara*-type**T** | 0.11 | 0.06 | 0.94 | 0 | URT |
| *Betula* | 0.05 | 0.43 | 0 | 0.57 | ORT |
| *Rhinanthus*-type**S** | 0.04 | 0.13 | 0.87 | 0 | URT |
| Ericaceae  | 0.02 | 0.19 | 0.74 | 0.57 | WAT |
| *Galium*-type**T** | -0.05 | 0 | 1 | 1 | UT |
| *Sphagnum* | -0.13 | 0.21 | 0.11 | 0.79 | WAT |
| *Dulichium*-type | -0.16 | 1 | 0 | 0 | SAT |
| *Pinguicula*-type**S** | -0.22 | 0 | 1 | 1 | UT |
| *Saxifraga oppositifolia*-type | -0.96 | 0.13 | 0.88 | 0 | URT |
| *Eriophorum*-type | -0.01 | 1 | 0 | 0 | SAT |

**Table 7**

Pollen indicator taxa for management regimes in boreal rich fens based on the results from the Wilcoxon signed rank test (relationship between vegetation and management regime) and the Spearman rank**-**correlation coefficient (relationship between plant and pollen percentages). The effect of traditional mowing on the relative vegetation cover (plants expressed as pollen taxa) in fens is displayed as: + positive effect of traditional mowing, • no effect, **-** negative effect). Results from earlier studies in the study areas are displayed in brackets (after Moen, 1990, 1995; Moen et al., 1999); see text for further details.

\**Pedicularis*-type pollen mainly increases with mowing, but single species are reduced with mowing.

|  |  |  |
| --- | --- | --- |
| **Pollen-vegetation relationship** | **Pollen/spore taxa** | **Effect of mowing** |
| Very good pollen indicator | *Thalictrum*  | + |
| Good pollen indicators | Cyperaceae*Eriophorum*-typePoaceae*Succisa pratensis**Pedicularis*-type | ++**-****-**+\* |
| Potential pollen indicators | *Potentilla*-typeRosaceae*Selaginella selaginoides* | (**-**)(**-**)(+) |
| Pollen type reflecting unidentified factors in present study | *Menyanthes trifoliata* | (+/•) |
| Pollen types reflecting plant cover in earlier studies | *Anemone*Asteraceae Cichorioideae (*Leontodon* spp./*Crepis* spp.)*Betula**Bistorta vivipara*-type*Calluna vulgaris**Dulichium*-type*Drosera rotundifolia*-typeEricaceae*Galium*-type *Juniperus communis* *Pinguicula*-type*Rhinanthus*-type (*Euphrasia* spp./*Bartsia* spp.)*Salix**Saxifraga oppositifolia*-type*Sphagnum**Solidago*-type | (+/-)(**-**)(+)(-)(+/•/**-**)(+)(-) (**-**)(+)(+)(+/-)(+)(**-**)(**-**) |