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Surface pollen deposition on glacier forelands in southern Norway I: local patterns of representation and source area at Storbreen, Jotunheimen

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Abstract: The relationship between vegetation and surface pollen deposition is examined at Storbreen glacier foreland where a clear plant succession exists. The aim is to determine whether the distinct plant communities present produce characteristic pollen assemblages. The influence of environmental factors is also considered. Pollen assemblages from moss polsters, collected from 22 paired sampling sites across the foreland, are compared with local vegetation. Two-way indicator species analysis and detrended correspondence analysis are employed to identify clusters and sequences, initially in the vegetation data and subsequently in the pollen data sets. Vegetation and pollen data are compared simultaneously using canonical correspondence analysis. Three main plant communities are distinguished: pioneer, heath and snowbed. Broadly, each community produces characteristic pollen assemblages. Boundaries between groups are not clear-cut, reflecting the mosaic of plant communities present. Recognition of distinct plant communities is hampered by the prevalence of long-distance arboreal pollen and poor representation of entomophillously pollinated taxa. Late in the succession up to 78% of pollen could originate locally. Use of the non-arboreal pollen sum significantly improves correspondence with vegetation. The importance of indicator taxa is considered and both *Salix* and *Empetrum* are found to distinguish successfully early phases of succession from later phases. Strong correlations exist between the primary ordination axes of vegetation and pollen and with terrain age and altitude (for example, the correlation between altitude and total land pollen Axis 1 is $r = -0.76$). The surface data add new information to the interpretation of tree colonization in the area during the Holocene.

Key words: Surface pollen, pollen representation, plant succession, classification and ordination, relevant source area of pollen, moss polster, glacier foreland, Jotunheimen, Norway.

Introduction

This study forms part of a series of papers examining the relationship between surface pollen and vegetation at 26 glacier forelands from Jotunheimen and Jostedalsbreen, southern Norway (Caseldine, 1989; Pardoe, 1992, 1996, 2001; Caseldine and Pardoe, 1994). At Storbreen (Figure 1) there is a clear succession of plant communities that can be related to length of time since deglaciation and terrain stability. This chronosequence of relatively discrete communities (Matthews, 1974, 1975, 1977; Whittaker, 1987) provides the ideal basis for examining the relationship between vegetation and pollen, since several environmental variables are constant and the source of pollen is relatively well defined.

Vegetation succession at Storbreen is extremely well documented (Matthews, 1976, 1978a,b, 1979, 1979a,b; Whittaker, 1985, 1987; Matthews and Whittaker, 1987; Crouch, 1991). The most comprehensive study by Matthews (1976) involved collecting vegetation data from 638 sites on the foreland in a systematically stratified random design. Matthews (1976, 1978b) identified three species groups: heath species; snowbed species and pioneer species, each with a core of highly intercorrelated species that are related to terrain age and topographic position. Each species occupies a limited age range and a limited range of environments. The pioneer species form the initial phase of the succession. Other species, including woody dwarf-shrubs become increasingly important as the local environment changes. The pioneer species group is replaced by 'snowbed' species at high altitudes and by heath species at lower altitudes. Matthews (1978b) stressed the

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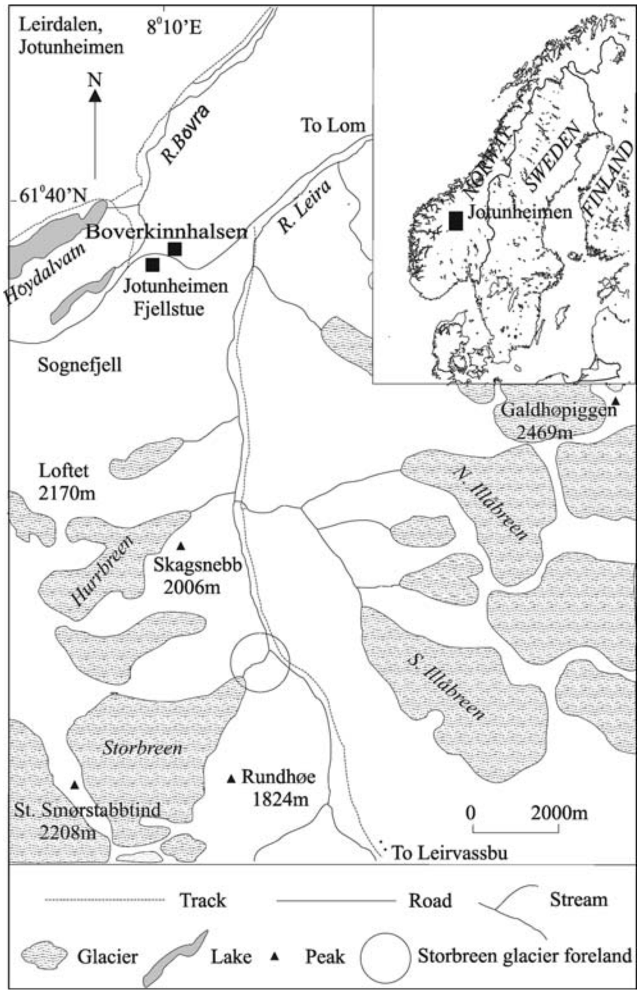


Figure 1 Location of Storbreen foreland (after Matthews, 1978a)

dynamic nature of succession and suggested that the vegetation is still not in dynamic equilibrium with the environment after 220 years.

At Storbreen a number of environmental variables are strongly intercorrelated, including time since deglaciation, altitude and nutrient status of the soil. It is impossible, therefore, to isolate one factor as being solely responsible for the distribution of plant communities. Nevertheless, the terrain age factor complex, with the addition of altitude, appears to be the major determinant of the distribution of plant communities (Whittaker, 1985). Whittaker states that the spatial and successional patterns of the communities at Storbreen are the product of the interaction of dynamic plant populations with a complex and equally dynamic environment.

The scale of the glacier foreland is particularly appropriate for pollen–vegetation studies, including investigation of pollen source, since the foreland is relatively small and clearly delimited and yet, within this area, a succession of plant communities exists so the likely source of pollen is relatively well defined. The sequence of plant communities on terrain of known age is useful for comparison with pollen samples from peat cores.

There have been few studies of pollen deposition on glacier forelands. In a series of pioneering studies Jochimsen (1972, 1979) showed how pollen deposition could be related to vegetation at the Fernau, Rotmoos and Hintereis glacier forelands in the Alps. Later, Birks (1980a) elegantly demonstrated the relationship between vegetation and pollen deposition at the Klutlan Galcier, Yukon, using canonical variates analysis. Birks (1980b) subsequently compared the surface assemblages with fossil spectra, demonstrating the existence of modern analogues.

The dominance of long-distance pollen is a major problem in open arctic-alpine environments. Interest in patterns of surface pollen deposition in such habitats has increased in recent years (eg, Hicks, 1985, 1994; Hicks and Birks, 1996; van der Knaap *et al.*, 2001; Oswald *et al.*, 2003a; Bennett and Hicks, 2005). Oswald *et al.* (2003a) used palynology to explore questions regarding the landscape-scale heterogeneity of past tundra vegetation. They noted that late-Quaternary pollen from the Arctic are notoriously difficult to interpret because of the over- and under-representation of key taxa, the inability to differentiate pollen types within many genera or families and the unclear spatial resolution of the data. They compared modern pollen spectra, taken from lake sediments on two contrasting glaciated surfaces from the Arctic Foothills, northern Alaska, using various statistical techniques. They used dissimilarity metrics to determine whether the samples from the different surfaces could be differentiated based on their pollen spectra. Discriminant analysis was used to determine which taxa were most useful for discriminating between the two surfaces and samples from the different glaciated surfaces were effectively distinguished. Oswald *et al.* (2003a) also found that the ratio of *Betula* to extra-local pollen (*Alnus*+*Picea*) could be used to distinguish surfaces, indicating different pollen productivity on contrasting glaciated surfaces.

Oswald *et al.* (2003b) went on to analyse Holocene pollen records from two lakes in northern Alaska located on glaciated surfaces with contrasting soil texture, topography and tundra communities. Using indicator taxa, pollen accumulation rates (PARs) and modern pollen assemblages they successfully reconstructed vegetational changes at the two lakes.

Hjelle (1997, 1998, 1999) produced a series of interesting and relevant studies investigating grazed and mown vegetation types in western Norway, with the aim of describing their modern pollen/vegetation relationships as an aid to the interpretation. In the latter paper she used a range of multivariate techniques to identify gradients within her data. The studies demonstrated that mown meadow communities could be identified from pollen assemblages and the importance of indicator taxa was also emphasized.

The present study builds on existing studies at Storbreen that have related pollen to vegetation at a range of altitudes, terrain ages and scales (Caseldine, 1989; Pardoe, 1992, 1996). The former study was based on a total of 38 sites from across the foreland, taken from a broad range of terrain ages, altitudes, aspects and vegetation types. The results demonstrate a broad, tripartite division in the pollen record, which reflects the three major vegetation types. The pollen assemblages are dominated by a combination of extremely local or distant (regional) pollen while the 'extra-local' component appears to be consistently low, reflecting very little transport of pollen from sources within the alpine communities over the foreland. However, the data tend to be quite noisy partly because of occasional over-representation of taxa such as *Salix*, *Oxyria* and Cyperaceae, and partly because so many different environmental variables are involved.

Pardoe (1996) took several samples from three distinct vegetation types on the glacier foreland and the degree of local variation was examined. The results showed considerable variation in the composition of pollen assemblages within a few metres.

In the present study a different methodology was adopted; samples were collected from a transect of sites extending from the youngest terrain, close to the glacier snout, to terrain beyond the terminal moraine of the glacier, which is thought to be more than 9000 years old. By using data from a transect across the foreland the intention is to reduce the noise in the data by tying the pollen data closer to known regular changes in vegetation development away from the glacier. The primary environmental factors to change are altitude and age of terrain.

Methods

Field techniques

The vegetation sampling method employed was essentially a modification of the approach used by Matthews (1976, 1978a,b) and Whittaker (1985). A quadrat size of 4 m^2 was selected. Matthews (1978b) demonstrated that on an alpine foreland, where there is considerable local variation, a quadrat smaller than 4 m^2 was insufficient to provide reproducible results.

At each 4 m^2 quadrat from which the vegetation analyses were made, a composite moss polster was collected from a patch 'typical' of the vegetation community at that point in the succession. The pollen sampling followed the previously adopted procedure whereby moss polsters consisting of 20 pinches of moss were collected, since previous work has shown that a minimum of 20 pinches is necessary to overcome problems of local variability (Pardoe, 1992, 1996). The majority of subfossil data from this region has been collected from peat rather than lake sediments (Caseldine, 1983, 1984; Matthews and Caseldine, 1987; Shakesby *et al.*, 1990). Moss polsters provide the best basis for comparison with these fossil peat samples since the surface material is the same and both are terrestrial and efficient in collecting locally produced pollen.

Each quadrat was subdivided into one-hundred 20 cm × 20 cm squares and the presence of every vascular-plant species rooted in each subdivision recorded. The frequency of each species growing at a site was therefore expressed as a score, with a possible maximum of 100 if it occurred in every subdivision. This absolute measure of frequency ensured that each species was recorded independently. In dense vegetation, such as ericaceous heath, several species could have a score of 100.

Pollen preparation and counting

The 20 moss subsamples were combined by boiling gently for 2h in 0.1M sodium hydroxide solution and then shaking for a further 1h to suspend the pollen. The samples were then passed through a 180 μm sieve to removed coarse material. A 40 mL subsample was then prepared and counted using standard techniques, including hydrofluoric acid treatment and Erdtman's acetolysis (Moore and Webb, 1978; Moore *et al.*, 1991) (see Pardoe, 1992, for further details).

Two pollen and spore sums were employed in the analyses. The Total Land Pollen (TLP) sum includes all pollen and spore taxa except obligate aquatics, the Non-Arboreal Pollen (NAP) sum excludes all arboreal taxa and obligate aquatics. The NAP sum precludes possible effects of long-distance transport of arboreal pollen and has been found to reflect local vegetation characteristics better (Pardoe, 1992, 1996, 2001; Caseldine and Pardoe, 1994). For each sample a minimum of 500 TLP grains and a minimum of 100 NAP grains were counted (Figure 2).

Numerical analysis

Multivariate analysis

Multivariate analysis was used to distinguish the major trends and groupings within the data, as a basis of comparison for the pollen and vegetation data and also to examine the influence of environmental factors on the data sets. Three multivariate techniques were selected: two-way indicator species analysis (TWINSPAN); detrended correspondence analysis (DECORANA); and canonical correspondence analysis (CCA). The default options were selected unless otherwise stated.

Canonical correspondence analysis was applied in an unusual manner in this study, using the approach described in Pardoe (1996). Since the primary concern is the influence of the vegetation on the composition of the pollen spectra, rather than assessing the influence of environmental variables on vegetation, the pollen data sets were treated as analogous to 'species' data and the vegetation data were used in place of 'environmental' data. In the canonical correspondence analyses the number of vegetation taxa was restricted to 20. Taxa that were most abundant or present most consistently were selected.

Pollen indices

An alternative approach was used to assess the potential of indicator taxa to distinguish specific plant communities. Oswald *et al.* (2003a) stressed the importance of indicator taxa, in their study in the Yukon. They calculated indices expressing the representation of *Betula* and Cyperaceae as a ratio to the sum of extra-local pollen (*Alnus* and *Picea*). Similar indices were calculated for the Storbreen samples, although here *Alnus* and *Pinus* were the extra-local pollen taxa.

Pollen source area

In an attempt to estimate the most likely source of pollen for each of the moss polster samples the pollen and vegetation data were compared for each quadrat. Each pollen taxon was allocated to one of four categories: (i) pollen that could have come directly from the 4 m^2 quadrat; (ii) pollen from taxa that are known to grow on the foreland (J.A. Matthews, personal communication, 2005) but that are absent from the quadrat; (iii) arboreal pollen taxa (including *Pinus*, *Picea*, *Alnus*, *Quercus*, *Carpinus* and *Tilia*) that are known to be absent from the foreland, therefore likely to be long distance, and (iv) others with an unknown source (including *Corylus*, *Artemisia*, Chenopodiaceae and *Linum*). The sum of taxa in each category, expressed as a percentage of the TLP sum, was calculated.

Analysis

Classification and ordination of the vegetation data

Two-way indicator species analysis classification of the vegetation data shows clearly that samples are assigned to groups that correspond to the age of terrain and hence position in the vegetation succession (Figure 3a). The four groups correspond to four different communities: a 'pioneer' group of sites (Group 00) on very young unstable terrain where only a few specialized species have colonized; a group of sparsely vegetated sites (Group 01) where a greater range of herbs and shrubs have become established; a heath group dominated by *Salix* spp. (Group 10) and a group on the oldest terrain (Group 11) characterized by late successional herbs. At the four group level there is a degree of overlap between groups. The 'pioneer' group is found mainly on the youngest terrain but includes quadrats S7 and S8. This may suggest an area of slower or retrograde succession, possibly because the ground is unstable.

Species classification of this data produces four unequal-sized groups. The largest group consists of all the Ericaceae and Empetraceae species, together with the majority of herbs and grasses associated with the later phases of succession. There is a large group of pioneer species, a small group of

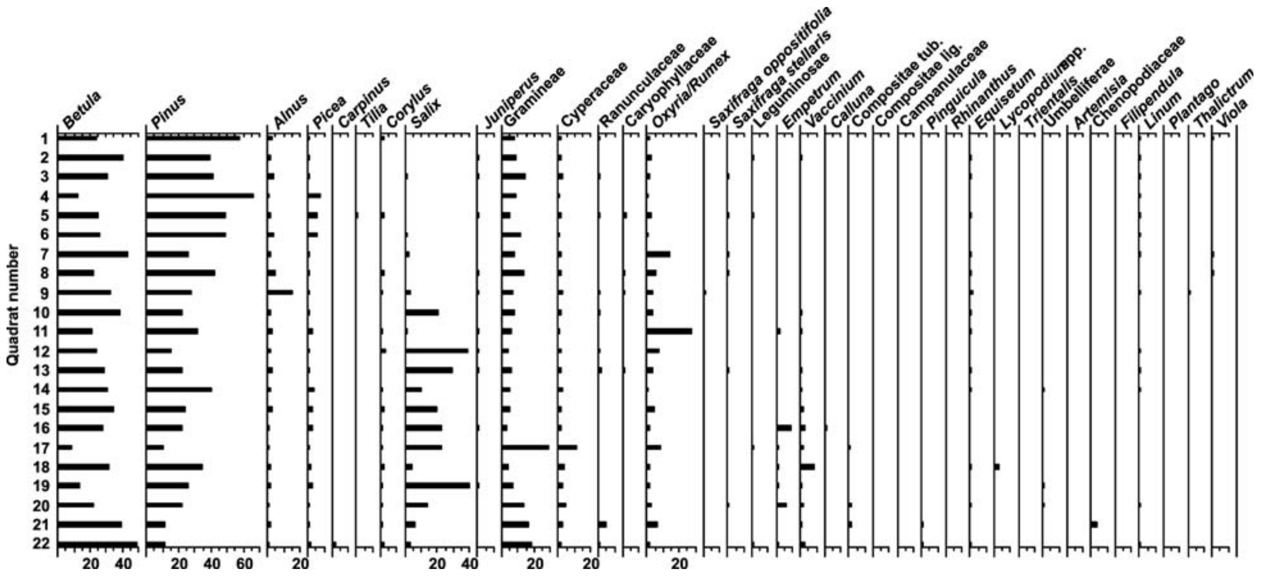
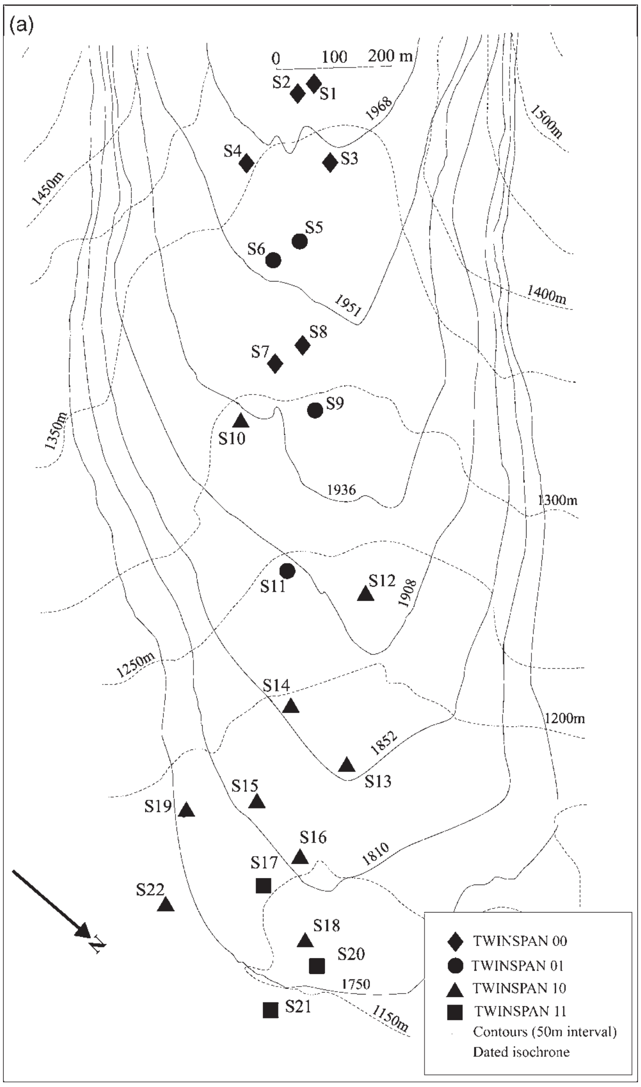


Figure 2 A summary of pollen percentage values, expressed as percent of total pollen, for moss polster samples at Storbreen glacier foreland

secondary colonizers and a small group consisting of *Festuca ovina*, *Salix glauca* and *Salix herbacea*, suggesting an open snowbed community.

Detrended correspondence analysis of the vegetation data set shows a clear progression of sites that corresponds with their position in the succession (Figure 3b). The first axis, associated with an eigenvalue of 0.812 (Figure 3b), indicating that it accounts for a high proportion of variation in the data, shows a clear separation between sites in the early stages of the succession (sites 1–8) and the later phases (9–22). The first ordination axis shows strong correlations with both altitude ($r = 0.94$, $p < 0.01$) and terrain age ($r = -0.43$, $p < 0.05$) (Table 1). The second ordination axis also shows a significant correlation with altitude ($r = 0.44$, $p < 0.05$). Sites are more broadly scattered on the second and third axes. In all the ordinations described in this paper the third axes are associated with low eigenvalues, suggesting that they account for relatively little variation in the data. Therefore, these axes are not discussed further.

Ordination of species shows the relationship between the shrub and herb taxa, which underlies the pattern of succession across the foreland. There is a gradual progression from a tight



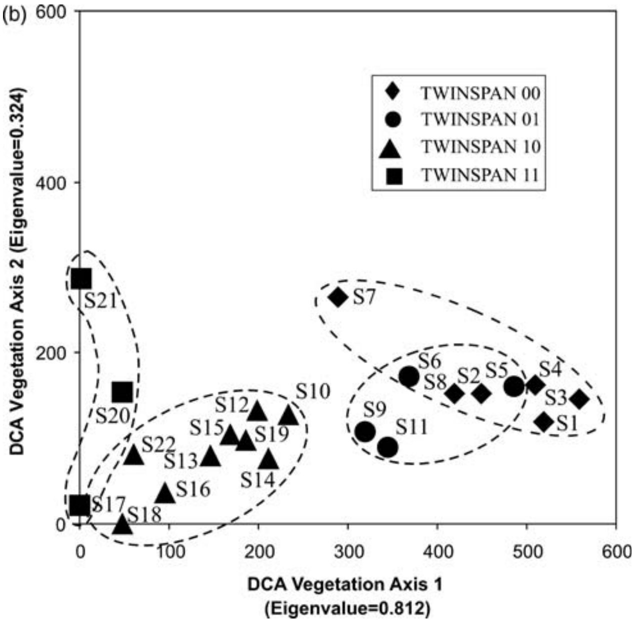


Figure 3 TWINSPAN classification and DECORANA ordination of the vegetation data. (a) The distribution of TWINSPAN classification groups over the Storbreen foreland; (b) classification and ordination in series – the distribution of sampling sites in TWINSPAN groups on the first two DECORANA axes

Table 1 The correlation between environmental variables and the axes produced by detrended-correspondence analysis and CCA ordination of the data from Storbreen foreland (Pearson's r) and between the axes produced by detrended-correspondence analysis

Axis	DECORANA				CCA			
	Altitude		Terrain age		Altitude		Terrain age	
	r	p	r	p	r	p	r	p
V851	**0.94**	< **0.01**	**−0.43**	< **0.05**				
V852	**0.44**	< **0.05**	0.27	> 0.20				
V853	0.21	> 0.20	−0.03	> 0.20				
TLP1	**−0.76**	< **0.01**	0.24	> 0.20	**−0.72**	< **0.01**	0.06	> 0.20
TLP2	0.21	> 0.20	**0.58**	< **0.01**	−0.24	> 0.20	**0.76**	< **0.01**
TLP3	0.03	> 0.20	0.21	> 0.20	0.18	> 0.20	−0.38	< 0.10
NAP1	**−0.70**	< **0.01**	−0.17	> 0.20	**−0.68**	< **0.01**	−0.16	> 0.20
NAP2	0.19	> 0.20	−0.20	> 0.20	−0.24	> 0.20	0.08	> 0.20
NAP3	0.03	> 0.20	−0.08	> 0.20	−0.15	> 0.20	−0.11	> 0.20

Axis	V851		V852		V853		TLP1		TLP2		TLP3		NAP1		NAP2	
	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p
V851																
V852	0.30	< 0.20														
V853	0.19	> 0.20	0.01	> 0.20												
TLP1	**−0.81**	< **0.01**	−0.25	> 0.20	−0.26	> 0.20										
TLP2	0.06	> 0.20	**0.48**	< **0.05**	0.06	> 0.20	−0.25	> 0.20								
TLP3	0.03	> 0.20	−0.08	> 0.20	0.23	> 0.20	−0.41	< 0.10	0.30	< 0.20						
NAP1	**−0.64**	< **0.01**	**−0.50**	< **0.02**	−0.23	> 0.20	**0.76**	< **0.01**	**−0.70**	< **0.01**	**−0.46**	< **0.05**				
NAP2	0.23	> 0.20	−0.30	< 0.20	0.12	> 0.20	**−0.51**	< **0.02**	0.17	> 0.20	**0.59**	< **0.01**	−0.38	< 0.10		
NAP3	0.04	> 0.20	−0.27	> 0.20	−0.20	> 0.20	−0.10	> 0.20	−0.39	< 0.10	0.26	> 0.20	0.05	> 0.20	−0.05	> 0.20

Statistically significant values ($p \leq 0.05$) are printed in bold.

cluster of pioneer species, to a cluster of *Salix* species, through to Ericaceae and Empetraceae and associated herbs. The second ordination axis separates woody shrubs such as *Betula nana*, *Vaccinium vitis-idaea* and *Loiseleuria procumbens* from non-lignified herbs such as *Campanula rotundifolia* and *Taraxacum* spp. characteristic of moister sites on older ground. This axis may be related to stability and soil moisture.

Classification and ordination of the pollen data

Total land pollen

In the early stages of the succession arboreal pollen dominates the TLP spectra, with the total of arboreal pollen reaching a maximum of 80% (Figure 2). This indicates an open pioneer community where regional pollen predominates and there is very little herb pollen and virtually no shrub pollen. As succession proceeds, the importance of shrub and herb pollen increases substantially. Gradually the proportion of shrub pollen increases at the expense of both herb and arboreal pollen, reflecting the development of a dense scrub or heath community. This trend increases as far as the terminal moraine.

Beyond the terminal moraine both arboreal pollen and herb pollen regain their influence in the pollen spectra because, outside the foreland, the dense shrub layer tends to be replaced by a ground and field layer where late-successional herbs have an important role. The decrease in the shrub cover may produce an increase in the representation of arboreal pollen, which the shrubs may have filtered out in the earlier phases of succession (Pardoe, 2001).

TWINSPAN classification of the Storbreen TLP data shows a clear division of samples on the basis of age of terrain and position in the succession (Figure 4a). One group dominates the earliest phases of succession from the youngest terrain to ground deglaciated in AD 1852 (Group 00). Possibly at such open sites, where long-distance pollen dominates the pollen spectra, the samples are relatively monotonous and the local component is not strong enough to produce characteristic pollen assemblages. The preferential species are represented by low frequencies of *Juniperus*, *Artemisia*, *Lycopodium selago*, *Selaginella*, *Rhinanthus*, *Linum*, *Salix*, *Picea*, *Alnus* and Cyperaceae.

Only on ground deglaciated prior to 1852, where a closed heath community exists, does the local component make its mark on the pollen spectrum. The preferential species include *Juniperus communis*, *Empetrum*, *Vaccinium* and *Betula*. These taxa are all present locally. *Corylus*, *Picea* and *Pinus* are also preferential species, indicating that there is still a significant long-distance component.

Samples taken from older ground inside the terminal moraine are, with one exception, classified into one group (10). Group 11 consists of two sites, S21 and S17. These sites were also isolated in the classification of vegetation data, together with S20. The preferential species consist of a variety of late-successional herbs, suggesting mature, diverse, luxuriant vegetation typical of the 'climax' outside the terminal moraine.

The final TWINSPAN group (01) consists of three apparently anomalous sites scattered over the foreland from the very youngest terrain to the oldest. Exactly what links these three sites is unclear. TWINSPAN classification of species produces four broad groups: pioneer herbs, tree species, heath taxa and rare taxa.

Strong correlations exist between the primary ordination axes of vegetation and pollen (for example, the correlation between vegetation Axis 1 and TLP Axis 1 is $r = -0.81$ (see Table 1)). DECORANA ordination of the TLP data shows a degree of correspondence between the arrangement of samples on the first axis and their position in the transect (Figure 4b). The first axis is strongly correlated with altitude ($r = -0.76$, $p < 0.01$) (Table 1). Sites 1–9 form quite a tight cluster. The remaining sites are scattered, but those around the terminal moraine show some association. However, the arrangement of samples on the second axis is not clearly related to their location on the foreland. Nevertheless, the second axis and terrain age are significantly correlated ($r = 0.58$, $p < 0.01$).

DECORANA ordination of species produces three main clusters: a tight cluster of long-distance arboreal and herb taxa around the origin; a group of herb taxa, possibly locally produced in the early successional phases; and a third cluster, mainly consisting of heath taxa found on older terrain. Superimposed is a scattering of exotic herbs.

Canonical correspondence analysis of the TLP data produces an ordination where many taxa are clustered close to the origin and there is little separation of the plant communities, especially on the second axis. All the eigenvalues produced by the CCA analyses are relatively low (less than 0.19), possibly because these are quite noisy data sets. Furthermore, the environmental variables used in the analyses are NAP taxa that would not explain variation in the arboreal pollen that dominates this data set. The first axis is strongly correlated to altitude ($r = -0.72$, $p < 0.01$) suggesting that altitude is a major influence on the data structure (Table 1). Terrain age and the second axis are significantly correlated ($r = 0.76$, $p < 0.01$) suggesting that this factor is also important.

Non-arboreal pollen

TWINSPAN analysis of the NAP data shows a familiar pattern; the younger terrain is dominated by one large group (01) (Figure 5a), including almost all ground deglaciated since AD 1852 and one site outside the terminal moraine.

Three groups are sited on the older terrain, occupying only a small portion of the foreland. Group 00 spans terrain deglaciated since 1936 to ground deglaciated more than 9000^{14}C yr BP. The indicator species of this group is a high percentage of *Salix*. The sites correspond to the large areas of shrub *Salix,* located to the east of the foreland, suggesting a strong signal from locally produced pollen. The other two small groups (10 and 11), are located on ground deglaciated between AD 1750 and the early nineteenth century. Their characteristic indicator species are heath species including *Vaccinium*, *Empetrum* and *Salix* spp. This suggests that the vegetation at these sites, within the heath community, is producing a characteristic pollen assemblage.

There is a marked contrast in this data set between the majority of similar sites, which occupy most of the foreland, and the mixture of sites between the AD 1810 moraine and beyond the terminal moraine. This suggests that the NAP pollen spectra are relatively monotonous at the younger, open sites but the data are sensitive to, and reflect, the mosaic of closed communities on the older ground.

Classification of species produces three distinct clusters: a cluster of heath taxa; a group of taxa, probably locally produced in the early stages of succession, but which equally could have a regional source; and a group of pioneer herb species, probably growing locally, together with some exotic herbs.

DECORANA ordination of NAP data produces a very similar pattern to ordination of TLP data (Figure 5b). There is a tight cluster of pioneer sites (1–9) on the first axis followed by a broader spread of sites on older terrain. The first axis is strongly correlated with terrain age ($r = -0.70$, $p < 0.01$) (Table 1). As in TWINSPAN, S11 tends to be associated with

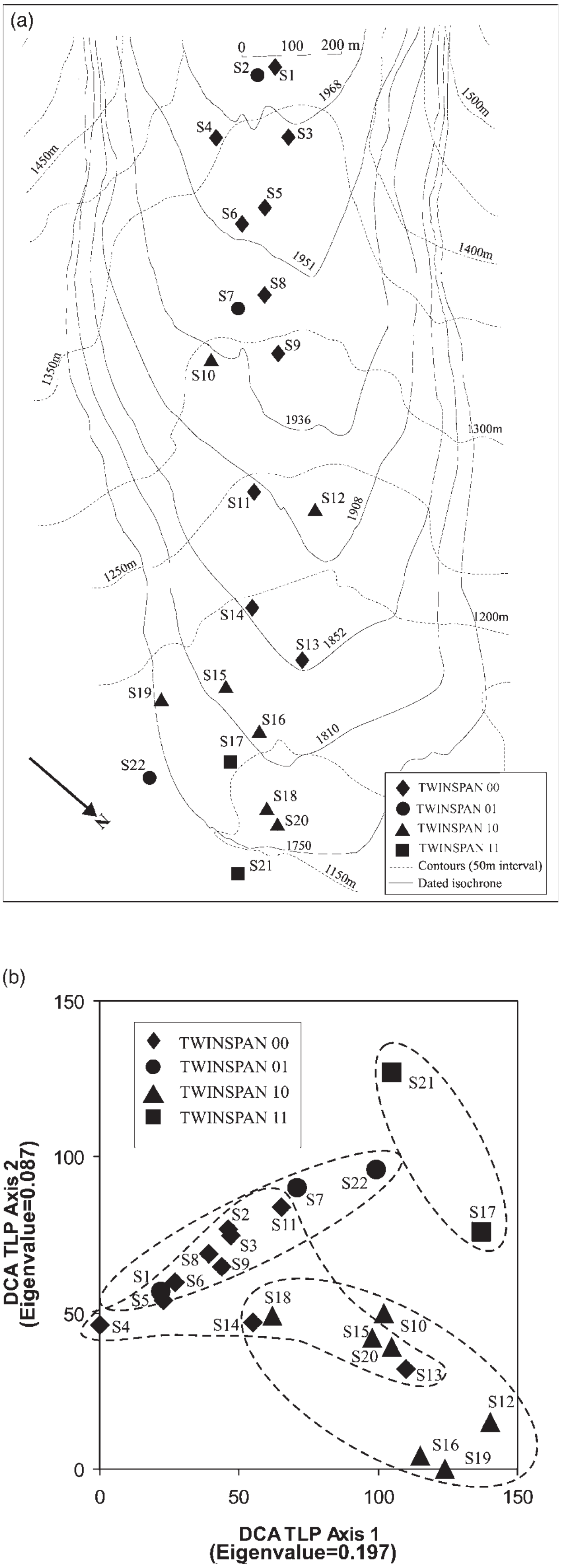


Figure 4 TWINSPAN classification and DECORANA ordination of the total land pollen data. (a) The distribution of TWINSPAN classification groups over the Storbreen foreland; (b) classification and ordination in series – the distribution of sampling sites in TWINSPAN groups on the first two DECORANA axes

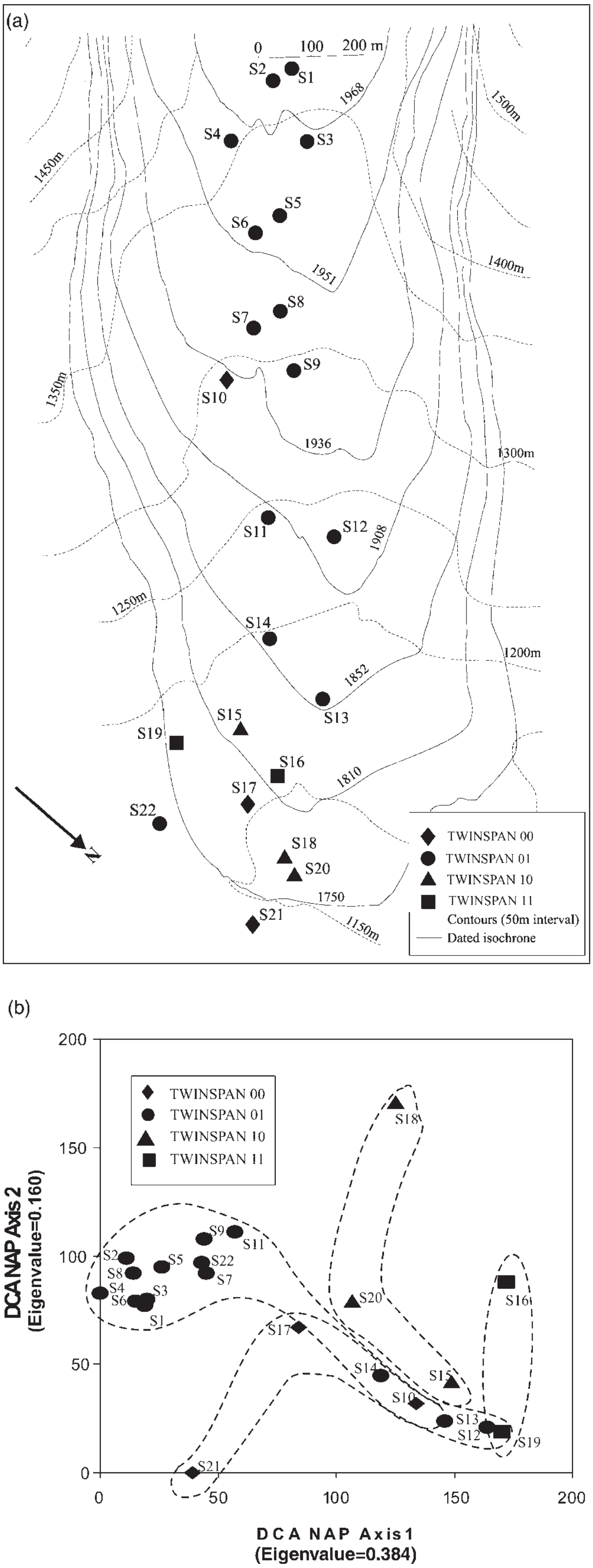


Figure 5 TWINSPAN classification and DECORANA ordination of the non-arboreal pollen data. (a) The distribution of TWINSPAN classification groups over the Storbreen foreland; (b) classification and ordination in series – the distribution of sampling sites in TWINSPAN groups on the first two DECORANA axes

the pioneer sites whereas S10 is placed with the older sites. This may simply reflect the mosaic of plant communities on the local scale or could suggest that the AD 1936 moraine represents the boundary between the pioneer community and the snowbed community.

Samples on older ground show a greater scatter, unrelated to terrain age. Samples on the oldest terrain occupy an intermediate position between the pioneer samples and the samples from the later phases of the succession within the 1810 moraine. On axis 1, three samples from ground deglaciated between 1750 and 1936 form another cluster. Again, there is no clear correspondence between the arrangement of the samples on the higher DECORANA axes and their relative position on the foreland.

The ordination of species is similar to both the DECORANA species ordination of the TLP data and the TWINSPAN classification of the NAP data. Three groups can be identified (see also, Pardoe, 2001).

(1) The heath species, eg, *Vaccinium*, *Empetrum*, *Calluna* and *Lycopodium*, which generally have a local source.
(2) A cluster typified by *Oxyria*, Gramineae, Cyperaceae, *Thalictrum* and Campanulaceae, whose source is difficult to determine. These are likely to have primarily a very local source, possibly supplemented by some long-distance pollen.
(3) A cluster, including *Saxifraga oppositifolia*, *Trientalis europaea*, Leguminosae, *Equisetum*, *Saxifraga stellaris* and *Linum*. This group, comprising taxa that are generally present at low frequencies, includes both low pollen producers, present in the vegetation, and also, extralocal taxa. There is the suggestion of a fourth group consisting of *Salix* spp., *Lycopodium selago*, Compositae tub. and Ranunculaceae, which may be characteristic of the *Salix*-dominated snowbed community.

Superimposed on the main clusters is an apparently random scatter of mainly exotic herbs (eg, Umbelliferae and *Artemisia*). These taxa are rare so their positions on the ordination axes are unlikely to be significant. *Viola* and Umbelliferae appear to be closely linked and distinct from other species. These taxa could be indicators of the ‘climax’ community outside the terminal moraine. The representation of individual taxa is described in greater detail in Pardoe, (2001).

CCA of the NAP data, using the 20 most abundant taxa as environmental variables, produces a much clearer separation of the plant communities than analysis of the TLP data (Figure 6a, b). The arrangement of the pollen taxa on the first axis based on the NAP data set can be clearly related to the frequency of that taxon in the vegetation in the plant succession. This axis is strongly correlated with altitude ($r = -0.68$, $p < 0.01$).

However, closer examination of the distribution of taxa on the axes suggests that other factors may also be involved. For example, *Vaccinium*, a taxon that is particularly sensitive to the length of growing season, is at one extreme of the ordination while taxa such as *Saxifraga oppositifolia*, *Salix herbacea* and *Luzula* that can tolerate prolonged snowlie and unstable condition are at the opposite extreme.

DECORANA ordination of pollen taxa produces groups that can be related to the origin and mode of pollen production whereas CCA ordination of the pollen and vegetation data simultaneously produces clusters that can be interpreted more easily in terms of the source plant community because the direct ordination restricts the pollen data by taking into account the vegetation taxa.

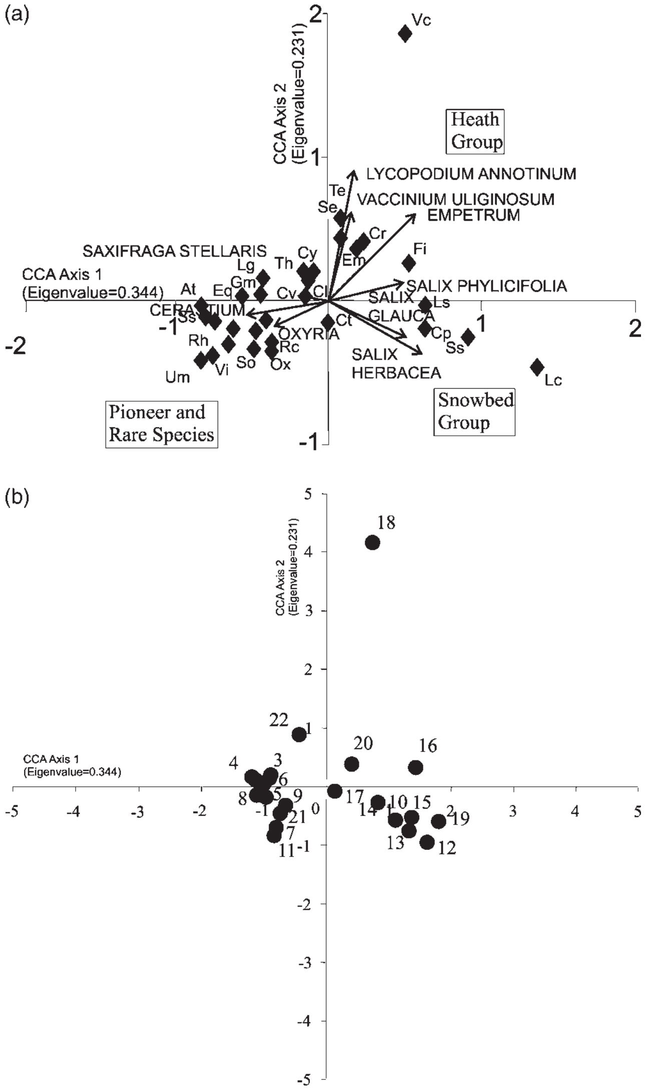


Figure 6 CCA ordination of vegetation and non-arboreal pollen data from Storbreen (excluding *Lycopodium* spp.). (a) Species scores. Key to pollen taxa: Eq, *Equisetum*; Ct, Compositae tub.; Cy, Cyperaceae; Cl, Compositae lig.; Cv, *Calluna*; Th, *Thalictrum*; At, *Artemisia*; Ss, *Saxifraga stellaris*; Rh, *Rhinanthus*; Um, Umbelliferae; So, *Saxifraga oppositifolia*; Ox, *Oxyria*; Rc, Ranunculaeae; Gm, Gramineae; Vc, *Vaccinium*; Te, *Trientalis*; Fi, *Filipendula*; Se, *Selago*; Cr, *Campanula*; Em, *Empetrum*; Ls, *Lycopodium selago*; Cp, Caryophyllaceae; Ss, *Salix* spp.; Lc, *Lycopodium clavatum*; Lg, Leguminosae. (b) Sample scores for each site (quadrat)

Three distinct groups can be identified.

(A) A group consisting of pioneer taxa and rare herbs. The pollen taxa in this cluster include *Oxyria*, Ranunculaceae and *Saxifraga oppositifolia*, while the vegetation taxa include *Oxyria*, *Saxifraga oppositifolia*, *Saxifraga cespitosa*, *Saxifraga stellaris*, *Poa alpina* and *Cerastium alpina*. The closeness of the same taxa in both data sets provides strong evidence of a local pollen source for many taxa and suggests that the pollen assemblage is representative of the local vegetation. This is significant because the CCA analysis demonstrates that, even in the pioneer community where AP dominates, the analysis is sensitive to locally produced pollen and that this community does produce a characteristic pollen assemblage, in contrast to the results of TWINSPAN and DECORANA analysis. This group includes some rare extra-local herb pollen taxa. For example, *Artemisia* is absent from the vegetation at Storbreen but found near Lom (approximately 35 km away). The group also includes rare taxa such as *Viola* and *Juniperus* that could have a local source since both grow on the foreland.

(B) A snowbed group. In this cluster pollen taxa such as *Salix* spp. and *Lycopodium clavatum* are located close to vegetation taxa such as *Salix herbacea*, *Salix glauca* and *Salix phylicifolia*. Again, this proximity suggests a local source of pollen and indicates that the snowbed community does produce a characteristic assemblage.

(C) A heath group. In this group pollen taxa such as *Empetrum*, *Trientalis europaea* and Campanulaceae are located close to vegetation taxa such as *Empetrum*, *Vaccinium uliginosum* and *Bartsia alpina*. This group tends to be more broadly scattered. *Lycopodium* spp. spores were excluded from the diagram because it was an extreme outlier. *Vaccinium* spp. pollen is also an outlier.

Pollen indices

The indices successfully distinguished the early phases of succession from the later phases of succession for both *Salix* and *Empetrum* (Figure 7 a, b). *Salix*, both from *Salix herbacea* and shrub *Salix*, is abundant in both the heath and snowbed communities and produces a clear signal in the pollen assemblage, while a high frequency of *Empetrum* is characteristic of the heath community. The results for *Oxyria* are inconsistent. Caryophyllaceae produces relatively high indices early in the succession (Figure 7c), where the vegetation has become established and *Cerastium alpina* and *Arabis alpina* are abundant, and also isolated peaks later in the succession but the results need to be treated with caution because Caryophyllaceae pollen is present only at low frequencies. Gramineae produced disappointing results, because of poor species resolution (Figure 7d). In the early phases of succession the source of Gramineae is likely to be either taxa such as *Poa alpina*, *Deschampsia alpina* and *Phleum*, present at low frequencies, or long distance pollen, whereas later in the succession more pollen might come from local species such as *Festuca rubra* and *Anthoxanthum oderata*.

Pollen source area

When the potential source of pollen is examined, the results (Figure 7e) show graphically changes in the likely source of pollen through the succession as the vegetation becomes denser and more diverse. For example, in the early phases of succession arboreal pollen accounts for up to 75% of the pollen assemblage and pollen that could originate from the quadrat less than 10%. As succession proceeds the proportion of arboreal pollen diminishes to only 15–30% while the proportion of pollen that could have come from the quadrat increases to 55–78%.

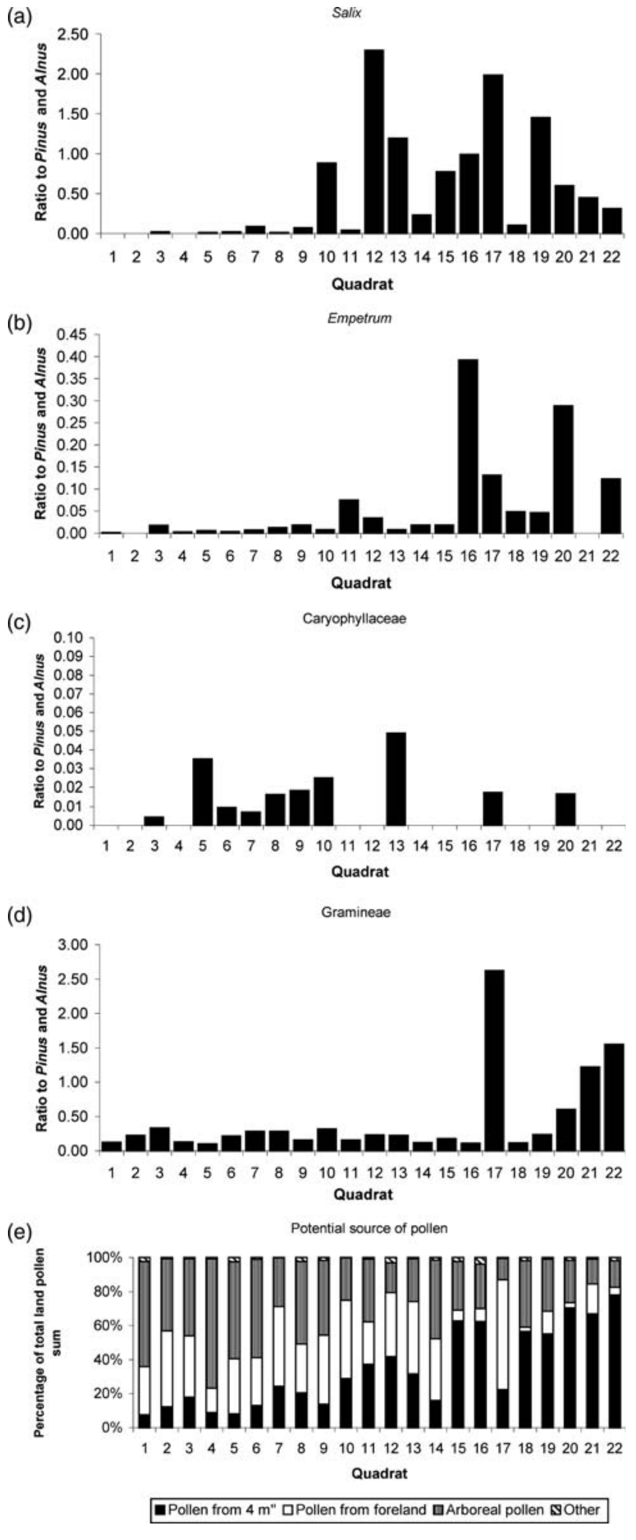


Figure 7 (a) Ratio of *Salix* pollen to the sum of *Pinus* and *Alnus* pollen. (b) Ratio of *Empetrum* pollen to the sum of *Pinus* and *Alnus* pollen. (c) Ratio of Caryophyllaceae pollen to the sum of *Pinus* and *Alnus* pollen. (d) Ratio of Gramineae pollen to the sum of *Pinus* and *Alnus* pollen. (e) The potential source of pollen in each assemblage. Note different scales on the vertical axis. Quadrat number refer to Figure 3a

Discussion

This study demonstrates that at Storbreen glacier foreland a strong relationship can be identified between vegetation and pollen deposition, both for whole plant communities and for individual taxa. Ordination and classification of the data bring out the broad trends and produce results that can be interpreted in terms of the major environmental variables. TWINSPAN analysis of both the vegetation and pollen data reveals that the three main plant communities, pioneer, heath and snowbed, can be distinguished. DECORANA ordination shows that the sequence of samples on the ordination axes can be related to the position of the sampling sites in the plant succession and that the axes can be directly related to both altitude and age of terrain. Multivariate analysis of the pollen data distinguishes the two extremes of the succession, the pioneer and heath communities, most successfully, but the intermediate succession stages are harder to identify, because the spectra they produce (particularly the TLP spectra) can be very similar despite deriving from different plant communities. Consequently, there is a high degree of overlap between pollen spectra from different plant communities and several transitional samples exist. In these circumstances indicator species can prove invaluable for differentiating plant communities and determining the source of pollen.

Three groups of taxa can be recognized at Storbreen (Pardoe, 2001): mostly insect-pollinated taxa that produce relatively strong plant–pollen correlations, including *Salix herbacea*, *Empetrum*, Caryophyllaceae and *Oxyria*/*Rumex*; wind-pollinated taxa, such as *Betula*, *Pinus* and Gramineae, that produce very poor correlations; and, finally, herb taxa that produce relatively little pollen and rarely register in the pollen spectrum. Taxa from the first category are most useful as indicators to differentiate spectra from separate plant communities.

Calculation of indices expressing the ratio of indicator taxa to the sum of extra-local pollen proved a valuable means of distinguishing different plant communities. The indices emphasize changes in the representation of specific taxa through the succession, especially *Salix* and *Empetrum*, but they are dependent on local changes in the extra-local component through time and space, so the context is important. The Storbreen results endorse the views of Oswald *et al.* (2003a) that it is preferable to rely on several indicators, in conjunction with multivariate analyses of the entire pollen assemblage.

Classification of the pollen data suggests that the ‘pioneer’ group is much larger and more extensive than the ‘pioneer’ group produced by classification of the vegetation data and identified in the field. In such an open environment, pollen with a regional source dominates both the TLP and NAP spectra, masking the local signal and producing relatively monotonous pollen spectra, making it difficult to detect relatively subtle changes in the vegetation in the early phases of plant succession. Nevertheless, even in the pioneer community a local signal can be recognized and this grows stronger as the vegetation becomes more established and the ground cover increases. CCA analysis of the data provides stronger evidence of the links between pollen deposition and vegetation than DECORANA, possibly because environmental factors such as altitude and terrain age have a major influence on the structure of the vegetation data and, indirectly, pollen data, so simultaneous ordination of the data sets reinforces the importance of these factors. Direct comparisons are possible between taxa in the pollen spectra, for example *Salix* spp. and the plants in the vegetation such as *Salix herbacea*, *Salix glauca* and *Salix phylicifolia* from which the pollen is derived. Analysis of the NAP data produces much clearer results and higher eigenvalues than analysis of TLP, probably because a higher proportion of pollen in the NAP sum has a local source so the signal from the local vegetation is stronger, providing a much clearer picture of the local plant community. However, the disadvantage of using the NAP sum is that it is relatively small. The eigenvalues derived from ordination of both data sets and both ordination techniques are all relatively low and this may be partly due to noise in the data.

There is not always a clear-cut division between the pollen groups, reflecting the mosaic of plant communities that are present at Storbreen (see also Pardoe, 1996), a consequence of local-scale variation in environmental factors such as soil stability, disturbance, length of snowlie and moisture conditions. The lack of sharp boundaries between plant communities suggests that ordination produces a more realistic result than classification of the data. Throughout the literature there seems to be a growing awareness of the importance of local-scale mosaics or patches of communities to the composition of the pollen assemblage (see, for example, Bunting, 2003; Bunting *et al.*, 2004; Räsänen *et al.*, 2004). Bunting (2003) notes that at her site in northwest Scotland ‘changes in non-arboreal components of pollen assemblages from mire communities therefore appear to reflect predominantly local patch dynamics rather than wider landscape changes’, and this phenomenon may also be important at Storbreen.

The source of pollen is the critical factor in understanding the pollen–vegetation relationship. In recent years there has been increasing interest in computer models of the source of pollen (Broström *et al.*, 2004, 2005; Bunting *et al.*, 2004, 2005). Sugita (1993, 1994) introduced the concept of the ‘relevant source area of pollen’ (RSAP), which he defined as the area beyond which the correlation with plant abundance does not improve. The RSAP is calculated for a specific landscape and time period. For example, the predicted and observed RSAP for small forest hollows in Michigan and Wisconsin was the area within a 75–100 m radius (Sugita, 1994, 1998; Calcote, 1995) but that is about one-tenth of the radius predicted for the landscapes of southern Sweden under the current environmental setting (Sugita *et al.*, 1999). The calculation is usually made for an area with a radius of several kilometres and the RSAP is constant for any point within that landscape. RSAP studies have generally been undertaken for forested sites. Sugita *et al.* (1999) found that it is difficult to quantify the area of open land from non-arboreal pollen percentages, suggesting that an area within 800–1000 m radius is still too small to obtain good estimates of pollen productivity. Bunting (2003) found relevant pollen source areas of the order of 2 m or less for *Calluna vulgaris* and *Vaccinium* type.

The computer models are most suitable for broad-scale studies since they effectively demonstrate the representation of dominant taxa, especially tree taxa. The models are also valuable for reconstructing the vegetation history of a site. However, the models are relatively crude tools for reconstructing the entire plant community. They are unable to provide detailed information about rare pollen types that, although present at only low frequencies, may be critical to understand the exact nature of the plant community.

The present study represents a different approach to understanding the pollen–vegetation relationship because it is small-scale and based on fine-resolution vegetation data collected in the field. Field-based studies can show in greater detail the relationship between pollen and vegetation and also highlight over- or under-represented taxa – features that may be overlooked by broad-scale models. The two approaches can be complementary. Inevitably, the models make unrealistic assumptions about the uniformity of environmental variables such as topography, soil type and stability. In contrast small-scale studies can highlight the importance of these factors on a local scale, producing a mosaic of communities. This study also has the advantage that the distribution of plant communities and of individual taxa is well known and relatively well defined at Storbreen, so it is possible to work out the probable source of pollen on the local scale to infer the representation of individual taxa.

The vegetation survey for the present study was carried out in such a way that the relative source area of pollen could not be calculated. However, it was considered worth exploring the potential source of pollen by comparing the pollen and vegetation data for each quadrat (Figure 7). These results relating to pollen source are consistent with the view of

Bunting (2003) that when sediment records from mires are used, the non-arboreal pollen and spore component of the pollen assemblage will be dominated by pollen from vegetation within a few metres of the sampling point.

The proportion of pollen that could have derived from the foreland is quite variable, depending on the diversity of the local vegetation. For example, in quadrat 17 where there are only seven taxa in the vegetation, only 22.5% of TLP could have come from the quadrat but 64.6% could have come from the remainder of the foreland, whereas in the adjacent quadrat (quadrat 18) where there are 19 plant taxa, 56.6% of TLP could have come from the quadrat and only 2.2% could have come from the remainder of the foreland. At both sites there is a continuous groundcover. This reinforces the concept that the mosaic of plant communities strongly affects the composition of the pollen assemblage. Both groundcover and the physiology and pollen productivity of the plants will also have an important influence. For example, one can imagine that an open, unstable, rocky substrate where small pioneer plants grow in isolation represents a very different depositional environment from the dense shrubby heathland at low altitudes near the edge of the foreland where there is a complete groundcover and several layers of plants. Although there is some variability the general trends are quite striking and the proportions of the different sources do change quite consistently across the foreland. The potential source of pollen is still many kilometres throughout the succession. However, the graphs suggest that the actual source area of pollen decreases significantly as succession proceeds and that for most of the samples, where there is a continuous ground cover (quadrats 15–22), the majority of pollen is likely to originate from the foreland, an area of approximately 1.2 km^2. Oswald *et al.* (2003a) suggest that the relevant source area for tundra is quite small because many of the pollen types are insect-dispersed, and also because the smaller stature of the vegetation may result in different dispersal patterns than in forests, and indicate that for their sites the RSAP may be of the order of 600–800 m, which is similar in scale to, although not directly comparable with, the results from Storbreen.

There are several limitations to this approach: (a) although the pollen potentially could have come from the area specified, it may have originated further afield; (b) the boundaries of both foreland and quadrat are quite arbitrary so the pollen assemblage might be influenced by an abundant source just outside the boundary; (c) the source of pollen is estimated based on presence/absence in the vegetation and this can make quite significant differences to the results. For example, the presence of a small clump of *Salix herbacea* in the quadrat would have the same influence on the results as a dense thicket of *Salix glauca*, *Salix reticulata* and *Salix phylicifolia*; (d) the allocation of *Betula* to a category represents something of a problem since, throughout the succession, but especially in the early phases of succession, the predominant source of pollen is likely to be long-distance *Betula pubescens* pollen. However, *Betula nana* grows on the foreland and, in the later phases of succession, it is abundant in the quadrats, so there is no choice but to include *Betula* in either the foreland or quadrat categories, even though this may skew the data, especially in the early phases of succession. Nevertheless this is a useful first step and demonstrates the value of estimating the most likely source of pollen. Throughout the succession the percentage of pollen whose source is difficult to determine is consistently 4% or less.

The present study demonstrates that plant communities do, broadly, produce characteristic surface pollen assemblages, so the applications of these results can be considered, the most obvious being the use of the modern samples as analogues for past vegetation and to improve our interpretation of subfossil cores. This approach has been attempted with limited success (Caseldine and Pardoe, 1994). The study was based on large regional-scale data sets that were inevitably quite noisy. However, the degree of correspondence might be significantly improved by using a smaller surface data set from a more limited area, and comparing the surface samples with a core collected within that area. The agreement might also be improved if local non-arboreal pollen were emphasized.

The method of moss polster collection is controversial. Several previous studies have used a moss polster consisting of a single pinch of moss from one point (Hjelle, 1998; Tonkov *et al.*, 2001) and some might argue that this provides the best analogue for a fossil core that is collected from a single point. However, the advantage of using a moss polster consisting of several pinches (in this study, 20) from a small area is that the effect of local variation is reduced and the pollen assemblage is more representative of the local plant community, providing a better modern analogue for the interpretation of fossil cores. The disadvantage of using a single pinch is that where there is a high degree of local variability (as has been previously demonstrated at this glacier foreland (Pardoe, 1996)) there is the danger that an unusual surface sample might not be representative of the whole community and will provide a poor analogue for past vegetation (see Pardoe, 1996).

The results from Storbreen also might be valuable to re-interpret results presented in Barnett *et al.* (2001) a paper that looked at changes in forest composition and extent in Leirdalen during the Holocene. In this paper Barnett *et al.* suggest that values of *Betula* spp. greater than 10% and values of *Pinus sylvestris* of 55% both indicate the local presence of these taxa, based on figures from Huntley and Birks (1983). However, in the surface samples from the early phases of succession at Storbreen such high values of arboreal pollen are characteristic of an open pioneer community rather than indicating the presence of woodland, although, to be fair, Barnett *et al.* (2001) do also consider concentration and influx values rather than percentage values alone. The data from Storbreen, being much closer to the Leirdalen site could provide a better modern analogue and a stronger foundation for the interpretation, possibly indicating that woodland migrated to this site later than previously thought.

In this study the pollen was extracted from moss polsters and the pollen counts were relative. These data are most suitable for comparison with relative data from palaeostudies, especially for pollen samples taken from peat cores. However, the increasing success of Hicks and her colleagues (Hicks, 2001; Hicks *et al.*, 2001; Autio and Hicks, 2004) has demonstrated the effectiveness of using Tauber traps to produce absolute pollen accumulation rates (PARs), to relate PARs to climatic parameters and also to provide insights into the representation of individual taxa. Currently there is growing interest in comparing pollen spectra collected from moss polsters and Tauber traps from the same location (Tonkov *et al.*, 2001; Räsänen *et al.*, 2004). If the nature of this relationship could be elucidated and quantified we could then draw on surface pollen data from both moss polsters and Tauber traps to improve our understanding of the relationship between modern vegetation and pollen deposition, to provide a clearer picture of the length of deposition and to facilitate our interpretation of subfossil data, in terms of past vegetation and palaeoenvironmental change. However, the disadvantage of using Tauber traps is that pollen deposition must be recorded over a period of several years to overcome problems caused by annual variation (Hicks, 1985; Autio and Hicks, 2004) so a sustained effort would be required to obtain better results.

Comparative studies of pollen deposition at a range of scales (Pardoe, 1992, 2001) suggest that the foreland scale is optimum since the plant communities present are relatively clearly defined and the major environmental trends can be identified. Other studies have revealed that at small scales local variation can become a major problem (Pardoe, 1996) whereas at larger scales major variation in environmental variables such as altitude, climate and aspect can produce a very noisy data set that is relatively difficult to interpret (Pardoe, 1992).

Conclusion

This paper demonstrates that the three main plant communities at Storbreen glacier foreland can be identified in both the vegetation and pollen data sets. This identification is facilitated by the use of numerical techniques. The application of canonical correspondence analysis demonstrates the strong correspondence between vegetation and pollen in terms of both plant communities and individual taxa.

The different phases of succession can be identified from the pollen data alone, despite the prevalence of long-distance pollen in open plant communities. This is important for the interpretation of samples from fossil cores because it demonstrates that distinct plant communities can be distinguished, even where long-distance pollen dominates the spectra. Indicator taxa have a critical role, indicating the composition and the openness of the local vegetation. Previous studies at Storbreen (Caseldine, 1989; Pardoe, 1996, 2001) have stressed the importance of indicator taxa but this study provides better quantitative evidence.

The source of pollen is crucial. Using qualitative and quantitative approaches it is possible to infer the likely source of pollen, but this is still quite crude. Calculation of pollen indices brings out contrasts in the representation of different taxa. For example, the representations of *Empetrum* and *Salix* in the pollen assemblage show strong links to their frequencies in the vegetation whereas the representations of Gramineae and *Oxyria* proved quite inconsistent.

Plant physiology, even on a very small scale, may have an important influence on patterns of pollen deposition. There is a mosaic of plant communities at Storbreen glacier foreland and, in consequence, the separation of plant communities is not clear-cut in either the vegetation or pollen data, especially in the early phases of succession. Similar mosaics are likely to have existed in the past, making it more difficult to elucidate the nature of past vegetation precisely.

Knowledge of surface samples can contribute to our understanding of past local vegetation history. More empirical local studies are needed to provide greater insight into the relationship between vegetation and pollen deposition. Whittaker (1985) stressed the dynamic nature of both plant populations and environmental variables on glacier forelands. When one adds to this situation differences in the source and representation of individual pollen taxa, in combination with the mosaic of plant communities that are present, it is little wonder that the results produce a complex picture of surface pollen deposition. Nevertheless a clear relationship can be demonstrated between vegetation and pollen and the understanding of this relationship can be considerably improved by the use of multivariate analysis and indicator taxa.

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