

Modern pollen rain, subantarctic Campbell Island, New Zealand

M. S. McGlone and C. D. Meurk

Landcare Research, P.O. Box 69, Lincoln 8152, New Zealand (E-mail: mcglonem@landcare.cri.nz)

Abstract: A modern pollen-vegetation data set of 46 samples is presented from subantarctic Campbell Island, 600 km south of the New Zealand mainland. The sampled vegetation includes all major community types: maritime turf and grassland, sedge flushes, dwarf forest, scrub, cushion bog, tussock grassland, and high altitude graminoid turfs and tundra. Macrophyllous forbs - characteristic plants of subantarctic islands - are common throughout. Most taxa have highly restricted pollen dispersal, largely due to the short stature of the vegetation and the high proportion of insect-pollinated species. Percentages of pollen or spores of the dominant taxa have a significant positive correlation with the percent vegetation cover of the corresponding species, the exceptions being the widespread ferns *Polystichum vestitum* and *Blechnum* spp., and the ubiquitous macrophyllous forb, *Bulbinella rossii*. The relationship between the vegetation cover of a given taxon and its pollen representation was usually not strong enough to give confidence in a quantitative reconstruction based on pollen frequency alone. However, the broad vegetation groupings have characteristic pollen and spore spectra clearly related to the abundance of their dominant plant species. Detrended correspondence analysis of the pollen spectra grouped most sites according to their source vegetation type and generated a pattern similar to that of vegetation data analysed in a similar fashion in previous studies of the island. This study, together with recent work on Auckland Island pollen and spore representation, has resulted in a combined modern palynological data base of more than 100 sites for the New Zealand subantarctic islands.

Keywords: Campbell Island; modern pollen rain; pollen dispersal; pollen representation; subantarctic islands.

Introduction

The isolated subantarctic islands to the south of the New Zealand mainland are covered by extensive blankets of peats and peaty soils that began forming more than 12 000 years ago. New Zealand subantarctic peats are for the most part highly humified and, with the exception of scattered wood layers, lack well preserved macrofossils. Inferences as to past vegetation change therefore mainly rely on pollen and spores. A number of pollen analytical studies have been published for the New Zealand subantarctic islands (Moar, 1958, 1973; Fleming *et al.* 1976; McGlone *et al.* 1997), showing that major vegetation and climatic change has occurred in the post-glacial period. These studies have generally been of low resolution and poorly dated, and there is great potential for further work.

The Campbell Island survey presented in this paper is part of a wider programme to improve the characterisation of the pollen rain of the New Zealand subantarctic islands. The subantarctic island flora is limited, and thus a high proportion of pollen taxa can be assigned to one or a few species. A study of the Auckland Islands (McGlone and Moar, 1997) demonstrated that modern pollen rain distinguished

the major vegetation types with a high degree of reliability but that the strength of the pollen-vegetation relationship was insufficient to quantitatively estimate vegetation composition from pollen spectra. Campbell Island lies south of the Auckland Islands, and has similar flora and vegetation. It lacks the tall forest of the Auckland Islands, but has a greater relative extent of tundra and macrophyllous forb communities. This present study sampled similar vegetation types to those of the Auckland Islands and, in particular, macrophyllous forb and tundra communities not well represented in the earlier study. The ultimate objective is to produce a comprehensive New Zealand subantarctic island modern pollen-vegetation data base to assist in making better quantified estimates of past vegetation and environments.

Environment and vegetation

Physical environment

Campbell Island (52° 34'S, 169° 09'E) lies approximately 600 km SSE of mainland New Zealand, and its nearest island neighbours are the Auckland

Islands, 300 km north-west, and Macquarie Island 700 km to the south-west. Marine erosion has cut steep cliffs on all exposed coastlines. Gentle to moderately steep slopes and broad U-shaped valleys characterise the lowlands; the uplands have rolling plateaux, fretted ridges, and cliffs. The highest point is Mt Honey (570 m). The island's surface of 113 km² is covered with peat, with the exception of slopes >35° and terrain above 400 m. Deep (c. 5 m) peat deposits are abundant on flat to undulating lowland surfaces, while thin peats and shallow peaty soils occur on steeper slopes and summits (Campbell, 1981).

Campbell Island lies in cool waters well south of the subtropical convergence, and in a zone of persistent westerly winds. The climate is cloudy, cool, moist and extremely windy (De Lisle, 1965). There are over 250 raindays a year but only a moderate annual average lowland rainfall of 1400 mm (New Zealand Meteorological Service, 1973). Sea-level air temperatures on the island track sea-surface temperatures, averaging 9.3°C in January and 4.6°C in July, with a small daily range. Uplands experience more rain (2000–2500 mm per annum), less sunshine, lower temperatures (c. 5°C lower at the summits), more frequent and severe frosts, and much stronger winds (6–8 m s⁻¹ at sea level versus 16–22 m s⁻¹ above 300 m) (Meurk and Given, 1990).

Flora and vegetation

The present vegetation has been strongly modified by introduced grazing animals and burning. Earlier accounts of the vegetation of Campbell Island include those of Cockayne (1904, 1909) and Oliver and Sorensen (1951). Meurk *et al.*, (1994) presented a quantitative analysis of the vegetation pattern of Campbell Island and its relationship to topographical, climatic, edaphic and biotic factors.

There are about 132 indigenous vascular taxa and 39 naturalised adventives in the Campbell Island flora. The flora of the southern islands of New Zealand contains a number of distinctive, large-leaved herbaceous species, often referred to as “megaherbs”. The term is inappropriate since their leaves are in the macrophyll class and some of the subantarctic tussocks (which are also herbs) are larger. Therefore, we will here, following McGlone *et al.* (1997), refer to them as “macrophyllous forbs”. Campbell Island has in this group *Anisotome antipoda*¹, *A. latifolia*, *Bulbinella rossii* (geophyte), *Stilbocarpa polaris*, *Pleurophyllum criniferum* (geophyte), *P. hookeri*, and *P. speciosum* (partial geophyte).

Meurk *et al.* (1994) identified 21 plant communities. Hard cushion bogs, dominated by

Centrolepis ciliata, *Oreobolus pectinatus*, *Astelia subulatus* and *Isolepis aucklandica* in the lowlands, and by *Centrolepis pallida* with *Rostkovia magellanica*, *Isolepis aucklandica* and bryophytes at high altitudes, are common throughout. The bogs form intricate mosaics with other vegetation types, and sites on them are assigned to the surrounding vegetation matrix. For the purposes of this study we have aggregated the non-cushion bog vegetation into the following six major groupings:

1. Maritime turf and grassland

Coastal Campbell Island is characterised by lichen crusts, cushions, and turfs along the littoral fringe, macrophyllous forb fields (*Anisotome latifolia*, *Stilbocarpa polaris*, *Pleurophyllum speciosum*), short and tall *Poa* tussock grasslands, and *Hebe* shrublands. Maritime short turfs are dominated by *Colobanthus* spp., *Crassula moschata*, *Isolepis aucklandica*, *Leptinella* spp. and *Puccinellia chathamica*. These communities receive substantial inputs of cations from sea-spray and are highly productive (Meurk *et al.*, 1994).

2. Carex flushes

Fertile flushes dominated by *Carex appressa*, *Coprosma* spp shrubs, *Blechnum* “sp.2” and *Hierochloa fusca* form on low to moderate angle slopes. *Polystichum vestitum*, *Pleurophyllum criniferum*, *Poa litorosa* and *Bulbinella rossii* are commonly present.

3. Forest-scrub

Dracophyllum longifolium and *D. scoparium* form low forest (up to 5 m tall) and scrub on low altitude, sheltered sites. *Myrsine divaricata* and *Coprosma* spp. shrubs occur within the forest and form dense divaricating scrub at low to mid altitudes on exposed or swampy sites. *Polystichum vestitum* and *Histiopteris incisa* ferns are abundant in gullies and canopy gaps.

4. Shrub-tussock

At mid altitudes, *Chionochloa antarctica* and *Poa litorosa* tussock grassland intergrades with shrub-fern communities dominated by *Dracophyllum* heath and divaricating *Coprosma* spp. and *Myrsine divaricata* stands, with *Polystichum vestitum* in gullies. These stands are regenerating in an induced meadow complex dominated by *Poa litorosa* and *Bulbinella rossii*.

5. Tussock grasslands

Low to mid altitudes support *Chionochloa antarctica* tall tussock grasslands, but sheep grazing has induced widespread *Poa* short tussock meadows. The tussock grasslands of the upper middle slopes become shorter and sparser as they interfinger with the rush turfs of the tundra. Macrophyllous forbs are common in these

¹Plant nomenclature follows that used by Meurk *et al.* (1994).

associations, and *Bulbinella rossii* is abundant under heavy grazing.

6. Tundra

The uplands are tundra-like with turf-herbfields dominated by the rushes *Marsippospermum gracile* and *Rostkovia magellanica*, the macrophyllous forbs *Bulbinella*, *Pleurophyllum hookeri*, *Anisotome antipoda* and *Stilbocarpa polaris*, and other smaller forbs, graminoids, and cryptogams. On extreme sites, fellfields dominate.

Human impact

Pastoral land use commenced 1895 and grazing finally ceased with the elimination of the last of the feral sheep and cattle at the end of the 1980s. During this pastoral era the highly palatable macrophyllous forbs and the maritime *Poa foliosa* tussock retreated to inaccessible habitats, and the already ubiquitous, unpalatable *Bulbinella rossii* became dominant over large areas. The *Chionochloa* tussock grasslands could not resist the combined pressure of burning and grazing, and were gradually replaced by short *Poa litorosa*-*Bulbinella* tussock meadows over a wide middle belt of the island (Meurk, 1977). Since removal of the feral grazers began in 1970 there has been a progressive recovery of the original elements (Meurk, 1989).

Methods

A total of 46 sites were chosen to represent the variation within major vegetation communities on the basis of previous survey work. Ten subsamples of moss (or surface litter where moss was absent) were collected at each site over an area of approximately 4 m² within the boundaries of a uniform vegetation type, and homogenised during processing to reduce local fluctuations in pollen representation. At the same site the cover of all species present was visually estimated over a radius of 5 m (bog, herbfield and fellfield) or 10 m (forest, scrub and grassland) and assigned to one of seven cover classes. The vegetation was assigned to one of the six broad groups (forest-scrub, scrub-grassland, maritime turf and grassland, tussock grassland, tundra) before pollen analysis. Altitude was recorded for each site, and an estimate made of relative soil fertility on a five point scale, based on work reported in Meurk *et al.* (1994).

Preparation of the surface samples followed standard palynological techniques (Moore and Webb, 1978) of boiling in 10% KOH, sieving, acetolysis and, in the case of some samples with a large amount of resistant organic matter, soaking in cold bleach for an hour. The preparations were then mounted in glycerine

jelly and counted at 40x magnification. A minimum of 250 pollen grains and spores were counted per sample.

A total of 44 indigenous pollen and spore types were encountered in this study, and 19 could be identified to species. Of those taxa common in the vegetation at our sites, only Juncaceae appear to be completely unrepresented, possibly because of their delicate, easily destroyed pollen grains. A number of pollen types could not be confidently assigned to a recognised taxon. *Pleurophyllum hookeri* type includes *P. criniferum*. Poaceae pollen was assigned by size to two categories (<40 µm, >40 µm). *Chionochloa* falls mainly into the larger size category, and *Poa* into the smaller size category; pollen of the other grasses is too poorly known to assign them. Three broad categories of Cyperaceae were recognised: *Carex* type; an *Isolepis* type; and a general Cyperaceae undifferentiated type. Individual Cyperaceae pollen grains are often highly variable, and it is possible that other sorts of Cyperaceae have been included in the two named types.

The surface pollen data set has been analysed by detrended correspondence analysis (DCA) using Decorana (Hill and Gauch, 1980; Tilia program version 1.12 - Eric C. Grimm, Illinois State Museum, Illinois, U.S.A., 1992). Following the recommendation of Hill and Gauch (1980) to remove outliers and rare species, taxa with five or fewer occurrences or which failed to register in any sample at >1% were excluded. Taxa which generally occurred at low values, but which had occasional high representation in a few samples (almost certainly due to inclusion of whole inflorescences or strobili), were also excluded from the data set.

A number of taxa are either infrequently represented in the pollen rain, or never attain substantial percentages. In order to assess their representation quantitatively, the occurrence of these taxa in both the vegetation and the pollen was analysed on the basis of presence or absence alone. The four possible combinations of the presence and absence of pollen and source taxon were tabulated for infrequently represented species and the significance of departure from a random distribution tested by Fisher's exact test (2-way), because of low sample size. As well, "fidelity" and "dispersibility" indices were calculated, similar to those used by Davis (1984) to analyse under-representation and over-representation. For the fidelity index, the number of sites where a given plant taxon was both recorded in the vegetation and in the pollen surface samples was expressed as a percentage of the total number of sites where the plant was present. The index ranges from 100% where the pollen is always recorded when the source taxon is present, to 0%, when the pollen is never recorded when the source taxon is present. For the dispersibility index, sites where the plant taxon is absent when its pollen is recorded in the surface sample are expressed as a percentage of all sites where the plant

was absent. The index ranges from 100%, where the pollen is always recorded in the absence of the plant, to 0%, where the pollen is never recorded if the plant is absent.

Results and discussion

Pollen percentages for the 46 modern surface sites are presented in Fig 1. Sites are ordered according to vegetation group, and arranged within each group from the top of the pollen diagram downwards in order of increasing altitude. Forty-nine island-sourced pollen types and 21 long-distance transported pollen types were recorded. Summary statistics for the pollen percentages of selected types according to the vegetation groupings are presented in Fig. 2. For the more abundant taxa with good pollen representation, we have plotted pollen percentages against vegetation cover percentage and calculated linear regressions (Fig. 3; Table 1). The height of the y-intercepts of the linear regression line is a guide to the amount of pollen originating outside the vegetation plot (Jackson and Dunwiddie, 1992). Results of the DCA ordination of the pollen taxa are presented in Fig 4, and of the sites in Fig. 5.

Representation of individual taxa

While most species on the island are insect-pollinated, many physiognomically important taxa such as the grasses, sedges, ferns, lycopods and *Coprosma* have wind-dispersed pollen or spores. Although mode of pollen dispersal is a major factor in taxa representation, there are a number of other important influences such as presentation of pollen within the flower, abundance of pollen and flowers, position of flowers on the plant, and height of the source plant (McGlone and Moar, 1997). Thus, an insect-pollinated shrub such as *Myrsine divaricata* may have nearly as good a representation in the pollen rain as wind-pollinated shrubs such as *Coprosma* due to these compensatory variables.

Woody taxa

Hebe was recorded only four times in the pollen spectra, and only in one of the four sites where it was present. *Hebe* species on the New Zealand mainland have very poor pollen representation (McGlone, 1982; Macphail and McQueen, 1993) and this is also a feature of the subantarctic species.

Dracophyllum pollen is significantly correlated with its plot abundance ($R^2=0.43$), and has a low y-intercept. *Dracophyllum* spp. have deeply inserted anthers in small tubular flowers, and as a result have low pollen dispersibility. However, *Dracophyllum* dwarf forest and scrub are abundant and, because of the

Table 1: Relationships between major pollen taxa percentage (y axis) and percentage vegetative cover of equivalent taxa (or other where indicated) in plots (x axis). The y-intercept is regarded as an indication of the degree to which the pollen is derived from outside the plot. See Fig. 3 for representative scatter plots and regressions.

Taxon	R^2	P^1	y-intercept
<i>Dracophyllum</i>	0.431	***	1.0
<i>Myrsine divaricata</i>	0.315	***	2.0
<i>Coprosma</i> undiff. vs <i>C. ciliata</i> & <i>C. cuneata</i> .	0.566	***	1.9
<i>Anisotome</i>	0.592	***	2.1
<i>Bulbinella rossii</i>	0.162	**	4.5
<i>Bulbinella rossii</i> vs altitude	0.414	***	2.3
<i>Pleurophyllum hookeri</i> type vs <i>Pleurophyllum hookeri</i> and <i>P. criniferum</i>	0.277	***	0.6
<i>P. speciosum</i>	0.309	***	0.2
Poaceae (>40 μm) vs <i>Chionochloa antarctica</i>	0.123	NS	10.6
Total Poaceae vs <i>Chionochloa antarctica</i>	0.029	*	19.6
Poaceae (<40 μm) vs <i>Poa</i> spp	0.438	***	0.8
Total Poaceae vs <i>Poa</i> spp	0.612	***	10.8
Total Poaceae vs all Poaceae spp	0.585	***	8.3
<i>Coprosma perpusilla</i>	0.573	***	0.1
<i>Carex</i>	0.873	***	1.7
<i>Isolepis</i> type vs <i>Isolepis aucklandica</i>	0.313	***	2.0
<i>Centrolepis</i>	0.786	***	0.4
Monolete fern spores vs all monolete spore bearing ferns.	0.032	NS	21.7
<i>Polystichum vestitum</i>	0.075	*	16.3
<i>Blechnum</i>	0.000	NS	4.4
<i>Hymenophyllum</i>	0.309	***	0.6
Long-distance pollen types vs altitude	0.598	***	0.1

¹*, **, *** = $P < 0.05$, 0.01, 0.001 respectively; NS = not significant at $P = 0.05$.

strong winds characteristic of the island, its pollen occurs sporadically in surface samples in all vegetation types. *Myrsine divaricata* has open flowers with exerted anthers, produces abundant pollen, and is therefore well represented where it is common in the local vegetation. It was recorded in a large proportion of sites where it was neither present nor close by at levels of up to 5%. Pollen percentages are only moderately correlated with its abundance in the vegetation ($R^2=0.32$).

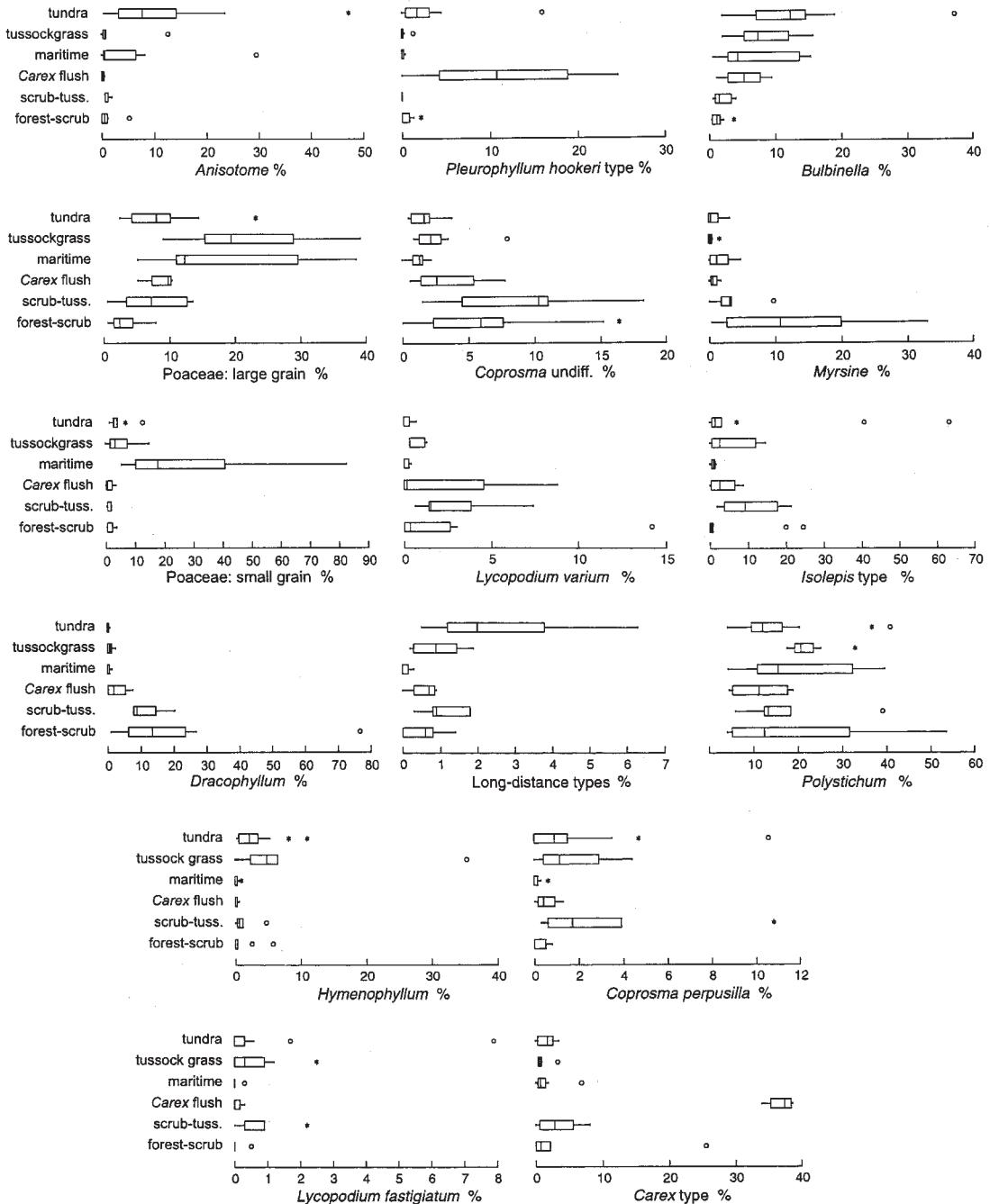


Figure 2. Boxplots (SYSTAT, 1992) of selected taxa in the modern pollen rain for the different vegetation groups. The box encloses the middle half of the data between the first and third quartiles. The bisecting line is at the value of the median. The horizontal lines extending from the top and bottom of the box indicates the range of typical data values. Outliers are displayed as “*” for outside values and “O” for far outside values. Note changes in scale.

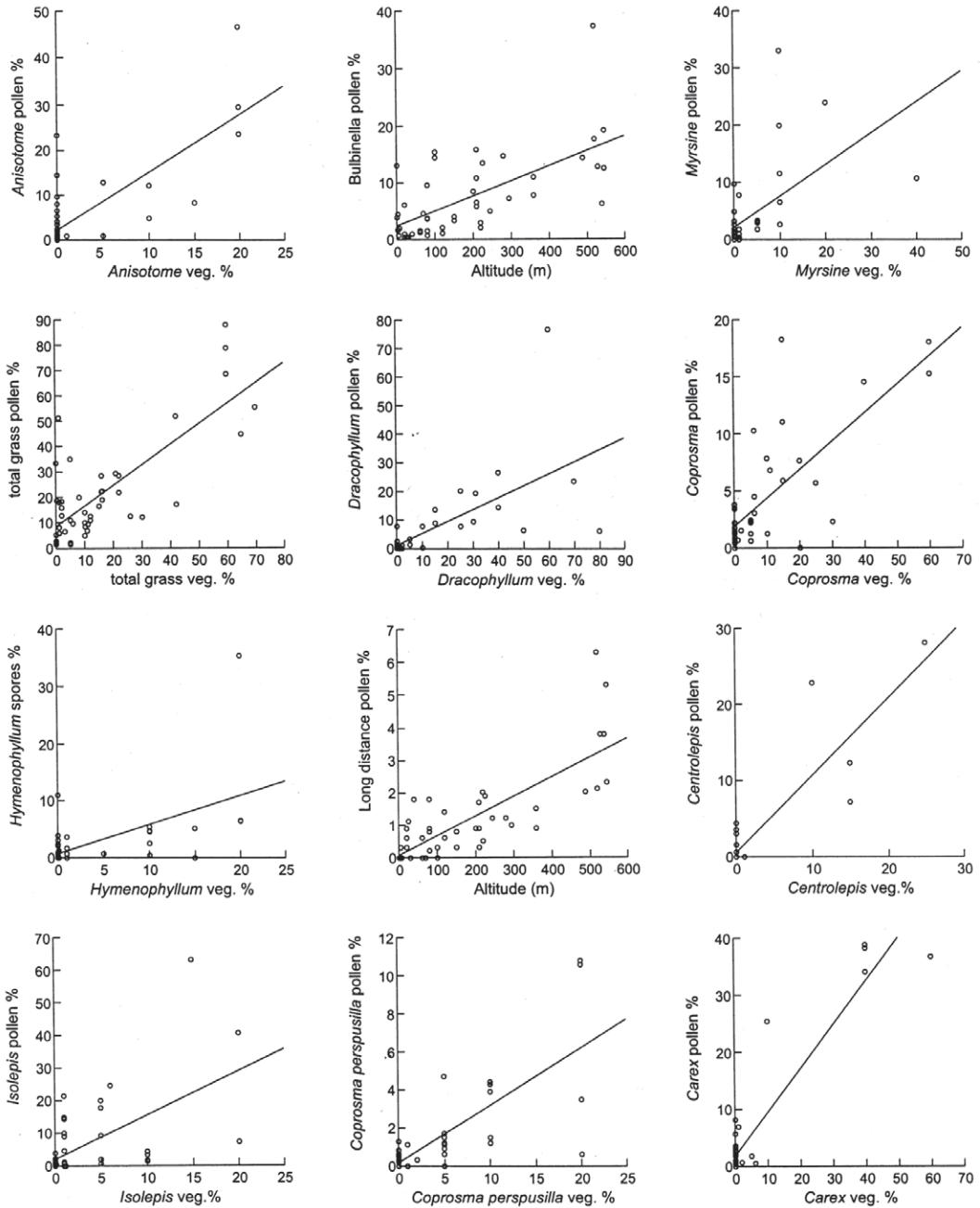


Figure 3. Percent pollen versus percent estimated vegetation cover (or altitude) with linear regression line, of selected taxa at each of 46 sites. Significance, y-intercepts and R^2 values given in Table 1. Y-intercepts can be regarded as a measure of the degree to which the pollen is derived from outside the plots.

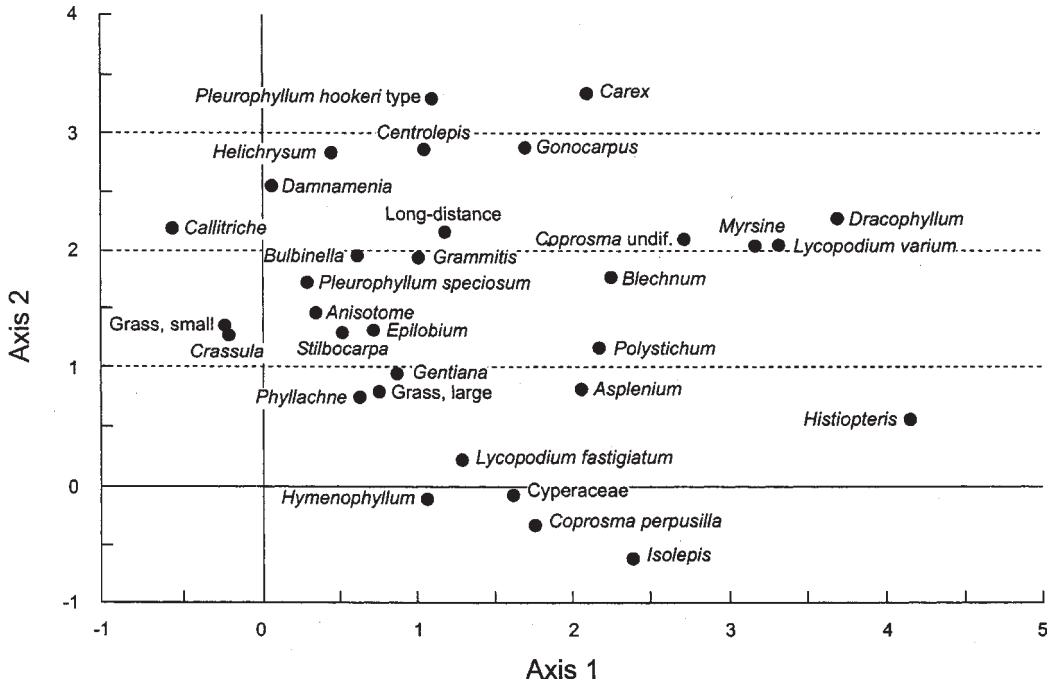


Figure 4. First 2 axes (eigenvalues: axis 1, 0.475; axis 2, 0.303) of inverse detrended correspondence analysis for 32 selected pollen taxa at 46 sites. Axis 1 contrasts grasses, macrophyllous forbs and herbs with woody species and some ferns. Axis 2 contrasts species of wetlands dominated by *Carex*, *Centrolepis* and *Pleurophyllum hookeri* with those dominated by *Isolepis aucklandica*, and *Coprosma perpusilla*.

Coprosma undiff. pollen is derived from wind-pollinated shrubs, its pollen percentage and vegetation cover values are closely associated ($R^2=0.57$), and its pollen is consistently represented at sites where it is absent from the vegetation.

Macrophyllous forbs

Stilbocarpa polaris was recorded in the vegetation at two sites, and in the pollen rain 14 times. One of the sites (site 33) where it was present in the vegetation had the highest pollen representation (3.5%), and the other had no pollen record. Therefore it has a high, but possibly spurious, pollen fidelity index (50%), and also a high pollen dispersibility index (30%), but the overall pattern was not statistically significant (Fisher's exact test: $P=0.490$). *Stilbocarpa polaris* is extensive on Macquarie Island, and pollen profiles from Macquarie peats have abundant (up to 80%) *Stilbocarpa* pollen (Selkirk *et al.*, 1988). Given that the plant was rare in our plots, the conclusion must be that it is a well distributed pollen type.

Both *Pleurophyllum hookeri* type and *P. speciosum* have significant but weak relationships between

vegetation cover and pollen percentages ($R^2=0.28$ and 0.31) and low y-axis intercepts. Both also show a high pollen fidelity index (86% and 63% respectively) and *P. hookeri* type a relatively high pollen dispersibility index (31%), and *P. speciosum* a low index (10%), the patterns being highly significant (Fisher's exact test: $P<0.001$). Whether the dispersibility index difference reflects a real difference is uncertain, as these species have very similar flowers and inflorescences.

Anisotome has a strong pollen-vegetation correlation ($R^2=0.59$), its pollen is well dispersed as it is present in virtually all sites, and this consistent with its tall umbels (1-2 m high) and abundant flowers with exerted anthers.

Bulbinella rossii has the highest pollen dispersal index (100%) and pollen fidelity index (100%) of all the macrophyllous forbs but, as it is also present in the vegetation at all but two sites, the patterns are not statistically significant. It has a weak but still significant relationship between pollen percentage and vegetation cover ($R^2=0.16$) and a relatively high y-intercept (4.5), suggesting that *Bulbinella rossii*, being ubiquitous in the vegetation and having well dispersed pollen, shows

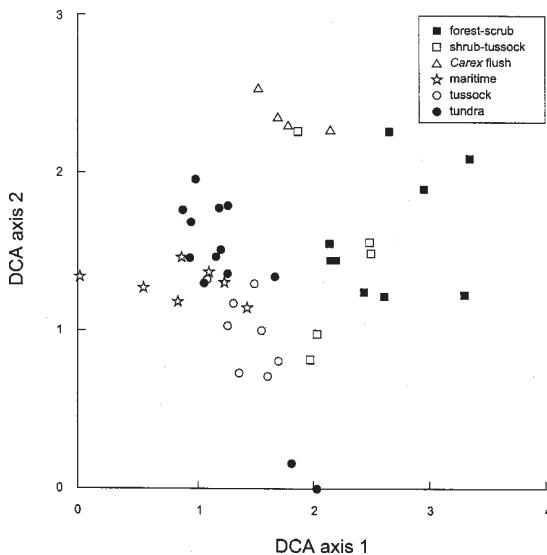


Figure 5. First 2 axes (eigenvalues: axis 1, 0.475; axis 2, 0.303) of inverse detrended correspondence analysis results for the modern surface samples. Symbols indicate vegetation communities on basis of field descriptions. Although different communities tend to cluster on the basis of their pollen spectra, shared species lead to considerable overlap between them.

no strong quantitative pollen relationship with its presence in the small plots for which vegetation cover was estimated. *Bulbinella rossii* has tall (up to 1 m) inflorescences, abundant flowers with exerted anthers and this is consistent with it having well dispersed pollen. Its pollen percentages have a moderately strong, highly significant relationship with altitude ($R^2=0.41$), but its vegetation cover has no detectable relationship with altitude ($R^2=0.03$). This relationship almost certainly comes from the enhancement of the percentage representation of a well dispersed pollen type by reduction of local total pollen production with increasing altitude.

Grasses

There is a strong ($R^2=0.59$) significant relationship between the total cover by grass and total grass pollen. It was hoped that the division of grass pollen into large and small sizes would capture, in part, the distinction between the generally large grains of *Chionochloa antarctica* and the small grains of *Poa*. There is no significant quantitative relationship between *Chionochloa antarctica* vegetation cover and larger pollen grain percentages, nor with total grass pollen. There is a moderate, significant relationship between *Poa* vegetation cover and small grass pollen percentages

($R^2=0.44$) but an even stronger relationship with all grass pollen grains ($R^2=0.61$). It may be that some of the *Poa* pollen grains as well of those of *Chionochloa antarctica* also exceed $40\ \mu\text{m}$, as there was a weak ($R^2=0.26$) but statistically significant relationship of *Poa* cover with large pollen grains.

Chionochloa tillers in subalpine situations on the mainland may take four to twelve years to flower (I. Payton, Landcare Research, Lincoln, N.Z., pers. comm. 1999) and it probably flowers irregularly on Campbell Island as it does on mainland sites (McKone *et al.*, 1998). *Chionochloa* is at present vigorously invading sites from which it was nearly eliminated by sheep grazing and the present populations at our sites probably have a preponderance of individuals that have yet to flower, and this may have contributed to the absence of a significant relationship. *Poa* on the other hand flowers regularly, and therefore is likely to be better represented in the pollen rain. We conclude that current grass pollen representation largely reflects the abundance of *Poa* spp.

Sedges and restiads

Carex pollen percentages have a strong statistically significant relationship ($R^2=0.87$) with *Carex appressa*, reflecting the abundance of this tall species in the flush sites. *Isolepis* type has a much weaker ($R^2=0.31$) but statistically significant relationship with *Isolepis aucklandica*. Although *Oreobolus pectinatus* is abundant in some wetland sites on the island, it was only recorded in one of our sites, and does not correspond with a high sedge pollen record. It is likely that this species is under-represented in the pollen rain. *Centrolepis* pollen has a strong statistically significant relationship with *Centrolepis* spp. ($R^2=0.79$), high fidelity (80%) and low dispersibility (17%), reflecting its low growth habit, but wind-pollinated status.

Forbs and lycopods

These pollen types tend to be poorly represented in the pollen rain, only rarely being represented at levels greater than 5%, and thus we used only the fidelity and dispersibility indices to examine their representation, and Fisher's exact test to assess the significance of the patterns. In Fig. 6 the fidelity index is plotted against the dispersibility index, and the resulting clusters assigned to one of three fidelity/dispersibility patterns (a fourth - low fidelity and high dispersibility - seems unlikely, as it is improbable that a species with widely dispersed pollen would not be recorded at source).

Pattern 1 - high fidelity (>50%) and low dispersibility (<20%) - includes *Centrolepis* spp., *Phyllachne clavigera*, *Crassulamoschata*, *Ranunculus* spp., *Damnania vernicosa*, *Abrotanella* spp., and *Gentiana antarctica*. These have moderate pollen representation (mean \pm S.E. of 8.9 ± 4.5 occurrences).

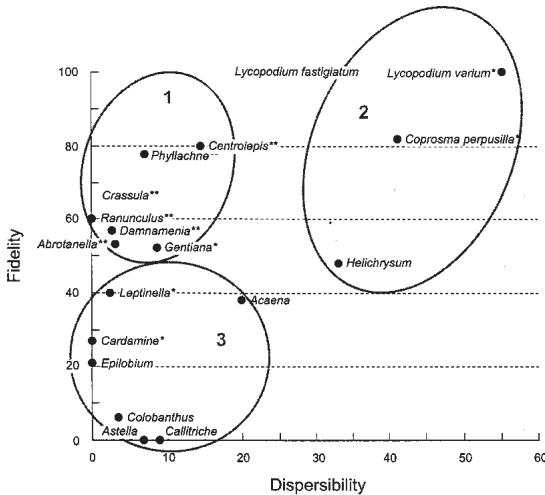


Figure 6. Dispersibility index (percent presence of pollen at sites without parent taxon) versus fidelity index (percent presence of pollen at sites with parent taxon) for minor taxa. Significant departure from random at the 0.001 level = ***, and at the 0.01 level = *. Three broad patterns are recognised (circled on graph): Pattern 1, high fidelity and low dispersibility; Pattern 2, high fidelity and high dispersibility; Pattern 3, low fidelity and low dispersibility

The pattern is significant or highly significant for all species ($P < 0.006$ in all cases). All of these taxa (except for *Crassula moschata* which occurs in maritime low turf) are common in the high altitude low turf, and this pattern probably arises from taxa with poor pollen dispersal growing in vegetation of low overall pollen production.

Pattern 2 – high fidelity (>50%) and high dispersibility (>30%) - includes *Coprosma perpusilla*, *Helichrysum bellidioides*, *Lycopodium fastigiatum*, and *L. varium*, but the pattern is significant only for *L. varium* and *C. perpusilla* ($P = 0.009$ and 0.007 respectively). They have relatively high pollen representation (mean \pm S.E. = 24 ± 5 occurrences). All but *Helichrysum bellidioides* have wind-dispersed spores or pollen, and all bear abundant flowers or strobili and have a scrambling habit.

Pattern 3 – low fidelity (<50%) and low dispersibility (<30%) - fits *Acaena*, *Astelia subulata*, *Callitriche antarctica*, *Cardamine*, *Colobanthus*, *Epilobium*, and *Leptinella*. They have very low representation (mean \pm S.E. = 5 ± 3.6 occurrences), which probably accounts for the non-significance of the pattern in all but two cases. The most important feature of this group is that they are plants with poor pollen dispersal and low pollen production, growing in mid-altitude to lowland sites where overall pollen

production is highest. It is likely that their pollen representation is drowned out by the background pollen rain of other species. Without this they would probably more closely resemble Pattern 1. *Acaena* spp. are scrambling plants that have abundant flowers with exerted anthers. The more central position of *Acaena* in the graph indicates a somewhat enhanced dispersibility.

If the influence of background pollen production is put to one side, it is clear that there are only two patterns for these low-growing forbs and lycophods: a relatively high pollen dispersibility pattern for wind-pollinated or well distributed scrambling plants with abundant flowers; and a low dispersibility pattern for largely insect-pollinated plants of a rosette or compact form, with few flowers. *Centrolepis* has low dispersibility, despite being wind-pollinated, because its flowers are held very close to the ground surface.

Even though they rarely make a significant contribution to the pollen rain these forbs and lycophods are useful indicators of the vegetation type and pollen production. The source taxon is in the local site vegetation at an average of 50% of the sites where the pollen is recorded in the spectrum. Where the source taxon is absent however, pollen is recorded at only 14% of the sites. If, as we suspect, Pattern 3 is simply a statistical consequence of very low representation, consistent records of any of these pollen types in a fossil pollen diagram should be a robust indicator of local presence of the source taxon. If a number of these usually under-represented types are present at a site, an open, sparse vegetation is indicated.

Ferns

Fern spores make up on average over one quarter of the pollen and spore pollen sum for all sites. Ferns are common in the vegetation, are recorded at most sites, but are dominant in none. *Hymenophyllum* has a moderate and statistically significant quantitative relationship (Fig. 3), and also high dispersibility and fidelity indices (54% and 85%). However, there is no significant vegetation-spore relationship for the two major fern types (*Polystichum vestitum* and *Blechnum* spp) nor for total monolete spore types versus total ferns. *Histiopteris incisa* spores are abundant at the only site (site 3) where it was common in the vegetation; it did not differ significantly from random in its presence/absence distributions.

Fern spores are well dispersed and common wherever ferns are present in the local vegetation, and thus it is surprising that they do not show a stronger vegetation-spore relationship. This lack of relationship between fern abundance and spore representation was also observed in the Auckland Island modern pollen rain study (McGlone and Moar, 1997). Either fern cover does not translate well into potential for spore production, or extra-local dispersal of fern spores is obscuring local relationships.

Long-distance transported pollen types

A total of 21 pollen types of taxa not present on Campbell Island are recorded (Fig. 1). They make up a low percentage of the average pollen rain (mean \pm S.E. = 1.2 ± 1.4 %) but a much higher proportion (mean \pm S.E. = 3.6 ± 1.6 %) in the tundra sites at or above 500 m altitude (site 40 and below in Fig. 1). There is a strong statistically significant relationship between long-distance transport types and altitude ($R^2=0.60$), probably reflecting the lower pollen production at higher altitudes rather than the openness of the vegetation, because the open maritime turfs recorded no long-distance types.

Of the total long-distance types, 11 are likely to be derived from the New Zealand mainland, five from Australia, and the remaining five either from Australia or New Zealand. The most common pollen types are *Nothofagus* subgenus *Fuscospora*, *Eucalyptus*, *Prumnopitys taxifolia*, *Phyllocladus*, Rhamnaceae and *Pinus*.

Community representation by pollen rain

DCA analysis

The first axis has an eigenvalue of 0.457 and separates samples dominated by woody species and some ferns with those dominated by grasses, macrophyllous forbs and herbs (Fig. 4). The first axis combines elements of both altitude and fertility gradients. Spearman Rank Correlation of axis 1 versus altitude gave a weak but statistically significant negative relationship ($R^2=0.33$; $P<0.05$); the soil fertility index gave a stronger negative relationship ($R^2=0.47$; $P<0.01$). Axis 1 therefore recognises the principal gradients identified in the vegetation analysis (Meurk *et al.*, 1994)

The second axis has an eigenvalue of 0.303, and separates wetland samples dominated by *Carex*, *Centrolepis*, and *Pleurophyllum hookeri* from those dominated by *Isolepis aucklandica*, *Coprosma perpusilla* and *Hymenophyllum*. Spearman Rank Correlations of axis 2 versus altitude and the soil fertility index were non-significant, and the axis does not seem to reflect any major environmental gradient other than wetland type.

The pollen sites cluster reasonably tightly into their vegetation groupings (Fig. 5). The sole major exception is for sites 34 and 35 (tundra group) which are low on axis 2 well away from other tundra sites, and which have high levels of *Isolepis aucklandica* and *Coprosma perpusilla*. The least clustered grouping is shrub-grassland, which occupies a poorly defined area between the grassland and tundra sites on one hand, and forest-scrub on the other. This positioning in the diagram reflects its transitional nature. We discuss the representation of the different vegetation types below.

Maritime

Low woody pollen percentages and the highest average grass percentages of all vegetation types (53% versus the island average of 21%), abundant small grass grains, plus substantial percentages of the macrophyllous forbs *Anisotome* and *Bulbinella rossii* (Fig. 2) result in more than half these sites overlapping in the DCA diagram with tundra and higher altitude tussock grassland sites (Fig. 5). However, these are the only sites that have significant percentages of *Crassula moschata*, *Leptinella* and *Callitriche antarctica*, which are typical of maritime turf communities. They also have the lowest proportion of long-distance transported types (Fig. 2). *Pleurophyllum* is also uncommon (Fig. 2). They are thus potentially distinguishable from tundra and high altitude tussock grassland in fossil samples.

Carex flush

A combination of very high *Carex* pollen percentages, high *Pleurophyllum hookeri* type (but derived from *P. criniferum*) (Fig. 2), and low but constant woody taxa pollen percentages (average 6.9%) clearly distinguish these sites.

Forest-scrub

These sites have high pollen percentages of *Dracophyllum*, *Myrsine divaricata*, and *Coprosma*, moderate to high levels of *Polystichum vestitum* spores, but low representation of all other types. The first 3 sites in this category (sites 1, 2 and 3) are from closed forest, and are clearly distinguished from all others through the highest average percentages for *Dracophyllum* (42.3%) and total woody taxa (57%), and lowest total grass types (2.0%). There is considerable overlap between the forest-scrub and the shrub-tussock categories in the DCA diagram (Fig. 5), as individual shrub-tussock sites may have woody taxa pollen percentages as high as some from the forest-scrub grouping.

Shrub-tussock

These sites share moderately high levels of woody taxa pollen percentages with the forest-scrub sites, in particular *Dracophyllum* and *Coprosma* undiff., and there is overlap on the DCA diagram as noted above. However, total grass levels are on average higher (largely due to the large grass grain group), *Myrsine divaricata* is lower, and *Lycopodium fastigiatum*, and *L. varium* more consistently present (Fig. 2), and they could very likely be distinguished on these grounds in peat profiles sites. The presence of *Coprosma perpusilla*, *Isolepis aucklandica* (Fig. 2), *Phyllachne clavigera*, and *Centrolepis* - derived from the cushion bogs that are common in this and the next two groupings - also help distinguish shrub-tussock from forest.

Tussock-grassland

While overall grass percentages are somewhat lower than in maritime sites (35% versus 53%), small grass grains are much less abundant, reflecting the dominance of *Chionochloa antarctica* (Fig. 2). The macrophyllous forb *Bulbinella rossii* is common, *Gentiana antarctica* and *Epilobium* consistently present, and *Hymenophyllum* more abundant than in any other site type. The presence of cushion bogs in this grouping results in the abundance of *Coprosma perpusilla*, *Isolepis aucklandica*, and *Phyllachne clavigera* pollen. Tussock grassland sites are mostly clearly separated from the tundra sites, but overlap with maritime sites because of their high grass levels.

Tundra

The open short turf of these sites, the low pollen production and representation of stunted plants and the abundance of *Marsippospermum* - which does not contribute at all to the pollen rain - is reflected in the low grass pollen percentages and the high percentage of long-distance transported pollen (Fig. 2). Otherwise sporadically recorded pollen types are abundant, especially at and above 500 m altitude (site 40 and below in Fig. 1). Included in this group are: *Pleurophyllum hookeri* type, *P. speciosum*, *Damnomenia vernicosa*, *Gentiana antarctica*, *Abrotanella*, *Helichrysum bellidioides*, *Myosotis*, *Centrolepis*, *Phyllachne clavigera*, and *Grammitis*. None of these are confined to upper altitudes, but a combination of their increased abundance in the short upland turfs and the lower local pollen production results in them being more prominent in the pollen rain.

Conclusions

The results of this study closely parallel those from the Auckland Island modern pollen rain study (McGlone and Moar, 1997). Each of the broad vegetation communities tends to have a distinctive pollen rain, as seen in the aggregated pollen statistics for the communities (Fig. 2) and the DCA analysis (Fig. 5). Where there is overlap in the pollen rain it is mainly because the parent communities have dominants in common, or are closely adjacent, and thus bear a strong resemblance to one another.

A reassuring feature of the pollen analytical signature of these subantarctic communities is that discrimination relies for the most part on the abundance of pollen types derived from dominants within them. Studies of alpine or open vegetation elsewhere are usually complicated by the dominance of pollen derived from distant lowland and montane vegetation. For instance, the relative proportions of some lowland pollen types can be greater in high altitude or high

latitude sites remote from the source taxon than sites close to them (Prentice, 1988). While statistical discrimination can be made between the various sites in these cases, the fact remains that there is generally only a weak quantitative relationship between the pollen spectra and the parent communities (e.g., Randall *et al.*, 1986; Horrocks and Ogden, 1994).

The quantitative relationships revealed in this study between pollen representation and source taxon vegetation cover are variable, being virtually non-existent in some cases, and moderately strong in others. Only a handful of taxa had strong relationships with R^2 values of 0.5 or higher (*Coprosma undiff.*, *Anisotome*, grass, *Carex*, *Centrolepis*, and *Coprosma perpusilla*) while a number of important components of the vegetation had very poor relationships (*Chionochloa antarctica*, *Bulbinella rossii*, and *Polystichum vestitum*). A major interpretive problem is presented by *Polystichum vestitum*, which is abundant as a plant and in the pollen rain below 200 m altitude, but is not common as a plant in the higher altitude sites although its spores are also abundant there. It therefore seems to be acting as an island-wide extra-local source. On balance, a one-to-one relationship between fossil pollen abundance and past vegetation cover of a species cannot be expected, although some broad cover class information can probably be extracted. A conclusion from the Auckland Island pollen rain study (McGlone and Moar, 1997) was that the small vegetation plots used may not adequately reflect the pollen rain catchment, and more experimentation would be needed to establish the appropriate vegetation plot size. However, given the very different pollen dispersal abilities revealed in this study, the pollen catchment will differ for each pollen taxon and no one site size will suit all.

There are several ways to deal with this problem of quantitatively reconstructing the vegetation from fossil pollen data. A network of both vegetation and surface pollen sites of sufficient density permits the generation of generalised pollen and vegetation surfaces, which can then be used to place fossil samples in the modern continuum. This has been done on a very large scale in North America (Webb *et al.*, 1993) with a large measure of success, and there is no reason why the same techniques could not apply to a much smaller scale in the subantarctic islands. Another technique is to statistically match individual fossil samples with the modern pollen data set to locate a group of close analogues which can be used to generate vegetation and environmental parameters (Overpeck *et al.*, 1985). Finally, DCA analysis of the modern data set can be performed with the fossil samples passively placed within the framework as has been done with one of the Auckland Island fossil sites (McGlone and Moar, 1997; McGlone *et al.*, 2000).

The past pollen rain of Campbell Island generally bears a close resemblance to the suite of modern pollen rain sites. The pollen spectra encountered in the Holocene sections of the three cores analysed (McGlone *et al.*, 1997) are clearly encompassed by the range of modern pollen spectra. However, there is no close match for the initial late-glacial sequences in which macrophyllous forbs are dominant in the absence of tussock grassland or sedge pollen types, although the high altitude tundra sites come closest. This suggests that the proposed vegetation reconstruction of "...tundra-like landscapes extending to near sea-level, with open expanses of stunted macrophyllous forbs and short turfy graminoids on raw mineral soils and incipient peats..." (McGlone *et al.*, 1997) is accurate, as the nearby presence of grassland would have, as with the modern sites, raised grass pollen levels above background levels.

Acknowledgements

We thank Rodney Russ and the staff of Southern Heritage Tours for logistical support on Campbell Island, and the Southland Office of the Department of Conservation for permission to sample vegetation and peat. We also thank Alison Watkins for pollen slide preparation, Trevor Partridge for advice on statistical analysis, and Janet Wilmshurst and Susan Wiser for their helpful comments on a draft of this paper. Colin Burrows made many useful suggestions as referee and we thank David Wardle and David Kelly for editorial comment. This research was funded by the Foundation for Research, Science and Technology under Contract No. C09313.

References

- Campbell, I.B. 1981. Soil pattern of Campbell Island. *New Zealand Journal of Science* 24: 111-135.
- Cockayne, L. 1904. A botanical excursion during midwinter to the southern islands of New Zealand. *Transactions of the New Zealand Institute* 36: 225-333.
- Cockayne, L. 1909. The ecological botany of subantarctic islands of New Zealand. In: Chilton, C. (Editor), *The subantarctic islands of New Zealand, Volume 1*, pp 182-235. Government Printer, Wellington, N.Z.
- Davis, O.K. 1984. Pollen frequencies reflect vegetation patterns in a Great Basin (U.S.A.) mountain range. *Review of Palaeobotany and Palynology* 40: 295-315.
- De Lisle, J.F. 1965. The climate of the Auckland Islands, Campbell Island and Macquarie Island. *Proceedings of the New Zealand Ecological Society* 12: 37-44.
- Fleming, C.A.; Mildenhall, D.G.; Moar, N.T. 1976. Quaternary sediments and plant microfossils from Enderby Island, Auckland Islands. *Journal of the Royal Society of New Zealand* 6: 433-458.
- Hill, M.O.; Gauch, H.G. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42: 47-58.
- Horrocks, M.; Ogden, J. 1994. Modern pollen spectra and vegetation of Mt Hauhungatahi, central North Island, New Zealand. *Journal of Biogeography* 21: 637-649.
- Jackson, S.T.; Dunwiddie, P.W. 1992. Pollen dispersal and representation on an offshore island. *New Phytologist* 122: 187-202.
- Macphail, M.K.; McQueen, D.R. 1983. The value of New Zealand pollen and spores as indicators of Cenozoic vegetation and climates. *Tuatara* 26: 37-59.
- McGlone, M.S. 1982. Modern pollen rain, Egmont National Park, New Zealand. *New Zealand Journal of Botany* 20: 253-262.
- McGlone, M.S.; Moar, N.T. 1997. Pollen-vegetation relationships on the subantarctic Auckland Islands, New Zealand. *Review of Palaeobotany and Palynology* 96: 317-338.
- McGlone, M.S.; Wardle, P.; Meurk, C.D. 1997. Late-glacial and Holocene vegetation and environment of Campbell Island, far southern New Zealand. *The Holocene* 7: 1-12.
- McGlone, M.S.; Wilmshurst, J.M.; Wiser, S.K. 2000. Late-glacial and Holocene vegetation and climate change on Auckland Island, subantarctic New Zealand. *Holocene* (in press).
- McKone, M.J., Kelly, D.; Lee, W.G. 1998. Effect of climate change on mast-seeding species - frequency of mass flowering and escape from specialist insect seed predators. *Global Change Biology* 4: 591-596.
- Meurk, C.D. 1977. Alien plants in Campbell Island's changing vegetation. *Mauri Ora* 5: 93-118.
- Meurk, C.D. 1989. Vegetation monitoring with special reference to the subantarctic islands of New Zealand. In: Craig, B. (Editor), *Environmental monitoring in New Zealand*, pp 209-219. Department of Conservation, Wellington, N.Z.
- Meurk, C.D.; Foggo, M.N.; Wilson, J.B. 1994. The vegetation of subantarctic Campbell Island. *New Zealand Journal of Ecology* 18: 123-168.
- Meurk, C.D.; Given, D.R. 1990. *Vegetation map of Campbell Island*. Department of Scientific and Industrial Research, Wellington, N.Z.
- Moar, N.T. 1958. Contributions to the Quaternary history of the New Zealand flora. 1. Auckland Island peat studies. *New Zealand Journal of Science* 1: 449-465.

- Moar, N.T. 1973. Late Pleistocene vegetation and environment in southern New Zealand. *In: van Zinderen Bakker, E.M. (Editor) Palaeoecology of Africa and the surrounding islands and Antarctica. Volume 8*, pp 179-198. Balkema, Cape Town, South Africa.
- Moore, P.D.; Webb, J.A. 1978. *An illustrated guide to pollen analysis*. Hodder and Stoughton, London, U.K.
- New Zealand Meteorological Service. 1973. *Summaries of climatological observations to 1970*. New Zealand Meteorological Service Miscellaneous Publications 143. New Zealand Meteorological Service, Wellington, N.Z.
- Oliver, R.L.; Sorensen, J.H. 1951. The vegetation. *In: Botanical investigations on Campbell Island*, pp. 5-24. Cape Expedition Series Bulletin 7(1). Department of Scientific and Industrial Research, Wellington N.Z.
- Overpeck, J.T.; Webb, T. III; Prentice, I.C. 1985. Quantitative interpretation of fossil pollen spectra: dissimilarity coefficients and the method of modern analogues. *Quaternary Research* 23: 87-108.
- Prentice, I.C. 1988. Records of vegetation in time and space: the principles of pollen analysis. *In: Huntley, B.; Webb, T. III (Editors), Vegetation history*, pp 17-24. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Randall, R.E.; Andrew, R.; West, R.G. 1986. Pollen catchment in relation to local vegetation: Ceann Ear, Monach Isles N.N.R., Outer Hebrides. *New Phytologist* 104: 271-310.
- Selkirk, D.R.; Selkirk, P.M.; Bergstrom, D.M.; Adamson, D.A. 1988. Ridge top peats and palaeolake deposits on Macquarie Island. *Papers and Proceedings of the Royal Society of Tasmania* 122: 83-90.
- SYSTAT Inc. 1992. *SYSTAT for Windows: Graphics, Version 5 Edition*. SYSTAT Inc, Evanston, Illinois, U.S.A.
- Webb, T. III; Bartlein, P.J.; Harrison, S.P.; Anderson, K.H. 1993. Vegetation, lake levels, and climate in eastern North America for the past 18,000 years. *In: Wright, H.E; Kutzbach J.E.; Webb T. III; Ruddiman, W.F.; Street-Perrott, F.A.; Bartlein, P.J (Editors). Global climates since the last glacial maximum*, pp 415-467. University of Minnesota Press, Minneapolis, U.S.A.