Patterns of variation in the climates, soils and vegetation of some subantarctic and antarctic islands

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Patterns of variation in the climate, soils and vegetation among 19 sites from 3 subantarctic and one maritime antarctic island were defined by principal component analyses (PCA) of abiotic and vegetation variables. The sites were classified on the same parameters by nearest neighbour/group mean clustering. The first two components from the PCA of the abiotic (climate and soil) data separated the islands along a climatic gradient, partly related to latitude. Sites within each island were separated along parallel series by edaphic factors and exposure. The third and fourth components reflected changes in soil chemistry caused by manuring by seabirds and seals. Cluster analysis on the abiotic variables showed that the main division was between high- and low-latitude islands, with a strong tendency to 'chaining'. PCA of the vegetation data resulted in few conspicuous or simple patterns but three environmental trends were indicated, which corresponded approximately to components II, III and IV from the PCA of the abiotic data. Animal manuring induces vegetation successions parallel to the soil changes noted in the abiotic analyses and these combine with radiative successions from fellfields to all other vegetation types to produce a complex, and somewhat ambiguous, pattern of sites. Cluster analyses on the botanical variables produced clear groupings but these varied markedly according to the life-form category used to classify two of the plant species. This instability reflects the wide ecological amplitude of the phanerogamic species, with single species often filling what would be a variety of niches in less isolated ecosystems. The results also emphasize the importance of bryophytes on the southern subpolar islands. The two sets of analyses, taken together, emphasize the special characteristics of subantarctic islands found in previous bipolar comparisons and also indicate the extreme sensitivity of these ecosystems to the introduction of alien species.

Wisselpatrone in die klimaat, gronde en plantegroei van 19 lokaliteite van drie subantarktiese- en een maritieme antarktiese eiland is deur middel van hoofkomponente-ontleding (PCA) van abiotiese- en plantegroeiveranderlikes omskryf. Die lokaliteite is langs dieselfde parameters deur naaste buurman/groepgemiddelde trosvorming, geklassifiseer. Die eerste twee komponente van die PCA van die abiotiese (klimaat en grond) data het die eilande langs 'n klimaatsgradiënt wat deels met die breedtegraad verband hou, geskei. Lokaliteite op 'n eiland is langs parallelle serieë deur edafiese faktore en blootstelling geskei. Die derde en vierde komponente het veranderings in grondchemie wat deur bemesting van seevoëls en robbe veroorsaak word, weerspieël. Trosontleding van die abiotiese veranderlikes het getoon dat die hoofverdeling tussen hoë- en lae breedtegraad-eilande lê, met 'n sterk neiging tot 'kettingvorming'. PCA van die plantegroeidata het enkele opvallende of eenvoudige patrone tot gevolg, maar omgewingsneigings wat min of meer met komponente II, III en IV van die PCA van die abiotiese data ooreenstem, is aangedui. Dierbemesting induseer plantsuksessies wat parallel met die grondveranderings wat in die abiotiese ontleding waargeneem is, verloop en dit kombineer met uitstralende suksessies van klipperige velde tot alle ander plantegroeitipes om 'n ingewikkelde, taamlik onduidelike patroon van lokaliteite te produseer. Trosontleding van botaniese veranderlikes het duidelike groeperings geproduseer, maar dit het skerp volgens die lewensvormkategorie wat gebruik is om twee plantspesies te klassifiseer, gewissel. Hierdie onstabiliteit weerspieël die wye ekologiese amplitude van die fanerogaamspesies; enige een van hierdie spesies vul dikwels dit wat in minder geïsoleerde ekostelsels 'n verskeidenheid van nisse sou wees. Die resultate benadruk ook die belangrikheid van briofiete op die suidelike subpolêre eilande. As die twee stelle ontledings in samehang gesien word, benadruk dit die uitstaande eienskappe van subantarktiese eilande wat in vorige bipolêre vergelykings gevind is en dit dui ook op die uiterste sensitiwiteit van hierdie ekostelsels teenoor die invoer van uitheemse spesies.

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Introduction

Comparisons based on multivariate analyses of climate, soil and vegetation parameters from a wide range of tundras and related habitats demonstrated several fairly consistent ecological patterns over the range (French 1974, 1981; French & Smith 1985). Many of the trends represented by the component vectors have been shown to be associated with the regulation of biological processes and populations in tundra-like ecosystems (e.g. Holding *et al.* 1974; Heal & French 1974; Heal *et al.* 1981).

These comparisons were all broad-based, bipolar studies but, except for French & Smith (1985), concentrated mainly on northern hemisphere patterns. Southern hemisphere subpolar areas form a coherent group, geographically and ecologically distinct from northern hemisphere tundras, and in this paper, we examine the patterns and interrelations among the soils, climates and vegetation of some southern subpolar tundras.

Analyses such as these tend to be exploratory, hypothesis-generating rather than hypothesis-testing. However, they can also form valuable environmental models for use in the study of related populations or processes (see above) and, while normally only of limited direct use in statistical hypothesis-testing, can often provide much confirmatory evidence for hypotheses derived from other studies (e.g. Walton 1984). Our earlier paper (French & Smith 1985) suggested, from bipolar comparisons, that the three most generally important features of the southern hemisphere tundras that distinguished them from the northern tundras were: oceanicity, geographical isolation, and degree of influence of large vertebrates such as seals and seabirds.

Oceanicity could be expected to lead to relatively small

effects of macroclimate or latitude on any type of ecosystem (between different islands) but larger effects of microclimate within islands. We would also expect moisture to be more important, overall, than temperature in explaining trends and differences in soils and vegetation.

Isolation, coupled with the relatively uniform conditions produced by oceanicity, should lead to convergence on similar arrays of vegetation and soil types over the entire southern subpolar region. In particular, we would expect little fundamental variation between islands in the range of combinations of plant growth-forms (though not so in species) except at the extremes of the range, and also a wide ecological amplitude of any one life-form.

Animal influences, especially the importance of manuring and physical disturbance and relative absence of heavy grazing, coupled with oceanicity, could account for at least some superficially anomalous combinations of soil climate and nutrients and/or vegetation. In the analyses that follow, we give particular attention to the evaluation of these factors.

Sites

Information was available for sites at Signy Island, South Georgia, Macquarie Island and Marion Island (Figure 1). These provide a representative sample of the geographical range of southern ocean islands, although data were available for only one site at Macquarie Island.

Brief descriptions of the sites at each island, with references to more detailed site descriptions, are provided below. The site codes used in the tables and figures are given in parentheses after each site name.

Signy Island; 60°S, 45°W (Collins *et al.* 1975)

Situated only 640 km from the Antarctic Peninsula, much of the island is covered by permanent ice and snow. The vegetation is almost entirely cryptogamic, the only two vascular species [*Deschampsia antarctica* Desv. and *Colobanthus quitensis* (Kunth) Bartl.] occurring mainly on well-drained, north-facing slopes in the coastal zone.
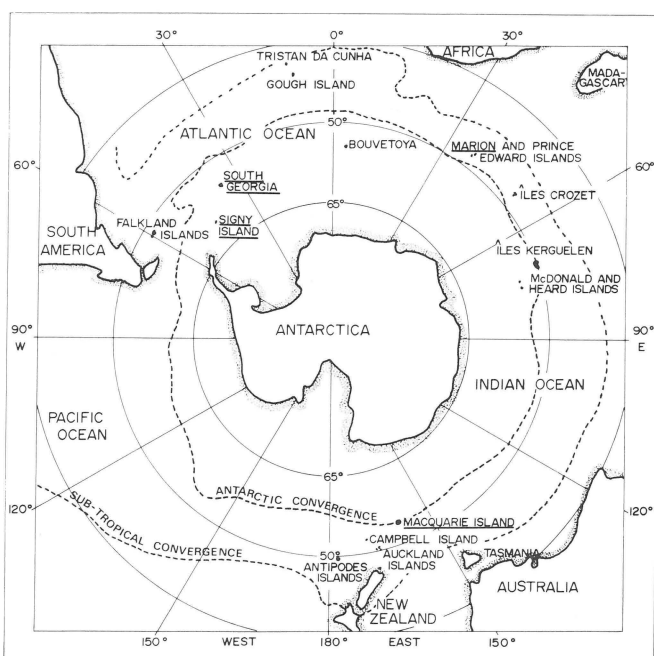

Figure 1 Map showing location of islands mentioned in text. Islands considered in the principal component analyses are underlined.

Moss turves (S.MT)

Deep peat banks formed by the moss *Chorisodontium aciphyllum* (Hook. f. et Wils.) Broth (some also have *Polytrichum alpestre* Hoppe. as co-dominant, but abiotic data herein are all from *Chorisodontium* turves).

Moss carpets (S.MC)

Shallow peats with *Drepanocladus uncinatus* (Hedw.) Warnst. and other carpet-forming mosses. Permanently wet, often with flowing water but with the mosses at least partly in contact with the mineral substrate.

Grass (S.DG)

Patches of *Deschampsia antarctica* on a mineral soil (brown earth or brown tundra soil, *sensu* Walton 1984) in sheltered areas, often below cliffs with nesting seabirds.

Old moraine (S.OM)

Mostly unvegetated morainic material with a low organic matter content.

Marble knolls (S.MK)

Unvegetated except for occasional scattered cryptogams (soil data in Table 1 are from unvegetated areas).

South Georgia: 54–55°S, 36–38°W, subantarctic, Magellanian Province (Lewis Smith & Walton 1975)

Situated *c.* 2 000 km east of Tierra del Fuego, the island has an alpine topography with most of the higher altitude regions covered by permanent ice and many large glaciers reaching the sea. A range of vegetation types, including extensive closed phanerogamic communities, occur around King Edward Cove on the north coast of the island.

Poa *grassland (G.PG)*

Large tussocks of *Poa flabellata* (Lam.) Hook. f. Considered to be a climax community at coastal areas up to *c.* 225 m above sea level (a.s.l.), this grassland is particularly luxuriant in areas manured by birds and seals.

Acaena magellanica *slope (G.AM)*

Acaena magellanica (Lam.) Vahl, codominant with the moss *Tortula robusta* Hook. et Grev. on moist, well-drained slopes.

Grassy heath (G.GH)

A mixed sward dominated by *Festuca contracta* T. Kirk, *A. magellanica*, plus abundant bryophytes and lichens. Occurring on fairly dry mineral soil at somewhat exposed sites.

Fellfield (G.FF)

Medium to high altitude, windswept ridges and plateaux vegetated by cryptogams (mainly lichens and cushion and turf-forming mosses) with occasional phanerogams in the lee of large stones.

Basin bog (G.BB)

On deep oligotrophic peat of wet valley floors, lake margins and rock basins, dominated by the rush *Rostkovia magellanica* (Lam.) Hook f., mosses and liverworts.

Eutrophic mire (G.EM)

Wet, eutrophic seepage slopes supporting a mixed mire vegetation, mainly *Juncus scheuchzerioides* Gandith. and

Table 1 Abiotic data. For site codes see text

	WST	CST	FFS	TSS	PPTN	EVAP	DS	H₂O_max	H₂O_min	pH	LOI	N	C/N	P	K	Ca	Mg
								H_2O_{max}	H_2O_{min}								
Signy Island																	
S.MT	4,0	− 3,5	42	330	(400)	[150]	(200)	1330	210	4,8	90,0	1,30	(38)	25	180	1500	1700
S.MC	(3,5)	(− 8,0)	(40)	(330)	(400)	[100]	(180)	1700	200	5,7	44,0	1,67	15	100	225	1800	650
S.DG	(5,0)	(− 0,5)	[80]	[700]	(450)	[300]	210	150	82	5,6	14,0	0,45	13	40	240	1500	830
S.OM	(5,0)	(−12,0)	(30)	(280)	(300)	[100]	[150]	50	14	6,2	2,0	0,06	9	70	90	490	130
S.MK	(5,0)	(−12,0)	30	(260)	(200)	[100]	[150]	28	1	8,5	1,6	0,06	1	10	20	6310	80
South Georgia																	
G.PG	6,0	(− 0,2)	(138)	(720)	2105	[400]	(225)	551	116	4,1	57,6	2,10	(14)	84	255	433	261
G.AM	5,4	(− 0,5)	(135)	(601)	2105	[400]	221	400	20	4,8	22,4	1,00	(11)	32	354	1520	450
G.GH	5,4	(− 0,5)	(135)	(601)	2105	[400]	(220)	136	29	4,5	16,4	0,66	(12)	17	100	213	106
G.FF	5,6	(− 6,0)	(83)	(461)	2105	[400]	(220)	51	7	5,0	5,1	0,12	(24)	26	23	50	20
G.BB	6,2	(0,0)	(140)	(838)	2105	[400]	(230)	585	299	4,1	73,1	2,20	(17)	38	250	1420	526
G.EM	5,8	(− 1,0)	(135)	(680)	2105	[400]	(220)	1444	450	5,6	73,9	2,50	(15)	93	627	10460	692
Macquarie Island																	
Q.PG	6,5	1,8	234	(1200)	926	445	30	400	50	6,4	18,5	(0,8)	(12)	(13)	280	122	1020
Marion Island																	
M.FB	8,6	4,7	[273]	2197	2576	536	[70]	1041	269	4,3	83,6	1,82	15,7	25	547	1120	1118
M.DL	(9,9)	(4,6)	[273]	2394	2576	536	80	2000	210	4,7	70,3	2,50	17,2	19	391	2700	2005
M.PG	10,1	5,4	[273]	2737	2576	536	[70]	750	201	4,1	70,7	1,60	14,1	74	117	540	377
M.FF	8,6	4,7	[273]	2299	2576	536	[90]	380	10	5,4	31,6	0,69	25,2	11	156	120	219
M.MI	9,9	4,6	[273]	2394	2576	536	80	3180	290	4,8	79,9	2,25	19,0	27	273	320	377
M.SS	9,0	4,5	[273]	2355	2576	536	80	1225	280	5,0	81,5	2,49	17,2	27	508	1640	3086
M.BI	9,7	4,5	[273]	2439	2576	536	80	2140	120	4,5	88,8	3,41	12,9	179	619	933	681

Abiotic variables

WST — mean soil temperature of warmest month at or near 5 cm depth (°C); CST — mean soil temperature of coldest month (°C); FFS — Frost-free days (soil); TSS — temperature sum degree days above 0°C (soil); PPTN — total precipitation (mm H_2O); EVAP — total evaporation (mm H_2O); DS — days snow lying; H_2O_{max} — maximum soil moisture (% dry wt); H_2O_{min} — minimum soil moisture (% dry wt); pH — soil pH; LOI — loss on ignition (% dry wt); N — total nitrogen (% dry wt); C/N — carbon to nitrogen ratio; P, K, Ca, Mg — 'extractable' (ppm dry wt).

Values in parentheses are estimated from incomplete bases, ie. with some interpolation of missing days' data, or from a series of spot measurements rather than continuous recording (climate) or, in soil data, from variables not measured directly (C/N from N and LOI) or with an estimated correction to allow for differences in analytical methods (N & P, Macquarie). Those in square brackets are approximations based on a general appreciation of the site and/or similar sites

bryophytes, although *Acaena magellanica* and *Rostkovia magellanica* are often associated.

Macquarie Island; 54°S, 159°E, subantarctic, New Zealand Province (Jenkin 1975)

Approx. 1 500 km SSE of Tasmania. Very oceanic. No permanent ice. Variety of vegetation types, many formed by closed swards of phanerogams. Bryophytes abundant.

Poa *grassland (Q.PG)*

Tussocks of *Poa foliosa* Hook. f., at 45 m a.s.l. on a thin layer of peat overlying wind-blown beach sand.

Marion Island; 47°S, 38°E, subantarctic, Kerguelen Province (Huntley 1971; Smith 1978, 1987a; Gremmen 1981)

Approx. 1 800 km SSE of Africa. Very oceanic, only a small permanent ice cap. Actively volcanic, well vegetated below *c.* 300 – 400 m a.s.l., many communities dominated by phanerogams but bryophytes very abundant.

Fernbrake (M.FB)

Dense carpet of short, hardy fronds of *Blechnum penna-marina* (Poir.) Kuhn., usually with cushions of *Azorella selago* Hook. f., and often with *Acaena magellanica* and *Poa cookii* Hook. f. Dominates the well-drained slopes of low altitude (< 250 m a.s.l.) areas.

Drainage line (M.DL)

Wet depressions and drainage lines in slope areas dominated by *Acaena magellanica, B. penna-marina* and *Brachythecium rutabulum* (Hedw.) B.S.G. Physiognomically similar to G.AM.

Grassland (M.PG)

Slope areas influenced by burrowing birds, but also on sea-facing slopes of the shore-zone where manuring by animals occurs. Dominated by tussocks of *Poa cookii*.

Fellfield (M.FF)

Windswept rocky ridges dominated by cushions of *Azorella selago* and cushion and ball-forming mosses at higher altitudes (> 300 m a.s.l.). Below this altitude (as in the sites represented in this study) *Agrostis magellanica* Lam. occurs epiphytically on the *A. selago* cushions. Skeletal mineral soil relatively low in organic matter.

Mire (M.MI)

Wet, graminoid and bryophyte-dominated vegetation on peat deposits of gently sloping lowland areas. In ill-drained basins the importance of bryophytes is increased and a bog vegetation develops.

Salt-spray (M.SS)

Sites on a narrow belt along the shore zone, experiencing

heavy deposition of wind-blown salt-spray and occasional inundation by waves. Dominated by *Crassula moschata* Forst. f. and *Cotula plumosa* Hook. f., generally on a dark fibrous peat.

'Grossly biotically influenced' (M.BI)

Mainly shore-zone sites, extremely heavily influenced by vertebrate excretion (e.g. seal wallowing areas and the sur- roundings of penguin rookeries). Dominated by tussocks of *Poa cookii*, mat-forming dicots such as *Callitriche antarctica* Engelm., *Montia fontana* L. and luxuriant rosettes of *Cotula plumosa*.

Methods

Principal component analysis (PCA) was used to examine interrelations in the climatic, soil chemistry and vegetation variables, followed by nearest neighbour/group mean clus- tering of the sites by their scores on what were considered to be the significant components. In all cases, we used an R- mode analysis, taking vectors of the correlation matrix (between variables) and deriving component scores from application of the resulting vector loadings to the original standardized data. This procedure weights all variables approximately equally, enables direct interpretation of the vectors in terms of the original variables, and gives vector loadings which can be used to fit new data to the pattern derived. Vectors were extracted until either a vector accounted for less than 5% of the total variance or until two or more vectors in succession were not ecologically interpretable. The vectors listed in the tables are all standardized loadings. We have given percentage variance accounted for, rather than eigenvalues, as we feel this is a more relevant figure in ecological terms. The eigenvalues, however, may be derived very simply from the percentage variance accounted for, as the latter is calculated as eigenvalue divided by the number of variables (because the vectors are of the correlation matrix, where all diagonal elements are 1).

Because PCA is frequently said to be a relatively poor technique for vegetation ordination (e.g. Beals 1973), Bray- Curtis geometric ordination, reciprocal averaging, and de- trended correspondence analysis were also tried, but none gave clearer or more interpretable results than PCA.

Cluster analyses of site scores in component space or, in the case of vegetation, of the original data, were used to group the sites into ecologically similar clusters, and to form a hierarchical classification. Euclidean distance was the dis- similarity measure. The procedure used was a combined nearest neighbour and group mean clustering in which, at each level, sites or group centroids were clustered with their nearest neighbours, then the centroids of the new clusters calculated and used in nearest neighbour clustering at the next level. At each stage, a distance constraint was set, beyond which sites (or groups) were to be considered 'outliers'.

The dendrograms have Euclidean distance as the 'dif- ference' axis. However, because distances were recalculated between sites/groups at each level, and the distances in the dendrogram are of each site or group to its nearest neighbour at the level at which it is first clustered, it would be misleading to use this as a truly quantitative index of relationships between sites. Outliers, especially, will have their nearest neighbour distances inflated as the clusters to which they are closest expand and the centroids move farther apart. Distance scales have therefore not been included. The important features of the dendrograms are the links between sites, and the order of those links. Details of the programs used are

available from D.D. French.

Abiotic data for each site are provided in Table 1. Air temperatures were not considered since the available data were not sufficiently detailed to distinguish individual sites within each island. Details of the chemical analytical methods used on the soil samples are provided by Brown & Veum (1974) for Macquarie Island, Signy Island and South Georgia and by Smith (1987b) for Marion Island.

Botanical data for the sites (Table 2) are in the form of relative cover ($\times 10$) of plant life-forms defined by Webber (1978) plus a simple 'total cover index' (French 1981), with three values corresponding to 'sparse' (33%), 'incomplete but fairly dense' (67%) and 'complete' (100%). Relative cover refers to the percentage contribution by a particular life-form to the total aerial vegetation cover.

Blechnum penna-marina cannot be satisfactorily classified as one of the life-forms used by French (1981) since, although a pteridophyte, it behaves phenologically and ecologically as a shrub. Similarly, *Crassula moschata*, while strictly an 'erect dicot', usually forms a pseudo-mat in the salt-spray zone where it typically occurs. Two botanical data sets are provided in Table 2, the first with *B. penna-marina* as a pteridophyte and *C. moschata* distinguished from other mat and/or erect dicots, the second including *B. penna-marina* in the 'deciduous shrub' category and *C. moschata* with 'mat dicots'. (Other combinations are, of course, possible, but these two suffice to illustrate the effects of different classifications on the final result). *Acaena magellanica* is strictly a suffruticose herb but is often referred to as a deciduous dwarf shrub (Lewis Smith & Walton 1975; Lewis Smith 1984) and is considered as such in this account.

Separate PCAs were computed for the abiotic (climate and soil chemistry) and botanical data. Two botanical PCAs were performed, one with *B. penna-marina* as a pteridophyte and *C. moschata* distinguished from other dicots, the other including *B. penna-marina* in the deciduous shrub category and *C. moschata* with mat dicots.

Results

Abiotic analyses

As in previous bipolar analyses (French & Smith 1985), all climatic variables are highly intercorrelated (Table 3). Amongst the southern sites there is a much higher correlation than in the bipolar analyses between mean soil temperature of the warmest month and other climatic variables, especially tem- perature of the coldest month. The number of days with snow lying is also associated with summer, rather than winter, parameters. Seasonal temperature range is therefore less important at these sites than in the northern hemisphere. An outstanding feature of the southern islands which was empha- sized in the bipolar analyses, i.e. their extreme oceanicity, is therefore also prominent in this analysis.

Also related to oceanicity is the positive correlation of potassium and magnesium (rather than calcium as in previous analyses) with climatic variables. The main source of elements to many of the southern island ecosystems is the surrounding ocean, rather than weathering of parent rock (Allen *et al.* 1967; Jenkin 1975; Smith 1977; Walton & Lewis Smith 1980; Walton 1984).

Soil temperature of warmest month was positively corre- lated with precipitation and evaporation, reflecting the zonal decrease in precipitation with latitude in the subantarctic region. Loss-on-ignition (LOI) and soil nitrogen were well correlated with the climatic variables, while maximum soil water content and soil acidity were correlated with soil

Table 2 Botanical data. For site codes see text.
(a) *Blechnum penna-marina* = Pteridophyte, *Crassula moschata* separate from other dicots
(b) *B. penna-marina* = DS, *C. moschata* = MD (sites other than the Marion Island sites listed are as in version (a)

	Botanical variable											
	DS	SG	CG	CD	MD	Cm	RD	ED	PTER	BRYO	LICH	TOT
(a)												
S.MT	0	0	0	0	0	0	0	0	0	608	392	100
S.MC	0	0	0	0	0	0	0	0	0	1000	0	100
S.DG	0	592	0	58	0	0	0	0	0	258	92	67
G.PG	14	959	0	0	27	0	0	0	0	0	0	33
G.AM	742	7	0	0	7	0	0	0	0	244	0	100
G.GH	114	513	19	0	6	0	0	0	0	285	63	100
G.FF	38	105	0	0	0	0	0	0	0	495	362	33
G.BB	16	21	365	0	5	0	0	0	0	484	109	67
G.EM	115	19	167	0	13	0	0	0	0	686	0	100
M.FB	40	130	0	150	0	0	0	0	550	90	40	100
M.DL	410	40	0	10	40	0	0	10	30	460	0	100
M.PG	20	790	0	10	50	0	10	0	0	120	0	100
M.FF	0	70	0	340	0	0	0	0	0	390	200	33
M.MI	10	200	30	30	110	0	0	0	30	570	10	100
M.SS	0	10	0	120	90	460	280	0	0	20	20	67
M.BI	0	400	0	0	410	0	180	0	0	10	0	100
(b)												
M.FB	590	130	0	150	0	–	0	0	–	90	40	100
M.DL	440	40	0	10	40	–	0	10	–	460	0	100
M.MI	60	200	30	30	110	–	0	0	–	570	10	100
M.SS	0	10	0	120	550	–	280	0	–	20	20	67

Botanical variables
DS — deciduous shrub; SG — single-shoot graminoid; CG — caespitose graminoid; CD — cushion dicot; MD — mat dicot; Cm — *Crassula moschata*; RD — rosette dicot; ED — erect dicot; PTER — pteridophyte (= *Blechnum penna-marina*); BRYO — bryophyte; LICH — lichen; TOT — total cover index (see text)

Table 3 Correlation matrix of abiotic variables. Variable codes as in Table 1

WST	1																
CST	0,80***	1															
FF(S)	0,94***	0,92***	1														
TS(S)	0,97***	0,84***	0,95***	1													
PPTN	0,78***	0,79***	0,81***	0,73***	1												
EVAP	0,85***	0,93***	0,93***	0,83***	0,92***	1											
DS	−0,75***	−0,51*	−0,76***	−0,80***	−0,29	−0,50*	1										
H_2O_{max}	0,50*	0,43	0,46	0,52*	0,35	0,33	−0,38	1									
H_2O_{min}	0,28	0,38	0,29	0,30	0,33	0,27	−0,07	0,64**	1								
pH	−0,40	−0,65**	−0,45	−0,41	−0,68**	−0,59**	−0,07	−0,30	−0,36	1							
LOI	0,53*	0,62**	0,53*	0,57*	0,51*	0,46*	−0,28	0,74***	0,81***	−0,60**	1						
N	0,56*	0,61**	0,57*	0,56*	0,58**	0,53*	−0,25	0,77***	0,73***	−0,54*	0,88***	1					
C/N	0,03	0,25	0,08	0,11	0,15	0,13	0,07	0,26	0,25	−0,45	0,43	0,13	1				
P	0,08	0,01	0,01	0,08	0,07	−0,02	0,04	0,33	0,20	−0,21	0,32	0,53*	−0,17	1			
K	0,41	0,55*	0,51*	0,43	0,45	0,49*	−0,26	0,54*	0,62**	−0,32	0,66**	0,79***	−0,02	0,42	1		
Ca	−0,20	−0,24	−0,22	−0,25	−0,16	−0,22	0,20	0,08	0,44	0,47*	0,07	0,15	−0,26	0,11	0,34	1	
Mg	0,29	0,38	0,35	0,36	0,13	0,24	−0,35	0,35	0,45	−0,16	0,53*	0,45	0,31	−0,15	0,52*	0,07	1
	WST	CST	FFS	TSS	PPTN	EVAP	DS	H_2O_{max}	H_2O_{min}	pH	LOI	N	C/N	P	K	Ca	Mg

* $P = 0,05$; ** $P = 0,01$; *** $P = 0,001$

temperature, LOI and soil N. This reflects the waterlogged, acid, organic nature of many of the southern island soils.

Weightings of the variables on the first four vectors derived from the PCA of the abiotic variables, with interpretations of the main trends, are presented in Table 4. These vectors accounted for 83% of the total variance. The first vector is similar to that of previous analyses (French 1981; French & Smith 1985) but is associated with a different soil trend, especially in that calcium is replaced by magnesium and potassium in the weightings (this follows from the correlations).

The continental – oceanic gradient that was a major feature of the bipolar analyses is absent since all the southern subpolar sites considered here are oceanic. Vector I, therefore, represents a gradient from 'warm, wet, organic, acid, high N, K and Mg' to 'cold, dry, mineral, basic, low soil nutrients'.

Vector II is from 'warm, dry soil, mineral, low soil nutrients' to 'cold, wet, organic, higher soil nutrients', reflecting the influence of exposure on sites within the main island areas. Exposed, low-altitude, rocky plateaux and ridges at the subantarctic islands, in particular, have skeletal sandy soils

Table 4 Vector weightings (first four vectors) from PCA of abiotic variables. Variable codes as in Table 1

Variable	Vector I	Vector II	Vector III	Vector IV
WST	0,30	0,21	0,17	0,03
CST	0,31	0,15	−0,07	−0
FF(S)	0,32	0,22	0,14	−0,01
TS(S)	0,31	0,20	0,15	−0,04
PPTN	0,28	0,15	−0,10	0,23
EVAP	0,30	0,23	−0,01	0,11
DS	−0,20	−0,23	−0,38	0,24
H_2O_{max}	0,24	−0,25	0,03	−0,07
H_2O_{min}	0,20	−0,40	−0,04	−0,13
pH	−0,22	−0,02	0,51	−0,24
LOI	0,28	−0,27	−0,15	−0,09
N	0,29	−0,29	0	0,14
C/N	0,09	−0,04	−0,56	−0,37
P	0,07	−0,29	0,08	0,56
K	0,24	−0,29	0,17	0,07
Ca	−0,04	−0,39	0,37	−0,07
Mg	0,17	−0,15	0,02	−0,56
% variance accounted for:	49	16	10	8

Direct interpretations (positive end of each vector)

I   : Warm, wet, organic, acid, high N, K (Mg)
II : Warm, high pptn, evap, dry soil (= exposed and/or well drained), mineral, nutrient-poor (Mg marginal)
III : Warm summer, low snow (= exposed?), alkaline/high Ca, low C/N
IV : High P, (N), low C/N, Mg

Figure 2 Weightings of variables on vectors I and II in the PCA of the abiotic data, with vector III weightings indicated approximately as into (−ve) or out of (+ve) the page.

Figure 3 Site scores on components I and II in the PCA of the abiotic data. Site codes explained in text. Circle diameters are proportional to the site scores on component III. Dashed lines indicate climatic/−edaphic bands (see text).

low in organic matter and hence in water retention capacity, in contrast to the waterlogged peats of adjacent more sheltered areas.

Vector III is from acid (organic) sheltered soils with high C/N ratios to exposed alkaline calcareous (mineral) soils with low C/N ratios. The C/N ratio gradient does not indicate a strong organic-mineral gradient as it is not coupled with a high weighting of LOI (although they are weighted in the same direction).

In vector IV the opposite weightings of Mg and P and the negative weighting of C/N ratios contrast the input of nutrients via vertebrate excretion and that in salt-spray.

Vectors I and II can be considered together as a linked pair reflecting the main differences between and within islands in climate (including soil climate), II and III as an expression of mainly abiotically-driven soil differences and vector IV as an index of the relative importance of vertebrates as soil modifiers. A small rotation of the first two vectors, in particular, gives a very clear distinction between effects of (i) temperature and aerial climate, (ii) soil moisture and nutrients, (iii) acidity, especially as related to Ca and (?) exposure and drainage (Figure 2).

The sites are plotted according to their scores on component I and II in Figure 3. The diameters of the circles are proportional to the site scores on component III. Dotted lines in the figure separate the islands along a gradient of overall climatic mildness (partly related to latitude). Within each island the sites are positioned along parallel series according to edaphic factors and exposure (cf. vector patterns in Figure 2).

On components III and IV (Figure 4) the sites are fairly well grouped according to the degree of animal influence, with the Marion Island 'grossly biotically influenced' sites at one extreme on component IV followed, after a gap, by South
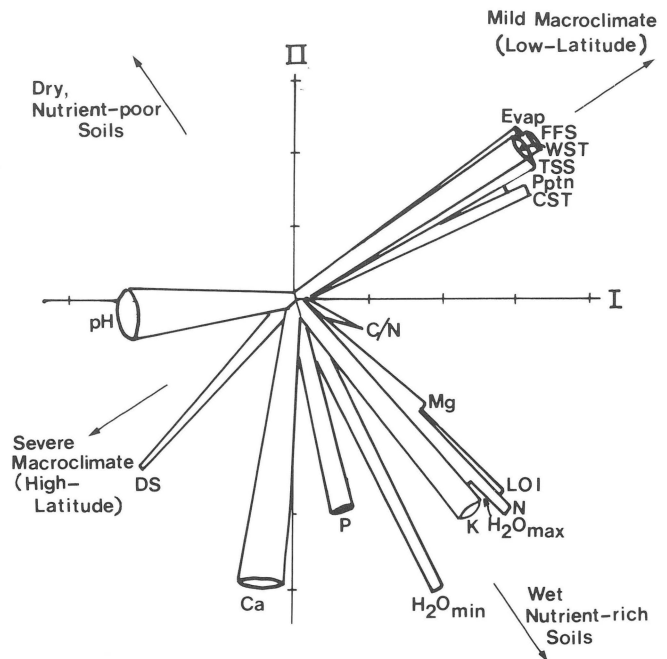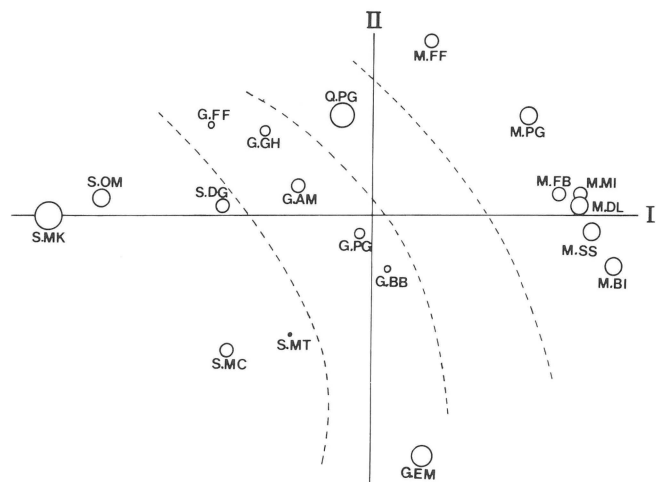
Georgia *Poa flabellata* tussock grassland — an area heavily used by elephant seals for wallows. Then there is a transitional band across the middle of component IV, from Marion Island *Poa cookii* grassland (strongly influenced by burrowing birds) through sites like South Georgia eutrophic mire and Signy Island grass sites, where there is some animal input, mainly by birds (but not enough to radically alter soil chemistry), to sites with little or no animal influence and little affected by sea-spray (e.g. M.FB, M.FF, S.MC). At the opposite extreme are the sites where any minor effects of vertebrate use are completely overridden by a high direct input of sea-spray (e.g. M.SS, S.MK, Q.PG). Thus, the low score of Marion 'salt-spray' on component IV, despite its unexceptional soil N and P, is attributable to its very high levels of magnesium (> 3 000 ppm d.w.t.) and is a true reflection of the difference in animal usage between it and the seal wallows
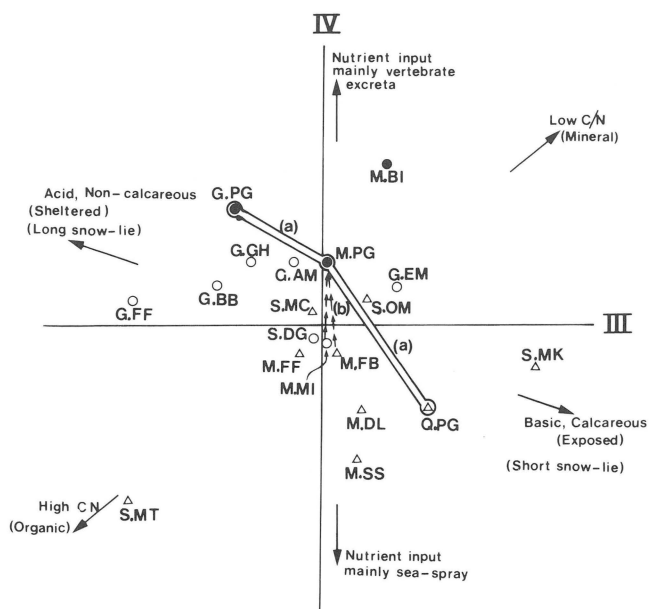
Figure 4 Site scores on components III and IV in the PCA of the abiotic data, with vector trends indicated. Solid circles; sites heavily influenced by vertebrate manuring. Open circles; sites which may have some manuring input but not enough significantly to alter soil chemistry. Triangles; sites with little or no vertebrate influence. For explanation of group (a) and arrows (b) see text.
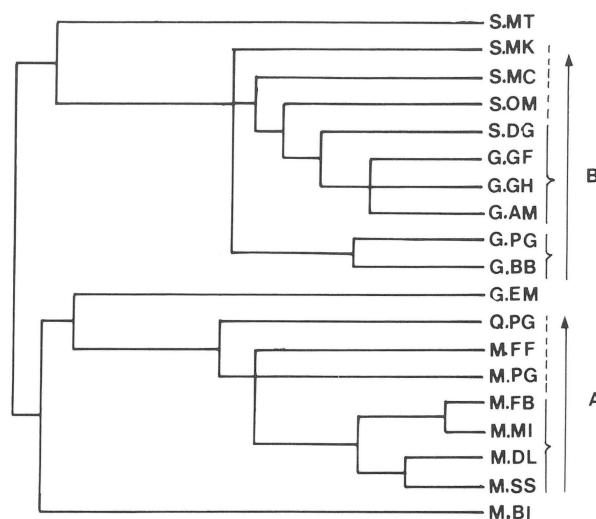

Figure 5 Clustering of the sites by their scores on the first four components from the analyses of the abiotic data. The arrows indicate the two main 'chains' of sites, pointing in the direction of increasing environmental severity (see text).

Figure 6 Minimum spanning tree on the first four components from the analyses of the abiotic data. Arrows indicate the two 'chains' of sites, in the direction of increasing environmental severity.

and penguin rookeries that make up the 'biotically influenced' sites. A similar distinction can be made between e.g. Signy Island grass, which receives N and P in downwash from bird colonies upslope, and Signy moss turves, with little input of nutrients, especially N and P (other than what is generally deposited all over the island by wind, rain, etc.) from any source (cf. Collins *et al.* 1975).

The relative positions of the three tussock *Poa* sites (Q.PG, M.PG, S.PG) on components III and IV (group 'a' in Figure 4) contrast the effect of wind exposure and blown sand at Macquarie Island where there is also strong exposure to sea-spray and (at the site used for this analysis) little or no significant seal activity, with the very high input of nutrients in elephant seal excreta at South Georgia. The Marion Island grasslands are intermediate, with nutrient input from petrels and other birds rather than seals, but also some exposure to wind-borne sea-spray. The ornithogenic succession from mires and fernbrakes to tussock grassland on Marion Island (Smith 1976) is indicated by the arrows (b) in Figure 4.

Clustering the sites by their positions on the first four components gives the dendrogram of Figure 5. There is a strong tendency to chaining, also shown in the minimum-spanning tree (Figure 6), where there are no very long links or discontinuities except to the three sites which are outliers in the dendrogram (S.MT, G.EM, M.BI). If these outliers are ignored, both figures show two parallel series of sites (indicated by the arrows on Figures 5 and 6): a low latitude series (A; Marion and Macquarie Islands) and a higher-latitude one (B; South Georgia and Signy Island). Each series follows a gradient from milder to harsher environments, i.e. from low-altitude, relatively sheltered soils without extremes of temperature or moisture (especially coldness and dryness) and with an adequate and well-balanced nutrient supply, to higher-altitude or exposed sites experiencing extremes of temperature and moisture and deficient in all or some major nutrients. The Marion Island drainage lines, for example, are warm, moist, sheltered and well supplied with all major nutrients.
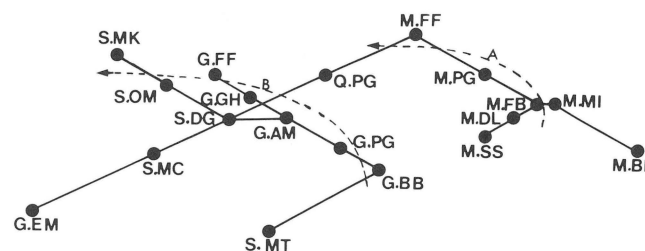
The *Poa cookii* grasslands are similarly warm and moist but are generally more exposed and acid, with lower N, K, Ca and Mg, while the fellfields, as well as having much lower levels of all nutrients (although a higher pH), are also colder and drier. At the 'severe' end of this series, the Macquarie Island site has nutrient and soil moisture levels comparable with the Marion fellfields and is still colder, with less precipitation (see data in Table 1). A similar gradation of increasing climatic and/or edaphic severity can be traced from the South Georgia *Acaena magellanica* (G.AM and G.GH) and *Poa flabellata* (G.PG) and basin bog (G.BB) sites to the Signy Island marble knolls (S.MK).

If component IV is omitted from the clustering, the Marion biotically influenced sites are no longer outliers but link closely with the other low-ground sites on Marion, while the more exposed mineral sites in each chain (M.FF, S.OM, S.MK) become new outliers and the Signy Island moss turves join the other acid bog sites. These changes emphasize the importance of vertebrate inputs to the soils of the southern islands.

Botanical analyses

As in the bipolar analyses (French 1981; French & Smith 1985), there is a generally low correlation between the various plant life-forms at the southern subpolar sites (Table 5) and therefore the statistical significance of individual correlations is not very meaningful. Rather more important is the overall pattern, which is comparable with that in French & Smith

Table 5 Correlation matrix of botanical variables. Variable codes as in Table 2

	DS	SG	CG	CD	MD	Cm	RD	ED	PTER	BRYO	LICH	TOT
DS	1 *1*											
SG	−0,26 *−0,28*	1										
CG	−0,09 *−0,14*	−0,25	1									
CD	−0,21 *0*	−0,19	−0,19	1								
MD	−0,15 *−0,23*	0,16 *−0,04*	−0,13 *−0,16*	−0,14 *0,07*	1 *1*							
Cm	−0,13	−0,20	−0,10	0,22	0,11	1						
RD	−0,18 *−0,22*	−0,08	−0,15	0,11	0,62* *0,98****	0,83***	1					
ED	0,42 *0,35*	−0,17	−0,10	−0,10	−0,02 *−0,06*	−0,07	−0,10	1				
PTER	−0,06	−0,11	−0,11	0,30	−0,11	−0,08	−0,11	−0,02	1			
BRYO	−0,03 *−0,16*	−0,55*	0,26	−0,18	−0,38 *−0,46*	−0,32	−0,47	0,10	−0,23	1		
LICH	−0,25 *−0,28*	−0,27	−0,03	0,14	−0,29 *−0,27*	−0,13	−0,21	−0,17	−0,11	0,26	1	
TOT	0,30 *0,38*	−0,19	−0,03	−0,41	0,22 *0,04*	−0,14	−0,01	0,18	0,21	0,20	−0,40	1

The main matrix is for the data set in which *Blechnum penna-marina* = pteridophyte and *Crassula moschata* is distinguished from other mat and erect dicots. Correlations in italics are for *B. penna-marina* = DS and *C. moschata* = MD. All other correlations are identical in both sets. Bracketed pairs indicate a significant change either in size or sign of the correlation. $*P = 0,05$; $**P = 0,01$; $***P = 0,001$

(1985) where, however, there were more significant single correlations, mainly because of the much larger sample size. The main differences from the bipolar analyses of French & Smith (1985) are in the correlations of single shoot graminoids with bryophytes (− 0,55 versus − 0,28 in the bipolar analysis), caespitose graminoids with bryophytes (0,26 versus − 0,38) and lichens (− 0,03 versus − 0,26), and pteridophytes with cushion dicots (0,30 versus 0,07). Mat dicots (excluding *Crassula moschata*) correlated positively with total cover in the present analysis, in contrast to a negative correlation in the bipolar analysis. The correlation between bryophytes and lichens also changed sign between the two analyses (− 0,28 for the bipolar data set versus + 0,26 in the southern subpolar set). Most of these changes arise from the more restricted phanerogam flora in the southern islands, together with the much greater importance of bryophytes.

The bracketed differences between versions of the southern data in Table 5 indicate changes in size or sign of the correlations which can be related to the ecology of the plants involved. Thus, the cushion plant *Azorella selago* occurs with *Blechnum penna-marina* in many of the Marion Island communities (CD:PTER) but not with *Acaena magellanica* (CD:DS) in the drainage lines and other wetter habitats. The differing habitats of *Crassula moschata* and all the other mat dicots are shown by the bracketed differences in the MD:SG, MD:CD and MD:TOT correlations. However, the strong association of *C. moschata* and other mat dicots with the rosette-forming *Cotula plumosa* is shown in the high MD:RD correlations. *C. moschata* is co-dominant with *C. plumosa* at sites heavily influenced by sea-spray. At sites manured by animals, other mat-forming dicots occur with *C. plumosa*, especially *Callitriche antarctica* and *Montia fontana*. Hence, including *C. moschata* as a mat dicot in the life-form classification reinforces the RD:MD correlation.

Despite these differences, the vectors (Table 6) indicate similar general trends in both versions of the PCA. The first vector in both is from sites with a high proportion of bryophytes and no mat and rosette dicots, to sites with abundant mat and rosette dicots but little or no bryophyte cover. This roughly corresponds to a gradient from inland bogs to coastal areas. The second vector, contrasting total cover, erect dicots, and 'shrubs' (*Acaena magellanica* or *A. magellanica* plus *B. penna-marina* with cushion-plants and lichens, is essentially a gradient from sheltered, edaphically rich sites to exposed, edaphically poor sites. The third vector separates single-shoot graminoids from other forms (especially mat and rosette dicots, and bryophytes) and seems to represent a gradient similar to vector IV of the ordination of the abiotic data. Subsequent vectors mainly pick out particular sites or groups rather than showing any general trend, and are different in the two versions.

However, given the degree of nonlinearity in the data, this is something of an over-simplification, and the component scores tend to form a 'dome' in the first three components. Taking into account the direct interpretation of the vectors (above), and the positions of the points in component space (see below), the three main environmental influences appear to be: (a) distance from the sea, and altitude, (the two are inevitably confounded to some degree in the field), (b) amount *and source* of nutrient input, i.e. the degree to which there is significant nutrient input from sea-spray or from vertebrate manuring, combined in the latter case with physical mixing of the substratum, and (c) wind exposure and/or osmotic stress. These are illustrated schematically in Figure 7 (inset) in relation to the linear vectors from the PCA. The first three components yield site scores (Figure 7) which are also essentially consistent over both versions, separating the Marion Island coastal sites from all the rest in component I, fellfields from the floristically richer sites in component II and the tussock grass sites from the rest in component III. The pattern can also be interpreted as a curvilinear 'traverse' (cf. French & Smith 1985, p. 15) tracking along the three environmental
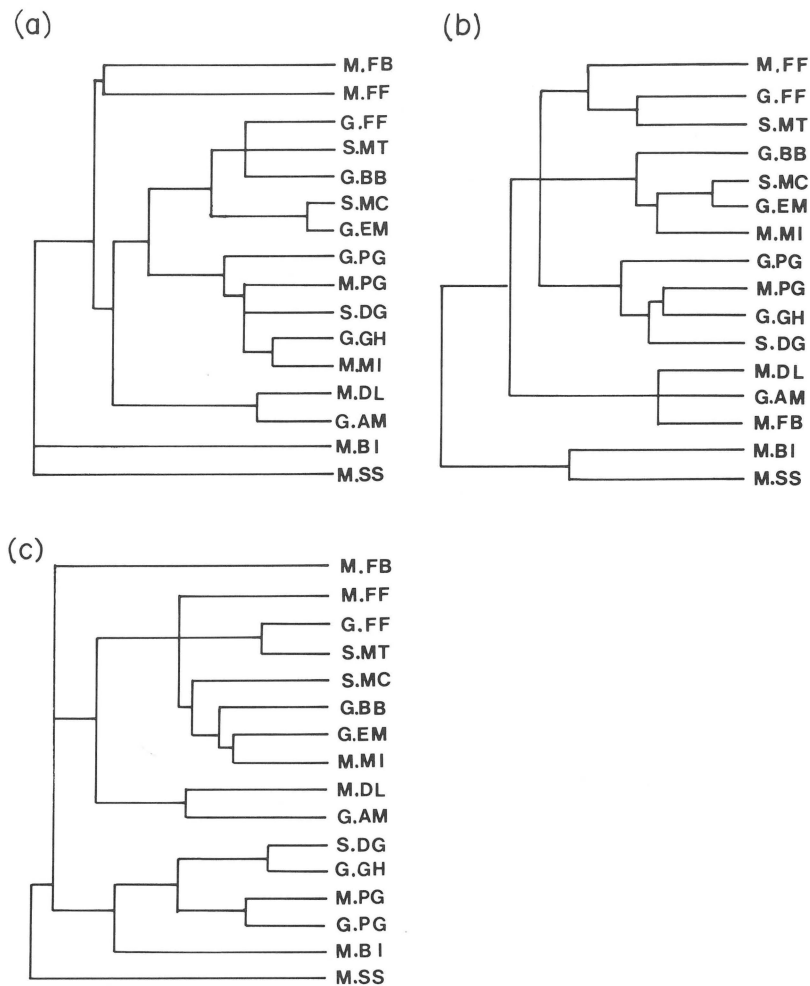
Table 6 Vector weightings (first five vectors), PCA of botanical variables. Variable codes as in Table 2

| | (a) *Blechnum* = PTER *Crassula* = Cm MD | | | | | (b) *Blechnum* = DS *Crassula* = MD | | | | |
| | Vector | | | | | Vector | | | | |
Variable	I	II	III	IV	V	I	II	III	IV	V
DS	0,17	0,41	0,14	0,25	0,38	0,14	0,47	0,09	0,44	0,29
SG	−0,20	0,02	−0,70	−0,06	0,14	−0,22	−0,08	0,70	−0,24	−0,07
CG	0,19	−0,05	0,14	−0,39	−0,34	0,20	−0,07	−0,25	−0,45	0,69
CD	−0,15	−0,36	0,18	0,47	−0,03	−0,13	−0,26	−0,12	0,60	0,34
MD	−0,38	0,26	−0,04	−0,24	−0,14	−0,54	0,11	−0,35	−0,09	−0,10
Cm	−0,41	−0,07	0,45	−0,04	0,10					
RD	−0,53	0,06	0,33	−0,16	0	−0,54	0,07	−0,37	−0,06	−0,07
ED	0,13	0,34	0,18	0,23	0,42	0,12	0,37	−0,03	0,29	−0,22
PTER	−0,02	0	−0,03	0,60	−0,56					
BRYO	0,46	−0,04	0,27	−0,24	−0,09	0,47	−0,05	−0,34	−0,16	−0,26
LICH	0,19	−0,46	0,10	−0,07	0,17	0,20	−0,48	−0,17	0,18	−0,39
TOT	0,09	0,52	0,10	0,02	−0,40	0,10	0,55	−0,11	−0,20	−0,18
% variance accounted for:	23	18	14	12	10	26	20	15	14	9

Figure 7 Site scores on components I and II from the PCA of the botanical data (*Blechnum penna-marina* = pteridophyte, *Crassula moschata* distinguished from other mat dicots), with circle diameters proportional to the scores on component III. The inset shows the three main environmental gradients derived from the vector weightings (Table 6a). When *B. penna-marina* = 'shrub', the pattern is nearly identical except that M.FB moves to a position between G.GH/M.MT and G.AM.

gradients (distance to sea/altitude, nutrient supply/source, water stress) described above and illustrated in the figure. Allowing for this curvilinearity, there is a notable correspondence between the first three botanical components and abiotic components II to IV, but little sign of the macroclimatic differences between islands (abiotic component I) in the ordination of the botanical data.

Components IV and V are less consistent and the patterns they represent diverge depending on the life-form classification of *B. penna-marina* and its association with other life-forms. When it is classified as a pteridophyte, Marion Island fernbrake (M.FB) is distinguished from the rest of the sites on components IV and V. Otherwise M.FB is linked closer to the wet, *Acaena magellanica*-dominated communities on Marion and South Georgia. Within the subantarctic, fernbrake communities dominated by *B. penna-marina* are restricted to the Kerguelen biogeographical province and are best developed at Marion Island where they dominate large slope areas of the eastern coastal plain. Fernbrakes do not occur at Macquarie, South Georgia, Heard or MacDonald islands but are more common at more temperate islands such as the Falklands (Moore 1968), Tristan da Cunha (Wace & Holdgate 1958) and Gough Island (Groves 1981).

Clustering the sites on the first four components produces the dendograms of Figure 8a and b. The difference between the cluster patterns results from the differing classifications of *Blechnum penna-marina* and, to a lesser extent, *Crassula moschata*.

When *B. penna-marina* is classed as a pteridophyte (Figure 8a) the Marion Island fernbrakes are linked with Marion fellfields, probably because of the importance of the cushion plant *Azorella selago* at both sites. The South Georgia fellfield is linked with two deep peat sites: Signy Island moss turves and South Georgia basin bog. At a higher level this group of sites is linked to the moss carpet and eutrophic mire sites (S.MC and G.EM). The Marion Island mire is not clustered with this main group of bryophyte-dominated sites but is linked closely with the grassland communities from all three islands, especially the South Georgia grassy heath, due to the importance of single-shoot graminoids at both sites (*Agrostis magellanica* in M.MI, *Festuca contracta* in G.GH). The *Poa* tussock sites join this group by linking with the Signy Island grass site in a 'chain' rather like those occurring in the abiotic analyses.

Classifying *B. penna-marina* as a deciduous shrub markedly affects the clustering of nearly all the sites (Figure 8b). The Marion Island fellfield now clusters with the South Georgia fellfield which in turn remains closely linked with Signy Island moss turves. This suggests that S.MT is not analagous to northern hemisphere bogs as previously supposed (e.g. Baker

Figure 8 (a) & (b) Clustering of sites by their scores on components I – IV of the PCA of the botanical data. (a) *Blechnum penna-marina* = pteridophyte, *Crassula moschata* distinguished from other mat dicots; (b) *B. penna-marina* = deciduous shrub, *C. moschata* = mat dicot. (c) Clustering on raw botanical data; *B. penna-marina* and *C. moschata* classified as in (a).

1972) but is better thought of as an extreme type of fellfield with unusually large moss cushions. The Marion Island fernbrakes, no longer separated by a high 'pteridophyte' cover, now link closely with other 'shrub'-rich sites (Marion Island drainage lines and South Georgia *Acaena magellanica* community). Secondary effects of the different classification of *B. penna-marina* are that the grassland group no longer includes the Marion Island mires, which are now included in a cluster of all the bog and mire sites.

The life-form classification of *Crassula moschata* only affects the Marion Island coastal sites. In the analyses leading to Figure 8a, *C. moschata* was considered to be in a life-form class of its own so that the Marion Island salt-spray and grossly biotically influenced sites are separate from each other as well as from all other sites. In Figure 8b, *C. moschata* was considered a mat dicot and the two coastal sites are linked fairly closely because of the abundance of *Cotula plumosa* at both sites, together with the occurrence of mat dicots other than *C. moschata* at biotically influenced sites.

Since the botanical data in Table 2 are of relative cover, clustering can also be performed directly on the original data. The resulting dendrogram (Figure 8c; *B. penna-marina* = Pteridophyte, *C. moschata* distinguished from other mat dicots) is intermediate between figures 8a and b, emphasizing the unique characters of the fernbrake and salt-spray sites as in Figure 8a, but partitioning the mire, bog and grassland sites more similarly to Figure 8b so that the Marion Island mires are grouped with other bryophyte-dominated wet communities

on South Georgia and Signy Island, and South Georgia fellfield is again closely linked with Signy Island moss turves. Interestingly, clustering on the raw data links the Marion Island grossly biotically influenced sites with tussock grasslands on South Georgia and Marion Island (G.PG and M.PG), sites also experiencing manuring by animals.

The instability of the clustering is partly a function of the distance matrices. For example, the distances between M.MI, G.GH, G.EM and S.MC differ by as little as 1%. A small change in the weighting of one or more variables can, therefore, give rise to disproportionately large changes in the final clusters.

Discussion

Subantarctic and maritime antarctic terrestrial ecosystems possess three characteristics which distinguish them from northern hemisphere tundras (French & Smith 1985). These are: oceanicity (with the associated importance of wind as a climatic factor), geographical isolation, and a high degree of animal influence. All these characteristics are manifested in the analyses presented in this paper.

Oceanicity is most clearly shown in the PCA of the abiotic variables, especially in the temperature patterns (small seasonal temperature range) and the importance of Mg and K, rather than of Ca, in the first component. The linking of climate with the common occurrence of acid, waterlogged, organic soils also implies (cf. French & Smith 1985) that the oceanic climates of the southern subpolar islands favour peat

development, especially by providing conditions conducive to high primary production (long growing season, absence of very cold temperatures, substantial nutrient input from the marine ecosystem), yet retarding the decomposition of this plant material through the maintenance of waterlogging and the absence of a warm summer. Heal *et al.* (1981) arrived at a similar conclusion from consideration of input and accumulation rates of organic matter over a wide range of tundra sites. In the botanical analyses, oceanicity is shown mainly in the lack of any botanical trend corresponding to the first abiotic component and in the curvilinear 'traverse' in the first two components from low-altitude sites in the salt-spray zone to high-altitude sites relatively far inland. Similarly, in the clustering, the coastal sites most influenced by sea-spray (M.SS, M.BI) separate out first, while wind exposure and osmotic stress together form a strong element of component II.

Geographical isolation is reflected most in the botanical results, especially in the wide ecological amplitude of the phanerogamic species and the tendency of some species to form rather specialized communities, often peculiar to a single island or island group (e.g. *Blechnum penna-marina, Crassula moschata* and, to a lesser extent, the graminoids *Agrostis magellanica* and *Rostkovia magellanica*). The paucity of vascular species and absence of some plant life-forms (especially woody forms) common at many northern hemisphere tundra sites also attest to the geographical isolation and, more subtly, to the oceanicity of the southern subpolar sites.

Another major consequence of the combination of oceanicity and geographical isolation is the overwhelming importance of bryophytes in the vegetation of the islands, not only as primary colonists but in the formation of mature communities. This is illustrated by the close linkage of Signy moss turves and South Georgia fellfield (Figure 8) and between all the fellfields, moss-dominated communities and bog and mire sites in Figure 8c. Aided by the extreme climatic wetness, bryophytes assume the role that would be filled in northern hemisphere tundras by a variety of cushion and mat dicots (and by lichens). This importance of bryophytes in the southern islands has been well documented in phytosociological studies (Lewis Smith 1972; Gremmen 1981) and contradicts the statement by Aleksandrova (1980) that 'even if mosses do take part in the composition of a number of associations, their role is insignificant in the majority of cases. The typical wetland vegetation on the subantarctic islands is, as already mentioned, mainly plant cushions which appear to be the main peat formers'. Although cushion-forming species (including bryophytes) probably initiate peat formation on new rock substrates (e.g. lava flows or post-glacial surfaces), bryophytes and graminoids are equally important (though possibly secondary) agents of peat accumulation in the subantarctic.

Besides increasing enormously the importance of the bryophyte flora, the geographical isolation of the southern islands allows for many 'vacant niches' which may be exploited by exotic invaders. The alarming spread of *Agrostis stolonifera* on Marion Island (Gremmen & Smith 1981) since its accidental introduction in the early 1960s is one example of this.

Animal influences are most clearly shown in the abiotic PCA, where the fourth vector is a measure of nutrient input via vertebrate excretion. Soils manured by seabirds on Marion Island have lower C/N ratios, and higher amounts of inorganic nutrients, than surrounding uninfluenced soils (Smith 1976). Similarly, in a PCA of botanical variables for 21

Marion Island sites (Smith & Steyn 1982) the main component (explaining 34% of the total variance) could be ascribed to the manuring influence of seabirds and seals. This is not so obvious in the botanical analyses presented here (cf. Figure 7) but the instability of the clustering may be partly due to the dynamics of animal influences. On Marion Island, tussock grasslands replace fernbrake where burrowing petrels and prions establish burrows (Smith 1976) and mires change in a similar manner around albatross nests. 'Grossly biotically influenced' sites are most often derived from 'salt-spray' vegetation, as are many tussock grasslands. The interactions of these (partly cyclic) vegetation changes, caused by vertebrate manuring and disturbance, with the radiative succession from *Azorella selago*-dominated vegetation to all other communities (Smith 1987a) helps to explain the ambiguity of the clusterings of Marion Island sites in Figure 8, and similar mechanisms are likely to apply on the other islands (cf. Lewis Smith & Walton 1975).

In this paper, we have shown how the use of suitable multivariate techniques can describe, and partly explain, some of the main patterns of variation in subantarctic ecosystems. A full analysis of the importance of these patterns over the whole subantarctic zone requires data from other subantarctic islands of the Kerguelen Province, fuller and better data from Macquarie Island and sites in the Magellanian Province, and probably also the inclusion of more maritime antarctic sites and some cool-temperate islands like those of the New Zealand shelf, the Falkland Islands and islands of the South Atlantic Ridge such as Gough and Tristan da Cunha. It would then be possible not only to examine the interrelations between southern hemisphere tundras and tundra-like ecosystems generally, but also to test the consistency of the ecological patterns within and between the main geographical groups.

Acknowledgements

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