Epilithic macrolichen vegetation of the Argentine Islands, Antarctic Peninsula

N.J.M. GREMMEN, A.H.L. HUISKES and J.W. FRANCKE

Netherlands Institute of Ecology, Centre for Estuarine and Coastal Ecology, Vierstraat 28, 4401 EA Yerseke, The Netherlands

Abstract: Classification of 162 sample plots of lichen vegetation from the Argentine Islands region, Antarctica, yielded two main groups, the *Usnea* complex and the *Mastodia-Rinodina* complex, comprising four and six subordinate communities, respectively. Communities of the *Usnea* complex typically occur in inland sites with steep slopes, characterized by low chloride, ammonia and phosphate concentrations. Communities of the *Mastodia-Rinodina* complex occur close to the shore and in areas occupied by birds, where concentrations of chloride, ammonia and phosphate were relatively high. Within each vegetation complex species composition is related to factors indicating nutrient status (chloride and ammonia concentration, distance from the sea), as well as to variables indicating different microclimatic conditions (elevation, aspect, exposure, moisture, and gradient). In canonical correspondence analyses of the data a large part of species variation could not be explained by the environmental variables studied (elevation, gradient, slope aspect, distance from the sea, direction of the sea, presence of guano, exposure, moisture, chloride, ammonia, phosphate and nitrate concentrations). It is suggested that temporal variability in mineral concentrations and the lack of information on differences in length of the growing season at the sample sites are, to a large extent, responsible for this.

Received 16 January 1994, accepted 26 May 1994

Key words: lichen, community classification, ordination, environment, maritime Antarctic

Introduction

Lichens are the dominant plant group throughout most of the Antarctic (Smith 1984). In the Argentine Islands, off the mid-west Antarctic Peninsula, they cover much of the exposed rock surface, and grow abundantly in moss banks. Although the vegetation of the Argentine Islands has been described (Smith & Corner 1973), little is known of the relation between the distribution of lichen species and environmental factors. In the present paper a detailed account is presented of the epilithic macrolichen vegetation of the Argentine Islands and some neighbouring islands.

This study is part of the Antarctic Coastal Ecology project of the Centre for Estuarine and Coastal Ecology of the Netherlands Institute of Ecology, in cooperation with the British Antarctic Survey (Huiskes & Kromkamp 1990, Gremmen *et al.* 1991). Fieldwork took place during the 1990/1991 southern summer at the British Antarctic Survey research station Faraday, Argentine Islands (65°S, 64°W; Fig. 1).

Study area

The Argentine Islands are a group of small islands, situated off the mountainous and glacierized west coast of the Antarctic Peninsula. Individual islands are less than 1 km² in area, and up to 64 m above sea level. The climate of the Argentine Islands has been summarized by Smith & Corner (1973). Small icecaps covering most of the islands are thought to be relics of a former coastal ice shelf (Thomas 1963). There is

evidence suggesting a recent recession of the ice in some of the islands (Corner & Smith 1973). Part of the terrain, especially on the north and west sides of the islands, is free from snow and ice during summer. The study area included the Argentine Islands, Yalour Islands and Petermann Island (Fig. 1).

The Argentine Islands consist of igneous rocks. Elliot (1964) discerns two groups, an Upper Jurassic Volcanic Group, and an Andean Intrusive Suite. Our study sites in the Argentine Islands were located on islands belonging to the Upper Jurassic Volcanic Group.

The flora of the Argentine Islands includes both Antarctic vascular plants, but moss banks and lichens dominate the vegetation. Of the vascular plants *Deschampsia antarctica* Desv. is not uncommon, occasionally forming dense swards of several square metres, whereas *Colobanthus quitensis* Bartl. is rarer, occurring in fewer localities (Corner 1971). Both species have increased dramatically over the past 30 years (Fowbert & Smith 1994). In mesic habitats moss banks dominated by *Polytrichum alpestre* Hopp. occur on many of the islands, ranging in size from a few m² to several hundreds m². In wet habitats small patches of carpet-forming mosses (e.g. *Brachythecium austro-salebrosum* (C. Muell.) Kindb. and *Drepanocladus uncinatus* (Hedw.) Warnst.) occur. On well drained sites species of *Bryum* occur. Most of the exposed rock surfaces in the islands are covered by lichen-dominated vegetation, locally with cushion-forming mosses. Smith & Corner (1973) describe a fruticose lichen and moss

Fig. 1. Map of the study area.

cushion sub-formation, dominated by species of *Usnea* and *Umbilicaria*, and a crustose lichen sub-formation, in which macrolichens are rare or absent.

The Argentine Islands contain small colonies of cormorants and gulls, and small numbers of skuas, terns and petrels occur (Stark 1990). There are large penguin colonies on Petermann and Yalour Islands.

Methods

Data collection

Data on the occurrence of plant species and on site characteristics were collected from sample plots containing epilithic macrolichens in the study area. Plots were chosen to cover all different habitat types, and to represent the variation in species composition of macrolichen vegetation. Thus an initial set of plots was chosen on the basis of habitat type, more or less randomly distributed. This first set of quadrats included sites close to the shore and farther inland, at sea level and on hilltops, sheltered and exposed, facing in different directions, with different gradients, close to and far from bird colonies. In addition plots were selected whenever a species combination was observed not covered in the previous set of sample plots. A relatively large number of plots was analysed in

vegetation containing the foliose lichen *Mastodia tessellata*, the main subject of our ecophysiological studies (Gremmen *et al.* 1991).

Commonly in studies of Antarctic lichen vegetation some, or even most, of the species cannot be identified in the field (Follmann 1965, Kappen 1985). This makes a precise estimate of abundance and cover of these species in the field impossible (Kappen 1985). For an efficient collection of data on the distribution of the species the following strategy was chosen: after a preliminary study of the lichen flora of the study area, we listed the species which we felt we were able to identify in the field from all other species. The cover percentages of these species are believed to be accurate. Subsequent identification of a large number of samples of these species has shown our field identifications to be correct in most cases. One or two species from our original list appeared not always to have been recognised in the field, as several unidentified samples proved to belong to these species. These species have been left out of the analysis. The result is a species list which represents the species composition of the vegetation with respect to the macrolichens and bryophytes completely, but is incomplete for the crustose lichens. Of the species listed, however, not only the observation of their presence, but also of their absence is accurate. For the species collected as unidentified samples from our sample plots (Appendix I) the presence data are accurate, but there may be large errors in the absence data. Thus none of these species have been included in the analysis.

For each 50 × 50 cm sample plot the cover of all species which could be identified with sufficient certainty in the field was recorded. These included all macrolichens and all mosses, as well as a number of crustose lichen species and one species of alga (Table II). Cover and abundance data were transformed to the 9 point ordinal scale of van der Maarel (1979). For each sample plot the following site characteristics were measured or estimated:

elevation in m above sea level;

slope gradient and direction, in degrees;

distance and direction to the nearest shore;

abundance of bird guano and intensity of trampling by animals, estimated on a 3-point scale, in which 1 = no evidence of trampling or guano, 2 = little influence and 3 = much trampling and/or guano;

degree of exposure, estimated on a 5-point scale, in which 1 = strongly sheltered and 5 = strongly exposed;

moisture status: degree of wetness of the site, estimated on a 3-point scale, in which 1 = dry, 2 = moist and 3 = wet, i.e. a regular supply of water from rain or meltwater;

To gain an impression of the nutrient status of the sites, material for chemical analysis was obtained using the following procedure: within the sample quadrat three paper filter disks of 8.5 cm diameter were placed on the rock surface, and

sprayed with 3 ml of deionized water. The disks were pressed closely against the rocks with a stainless steel spatula, and left for 30 minutes. Subsequently the disks were put into a 50 ml glass sample bottle. In the laboratory 45 ml of deionized water was added to each sample bottle. The bottles were well shaken and left to stand for two hours. The contents of the bottle were filtered and the resulting solution was analysed for chloride, phosphate, nitrate and ammonia using standard Merck Microquant analysis kits and a Vitatron spectrophotometer. Blanks were provided by spraying paper filter disks in the field without placing them on the rock surface. Results are expressed as concentrations in the final filtered solution.

Data analysis

A classification of the sites, based on species composition, was made by relocative centroid sorting, using the program FLEXCLUS (van Tongeren 1986). Final adjustments were made by hand, following the principles of Braun-Blanquet tabulation (Braun-Blanquet 1964, Mueller-Dombois & Ellenberg 1974, Westhoff & van der Maarel 1973). Basic communities in the classification were formed by clusters possessing at least one character species (Westhoff & van der Maarel 1973). Based on floristic similarities communities were grouped into complexes (Gremmen 1981), while floristic variation within some communities warranted the distinction of variants. Values of environmental variables were compared between clusters using the F-statistic in an analysis of variance.

A formal analysis of the variation in species composition of the sites, and of the relation between species and environment, was made using a number of techniques. Firstly correspondence analysis (CA) was used to describe the vegetational patterns. CA is an ordination method which uses a unimodal species response model (ter Braak 1985). Detrended correspondence analysis (DCA) was used to correct for possible effects of compression of the ends of the ordination axes and of a systematic relation of the second with the first axis (Hill & Gauch 1980, ter Braak 1987). To explain the pattern of variation in the species data by the observed values for the environmental variables, we used canonical correspondence analysis (CCA). CCA is similar to correspondence analysis, but the ordination axes are constrained to be linear combinations of the environmental variables (ter Braak 1987).

In CCA a minimal set of environmental variables to explain the species data was chosen by the method of forward selection. At each step the variable adding most to the explained variance of the species data was selected (ter Braak 1990). The significance was tested using Monte Carlo permutation tests (Manly 1990), with 99 permutations, and a significance level of 5%. No more variables were added to the regression model when the next best variable would explain less than 5% of the total variance explained by all variables.

All analyses were performed using the program CANOCO,

version 3.12 (Ter Braak 1988, 1990). Ordination diagrams and species-environmental variables biplots were plotted using the program CANODRAW, version 3.00 (Smilauer 1992). Species occurring only once or twice in the data were left out of the diagrams. For the interpretation of bi- and triplots we refer to ter Braak (1987). Samples with extreme values in the explanatory variables may unduly influence the ordination results in direct gradient analysis. Generally, samples with a leverage (Montgomery & Peck 1982) of more than 20 times the average have been made passive in the analysis. This was the case for one or two samples in most analyses. Species which could not be identified in the field have been left out of the analysis.

Directional variables were measured in the field in degrees from north. As this is a circular scale, in which the extreme values actually indicate similar situations, it is not suitable for direct numerical analysis. Therefore slope aspect and direction of the nearest shore were each transformed into two linear variables: one indicating the northerly component, defined as the cosine of the compass angle, the other indicating the easterly component, defined as the sine of the compass angle.

Authorities for species names are given in Table II and in Appendix I.

Results

The lichen vegetation and the site characteristics were described in 162 sample plots (Argentine Islands, 89 plots; Yalour Islands, 39 plots; Petermann Island, 34 plots). In the plots we identified 38 lichen, 6 moss and 1 alga species in the field. Collections from the plots yielded a further 23 species of crustose lichens (Appendix I), but these have not been used in the data analysis, as they have not always been recognized in the field.

Table 1. Epilithic lichen communities of the Argentine Islands, as classified using FLEXCLUS.

1	<i>Usnea</i> complex
1.1	community of <i>Usnea antarctica</i> , <i>Umbilicaria propagulifera</i> and <i>Pseudephebe pubescens</i>
1.2	community of <i>Usnea antarctica</i> and <i>Umbilicaria antarctica</i>
1.2.a	variant with <i>Pseudephebe minuscula</i>
1.2.b	variant with <i>Andreaea depressinervis</i>
1.3	species poor <i>Usnea antarctica</i> community
1.4	community of <i>Usnea antarctica</i> and <i>Physcia caesia</i>
2	<i>Mastodia-Rinodina</i> complex
2.1	community of <i>Rinodina petermannii</i> and <i>Acarospora macrocyclos</i>
2.2	community of <i>Mastodia tessellata</i> and <i>Physcia caesia</i>
2.3	community of <i>Caloplaca lucens</i>
2.3.a	variant with <i>Rinodina petermannii</i>
2.3.b	variant with <i>Rinodina petermannii</i> and <i>Mastodia tessellata</i>
2.3.c	variant with <i>Mastodia tessellata</i>
2.4	community of <i>Mastodia tessellata</i>
2.5	community of <i>Mastodia tessellata</i> and <i>Verrucaria elaeoplaca</i>
2.6	community of <i>Lecania brialmontii</i>

Table II. Synoptic table of the species composition of the epilithic lichen communities. Roman figures indicate species frequency (I = 1–20%; II = 21–40%; III = 41–60%; IV = 61–80%; V = 81–100%). Arabic figures indicate range of cover/abundance values (1 = very few individuals and cover < 5%; 2 = few individuals and cover < 5%; 3 = many individuals and cover < 5%; 4 = very numerous and cover < 5%; 5 = cover of 5–12.5%; 6 = 12.5–25%; 7 = 25–50%; 8 = 50–75%; 9 = 75–100%). Figures for the environmental variables represent the means per community. See Table III for units. ++ and — indicate a significant higher and lower value respectively in the *Usnea* complex as compared to the *Mastodia-Rinodina* complex (tested using the F-statistic of an ANOVA).

	<i>Usnea</i> complex					<i>Mastodia-Rinodina</i> complex							
cluster number	1.1	1.2.a	1.2.b	1.3	1.4	2.1	2.2	2.3.a	2.3.b	2.3.c	2.4	2.5	2.6
number of sites	16	9	6	6	3	12	15	13	10	7	48	15	2
elevation ++)	18	21	23	12	7	14	10	16	6	13	12	8	6
slope angle ++)	78	56	76	35	84	50	63	28	28	43	30	32	89
E-aspect —)	-0.3	0.1	0.1	0.2	-0.7	0.1	0.0	0.5	0.0	-0.2	0.3	0.5	0.4
N-aspect ++)	0.6	0.2	0.8	-0.2	0.5	0.2	0.4	-0.1	0.4	0.7	0.0	-0.6	-0.7
distance sea ++)	84	65	92	26	9	47	22	38	16	23	28	21	9
sea-to-east	0.0	-0.1	-0.2	-0.4	-0.1	-0.2	-0.3	-0.1	-0.4	0.0	-0.1	-0.3	-0.9
sea-to-north ++)	0.9	0.3	0.8	0.0	0.5	0.4	0.3	0.6	0.4	0.8	0.2	0.3	0.5
guano —)	0.0	0.1	0.0	0.3	0.1	1.0	0.9	1.2	1.2	1.2	1.5	1.3	0.1
exposure	3.3	3.6	3.1	3.7	3.0	3.4	3.2	4.1	3.9	4.0	3.3	3.5	1.0
moisture	1.3	1.0	2.3	1.2	1.0	1.5	1.2	1.0	1.3	1.1	1.2	1.2	2.0
Cl- —)	9	12	9	9	6	12	11	12	10	11	23	9	3
NO ₃ ++)	0.9	0.6	0.7	0.2	0.1	0.4	0.2	0.4	0.3	0.4	0.2	0.4	0.0
NH ₄ —)	0.1	0.2	0.0	0.2	0.1	0.3	0.6	0.6	0.5	0.5	1.2	0.9	0.1
phosphate —)	0.0	0.1	0.1	0.1	0.0	0.1	0.3	0.2	0.6	0.8	0.6	0.2	0.0
mean number of species: macrolichens	6.4	5.3	3.7	2.	3.3	3	2.9	1.2	1.8	2.1	1.3	1.7	2
mean number of species: mosses	0.5	0.4	1.2	0.3	0	0.2	0	0	0.1	0	0	0	0

Classification

Classification of the plots yielded two main groups, the *Usnea* complex and the *Mastodia-Rinodina* complex. Both groups in turn were divided into a number of subgroups (Table II). The species composition of each cluster, and average values of environmental variables, are given in Table II. The two main groups may be characterized as follows:

The *Usnea* complex.

This is characterized by the macrolichens *Usnea antarctica*, *Umbilicaria antarctica*, *U. propagulifera*, *U. decussata*, *Pseudophebe pubescens*, *P. minuscula* and *Parmelia saxatilis*, the crustose lichens *Rhizocarpon geographicum* and *Ochrolechia frigida* and the moss *Andreaea depressinervis*. This vegetation covers most of the inland rocks with a sufficiently long snow-free period to allow for the development of macrolichen vegetation. Along the shores of the narrow creeks between some of the islands, and distant from bird colonies, *Usnea* vegetation may be found right down to the high water mark. In nearly all of the studied environmental variables the *Usnea* complex differed significantly from the *Mastodia-Rinodina* complex (Table II). Sites of the *Usnea* complex were significantly higher in elevation, had steeper slopes, a greater distance from the sea, less influence by bird guano, and lower phosphate and ammonia concentrations. Nitrate concentrations were higher in sites of the *Usnea* complex. Within the *Usnea* complex four communities have been discerned (Table II).

The *Mastodia-Rinodina* complex

This group of communities is characterized by *Acarospora macrocyclos*, *Caloplaca lucens*, *Candelaria murrayi*, *Lecania brialmontii*, *Mastodia tessellata*, *Rinodina petermannii*, *Verrucaria elaeoplaca*, and *Xanthoria candelaria*. This vegetation is characteristic of sites strongly influenced by animals or by sea-spray, such as close to penguin colonies, and on coastal rocks. Concentration of chloride, ammonia and phosphate are significantly higher than in the *Usnea* complex (Table II). Vegetation of the *Mastodia-Rinodina* complex occurs up to over 100 m inland in areas influenced by penguins on Yalour and Petermann Islands. In the Argentine Islands these communities are largely restricted to a narrow coastal zone. Only small stands of this vegetation, especially of the *Caloplaca lucens* community, occur inland, on rocks used by skuas or gulls for perching or breeding sites. The *Mastodia-Rinodina* complex has been subdivided into six communities (Table II).

Ordination

The results of a correspondence analysis (CA) of the species data showed a pronounced arch effect (Hill & Gauch 1980, ter Braak 1987). To avoid this artefact the analysis was repeated using detrended correspondence analysis (DCA; Hill & Gauch 1980). The resulting ordination diagram (Fig. 2) showed a separation of the *Usnea* complex and the *Mastodia-Rinodina* complex along the first ordination axis. Environmental parameters most strongly correlated with this axis were guano ($r=0.53$), gradient ($r=0.46$) and distance from the shore ($r=0.40$). The second ordination axis could not be interpreted in terms of environmental variables.

Table II. continued.

cluster number	<i>Usnea</i> complex						<i>Mastodia-Rinodina</i> complex						
	1.1	1.2.a	1.2.b	1.3	1.4	2.1	2.2	2.3.a	2.3.b	2.3.c	2.4	2.5	2.6
number of sites	16	9	6	6	3	12	15	13	10	7	48	15	2
characteristic species of the <i>Usnea</i> complex													
Usan <i>Usnea antarctica</i> Du Rietz	V(3-6)	V(3-7)	V(3-5)	V(3-8)	V(1-6)	III(3-5)	II(1-3)	I(1)	I(3)	I(1)			
Rhge <i>Rhizocarpon geographicum</i> (L.) DC	II(3-6)	III(2-5)	III(3)	II(5-7)	V(3-5)								
Ocfr <i>Ochrolechia frigida</i> (Sw.) Lyngb	III(1-7)	IV(2-6)	IV(1-7)	I(2)									
Pasa <i>Parmelia saxatilis</i> (L.) Ach.	IV(3-5)	I(1)	I(1)										
Pspu <i>Pseudephebe pubescens</i> (L.) Choisy	V(3-8)		I(3)		II(3)								
Umde <i>Umbilicaria decussata</i> (Vill.) Zahlbr.	III(3-5)	II(3)											
Umpr <i>Umbilicaria propagulifera</i> (Vain.) Llano	V(1-8)	II(3)											
Uman <i>Umbilicaria antarctica</i> Frey et Lamb	II(3)	V(1-6)	V(1-8)	I(1)		II(3-5)							
Psmi <i>Pseudephebe minuscula</i> (Nyl. ex Arn.) Brodo & Hawksw.	IV(3-8)	IV(3-7)	II(1-3)										
Ande <i>Andreaea depressinervis</i> Card.		I(3)	V(2-8)	I(3)		I(3)							
characteristic species of the <i>Mastodia-Rinodina</i> complex													
Acma <i>Acarospora macrocyclos</i> Vain.	I(5)					IV(3-8)	I(3)	I(3-5)	I(3)		I(3)	I(3)	III(6)
Ripe <i>Rinodina petermannii</i> (Hue) Darb.	I(3)			III(3-5)		V(3-9)	III(3-9)	V(3-9)	V(3-8)		I(1-8)	III(1-6)	III(8)
Phca <i>Physcia caesia</i> (Hoffm.) Fuernr.	I(3)	I(3)			V(3)	II(5-7)	V(2-6)			I(3)	I(1)		III(3)
Mate <i>Mastodia tessellata</i> (Hook.f. et Harv.) Hook.f. et Harv.						II(3-6)	V(3-9)		V(3-8)	V(3-8)	V(3-9)	V(1-8)	III(5)
Calu <i>Caloplaca lucens</i> (Nyl.) Zahlbr.		I(3)				IV(2-8)	V(3-9)	V(3-8)	V(3-9)	I(3)	I(1-6)		
Veel <i>Verrucaria elaeoplaca</i> Vain.						I(3)					I(3)	V(3-9)	III(5)
Lebr <i>Lecania brialmontii</i> (Vain.) Zahlbr.						I(3)	I(3)	II(2-3)	I(5)	I(1-3)	III(1-3)	V(5-6)	
Xaca <i>Xanthoria candelaria</i> (L.) Th.Fr.		I(3)				I(3)	I(3-7)	II(3)	I(3)				
Camu <i>Candelaria murrayi</i> (Dodge) Poelt				I(2)		II(3-6)	II(3)		III(3)	I(2-3)	I(3)		
Casu <i>Caloplaca sublobulata</i> (Nyl.) Zahlbr.							I(3)		I(3)	I(3)			
Ca <i>Caloplaca</i> sp.							I(1-3)			I(5)	I(3)	I(3)	III(3)
companion species:													
Prer <i>Prasiola crispa</i> (Lightf.) Menegh.		I(3)	IV(1-3)			II(3-7)			I(3)		I(3)	I(3)	
Rhas <i>Rhizoplaca aspidophora</i> (Vain.) Redon	II(3)	IV(1-3)	II(2-3)	III(2-3)		IV(3)	I(3)	II(2-3)	I(3)	I(3)			
Rhme <i>Rhizoplaca melanophthalma</i> (Ram.) Leuck & Poelt	I(3)				V(3-5)	III(3-5)	I(3-6)	II(3)	I(3)	I(3)	I(5)	I(3)	
Drun <i>Drepanocladus uncinatus</i> (Hedw.) Warnst.	I(3)	II(1-3)		I(1)		I(3)			I(3)		I(1)		
crustose lichens	V(6-9)	V(3-9)	V(6-8)	V(7-9)	V(7-8)	IV(3-9)	III(3-8)	IV(3-7)	IV(3-5)	IV(3-6)	I(3-8)	II(3-4)	V(4-8)

Species rarely occurring:

Community 1.1: *Andreaea gainii* I (3), *Candelariella halletensis* I (3), *Cladonia pleurota* I (1), *Cornicularia aculeata* I (3), *Cornicularia epiphorella* I (3), *Rinodina turfacea* I (3), *Schistidium antarctici* I (3), *Stereocaulon glabrum* I (3), *Tortula princeps* I (3), *Usnea aurantiaco-atra* I (3); community 1.2.a: *Cetraria subscutata* I (3), *Ochrolechia tartarea* I (3), *Usnea aurantiaco-atra* I (4); community 1.2.b: *Bryum spec.* I (3), *Candelariella vitellina* I (3), *Cladonia pleurota* I (3), *Tortula princeps* I (3); community 2.1: *Candelariella halletensis* I (3); community 2.3.b: *Xanthoria elegans* I (8); community 2.3.c: *Caloplaca millegrana* I (3).

In a direct gradient analysis, using canonical correspondence analysis (CCA; ter Braak 1987), all 14 environmental variables represented in the data (Table III) added significantly to the explanation of the species variance. In the analysis of all sites six environmental variables were chosen by forward selection: chloride concentration, guano, exposure, moisture, gradient and northerly aspect. The first two axes of the ordination explained 7.4% of species variance, and 62.3% of variance of the species-environment relation. This compares with 10.3

and 48.8% respectively for an analysis comprising all 14 environmental variables. The *Usnea* complex is found on steeper slopes, with little or no guano and a low chloride concentration (Fig. 3). In contrast, the *Mastodia-Rinodina* complex is found on less steep slopes, with a more southerly aspect, influenced by guano, and with a relatively high chloride concentration.

Separate canonical correspondence analyses for the *Usnea* complex and the *Mastodia-Rinodina* complex showed

Fig. 2. Ordination diagram of a detrended correspondence analysis of the complete data set, showing the centroids of the lichen communities and the position of the species (see Table II for an explanation of the labels). Eigenvalues of axes 1 (horizontal) and 2 (vertical) are 0.86 and 0.50 respectively. Percentage variance of species data explained by axis 1 is 11.5% and by axes 1 + 2 is 18.2%.

differences in the environmental variables explaining species variation. Forward selection of the explanatory (environmental) variables showed gradient, northerly aspect, distance from sea and moisture to be the most important parameters explaining the variation in species composition within the *Usnea* complex. The first two axes of the CCA of the *Usnea* complex (Fig. 4), using the four most important environmental variables mentioned above, explained 13% of

Table III. Environmental variables used in the numerical analyses.

variable	range	data type
elevation	0-50	m above sea level
gradient	0-97	° from horizontal
northerly aspect	-1-1	from 1 = N to -1 = S
easterly aspect	-1-1	from 1 = E to -1 = W
distance from sea	0-200	m
sea towards north	-1-1	from 1 = N to -1 = S
sea towards east	-1-1	from 1 = E to -1 = W
guano	1-3	from 1 = none to 3 = much
exposure	1-5	from 1 = strongly sheltered to 5 = strongly exposed
moisture	1-3	from 1 = dry to 3 = wet
chloride	0-104	ppm in final solution; see text
nitrate	0-3.2	ppm in final solution; see text
phosphate	0-10	ppm in final solution; see text
ammonia	0-5.4	ppm in final solution; see text

Fig. 3. Results of canonical correspondence analysis of all sites, using six environmental variables (see text). Triplot showing the position of species, the centroids of the communities, and the environmental variables (arrows) on the first (horizontal) and second (vertical) ordination axis. Eigenvalues of the axes are respectively 0.41 and 0.15; percentage variance of species data accounted for in this ordination by axis 1 + 2 = 7.4%; percentage variance of species-environment relation accounted for by axes 1 + 2 = 62%. Labels for communities and species as in Table II. In this figure the scale for the environmental variables has been reduced by 50%.

the species variance and 68% of the species-environment relation. This compares with 16 and 36% respectively for an analysis comprising all 14 environmental variables observed. The ordination shows moisture to be the most important environmental variable. At the wet end of the moisture gradient are the *Andreaea depressinervis* variant of the community of *Usnea antarctica* and *Umbilicaria antarctica* (1.2.b in Table II), with the moss *Andreaea depressinervis* and the alga *Prasiola crispa*. All lichens have their optima in drier conditions. Within this group of lichens *Umbilicaria antarctica* shows a preference for damper sites. The community of *Usnea antarctica* and *Physcia caesia* (1.4) appears at the left hand side of the ordination diagram (Fig. 4), indicating its occurrence at dry sites, close to the sea. The diagram shows a positive correlation of the occurrence of the community of *Usnea antarctica*, *Umbilicaria propagulifera* and *Pseudophebe pubescens* (1.1) with steepness of the slope.

A canonical correspondence analysis of the *Mastodia-Rinodina* complex, using all 14 available environmental variables, explained 9.5% of the species variance by the first two ordination axes, and 43.3% of the species-environment relation. Using forward selection of the environmental variables a model comprising the six best explanatory variables (ammonia concentration, chloride concentration, elevation, exposure, northerly aspect and gradient; Fig. 5) was found to explain 7.5% of the species variance and 60.7% of the

Fig. 4. Results of canonical correspondence analysis of the *Usnea* complex. Triplot showing the position of species, centroids of the communities, and of environmental variables (arrows) on the first (horizontal) and second (vertical) ordination axis. Eigenvalues of the axes are respectively 0.29 and 0.23; percentage variance of species data accounted for by axis 1 = 7%, and by axes 1+2 = 13%; percentage variance of species-environment relation accounted for by axes 1 = 38%, and by axes 1 + 2 = 68%. See Table II for an explanation of the labels. In this figure the scale for the environmental variables has been reduced by 50%.

species-environment relation in the first two axes. The sites of the *Lecania brialmontii* community (2.6 in Table II) proved to be outliers, and were made passive in these analyses. This community typically occurs in sheltered, damp crevices in rocks close to the shore. The ordination diagram shows a positive correlation between the occurrence of the *Mastodia tessellata* community (2.4) and high chloride and ammonia concentrations. The *Verrucaria elaeoplaca* community (2.5) occurs at high ammonia concentrations, but does not appear to be dependent on high chloride concentrations. Within the *Mastodia-Rinodina* complex the occurrence of the community of *Mastodia tessellata* and *Physcia caesia* (2.2) is related to the steepness of the slope and the northerly aspect (Fig. 5), while the *Caloplaca lucens* community with *Rinodina petermannii* (2.3.a), as well as the variant with *R. petermannii* and *Mastodia tessellata* (2.3.b) occur in relatively exposed habitats.

Discussion

The main habitat difference between the *Usnea* complex and the *Mastodia-Rinodina* complex appears to be the nutrient status. This is in agreement with observations from many parts of the Antarctic (e.g. Allison & Smith 1973, Lindsay 1971, Smith 1972). Higher concentrations of ammonia and phosphate in the *Mastodia-Rinodina* complex can be explained

Fig. 5. Results of canonical correspondence analysis of the *Mastodia-Rinodina* complex. Triplot showing the position of the species, the centroids of the communities, and of the environmental variables (arrows) on the first (horizontal) and second (vertical) ordination axis. Eigenvalues of the axes are respectively 0.20 and 0.15; percentage variance of species data accounted for in this ordination by axes 1+2 = 7.5%; percentage variance of species-environment relation accounted for by axes 1 = 35%, and by axes 1 + 2 = 61%. See Table II for an explanation of the labels. In this figure the scale has been reduced by 50% for the environmental variables.

by the addition of these compounds to the environment via bird excreta (cf Lindeboom 1979, Ryan & Watkins 1989). Concentration of nitrate was significantly higher in the *Usnea* complex. This is contrary to our expectations, as animals seem to be the most important source of nitrogen in our study area. The phenomenon of the appearance of coastal communities inland at sites influenced by birds, as seen in our *Caloplaca lucens* community, has been noted elsewhere in the Antarctic as well as in the Arctic (Fletcher 1976).

Within both complexes species composition is influenced by mineral concentrations, as is shown by the importance of distance from the sea in the ordination of the *Usnea* complex and of chloride and ammonia concentrations in the CCA of the *Mastodia-Rinodina* complex. The contribution of elevation, gradient, aspect and exposure towards explaining species variation within the complexes indicates the importance of microclimatic conditions.

Vegetation similar to both complexes exists in various parts of the maritime Antarctic (e.g. Allison & Smith 1973, Smith 1972, Smith & Corner 1973, Engelskjøn 1987, Follmann 1965, Lindsay 1971, Longton 1979, Olech 1990) and the subantarctic (Lindsay 1974), but differences in methods used or incompleteness of published species data make a quantitative comparison of species composition in the different areas problematical. In the *Rinodina-Mastodia* complex the lichen which we identified in the field as

Xanthoria elegans turned out to be mostly *Caloplaca lucens*. As these species have often been confused (Søchting & Øvstedal 1992, D.O. Øvstedal, personal communication), we assume that our records of *Caloplaca lucens* and references to *Xanthoria elegans* in the literature generally represent the same lichen.

In the direct gradient analyses a significant relation between species composition and environmental variables was established, but this relation explained only a small part of the total species variation. Unfortunately little information is available on the percentage of explained variance by direct gradient analyses in other studies. It is therefore not possible to judge if the values presented here are exceptional. In species lists of temperate grasslands and subantarctic bryophyte communities some 10% of the species were erroneously listed or had gone unobserved, even by experienced observers (Gremmen, unpublished data). In our species lists, in which we listed only those species which we could identify in the field, a similar error percentage may be expected. Another source of inaccuracy is the fact that data on mineral concentrations were the result of incidental measurements. Mineral concentrations, especially in the coastal environment, probably fluctuate strongly in time, due to fluctuations in sea spray because of variation in windspeed and ice cover of the sea, seasonality in the presence of birds, variation in snow melting, etc. Without more knowledge about these fluctuations, and their dependence on local conditions, it is difficult to assess the value of a single measurement as indication of the mineral status of a site.

We feel that inaccuracy in quantifying the environmental variables and errors in the species data alone are insufficient to explain the large amount of residual species variation. We suggest that not all relevant environmental factors have been included in our study. Most important of these is possibly the length of the growing season as determined by the local duration of snow cover. This is known to have a profound influence on species composition of the vegetation in maritime Antarctic regions (Smith 1972). Also the contribution of minerals released from melting snow may play a role. This may be the case in the community with *Umbilicaria antarctica* and *Andreaea depressinervis*, occurring in seepage lines on rock faces. Lindsay (1971) stated that, in the South Shetland Islands, *Umbilicaria antarctica* was restricted to sites irrigated by slightly nitrophilous water. Although in the Argentine Islands nutrient concentrations in the habitat of the *Umbilicaria antarctica* - *Andreaea depressinervis* community appear to be low (Table II), the frequent supply of minerals in the meltwater may result in a comparatively high nutrient availability in these seepage lines (cf. Sparling 1966).

Acknowledgements

This work was funded by the Netherlands Antarctic Research Programme 1989/1993, administered by the Foundation for Marine Research. We wish to express our thanks to all

members of the British Antarctic Survey, in Cambridge as well as in the Antarctic, who helped us in the planning and execution of this study. Specifically we thank Dr. D.W.H. Walton and Dr. R.I.L. Smith. This paper has benefitted considerably from constructive review of an earlier version of the manuscript by Dr. R.I.L. Smith, and from the comments of Prof. L. Kappen, Dr. P. Marino and Dr. P.L. Nimis. The help of Dr. D.O. Øvstedal, University of Bergen, Norway, in the identification of the lichens is gratefully acknowledged. This is publication number 750 of the Netherlands Institute of Ecology, Centre for Estuarine and Coastal Ecology.

References

- ALLISON, J.S. & SMITH, R.I.L. 1973. The vegetation of Elephant Island, South Shetland Islands. *British Antarctic Survey Bulletin*, No. 33-34, 185-212.
- BRAUN-BLANQUET, J. 1964. *Pflanzensoziologie*. 3. Aufl. Wien: Springer, 865 pp.
- CORNER, R.W.M. 1971. Studies in *Colobanthus quitensis* (Kunth) Bartl. and *Deschampsia antarctica* Desv.: VI. Distribution and reproductive performance in the Argentine Islands. *British Antarctic Survey Bulletin*, No. 26, 41-50.
- CORNER, R.W.M. & SMITH, R.I.L. 1973. Botanical evidence of ice recession in the Argentine Islands. *British Antarctic Survey Bulletin*, No. 35, 83-86.
- ELLIOT, D.H. 1964. The petrology of the Argentine Islands. *British Antarctic Survey Scientific Reports*, No. 41, 31 pp.
- ENGELSKJØN, T. 1987. Botany of Bouvetøya, South Atlantic Ocean. II. The terrestrial vegetation of Bouvetøya. *Polar Research*, 5, 129-163.
- FLETCHER, A. 1976. Nutritional aspects of marine and maritime lichen ecology. In BROWN, D.H., HAWKSWORTH, D.L. & BAILEY, R.H. eds. *Lichenology: progress and problems*. London: Academic Press, 359-384.
- FOLLMANN, G. 1965. Una asociación nitrófila de líquenes epitéricos de la Antártica Occidental con *Ramalina terebrata* Hook. f. & Tayl como especie caracterizante. *Instituto Antártico Chileno Publicacion*, 4, 1-18.
- FOWBERT, J. & SMITH, R.I.L. 1994. Rapid population increases in native vascular plants in the Argentinian Islands, Antarctic Peninsula. *Arctic and Alpine Research*, 26, 290-296.
- GREMMEN, N.J.M. 1981. *The vegetation of the subantarctic islands Marion and Prince Edward*. The Hague: Junk, 145 pp.
- GREMMEN, N.J.M., HUISKES, A.H.J. & FRANCKE, J.W. 1991. Ecology of lichens in the coastal regions of the Argentine Islands, Antarctic Peninsula - a preliminary report. *Circumpolar Journal*, 6(1-2), 3-10.
- HILL, M.O. & GAUCH, H.G. 1980. Detrended correspondence analysis, an improved ordination technique. *Vegetatio*, 42, 47-58.
- HUISKES, A.H.J. & KROMKAMP, J.C. 1990. The role of the Delta Institute for Hydrobiological Research in the Netherlands Antarctic Research Programme. *Circumpolar Journal*, 5(2), 22-26.
- KAPPEN, L. 1985. Vegetation and ecology of ice-free areas of northern Victoria Land, Antarctica. 1. The lichen vegetation of Birthday Ridge and an inland mountain. *Polar Biology* 4, 213-225.
- LINDEBOOM, H.J. 1979. *Chemical and microbiological aspects of the nitrogen cycle on Marion Island (sub-Antarctic)*. PhD thesis, University of Groningen, 138 pp. [unpublished].
- LINDSAY, D.C. 1971. Vegetation of the South Shetland Islands. *British Antarctic Survey Bulletin*, No. 25, 59-83.
- LINDSAY, D.C. 1974. The macrolichens of South Georgia. *British Antarctic Scientific Reports*, No. 89, 91 pp.
- LONGTON, R. 1979. Vegetation ecology and classification in the maritime Antarctic zone. *Canadian Journal of Botany*, 57, 2264-2278.
- LONGTON, R. 1988. *The biology of polar bryophytes and lichens*. Cambridge: Cambridge University Press, 391 pp.
- MANLY, B.F.J. 1990. *Randomization and Monte Carlo methods in biology*. London: Chapman and Hall, 256 pp.

- MONTGOMERY, D.C. & PECK, E.A. 1982. *Introduction to linear regression analysis*. New York: Wiley.
- MUELLER-DOMBOIS, D. & ELLENBERG, H. 1974. *Aims and methods of vegetation ecology*. New York: Wiley, 547 pp.
- OLECH, M. 1990. Preliminary studies on ornithocoprophilous lichens of the Arctic and Antarctic regions. *Proceedings of the NIPR Symposium on Polar Biology*, 3, 218-223.
- RYAN, P.G. & WATKINS, B.P. 1989. The influence of physical factors and ornithogenic products on plant and arthropod abundance at an inland nunatak group in Antarctica. *Polar Biology*, 10, 151-160.
- SMILAUER, P. 1992. *CanoDraw 3.0 guide*. [Unpublished.]
- SMITH, R.I.L. 1972. Vegetation of the South Orkney Islands with particular reference to Signy Island. *British Antarctic Survey Scientific Reports*, No.68, 1-124.
- SMITH, R.I.L. 1984. Terrestrial plant biology of the sub-Antarctic and Antarctic. In LAWS, R.M. ed. *Antarctic Ecology*, Vol.1. London: Academic Press, 61-162.
- SMITH, R.I.L. & CORNER, R.W.M. 1973. Vegetation of the Arthur Harbour - Argentine Islands region of the Antarctic Peninsula. *British Antarctic Survey Bulletin*, Nos 33-34, 89-122.
- SØCHTING, U., ØVSTEDAL, D.O. 1992. Contributions to the Caloplaca flora of the eastern Antarctic region. *Nordic Journal of Botany*, 12, 121-134.
- SPARLING, J.H. 1966. Studies on the relationship between water movement and water chemistry in mires. *Canadian Journal of Botany*, 44, 747-748.
- STARK, P. 1990. *Wildlife Report. April '89 to February '90*. Unpublished report. British Antarctic Survey Archives, No. F/1989/NG1.
- TER BRAAK, C.J.F. 1985. Correspondence analysis of incidence and abundance data: properties in terms of a unimodal response model. *Biometrics*, 41, 859-873.
- TER BRAAK, C.J.F. 1987. ORDINATION. In JONGMAN R.H.G., TER BRAAK, C.J.F. & VAN TONGEREN, O.F.R. eds. *Data analysis in community and landscape ecology*. Wageningen: Pudoc, 91-173.
- TER BRAAK, C.J.F. 1988. *CANOCO - a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis (version 2.1)* Wageningen: GLW-DLO.
- TER BRAAK, C.J.F. 1990. *Update notes: CANOCO version 3.10*. Wageningen: Agricultural Mathematics Group.
- THOMAS, R.H. 1963. Studies on the ice cap of Galindez Island, Argentine Islands. *British Antarctic Survey Bulletin*, No. 2, 27-43.
- VAN DER MAAREL, E. 1979. Transformation of cover-abundance values in phytosociology and its effects on community similarity. *Vegetatio*, 39, 97-114.
- VAN TONGEREN, O.F.R. 1986. FLEXCLUS, an interactive program for classification and tabulation of ecological data. *Acta Botanica Neerlandica*, 35, 137-142.
- WESTHOFF, V. & VAN DER MAAREL, E. 1973. The Braun-Blanquet approach. In WHITTAKER, R.H. ed. *Ordination and classification of communities. Handbook of vegetation science 5*. The Hague: Junk, 617-726.

Appendix I. Species identified in collections from the sample plots, but not used in the data analysis. A number of specimens, belonging to the genera *Buellia*, *Lecanora*, *Lecidea*, *Phaeophyscia*, *Rhizocarpon* and *Thamnolecania*, could not be identified to species level. Figures indicate the frequency of each species in the communities described in Table II.

	c1.1	c1.2a	c1.2b	c1.3	c1.4	c2.1	c2.2	c2.3a	c2.3b	c2.3c	c2.4	c2.5	c2.6
<i>Buellia anisomera</i> Vain.				17		17		23					
<i>Buellia augusta</i> Vain.				33	67		40	8		14	4	7	50
<i>Buellia babingtonii</i> (Hook.f. & Tayl.) Lamb ex Dodge												7	
<i>Buellia cladocarpiza</i> Lamb	13					8	13	15					
<i>Buellia coniops</i> (Wahlenb. ex Ach.) Th.Fries				17								7	
<i>Buellia falklandica</i> Darb.							7						
<i>Buellia granulosa</i> (Darb.) Dodge							13						
<i>Buellia illaetabilis</i> Lamb		11	17										
<i>Buellia inordinata</i> (Hue) Darb.				17									
<i>Buellia latemarginata</i> Darb.				33		8							
<i>Buellia melanostola</i> (Hue) Darb.				17									
<i>Buellia russa</i> (Hue) Darb.				33		25		23					
<i>Carbonea assentiens</i> (Nyl.) Hertel											2		
<i>Cladonia cf. gracilis</i> (L.) Willd.	6												
<i>Haematomma erythromma</i> (Nyl.) Zahlbr.													10
<i>Huea grisea</i> (Vain.) Darb.				33		8	7						10
<i>Lecanora polytropa</i> (Hoffm.) Rabenh.	6												
<i>Lecania racovitzae</i> Vain.													10
<i>Physcia dubia</i> (Hoffm.) Lettau							7						
<i>Rhizocarpon grande</i> (Floerke ex Flotow) Arnold	13		33										
<i>Rinodina cf. olivaceobrunnea</i> Dodge et Baker	6												
<i>Tephromela atra</i> (Huds.) Hafellner		11		17			7	15	10				
<i>Umbilicaria nylanderiana</i> (Zahlbr.) Magnusson	13						8						