

The Influence of Microclimate on the Composition of Lichen Communities along an Altitudinal Gradient in the Maritime Antarctic

ANA PINTADO^{1*}, LEOPOLDO G. SANCHO¹, and
FERNANDO VALLADARES²

¹*Departamento de Biología Vegetal II, Facultad de Farmacia, Universidad Complutense, 28040 Madrid, Spain, Tel. +34-91-3941771, Fax. +34-91-3941774, E-mails. apintado@eucmos.sim.ucm.es and sancholg@eucmax.sim.ucm.es*

²*Centro de Ciencias Medioambientales, CSIC, Serrano 115 dpdo. 28006 Madrid, Spain, Tel. +34-91-7452500 (ext. 1287), Fax. +34-91-5640800, E-mail. valladares@ccma.csic.es*

Received November 1, 2000; Accepted February 6, 2001

Abstract

The influence of microclimate on diversity and abundance of lichen communities was studied along an altitudinal gradient on Livingston Island, South Shetland Islands, maritime Antarctic. Whilst biodiversity overall is high, it appears to decrease drastically within a few hundred meters from the coast towards higher altitudes. Microclimatic data and community composition were investigated at different sites and slope exposures from near sea level to the summit of Mount Reina Sofia (274 m a.s.l.) near the Spanish Antarctic research station Juan Carlos I. Microclimatic measurements were made over a period of 43 days during a summer. A remarkable decrease in lichen diversity and biomass was found with increasing altitude which correlated with a decrease in 2.37°C mean thallus temperature over

Presented at the Fourth International Association of Lichenology Symposium, September 3–8, 2000, Barcelona, Spain

*The author to whom correspondence should be sent.

0334-5114/2001/\$05.50 ©2001 Balaban

an altitudinal range of 266 m. Neither air humidity nor irradiance seems to influence lichen biodiversity over this altitudinal range. The results indicated slight changes in air temperature as limiting the distribution of lichens, the major photosynthetic organism in this area.

Keywords: Biodiversity, altitudinal range, lichen ecology, Antarctica, distribution limit

1. Introduction

The biodiversity and the distribution of vegetation in Antarctica are determined by isolation and biotic, edaphic and, most importantly, climatic factors (Seppelt, 1995; Green et al., 1999). Holdgate (1964), Longton (1979) and Smith (1984) distinguished between maritime and continental regions, the former comprising the northern Antarctic Peninsula and adjacent Antarctic islands. In the maritime Antarctic summer temperatures are generally milder and light rainfall may occur. Compared with continental Antarctic, maritime Antarctic tundra has a higher diversity and a larger biomass, with lichens as the dominant elements of vegetation but also with the presence of the two only phanerogams growing in Antarctica (Smith, 1984; Kappen, 1988; Seppelt, 1995; Green et al., 1999). For some authors this fact is related to the lesser water availability in continental Antarctic (Kennedy, 1993) rather than to decreasing temperature (Green et al., 1999), although both factors are interrelated (Hovenden and Seppelt, 1995). However, in an area of relatively abundant precipitation as the maritime Antarctic – between 250–500 mm per annum (Schwerdtfeger, 1970; Green et al., 1999) – few investigations of the vegetation associated to natural thermal altitudinal gradients have been carried out that would clarify controls on the distribution of species. The distribution of individual species and communities in relation to environmental gradients is a very prominent feature of the vegetation of some maritime Antarctic islands (Lindsay, 1971; Smith, 1972). Taking a small area with remarkably large biodiversity, like the one investigated in the present work on Livingston Island, 161 plant species including 110 lichen species (Olech, M. 1989; Sancho et al., 1999), it is remarkable how diversity and biomass decrease within a few hundred meters from coastal areas towards higher altitudes when compared to temperate regions. This suggests that contrasting microclimatic conditions should occur within a small altitudinal range in the maritime Antarctic. A number of authors have pointed out that nutrient availability in coastal areas or bird-enriched localities of the maritime Antarctic drastically affect the distribution pattern of vegetation from coastal to inland sites. However, other environmental factors must also be taken into account. In recent work on

Livingston Island, Valladares and Sancho (2000) demonstrated that altitude caused a decrease of maximal net photosynthetic rates in *Usnea aurantiaco-atra*. They suggested that temperature could influence lichen distribution in the maritime Antarctic through its effect on both nutrient availability and photosynthetic capacity, but microclimatic data were not available to them.

Our objective here has been to explore the influence of altitude and the associated temperature decrease in the distribution of lichens in the maritime Antarctic, interpreting the results from an ecophysiological point of view. To achieve this, microclimate and vegetation abundance and diversity were measured along an altitudinal gradient in a species-rich site in South Bay, Livingston Island. Different slope exposures were studied because microrelief also changes significantly the influence of environmental factors such as wind, water availability, evaporation and temperature in the maritime Antarctic (Kappen and Redon, 1987).

2. Material and Methods

Study area

The investigation has been undertaken at the southern coast of South Bay, near the Spanish Antarctic Base Juan Carlos I, Livingston Island, South Shetland Islands (62°40' S, 60°23' W). This area is well described in Sancho et al. (1999). It consists of an ice-free area of about 3 km² from the coast to the summit of Mount Reina Sofía (274 m a.s.l.), exposed to the mild and humid north and north-west winds but protected against the cold and strong south winds. The mean summer (December–February) 1988–1993 air temperature is ca. 3°C, showing very little day/night oscillation, the average precipitation in summer is around 200 mm and the relative air humidity is frequently above 90% (Sancho et al., 1999). The relatively mild and humid summers contribute to the development of a rich and abundant cryptogamic flora with 110 species of lichens, 50 species of mosses and two flowering plants, forming different plant communities. Microclimatic data and community composition were investigated at eight different sites located at 8, 45, 180 and 274 m a.s.l. and at two different slopes: horizontal and vertical northern exposure.

Vegetation data

Vegetation pattern (diversity and cover of species) was determined by collection and analysis according to the Braun-Blanquet method (Braun-Blanquet, 1964). At each site, total vegetation cover was estimated, and species recorded together with an index of their relative abundance (+ = rare; 1 = 1–5%;

2 = 5–15%; 3 = 15–25%; 4 = 25–50%; 5 = >50%), in an area of ca. 0.3 m². Specimens whose identity was difficult to ascertain in the field were collected and brought to the laboratory at the Spanish Research Station for identification.

Microclimatic measurements

Microclimatic data of the different sites were recorded at five minute intervals during 43 days from mid January to the beginning of March 1991 using four data loggers (Squirrel, Grant Instruments, UK) at each of the investigated altitudes. Six species, representative of the different communities, were selected at the different sites in order to compare the effect on thallus temperature of different altitudes and exposures and to represent different exposure, altitudinal range distribution, and growth form: *Himantormia lugubris* (Hue) Lamb growing on vertical and horizontal slopes at 274 m, *Pseudephebe pubescens* (L.) Choisy growing on a vertical slope at 180 m, *Umbilicaria antarctica* Frey & Lamb growing on a vertical slope at 8 m, *U. nylanderiana* (Zahlbr.) H. Magn. growing on a vertical slope at 45 m, *Usnea antarctica* Du Rietz growing on a horizontal slope at 8 m and *U. aurantiaco-atra* (Jacq.) Bory from horizontal slopes at 45, 180 and 274 m and from a vertical slope at 274 m. At each site, 1–2 temperature sensors were inserted into the lichen cover (fruticose thalli) or beneath the lower surface (foliose thalli) of the selected thalli, and one humidity probe (Vaisala, Finland) and one photosynthetic photon flux density (PPFD) sensor (Li-Cor, USA) were placed in the vicinity of the lichen thalli studied. At horizontal sites PPFD sensors were placed horizontally while at vertical sites they were placed at ca. 90° of inclination and with a northerly exposure.

3. Results

Vegetation patterns following an altitudinal range

A list of species growing at the different sites and an index of their relative abundance as well as total percentage cover is given in Table 1. In total, 46 species of lichens, 5 species of mosses and 2 species of flowering plants occurred at the study localities. The most ubiquitous species were *Ochrolechia frigida* (Sw.) Lynge, *Rhizocarpon geographicum* (L.) DC, *Usnea antarctica* Du Rietz and *U. aurantiaco-atra* (Jacq.) Bory. The less common species were restricted to the lower sites with exception of *Rhizocarpon polycarpon* (Hepp) Th. Fr. which only appeared at 274 m a.s.l. Estimated total vegetation cover ranged from 115% at the lower horizontal site, where epiphytic growth occurred, to 74% at the vertical site at 45 m a.s.l. Lichens were dominant at all investigated

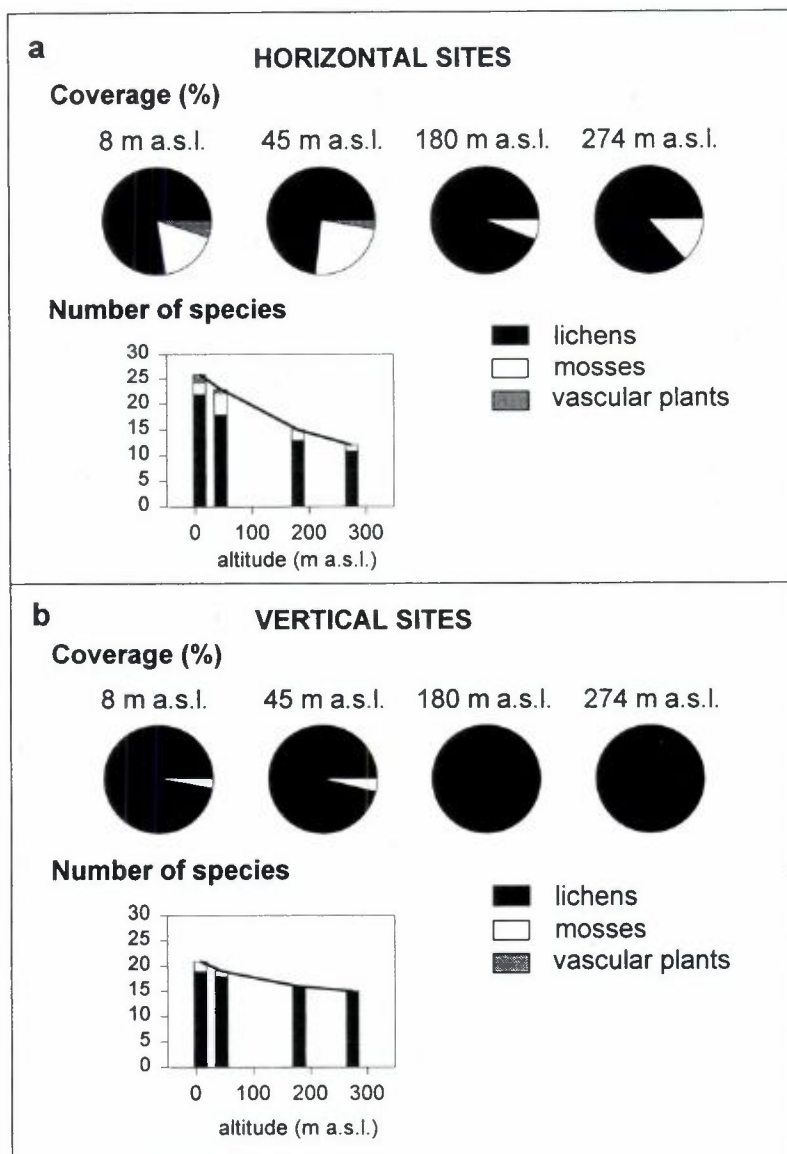


Figure 1. Elevational trends in relative coverage (as percentage of the total), and distribution of the number of species along a transect from 8 m (BAE) to 274 m a.s.l. (summit of Mount Reina Sofía) in Livingston Island. Different colours refer to lichens, mosses and vascular plants. a: horizontal slope, b: vertical slope.

sites, regardless of altitude or exposure, but species richness (including vascular plants and mosses) decreased with altitude for a given exposure (Table 1,

Fig. 1). At horizontal sites total coverage decreased with increasing altitude but this trend was not obvious for vertical sites. Remarkable differences were found between the horizontal and the vertical sites at the same altitude: percentage of cover was always higher in the horizontal sites except for the highest locations where coverage in both aspects was similar (around 75%, Table 1). On horizontal surfaces, the number of species declined with altitude (from 26 to 12) while, at the vertical sites, the reduction was less pronounced (Fig. 1). The presence of vascular plants was restricted to horizontal surfaces and only two mosses were found in vertical walls at low altitudes and always with little coverage (*Andreaea gainii* Card. and *Bartramia patens* Brid.).

Although the number of lichen species decreased with altitude for both exposures, lichen coverage did not follow this tendency and reached higher values at 180 m than at lower altitudes at horizontal exposures (92% at 180 m in contrast to 79% at 45 m). The latter was inversely related to vascular plant and moss competition.

Microclimatic results

The lichen species selected for microclimatic investigation showed different distribution patterns. *H. lugubris* and *P. pubescens* were more abundant in higher altitudes. *Umbilicaria antarctica* and *U. decussata* were restricted to the lower sites, while *Usnea antarctica* and *U. aurantiaco-atra* had broader altitudinal ranges.

Microclimatic parameters measured at the different sites during the investigated period showed that, in general, the mean thallus temperature for all species decreased with altitude (Table 2) ($P < 0.05$ except for the lower altitudes, between 8 and 45 m). Maximal thallus temperatures (T_{max}) were not significantly different, and minimal thallus temperatures (T_{min}) were only significantly different between the lowest and the highest sites. No significant differences were found between mean thallus temperatures at vertical and horizontal sites for any of the different species. Mean temperatures of lichen thalli during this summer season approximated to 0°C at the highest altitude (Table 2). The most common thallus temperatures during the investigated period were between $2\text{--}4^{\circ}\text{C}$ for the lowest localities and $0\text{--}2^{\circ}\text{C}$ for the highest localities for both slopes and all species (Fig. 2). The difference between mean thallus temperature of *Usnea* species from horizontal surfaces (highlighted in Table 2), was 2.37 K over 266 m. This gradient was evident both in cloudy and clear days. For example, during an overcast day with precipitation (Fig. 3) a maximal difference of 4.9 K was reached between thalli from the highest and the lowest altitudes. On the next day when the sun appeared the maximal differences reached more than 15 K.

Table 1. List of lichens, mosses and vascular plants recorded from vertical and horizontal slopes at 8, 45, 180 and 274 m a.s.l. in South Bay, Livingston Island. Indices express the relative abundance of each species in the study area (+ = rare; 1 = 1-5%; 2 = 5-15%; 3 = 15-25%; 4 = 25-50%; 5 = >50%).

Altitude	8 m a.s.l.		45 m a.s.l.		180 m a.s.l.		274 m a.s.l.	
	H	V	H	V	H	V	H	V
Exposure (H=horizontal; V=vertical)								
Number of species	26	21	23	19	15	16	12	15
Estimation of percentage cover (%)	115	106	108	74	98	82	75	77
Lichens								
<i>Amandinea coniops</i> (Walhlenb. in Ach.) Scheid.	1			+	+		1	1
<i>Austrolecia antarctica</i> Hertel								
<i>Buellia anisomera</i> Vainio	+		1					
<i>Buellia cladocarpiza</i> Lamb	+		+					
<i>Buellia granulosa</i> (Darb.) Dodge	1		+			+	1	
<i>Buellia latemarginata</i> Darb.								
<i>Buellia russa</i> (Hue) Darb.		1		1				
<i>Caloplaca athallina</i> Darb.			+		+			
<i>Caloplaca citrina</i> (Hoffm.) Th. Fr.	+							
<i>Caloplaca coralligera</i> (Hue) Zahlbr.	1	+						
<i>Caloplaca sublobulata</i> (Nyl.) Zahlbr.				1				
<i>Carbonea assentiensis</i> (Nyl.) Hertel	1	2				1		1
<i>Carbonea vorticosa</i> (Flörke) Hertel								
<i>Cladonia chlorophaea</i> (Flörke ex Sommerf.) Sprengel	+	+	+					
<i>Haematomma erythromma</i> (Nyl.) Zahlbr.	2	+					3	1
<i>Himantormia lugubris</i> (Hue) Lamb			1				1	1
<i>Lecanora intricata</i> (Ach.) Ach.			+				1	
<i>Lecanora margaritae</i> Hue								
<i>Lecanora polytropa</i> (Hoffm.) Rabh.	+	1		1		+	+	+
<i>Lecidea atrobrunnea</i> (Ram.) Schaerer				1		1	1	2

Table 1. Continued.

Altitude	8 m a.s.l.		45 m a.s.l.		180 m a.s.l.		274 m a.s.l.	
	H	V	H	V	H	V	H	V
Exposure (H=horizontal; V=vertical)								
Number of species	26	21	23	19	15	16	12	15
Estimation of percentage cover (%)	115	106	108	74	98	82	75	77
<i>Megaspora verrucosa</i> (Ach.) Haf. & V. Wirth			+					
<i>Ochrolechia antarctica</i> (M.Jl. Arg.) Darb.		+		+				
<i>Ochrolechia frigida</i> (Sw.) Lyngé	1		2		2	1	1	1
<i>Parmelia saxatilis</i> (L.) Ach.		1	+					
<i>Physcia caesia</i> (Hoffm.) Füllrohr	1	2	1		1			
<i>Physcia dubia</i> (Hoffm.) Lettau			1	+				
<i>Physconia muscigena</i> (Ach.) Poelt	2		+					
<i>Placopsis contortuplicata</i> Lamb					1		1	
<i>Pseudephebe minuscula</i> (Nyl. ex Arnold) Brodo & D. Hawksw.						1		2
<i>Pseudephebe pubescens</i> (L.) Choisy			1		1	+	2	1
<i>Psoroma hypnorum</i> (Vahl) Cray	1							
<i>Rhizocarpon geographicum</i> (L.) DC	1	2	1	2	1	3	2	2
<i>Rhizocarpon polycarpon</i> (Hepp) Th. Fr.								1
<i>Rinodina olivaceobrunnea</i> Dodge & Baker	1		1					
<i>Rinodina petermannii</i> (Hue) Darb.	1	1						
<i>Sporastatia testudinea</i> (Ach.) Massal.				1		1		1
<i>Stereocaulon alpinum</i> Laur.					1		2	
<i>Tephromela atra</i> (Huds.) Hafellner	1	1		+	1	+	+	+
<i>Tremolecia atrata</i> (Ach.) Hertel						1		1
<i>Umbilicaria africana</i> (Jatta) Krog & Swinscow				1		+		
<i>Umbilicaria antarctica</i> Frey & Lamb	1	1		+				
<i>Umbilicaria decussata</i> (Vill.) Zahlbr.				3				1
<i>Umbilicaria nylanderiana</i> (Zahlbr.) H. Magn.				2				

Table 1. Continued.

Altitude	8 m a.s.l.		45 m a.s.l.		180 m a.s.l.		274 m a.s.l.	
	H	V	H	V	H	V	H	V
Exposure (H=horizontal; V=vertical)	26	21	23	19	15	16	12	15
Number of species	115	106	108	74	98	82	75	77
Estimation of percentage cover (%)								
<i>Usnea antarctica</i> Du Rietz	3	4	2	1	1	1		1
<i>Usnea aurantiaco-atra</i> (Jacq.) Bory	2	2	4	2	4	4	3	3
<i>Xanthoria candelaria</i> (L.) Th. Fr.	1	+						
Mosses								
<i>Adreaea gainii</i> Card.	2	+	1		1		2	
<i>Bartramia patens</i> Brid.		1	2	1	1			
<i>Ceratodon purpureus</i> (Hedw.) Brid.			2					
<i>Dicranoweisia grimmii</i> (C. Müll) Broth.	2							
<i>Sanionia uncinata</i> (Hedw.) Loeske					1			
Vascular plants								
<i>Colobanthus quitensis</i> (Kunth) Bartl.	1							
<i>Deschampsia antarctica</i> Desv.	1		1					

Table 2. Microclimatic parameters at the different sites registered from January 19, 1991 up to March 3, 1992.

Altitude (m a.s.l.)	Exposure	Species	Mean Thallus T (°C)	T max (°C)	T min (°C)	SE1	n1	n2
8	Vertical	<i>Umbilicaria antarctica</i>	3.66	24.45	-2.40	0.03	12089	42
8	Horizontal	<i>Usnea antarctica</i>	3.71	24.63	-3.83	0.03	12089	42
44	Vertical	<i>Umbilicaria nylanderiana</i>	3.83	21.45	-1.70	0.03	12081	42
44	Horizontal	<i>Usnea aurantiaco-atra</i>	3.60	29.30	-4.75	0.04	9246	32
180	Vertical	<i>Pseudephebe pubescens</i>	3.38	35.7	-4.50	0.06	7450	26
180	Vertical	<i>Usnea aurantiaco-atra</i>	2.19	22.25	-5.15	0.03	12090	42
180	Horizontal	<i>Usnea aurantiaco-atra</i>	2.45	25.45	-4.15	0.03	12090	42
274	Vertical	<i>Himantormia lugubris</i>	1.26	15.45	-4.15	0.02	12086	42
274	Vertical	<i>Usnea aurantiaco-atra</i>	0.88	29.80	-5.45	0.03	12086	42
274	Horizontal	<i>Himantormia lugubris</i>	0.68	34.25	-7.80	0.06	12086	42
274	Horizontal	<i>Usnea aurantiaco-atra</i>	1.34	31.30	-6.35	0.06	12086	42

Altitude (m a.s.l.)	Exposure	Mean relative humidity (%)	SE	n	Mean PPFD	SE	n
8	Vertical	83.50	0.16	12089	164.54	2.68	12089
8	Horizontal	82.19	0.18	12089	202.82	2.78	12089
43	Vertical	86.13	0.15	12081	171.35	2.79	12081
43	Horizontal	81.14	0.17	12081	194.63	3.16	9246
180	Vertical				175.98	2.77	12090
180	Horizontal	87.57	0.16	12090	126.54	2.15	10650
274	Vertical				165.46	2.73	12086
274	Horizontal	93.34	0.20	4174	132.90	2.11	12086

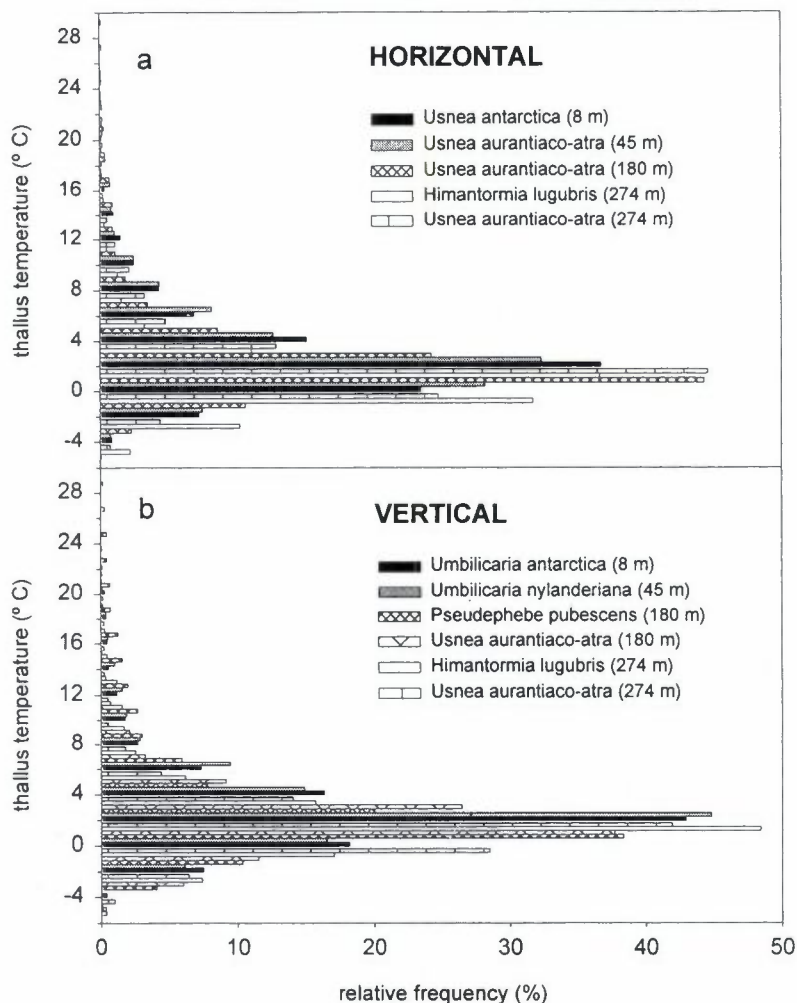


Figure 2. Frequency distributions of thallus temperature measured amongst selected lichen species along an altitudinal transect in South Bay, Livingston Island, maritime Antarctic, during a summer period. Each bar corresponds with a class of 2°C. a: horizontal slope, b: vertical slope.

The data did not show a significant altitudinal or exposure pattern for humidity or radiation although a trend towards a decrease in irradiance and an increase in relative humidity with increasing altitude was suggested for horizontal exposures (Table 2). Moreover, no differences were observed in the frequency distributions of radiation and relative humidity at the different sites (data not shown).

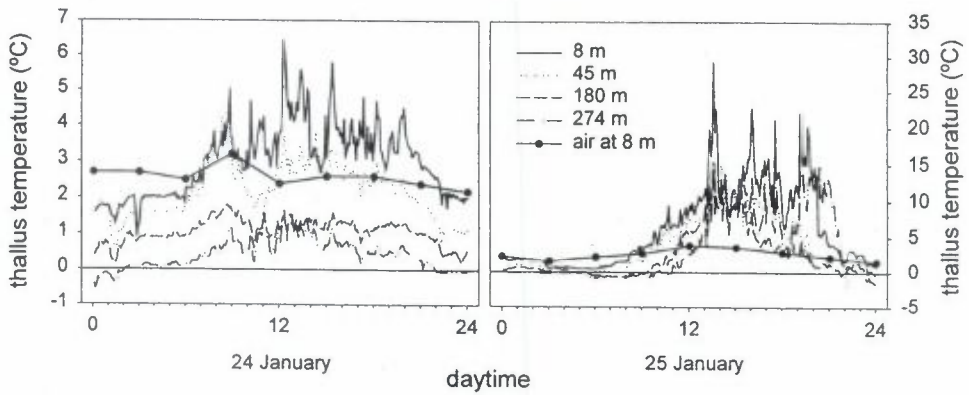


Figure 3. Daily course of temperatures experienced by *Usnea* spp. from horizontal surfaces at different altitudes in South Bay, Livingston Island, during a cloudy day with precipitation (January 24) followed by a clear day (January 25).

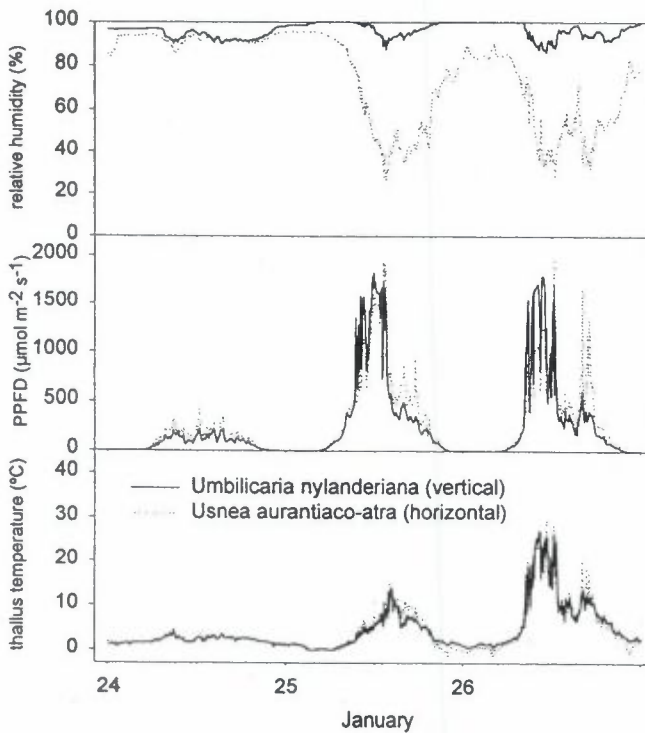


Figure 4. Daily courses of microclimatic parameters following a precipitation event in different slope exposures (..... vertical and (— horizontal) at 45 m a.s.l. in South Bay, Livingston Island, maritime Antarctic. PPF = Photosynthetic Photon Flux Density.

Although microclimatic parameters recorded during the investigated period did not show significant differences between vertical and horizontal sites, it is evident from daily courses that microhabitat influenced the observed differences in the vegetation pattern. As an example, Fig. 4 shows how, after a precipitation event, humidity is maintained at the vertical site where *Umbilicaria nylanderiana* grows, while at the more exposed horizontal site *Usnea aurantiaco-atra* rapidly dries out under similar conditions of radiation and temperature. Available data from microclimatic measurements also showed an increase in the mean relative humidity of the vertical slopes compared to the horizontal exposures (Table 2).

4. Discussion

The maritime Antarctic and in particular South Shetland and South Orkney Islands, are known to possess the greatest terrestrial biodiversity and community complexity of the entire Antarctic biome. Investigations carried out on some of these maritime Antarctic islands have shown that a remarkable feature of the vegetation is the influence of environmental gradients on the distribution of individual species and communities (Lindsay, 1971; Smith, 1972). Holdgate (1977), studying the distribution of the major vegetation types on Signy Island (South Orkney Islands) in relation to environment, concluded that altitude, degree of maritime influence, slope, aspect and substratum type were the dominant variables. Such areas with a large biodiversity and a vegetation distribution pattern correlated with environmental gradients are ideal for the investigation of factors delimiting the distribution of lichen communities in Antarctica. A comprehensive description of the flora and vegetation of South Bay, Livingston Island indicated the exceptional floristic richness of this small area and that this decreased from the coast to inland (Sancho et al., 1999). It was suggested that factors other than greater harshness of microclimate with increasing altitude may cause this decrease since the altitudinal range was only 274 m. They suggested as possible factors terrain recently uncovered by receding glaciers at the inland sites and variation in edaphic parameters such as salt deposition and nitrogenous compounds that could contribute to a greater species diversity in the coastal area. A recent study of lichen productivity and nutrient availability gradients in the same area indicated that altitude and nutrient availability are inextricably related in the maritime Antarctic because enriched sites are usually near the coast and the warmer temperatures of these low elevation sites accelerate geochemical cycles (Valladares and Sancho, 2000). However, no attempt has been made so far to quantify this decrease in species richness and abundance with increasing altitude and to relate it with microclimatic parameters.

We have found a direct relationship between decrease in biodiversity and decrease in temperature along an altitudinal gradient. If we consider the thermal gradient experienced by *Usnea* species from horizontal surfaces (highlighted in Table 2) we found a difference of 2.37 K in an altitudinal range of 266 m which represents approximately 1 K thallus temperature per 100 m. This is of major interest taking into account the estimate of the adiabatic lapse rate of 0.6 K air temperature per 100 m for alpine mountains (Körner, 1999). The larger lapse rate observed in the maritime Antarctic during the summer could be explained by its situation in a narrow fringe between the sea and the glacier plateau. This thermal gradient was evident both in cloudy and clear days. These summer days are crucial for lichen productivity in the maritime Antarctic (Sancho et al., 1997; Schroeter et al., 1995), so the ecophysiological implications of this thermal gradient are likely to be major. These results suggest that the low temperatures associated to increasing altitude can be considered a limiting factor for lichen growth and correlates well with the results of Valladares and Sancho (2000), where it was demonstrated that increased elevation resulted in a sharp decrease in net photosynthetic assimilation rates of *Usnea aurantiaco-atra*. The abundance of this species even at high altitudes must be due to lesser competition. Investigations in temperate regions have suggested that increasing diversity with increasing altitudinal range might be due mainly to large climatic differences (Dietrich and Scheidegger, 1997). In our case in the maritime Antarctic, it is remarkable how a small altitudinal range produces changes in microclimatic conditions that have important effects on lichen community composition. This result emphasizes that climatic conditions at the macroscale can give a very misleading impression of conditions actually experienced by organisms living at the ground surface.

The larger decline in biodiversity with altitude observed in horizontal sites with respect to vertical sites demonstrated how slope also influenced vegetation distribution. The lesser cover and species richness observed in all but the highest vertical sites with respect to the horizontal sites could be related to the more extensive accumulation of water, soil and nutrients on the latter sites which favour the growth of bryophytes and vascular plants. At the summit of Mount Reina Sofia strong wind and low temperatures seems to affect both types of sites to the same extent.

We conclude that plant biodiversity in the maritime Antarctic might well be extremely sensitive to slight changes in air temperature. This fact could explain the large number of species that reach the limit of their distribution in this area. Many lichen species have a restricted Antarctic distribution limited to the northern Antarctic Peninsula and nearby islands (Inoue, 1993) but range extensions including the sub-Antarctic islands and at least the colder southern continents are not uncommon. Seppelt (1995) suggested that perhaps the

occurrence of these species in Antarctica may be better considered as a southerly extension of their range. This is the case of *Usnea aurantiaco-atra* (Jacq.) Bory which reach its distribution limit in the maritime Antarctic. The results could also explain the sharp decline in biodiversity from the maritime Antarctic to the continental Antarctic. Species with a continental Antarctic distribution must possess ecophysiological adaptations that permit colonization and survival under a more rigorous climatic regime than that experienced by those species confined to the more northerly and climatically milder maritime Antarctic region. Another possibility is that species absent in this area lack some key processes that enables growth at cold temperatures.

It is obvious from the results the profound implications that climate change can have on the vegetation of Antarctic terrestrial habitats. Ecological changes in bryophyte and phanerogam communities in the maritime Antarctic have been detected as a direct response to increasing summer temperatures (Smith, 1994). As a result of the present investigation we believe that lichen communities will also be affected by changes in summer temperatures.

Acknowledgements

The authors want to thank the members of the 90-91 expedition to the Spanish Antarctic Base Juan Carlos I for help and companionship during the expedition. Financial support was provided by the Spanish Ministry of Science and Technology and CICYT ANT99-0680-C02-01 and by a grant to A.P. of the Spanish CICYT.

REFERENCES

- Braun-Blanquet, J. 1964. *Pflanzensoziologie*, 3rd ed. Wien, New York.
- Dietrich, M. and Scheidegger, C. 1997. Frequency, diversity and ecological strategies of epiphytic lichens in the Swiss Central Plateau and the Pre-Alps. *Lichenologist* 29: 237-258.
- Green, T.G.A., Schroeter, B., and Sancho, L.G. 1999. Plant Life in Antarctica. In: *Handbook of Functional Plant Ecology*. F.I. Pugnaire and F. Valladares, eds. Marcel Dekker, New York, Basel, pp. 495-543.
- Holdgate, M.W. 1964. Terrestrial ecology in the maritime Antarctic. In: *Biologie Antarctique*. R. Carrick, M. Holdgate and J. Prévost, eds. Hermann, Paris, pp. 181-194.
- Holdgate, M.W. 1977. Terrestrial ecosystems in the Antarctic. *Philosophical Transactions of the Royal Society (London)* 279: 5-25.
- Inoue, M. 1993. Floristic notes on lichens in the Fildes Peninsula of King George Island and Harmony Cove of Nelson Island, South Shetland Islands, the Antarctic. *Proceedings of the NIPR Symposium of Polar Biology* 6: 106-120.

- Kappen, L. 1988. Ecophysiological relationships in different climatic regions. In: *CRC Handbook of Lichenology*. M. Galun, ed. CRC Press, Boca Raton, pp. 37–100.
- Kappen, L. and Redon, J. 1987. Photosynthesis and water relations of three maritime Antarctic lichen species. *Flora* **179**: 215–229.
- Kennedy, A.D. 1993. Water as a limiting factor in the Antarctic terrestrial environment: a biogeographical synthesis. *Arctic and Alpine Research* **25**: 308–315.
- Körner, C. 1999. Alpine climate. In: *Alpine Plant Life. Functional Plant Ecology of High Mountain Ecosystems*. Springer-Verlag, Berlin, Heidelberg, New York. pp. 21–30.
- Lindsay, D.C. 1971. Vegetation of the South Shetland Islands. *British Antarctic Survey Bulletin* **25**: 59–83.
- Longton, R.E. 1979. Vegetation ecology and classification in the Antarctic zone. *Canadian Journal of Botany* **57**: 2264–2278.
- Olech, M. 1989. Preliminary botanical studies in Johnsons Dock area (Livingston, Antarctica). *Bulletin of the Polish Academy of Sciences. Biological Sciences* **37**: 223–230.
- Sancho, L.G., Pintado, A., Valladares, F., Schroeter, B., and Schlenz, M. 1997. Photosynthetic performance of cosmopolitan lichens in the maritime Antarctic. *Bibliotheca Lichenologica* **67**: 197–210.
- Sancho, L.G., Schulz, F., Schroeter, B., and Kappen, L. 1999. Bryophyte and lichen flora of South Bay (Livingston Island: South Shetland Islands, Antarctica). *Nova Hedwigia* **68**: 301–337.
- Schroeter, B., Olech, M., Kappen, L. and Heitland, W. 1995. Ecophysiological investigations of *Usnea antarctica* in the maritime Antarctic. I. Annual microclimatic conditions and potential primary production. *Antarctic Science* **7**: 251–260.
- Schwerdtfeger, W. 1970. The climate of the Antarctic. In: *Climate of the Polar Regions*. Orvig, S., ed. Elsevier, Amsterdam, pp. 253.
- Seppelt, R.D. 1995. Phytogeography of continental Antarctic lichens. *Lichenologist* **27**: 417–431.
- Smith, R.I.L. 1972. Vegetation of South Orkney Islands. *British Antarctic Survey Scientific Reports* **68**: 1–124.
- Smith, R.I.L. 1984. Terrestrial plant biology of the sub-Antarctic and Antarctic. In: *Antarctic Ecology*. Vol. 2. R.M. Laws, ed. Academic Press, London, pp. 61–162.
- Smith, R.I.L. 1994. Vascular plants as bioindicators of regional warming in Antarctica. *Oecologia* **99**: 322–328.
- Valladares, F. and Sancho, L.G. 2000. The relevance of nutrient availability for lichen productivity in the maritime Antarctic. *Bibliotheca Lichenologica* **75**: 189–199.