Antarctic Science 12 (3): 314–324 (2000) © British Antarctic Survey Printed in the United Kingdom

Some aspects of the great success of lichens in Antarctica

LUDGER KAPPEN

University of Kiel, Botanical Institute, Olshausenstrasse 40, D-24098 Kiel, Germany

Abstract: The terrestrial vegetation in Antarctica is restricted to small, very isolated, ice-free areas on the continent and on the islands adjacent to the Peninsula region. Lichens, a symbiosis between a fungus and an alga or cyanobacterium, form the most prominent component in the vegetation. They have the greatest number of species compared with other cryptogamic and unicellular organisms. They are able to colonize all types of solid substrata and have a low mineral nutrient demand. Their physiological vigour is derived from high freezing tolerance and the ability to be photosynthetically activated by water vapour uptake from snow at temperatures as low as *c.* -20°C. Long-term monitoring in their natural habitats demonstrates that lichens are photosynthetically active at suboptimal temperatures. Locally, however, they can benefit from meltwater on insolated rocks, but only for short periods in early summer. Although at this time they may be exposed to substrate temperatures of > 20°C and strong light they do not suffer from photostress. If, in winter, lichens are covered and kept dark by snow with temperatures close to 0°C, lichens enter a negative carbon balance. This effect may be relevant to lichens under conditions of global or regional warming.

Received 7 October 1999, accepted 21 February 2000

Key words: annual carbon balance, freezing tolerance, ice, lichens, low-temperature photosynthesis, photostress, snow

Introduction

In environments with a predominant stress component evolution of species is clearly directed to their adaptation to the stressor. For instance, hot and temperate deserts display an enormous spectrum of types and strategies against the impact of drought within a great diversity of plant taxa. In addition to high tolerance to desiccation, stress-avoidance mechanisms have evolved resulting in xeromorphous structures which give the plants a fascinating and exotic appearance. In arid hot regions, for example southern Africa, adaptive radiation can progress rapidly because of a short generation time (e.g. Ihlenfeldt 1994) resulting in great species richness within a few million years.

But how about cold environments? Ice-free habitats in polar regions are very young on the geological time scale. The Arctic glacial period commenced about 2–3 million years ago, and the Antarctic glaciation is believed to have commenced in earliest Oligocene after long geological periods with warmer climates (Barker *et al.* 1998). But interglacial warm periods are assumed during which plant life could have existed on the continent (Quilty 1990, Barrett 1996). Consequently, adaptive radiation of organisms might be expected to be more effective in the latter region. Cold stress is permanent and stronger in Antarctica than anywhere else offshore. The heat balances are everywhere negative (Engelskjön 1986) in Antarctica in contrast to most of the Arctic region where they are positive. Thus, the adaptive stimulus is clearly expressed. Another precondition that should favour speciation of plants is that Antarctica consists of a region with many small islands offshore and small, highly isolated ice-free areas called oases (Smith 1997a) on the Antarctic continent provides for the existence of isolated plant, animal or micro-organismic populations and might be a cause for special adaptive radiation (Greuter 1979). Conversely, it is well-known that islands or isolated areas are poorer in species than comparable areas of large land masses (McArthur & Wilson 1969). Moreover, species richness decreases drastically with increasing latitude (Woodward 1993).

Neither in the Antarctic nor in the Arctic regions have vascular plants ever evolved any effective mechanism to avoid cold stress (Crawford 1990). All of them are mesophytic perennials and similar to temperate climate species (Convey 1996). However, as a result of low energy income, many Arctic plant species are incapable of sexual reproduction, being apogamous, apomictic etc., favouring various ways of vegetative reproduction and distribution (pseudovivipary, bulbils, stolons, etc.). This has the consequence that many clonal species or polymorphisms have been generated (Crawford 1990, cf. Molau 1993) with a biodiversity of ecotypes, populations and modifications. In a wider sense this may be considered as adaptation to the cold environment. Bryophytes in Antarctica follow the same trend with increasing latitude. Sexuality is reduced, and sporophytes tend to fail (Smith 1997a, Seppelt *et al.* 1998). However, *Bryum pseudotriquetrum* (Hedw.) Gaertn. and *Hennediella heimii* (Hedw.) Zand. show marked genetic differences locally within populations or even colonies (Skotniki *et al.* 1997, 1998, Selkirk *et al.* 1998). Biodiversity at an intraspecific level is also evident with lichens as can be demonstrated with various morphotypes, reduced fertility and vegetative propagules. Intraspecific variance has been for example shown by Schipperges *et al.* (1995) with *Cetraria nivalis* (L.) Ach., a sterile lichen from different locations in the European Alps and the Arctic. Different physiotypes were also detected, e.g. in bacteria, by comparing Antarctic and non-Antarctic strains. Franzmann *et al.* (1997) have shown that Antarctic taxa have generally lower temperature optima for growth than their non-Antarctic counterparts.

Let us consider species diversity in Antarctica which comprises the maritime Antarctic region (western Antarctic Peninsula and the archipelagos of the South Shetland, South Orkney and South Sandwich islands; see Smith 1984) and the major landmass, the continental Antarctic region. Lichens, a symbiosis between an algal or cyanobacterial and a fungal biont, are represented by *c.* 360 taxa (Smith & Øvstedal personal communication 1999). In comparison *c.* 200 taxa of terrestrial algae (Broady 1996) and *c.* 70 taxa of microfungi are known (Vishniac 1996) and there are about 104 moss and 25 liverwort taxa (Ochyra *et al.* 1998). The number of bacteria for the whole Antarctic region is unknown. By contrast, vascular plants exist only in the "mild" maritime Antarctic region, and only two species contribute to the flora of Antarctica. Therefore lichens are numerically the most diverse group of visible terrestrial organisms and are also most conspicuous in the landscapes of ice-free regions in the Antarctic.

The unequal presence of plants and micro-organisms can hardly be explained by limited immigration into the Antarctic region. The meteorological conditions, with major airstreams from the pole to the margin of the Antarctic continent and circulation of depressions around the Antarctic continent only rarely large enough to cover the distance between Antarctica and other continents, are apparent obstacles to a continuous immigration of diaspores particularly for continental Antarctica. Yet micro-organisms and the spore producing cryptogams have been shown to have invaded the remotest regions by air spora (Broady 1996, Broady & Weinstein 1998). For instance, representatives of the moss genus *Campylopus* Brid., which have a scattered distribution on the globe, are present on top of some of the few volcanoes in Antarctica (Longton 1988, Bargagli *et al.* 1996). Various reports of the transport and deposition of pollen grains from other continents (see Marshall 1996) indicate that more organisms might potentially have become established in the Antarctic region than actually exist there at present. Since the establishment of a lichen depends on the simultaneous presence of the photobiont and the mycobiont it occurs most successfully with vegetative diaspores that consist of both symbionts. It is, however, remarkable that a major part of the Antarctic lichen vegetation is recruited from crustose species that usually form spores instead of vegetative diaspores. It is still poorly understood how these species find their suitable photobiont, particularly under the hostile conditions in Antarctica.

If it is assumed that the majority of organisms that existed in the early Tertiary in Antarctica were extinguished during the ice-ages, the time available during the Holocene for immigration has been about 10 000 yr. Of the lichens some taxa may have survived the ice ages and perhaps have dispersed around the continent between nunataks and oases particularly in interglacial periods (Kappen 1993a, Seppelt 1995). The Antarctic Peninsula and adjacent islands, however, being closest to a neighbouring continent (South America) appear to be a pathway for species immigrations (Kappen & Straka 1988, Marshall 1996). As a consequence, the biodiversity of lichens appears mainly limited by ecological conditions and the physiological adaptation of the organisms. This can be corroborated by the paucity of vascular plants in the Antarctic. Except for *Poa annua* Brid. in one locality, attempts to naturalise vascular plants from Patagonia and the sub-Antarctic region into the maritime Antarctic have failed because plants and seedlings died after one or two growing periods (Smith, R. 1996). By contrast, invasion of alien plants into sub-Antarctic islands appears to be a problem for the indigenous vegetation (Gremmen & Smith 1999).

Habitats and substrata

The dominance of lichens increases, in general, with increasing latitude in Antarctica, although in absolute terms species number and standing biomass is decreasing. Whilst they are competing with bryophytes and plants in the milder parts of the maritime Antarctic they are increasingly predominant polewards up to 86°S. Lichens are able to grow on all existing substrata such as solid rock, single stones, concrete, timber of old building material, rusted iron, bones, boots, and dead moss. As they have no roots and do not depend on mineral elements from soil they are not dependent on any soil formation. Only some taxa such as of *Cladonia* Hill ex P. Browne and *Peltigera* Willd. in the maritime Antarctic as far south as Alexander Island (Stenroos 1993) grow on soil.

Little is known about the effect of nutrients on the performance of lichens and mosses in Antarctica (Crittenden 1996) but obviously substratum structure is more relevant for lichens than chemistry (Melick *et al.* 1994, Hovenden & Seppelt 1995). Mineral contents of lichens mainly reflect the substratum or the deposition from nearby mineral and nutrient sources (Smith 1978, 1985). As in other regions of the world, a major distinction is possible between the mostly colourful eutrophic species that can cope with the fertilising effects from birds and seaspray, and the oligotrophic species that avoid sites with such fertilising effects. Among the bryophilous (growing on moribund moss) lichens some taxa are endemic to Antarctica such as *Buellia grimmiae* Filson and *Rinodina olivaceobrunnea* Dodge & Baker (Smith 1990a). The rarity of calcareous substrate (except concrete, bones, and marble in a few areas) in the Antarctic region and the absence of trees and shrubs and other phorophytes (except drift wood and timber of stations), may be one reason for the lower species diversity in the Antarctic compared to the Arctic.

Aspect plays a major role in the habitat selection of lichens. In the harsh climate of continental habitats lichens can only exist in protected or insolated sites that provide heat and facilitate snowmelt (Kappen 1985a). In windy regions, such as the coast of Wilkes Land, only leeward sites of rocks and sheltered niches are colonized by lichens. In the maritime Antarctic the crytogamic vegetation is more widespread but ceases near glaciers, in places with long-lasting snow, and in animal colonies.

Low temperature tolerance

When searching for adaptations the great physiological potential of the polar organisms to cope with low temperature conditions has been recognized. This has been particularly investigated in lichens. The ability of lichens to tolerate temperatures as low as -196°C, even in an hydrated state, can be considered a pre-adaptation of not only polar lichen taxa but also of taxa from warm and temperate climates (Kappen & Lange 1970). Photosynthesis of Antarctic lichens was found to continue even at *c.* -20°C according to laboratory experiments (Lange & Kappen 1972, Vestal 1988) and field measurements on *Usnea sphacelata* R. Br. and *Umbilicaria aprina* Nyl. (Kappen 1989, Schroeter *et al.* 1994).

Since metabolic activity is achieved in poikilohydrous organisms only if the thallus is sufficiently hydrated, water availability is a key problem. During summer maritime Antarctic lichens are frequently soaked by rainwater, fog or melting snow (Schroeter *et al.* 1995) which provide an optimum hydration state for photosynthetic activity (Fig. 1). On the continent rainfall rarely occurs and then only in coastal regions; normally precipitation is as snow. Typically, strong winds whirl up snow from the ground and cover lichens with drifted snow crystals. Under such conditions combined with ambient temperatures below 0°C, air-dry thalli become hydrated and can resume photosynthesis and respiration as was observed near Casey station, Windmill Islands (Kappen 1989). This has been experimentally confirmed with *Buellia frigida* (Darb.) Dodge in another region of the Antarctic continent, where chlorophyll *a* fluorescence was recorded over a 24-hr period (Schroeter *et al.* 1997a). The crustose thalli of this lichen were able to gain enough moisture from the humidity at the edge of a temporary snow patch on the rock without any visible melting process. As soon as the snow patch had retreated the thallus dried and became physiologically inactive.

The amount of moisture that was taken up from unmelted snow was measured by Schroeter & Scheidegger (1995). Under steady state conditions at -14°C, thallus water content increased by 22% dry weight raising it to near the minimum necessary for photosynthetic activity. At this low water content the fungal hyphae were still cavitated and the photobiont cells shrunk, thus demonstrating the considerable extent of water stress under which lichens can be active. If the water potential at -20°C is calculated the thallus is exposed to about -20 MPa (Kappen 1993b). This implies that the photobiont must develop a steep vapour gradient against the vapour pressure of the attached or surrounding snow crystals. Experiments to investigate osmotic stress in hot desert lichens revealed that they are able to photosynthesise even at water potentials as low as -38 MPa (Nash *et al.* 1990). Under these conditions photosynthetic rates are very low and can be considered more as a means of keeping the photosynthetic apparatus intact and producing frost-protective carbohydrates than for actual dry matter production.

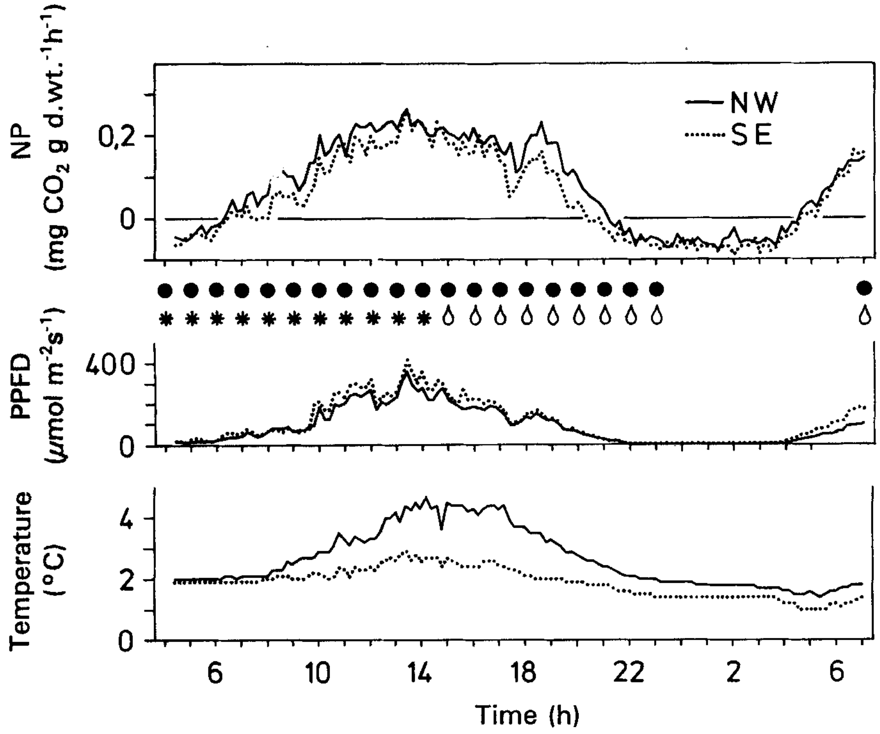

Fig. 1. Diurnal courses of net photosynthesis (NP) of the lichen *Usnea antarctica* Du Rietz near Arctowski station, King George Island (62°09'S; 58°28'W), in summer (December). The thalli were measured in a gas exchange chamber, oriented to the north-west and to the south-east. Photosynthetic photon flux density (PPFD) and thallus temperature (°C) are shown as well as the cloud cover (always overcast (●) and snowfall (✱) or rainfall (💧)). (After Kappen *et al.* 1987).

Fig. 2. Granitic rock with partial snow cover in the early summer season (November) near the beach of Botany Bay, south Victoria Land (77°01'S; 162°32'E). Snow melts off within a period of 3–4 days and irregular trickles of meltwater soak the thalli of *Buellia frigida* on the rock surface.

Meltwater-uptake

Snow melt is believed to be the major source of hydration for the productivity of lichens (Rudolph 1966, Schlensog *et al.* 1997). In the area of Granite Harbour (77°S) moistening by meltwater can be efficient for lichens on slightly inclined rock surfaces (Fig. 2). On clear, sunny days slowly running meltwater trickles keep the rock partially moist for several hours (Kappen *et al.* 1998a). It is reasonable to assume that the distribution of *Buellia frigida* thalli on the rock surface depends on the incidence and frequency of these melt trickles that occur here only in early summer until all snow has melted away. The moistened thalli can reach an over-air temperature of nearly 23 K (Fig. 3). This means that they can become as warm as 20°C at maximum. A temperature of 20°C may induce maximal productivity in *B. frigida*. Laboratory measurements of photosynthetic rates (Lange & Kappen 1972) show an optimum at 11°C and an upper compensation point near 28°C at maximum irradiance (Fig. 4). However, in the field, irradiance was much higher (1700 μmol m^{-2}s^{-1}) than in the experiment, and the photosynthetic optimum temperature should then be closer to 20°C. This is a comparatively high temperature value, as in other Antarctic habitats rock surfaces and the lichens attached to them usually dry out quickly under direct insolation. In the dry state, temperatures of up to 35°C may not be rare in Antarctica (see Smith 1999).

Resistance to photostress

Direct insolation may, however, be injurious to photosystem II, according to the experimental results by Demmig-Adams *et al.* (1990) with several lichen species. However, strong irradiance did not affect the meltwater moistened *Leptogium puberulum* Hue (Schlensog *et al.* 1997) and other species from the maritime Antarctic except for *Sphaerophorus globosus* (Huds.) Vain. which had the lowest carotenoid

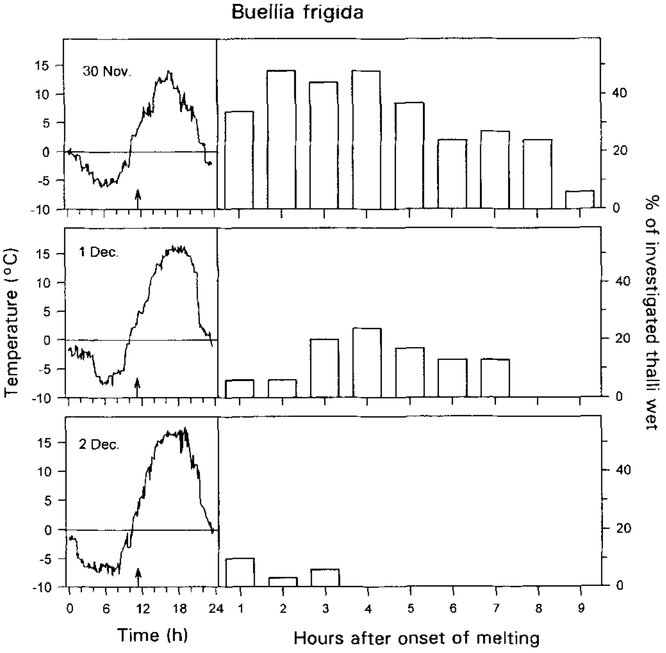

Fig. 3. Irradiance and the thallus temperatures at various positions on the granitic rock (see Fig. 2) were continuously recorded. This sequence of three days in Spring shows the diurnal course of thallus temperatures at a meltwater wetted site and, indicated by columns, the percentage of lichen thalli being moistened over periods of 1–9 h after onset of melting each day. Melting started generally after 11h00 local time (after Kappen *et al.* 1998a).

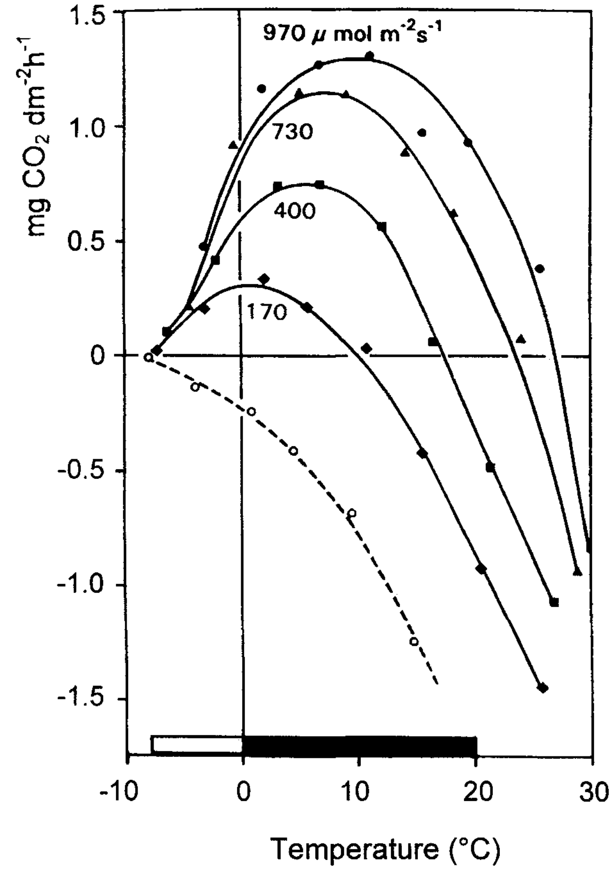

Fig. 4. CO$_2$ exchange of *Buellia frigida* from the Antarctic continent (material from Hallett station, 72°18'S; 170°18'E). The curves describe dark respiration (broken line) and the temperature-dependent net photosynthesis rates at various PPFD (170–970 μmol m^{-2}s^{-1}; laboratory measurements). The black and white bar indicate the thallus temperature range observed in the field at Botany Bay near the site described in Fig. 2 (after Lange & Kappen 1972 and Kappen *et al.* 1998a).

content (Valladares *et al.* 1997). Chlorophyll content in the thalli of the shade form was consistently higher than that of the sun form (Table I), which confirms a typical compensation that has been reported for other species (Kappen 1983). MAA (mycosporine-like amino acid derivatives) that are capable of absorbing UVB radiation in lichens with cyanobionts (Büdel *et al.* 1997) were also detected in both, shade and sun form thalli of *U. aprina*. Their concentration was higher in the sun form thalli than in the shade form thalli (Table I).

Table I. Pigments and UV-B absorbing mycosporine-like amino acid derivatives (MAA; mg g^{-1} dry wt) in sun and shade form thalli of *Umbilicaria aprina* from Granite Harbour, continental Antarctica (analysed by U. Karsten, Bremerhaven).

	Sun form	Shade form
chlorophyll *a*	1.8 ± 0.6	8.5 ± 2.3
chlorophyll *b*	4.2 ± 0.1	2.2 ± 0.4
pheophytin a	3.2 ± 0.2	1.2 ± 0.6
neoxanthin	2.4 ± 0.6	1.3 ± 0.1
violoxanthin	0.5 ± 0.3	0.5 ± 0.2
zeaxanthin	1.9 ± 0.2	1.2 ± 0.2
lutein	8.4 ± 1.2	5.9 ± 0.4
mycosporine-glycine	0.8 ± 0.03	0.58 ± 0.15
M-309*	0.06 ± 0.01	0.09 ± 0.03
M-313*	0.07 ± 0.01	–

*not identified, with maximum at 309, 313 nm.

Conditions for productivity, growth and colonization

Long-term monitoring of lichen thallus temperature in both the continental and the maritime Antarctic regions, has revealed that hydrated and active lichens generally do not become warmer than 12°C in their natural habitats (Table II). This confirms the hypothesis that lichens in Antarctic habitats usually become hydrated within similar temperature ranges, and lose water if thallus temperatures are higher than 10–12°C (Kappen 1985a). In this temperature range lichens reach only low photosynthetic rates compared to their potential at higher temperature and higher irradiance (Fig. 5). This may be one reason why these lichens are not very productive. At places like Granite Harbour (76°53'S; 162°44'E) the combination of high thallus temperature, high irradiance and free water lasts only for a few weeks in spring and early summer each year and ceases once all the adjacent snow has melted away. Therefore it was not surprising that the increase in thallus diameter of *B. frigida* was found to be insignificant over a period of 80 yr (Green *et al.* 1999).

Compared with vascular plants lichens generally have low photosynthetic rates and this is especially true for those of the Antarctic region (Table III). Moreover, the poikilohydrous lichens are heavily dependent on moisture availability for the frequency of their metabolic activity and therefore their annual productivity is low (Green *et al.* 1999). Growth, however, is not a direct function of photosynthetic productivity. As it is species-specific (Hale 1973) slow- and fast-growing species have also been identified for Antarctica (Smith 1995). Many of the fast-growing taxa are particularly responsive to nutrient

Table II. Temperature range for net photosynthesis in the field in Antarctica according to long-term measurements.

Species	Location	Directly measured or calculated thallus temperature (relevant to positive net photosynthesis)	Time period of observation (years)	Reference
Cryptoendolithic lichens	Asgard Range, McMurdo Dry Valleys	-7° to +7°C	3	Friedmann *et al.* 1993
Usnea antarctica	near Arctowski station, King George Island	+2° to +9°C	1	Schroeter *et al.* 1995
Usnea aurantiaco-atra	near Juan Carlos station, Livingston Island	+1° to +12°C	5	Schroeter *et al.* 1997b, in press

supply, for example, the ornithocoprophilous lichens (Smith 1985) and thalli of *Umbilicaria decussata* (Vill.) Zahlbr. whose size increased the closer they were to a bird colony (Ryan & Watkins 1989).

The wide distribution and ubiquity of the propagules (Smith 1991) suggest that lichens would potentially colonize all ice-free areas in Antarctica; however, actual colonization is not very homogeneous. The appearance of lichens on fresh substrates in Antarctica has been demonstrated in only a few localities (Smith 1984, Sancho & Valladares 1993). Smith (1995) demonstrated that lichens establish on fresh substrata only after a period of a few years, which is in accordance with the performance of lichens on lava fields in Hawaii (Smathers & Mueller-Dombois 1974, see also Bailey 1976). This lag phase indicates that substratum structure has to change by weathering until it is colonizable. This may take decades as was shown for Ellesmere Island, Canada (Fahselt *et al.* 1988). For Signy Island Smith (1990b) demonstrated that some lichens need only a few decades to grow from their first establishment to a dense canopy. Lichen assemblages may be stable for centuries if they are not disturbed by dislocation of the rock or changes in the microclimate (Smith 1993) or by being buried under snow for years (Valladares & Sancho 1995).

Changes due to regional warming

Continuous long-term monitoring of metabolic activity of lichens on Livingston Island, South Shetland Islands, revealed that snow-covered lichens can experience near or above freezing temperatures in the dark winter season (Schroeter *et al.* 1997b). A calculation on the basis of a photosynthesis model revealed for the year 1994 that the carbonlosses due to respiration were so high that the annual balance proved to be negative (Schroeter *et al.* in press). A negative annual carbon balance may not be uncommon for lichens in polar regions (Gannutz 1970, Lechowicz 1981), but if this happens repeatedly the lichens can be seriously affected. Long-lasting snow cover has been shown to have a negative effect on lichens in studies from other areas (Benedict 1990, Smith 1990b, Melick & Seppelt 1997). Winkler has studied the relationship between duration and depth of snow and the occurrence or absence of lichens in an ice-free area of King George Island (South Shetland Islands). Figure 6 illustrates that most macrolichens prefer open sites with shallow snow cover and early snow melt, whereas mosses and some crustose lichen taxa in contrast, are more resistant to long-lasting snow cover in depressions (Winkler *et al.* in press).

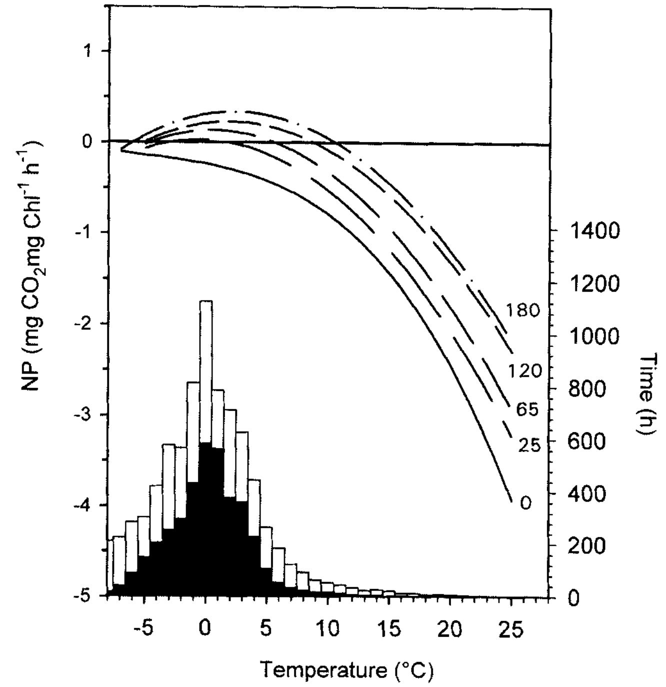

Fig. 5. CO$_2$ exchange (laboratory measurements of dark respiration and net photosynthesis at 25–180 µmol m^{-2}s^{-1} PPFD) of *Usnea aurantiaco-atra* from a site near Juan Carlos I station, Livingston Island, South Shetland Islands (62°39'S; 60°23'W). The columns indicate the cumulative time in hours of metabolic activity (black) and of inactivity (white) by temperature class. At PPFD >200 µmol m^{-2}s^{-1} no metabolic activity was observed in this year (1993). (After Schroeter 1997).

Interpreting the sequence of temperatures and carbon balances between 1992 and 1994 (Fig. 7) as a trend in terms of regional warming it becomes evident that a greater frequency of warm winters with more snow accumulation (Ye & Mather 1997) may cause a decrease in the viability of *Usnea aurantiaco-atra* (Jacq.) Bory, demonstrating also that this lichen can benefit from temperatures far below freezing point during the dark winter period.

This negative effect to *U. aurantiaco-atra* contrasts with reports on vascular plants in the maritime and sub-Antarctic regions where they have been growing more vigorously and

Table III. Maximal net photosynthesis rates of Antarctic cryptogams and phanerogams.

Type of organism	Rate (mg CO$_2$ g^{-1} dry wt h^{-1})	Rate (mg CO$_2$ dm^{-2} h^{-1})	Reference
crustose lichens	0.06–0.11	0.5.–2.50	Kappen 1988, 1993a, Kappen *et al.* 1990
foliose and fruticose lichens	0.20–0.80		Kappen 1985b, 1993a, Schlensog *et al.* 1997
bryophytes	0.50–4.00		Longton 1988, Convey 1994, Davey & Rothery 1996
phanerogams	12.50*–(20.71)*	8.80–14.50	Edwards & Smith 1988

*If 0.7 g dm^{-2} is taken instead of the quoted very low value of 0.07 g dm^{-2} leaf surface.

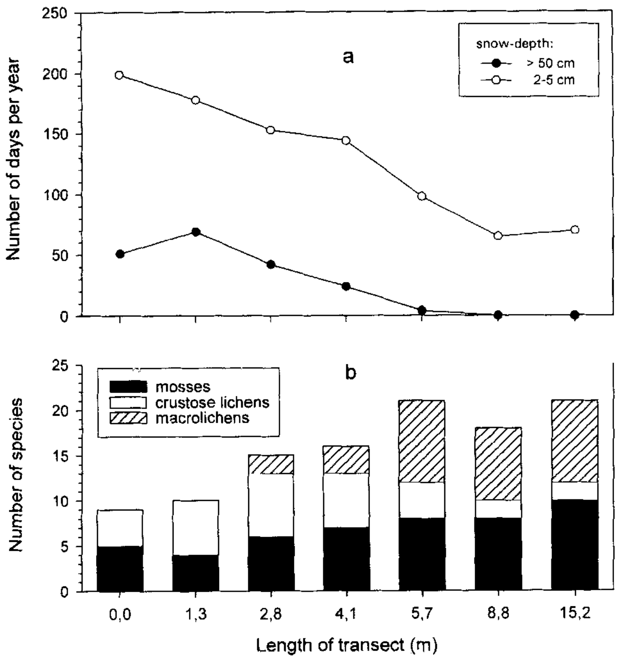

Fig. 6. a. Cumulative periods of snow cover during 1996 (for 50 cm depth and for 2–5 cm depth recorded at the same spot) along an ascending (4 m) transect *c.* 15 m long in the vicinity of Jubany station, King George Island (62°14'S; 58°40'W). **b.** Number of species of cryptogams at fixed points on the transect. It is evident that in the depression long-lasting deep snow cover allows only growth of bryophytes and crustose lichens, whereas macrolichens (mostly fruticose) are related to short and shallow snow cover (after Winkler *et al.* in press).

expanding in their area due to a warming tendency over the last 45 yr (Grobe *et al.* 1997, Smith 1990b, 1994, Gremmen 1997). Since *Colobanthus quitensis* (Kunth) Bartl. and *Deschampsia antarctica* Desv. reduce their photosynthetically active tissues to a minimum and stay in a resting stage during winter they do not suffer from high respiratory losses. Moreover, in summer these homoeohydrous vascular plants benefit from the warmer temperatures as they are permanently well hydrated, whereas the poikilohydrous lichens are more frequently dry and inactive during warmer periods in summer.

The contrasting physiology may not be the only reason for a different performance between lichens and vascular plants in the Antarctic because Smith (1990a) has recorded that the lichen *Usnea antarctica* has been spreading on Signy Island over a 24 yr period. It is interesting that according to Walker (1985) *U. antarctica* can be considered as the sorediate (asexual) counterpart of *U. aurantiaco-atra* in the sense of Poelt's (1970) concept of species pairs. The former species also has a wider distributional range than the latter (see Seppelt 1995), which confirms the general assumption that the asexual taxa of morphologically very similar species are more competitive and more successful. As a consequence, species composition may change accordingly in the maritime Antarctic in favour of vascular plants and of lichens with a wider ecological amplitude.

Whether the vegetation in the continental Antarctic region will be less influenced by climatic warming may be a matter of debate. According to Melick & Seppelt (1997) an increase of 0.086 K yr^{-1} in Wilkes Land between 1960 and 1985 was followed by a 0.1 K yr^{-1} decrease in the subsequent decade. Only at a long-time scale beginning 8–5000 BP, was an expansion of the vegetation after deglaciation suggested with a trend of expanding lichen cover and an increasing trend of the bryophyte vegetation to moist depressions due to a generally drier climate. By contrast, recent warming effects were stated for the McMurdo Dry Valleys based on changes of lake levels (Lyons *et al.* 1997)

Discussion and conclusions

It is suggested in this review that the success of lichens in the Antarctic can be explained mainly by their physiological capacity, in particular their high tolerance of low temperature stress and high resistance to photostress. Their capacity for being photosynthetically active at subzero temperatures is remarkable. Lichens with green algae as photobionts are able

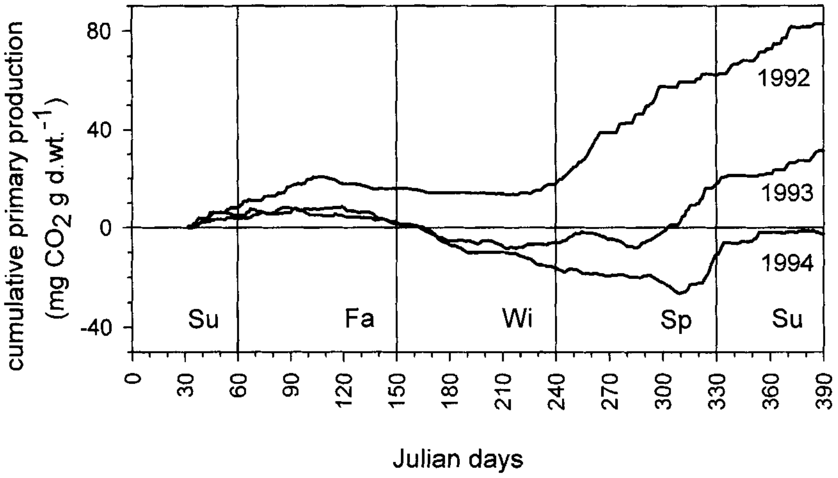

Fig. 7. Cumulative primary CO_2 prodution of *Usnea aurantiaco-atra* over the seasonal course (Su = summer, Fa = fall; Wi = winter, Sp = spring) of the years 1992–94 at the site described in Fig. 5. Due to respiratory carbon losses in late winter and early spring 1993 and 1994 the net carbon gain was negative (after Schroeter *et al.* in press).

to reactivate and to maintain photosynthesis by means of water vapour uptake, an important property of many desert lichens (Lange & Bertsch 1965). This has the consequence that lichens can also benefit from water vapour over ice and snow, as has been demonstrated for Antarctic species *in situ*, where melted snow is used in continental habitats for limited periods, mainly in the early summer season. Lichens with cyanobacteria as photobionts are not able to reactivate photosynthesis by means of water vapour (Lange *et al.* 1986). Their incapability of carrying out photosynthesis at temperatures below freezing (Green *et al.* 1999) means that their absence on the Antarctic continent is an indicator that liquid water is too rarely available. Free living cyanobacteria, however, are not rare in the continental Antarctic but depend on very wet habitats such as meltpools or streams. A few species of cyanolichens exist in the maritime Antarctic, where rainfall or meltwater is more frequently available (Kappen 1993a, Green *et al.* 1999). This, again, demonstrates to what extent physiological properties are decisive for the distribution of species. Nutrient availability from the substratum plays a minor role, as many of the lichens from inland habitats have a low demand for nutrients and derive them from airborne dust. Eutrophic conditions are selective for nitrotolerant species. The physiological capacitance of the lichens is less the result of a special adaptive evolution in the Antarctic region than a property of ubiquitous high-mountain species as many of the Antarctic species are (Sancho *et al.* 1997). New aspects may arise from comparative studies such as that on the ecophysiology of mediterranean high-mountain and maritime Antarctic populations of the lichen *Umbilicaria nylanderiana* (Zahlbr) H. Magn. The amount of algal cells and chlorophyll content in the thalli of the Antarctic population was much lower than in those of the Mediterranean population. As a consequence, maximal photosynthetic rates of the Antarctic samples were only 10% of the Mediterranean ones. The optimum temperature for photosynthesis was also lower, but dark respiration rates did not differ between Antarctic and Mediterranean samples. In the Antarctic habitat the total time period for metabolic activity was twice as long as in the Mediterranean high-mountain habitat (Sancho *et al.* in press).

The original assumption that Antarctic lichens represent a very specialised group of taxa, as more than 80% of the species were endemic (Dodge 1973) has been rejected (Castello & Nimis 1997). According to the most recent revision of Antarctic lichen species a figure of 30% endemic taxa is more correct (Smith, personal communication 1999). For endemic species the time span for an adaptive radiation and speciation is limited to a Holocene postglacial period of 10 000 yr, (in some regions on the continent to much shorter periods after deglaciation (Seppelt 1995)), or occurred during earlier interglacial phases or before the Oligocene. Some oases may have been ice-free over periods of a few million years (such as the McMurdo Dry Valleys (Friedmann & Weed 1987)) or habitats on nunataks were used, where species diversity is poor at present. The majority of the endemic species exists in the mild maritime Antarctic (see Kappen 1993a), and a higher percentage of endemism has been reported for the sub-Antarctic region (Hertel 1987). Interestingly, an adaptive radiation of testate amoebae is assumed to have occurred in Holocene in the Antarctic region (Smith 1996). Evidence of their descent from Mesozoic Antarctic ancestors was given by Marshall & Pugh (1996) for *Acari* (mites) species endemic to the Antarctic continent. At present it is not known where the endemic lichens have originated and whether some of them might have evolved on the continent. It is an open question also whether the endemic lichen species are particularly specialised to living conditions in Antarctica or what kind of properties they have developed. By comparison, the Antarctic moss flora has a very low level of endemism (about 7%; Ochyra *et al.* 1998) and it is postulated that these species must have immigrated from elsewhere.

It may be a matter of debate whether a high species diversity of lichens is of great relevance to Antarctic land ecosystems. But, together with bryophytes and, also in the absence of bryophytes, lichens form the largest amount of standing biomass in Antarctic landscapes with up to 950 g m^{-2} in continental and up to 1300 g m^{-2} in maritime Antarctic habitats (Smith 1984, 1990a, Kappen 1993a). They can build up a community structure like trees in a forest. It may be noted that many natural forests in temperate and boreal climatic belts are formed only by a few tree species, thus there is no general need for a high species diversity. High biodiversity is frequently taken as a prerequisite for ecosystem stability, and it is postulated that species interact strongly with each other and thus cause matter and energy fluxes (Peterson *et al.* 1998). In the Antarctic, functional groups in the sense of Körner (1993), may comprise lichens, bryophytes, fungi, algae, bacteria, protozoa, collembola, mites and nematodes at sheltered habitats (Davis 1981). Very little is known about interactions between species and about nutrient fluxes and food webs in Antarctic ecosystems.

Lichens are usually considered as pioneers, reaching frontier positions rather than starting the colonisation of terrestrial habitats (Kappen 1973). Smith (1993) considers them as secondary colonisers following micro-organisms such as bacteria and unicellular algae. In the maritime Antarctic lichens of the genera *Stereocaulon* Hoffm., *Cladonia* Hill ex Browne and *Sphaerophorus* Pers reach almost the size of *Deschampsia antarctica* and *Colobanthus quitensis* and therefore coexist as equal partners in the vegetation. In regions with harsher climatic conditions the vascular plants fail and leave the field to the lichens and bryophytes. While the latter are more competitive in moister sites, such as depressions, they are inferior to the lichens on solid substrata with changing surface moisture. It would be interesting to investigate in detail the reasons (long-lasting snow cover, substratum properties, exposure, microclimate etc.) for the very scattered occurrence or simply the absence of lichens in wide parts of ice-free areas in the Antarctic and where new colonisation processes could occur. Under present climatic conditions the vegetation structure remains stable, but any further drastic change of climatic conditions, air pollution or mechanical stress (e.g. animal and human activities and impact) would most likely alter or destroy the lichen vegetation (Kappen 1984, Adamson & Seppelt 1990, Smith 1997b). In this respect the lichen vegetation is highly vulnerable.

Acknowledgements

The author wishes to thank Dr Edith Fanta, for hosting our conference in Curitiba. Stimulating comments and language editing by Dr. R.I. Lewis Smith is gratefully acknowledged. Dr U. Karsten, AWI, Bremerhaven, is thanked for kindly analysing pigments in our samples. Many thanks to Mrs M. Mempel, M. Quandt and P. Cowles for assistance in preparing the manuscript. The author also thanks Dr R.I.L. Smith and an anonymous referee for their helpful suggestions.

References

ADAMSON, E. & SEPPELT, R.D. 1990. A comparison of airborne alkaline pollution damage in selected lichens and mosses at Casey Station, Wilkes Land, Antarctica. *In* KERRY, K.R. & HEMPEL, G., *eds. Antarctic ecosystems: ecological change and conservation.* Berlin: Springer Verlag, 347–353.

BAILY, R.H. 1976. Ecological aspects of dispersal and establishment in lichens. *In* BROWN, D.H., HAWKSWORTH, D.L. & BAILY, R.H., *eds. Lichenology: progress and problems.* London: Academic Press, 215–247.

BARGAGLI, R., BROADY, P.A. & WALTON, D.W.H. 1996. Preliminary investigation of the thermal biosystem of Mount Rittmann fumaroles (northern Victoria Land, Antarctica). *Antarctic Science,* **8**, 121–126.

BARKER, P.F., BARRETT, J.P., CAMERLENGHI, A., COOPER, A.K., DAVEY, F.J., DOMACK, E.W., ESCURIA, C., KRISTOFFERSEN, Y. & O'BRIEN, P.E. 1998. Ice sheet history from Antarctic continental margin sediments: the ANTOSTRAT approach. *Terra Antartica,* **5**, 737–760.

BARRETT, P.J. 1996. Antarctic palaeoenvironment through Cenozoic times - a review. *Terra Antartica,* **3**, 103–119.

BENEDICT, J.B. 1990. Lichen mortality due to late-lying snow, results of a transplant study. *Arctic and Alpine Research,* **22**, 81–89.

BROADY, P.A. 1996. Diversity, distribution and dispersal of Antarctic terrestrial algae. *Biodiversity and Conservation,* **5**, 1307–1335.

BROADY, P.A. & WEINSTEIN, R.N. 1998. Algae, lichens and fungi in La Gorce Mountains, Antarctica. *Antarctic Science,* **10**, 376–385.

BÜDEL, B., KARSTEN, U. GARCIA-PICHEL, F. 1997. Ultraviolet-absorbing scytonemin and mycosporine-like amino acid derivatives in exposed, rock-inhabiting cyanobacterial lichens. *Oecologia,* **112**, 165–172.

CASTELLO, M. & NIMIS, P.L. 1997. Diversity of lichens in Antarctica. *In* BATTAGLIA, B., VALENCIA, J. & WALTON, D.W.H., *eds. Antarctic communities - species, structure and survival.* Cambridge: Cambridge University Press, 15–21.

CONVEY, P. 1994. Photosynthesis and dark respiration in Antarctic mosses - an initial comparative study. *Polar Biology,* **14**, 65–69.

CONVEY, P. 1996. Reproduction of Antarctic flowering plants. *Antarctic Science,* **8**, 127–134.

CRAWFORD, R.M.M. 1990. *Studies in plant survival - ecological case histories of plant adaptation to adversity.* Oxford: Blackwell Scientific Publications, 296 pp.

CRITTENDEN, P.D. 1996. The effect of oxygen deprivation on inorganic nitrogen uptake in an Antarctic macrolichen. *Lichenologist,* **28**, 347–354.

DAVEY, M.C. & ROTHERY, P. 1996. Seasonal variation in respiratory and photosynthetic parameters in three mosses from the maritime Antarctic. *Annals of Botany,* **78**, 719–728.

DAVIS, R.C. 1981. Structure and function of two Antarctic terrestrial moss communities. *Ecological Monographs,* **51**, 125–143.

DEMMIG-ADAMS, B., MÁGUAS, C., ADAMS, W.W.I., MEYER, A., KILIAN, E. & LANGE, O.L. 1990. Effect of light on the efficiency of photochemical energy conversion in a variety of lichen species with green and blue-green phycobionts. *Planta,* **180**, 400–409.

DODGE, C.W. 1973. *Lichen flora of the Antarctic continent and adjacent islands.* Canaan, NH: Phoenix Publishing, 399 pp.

EDWARDS, J.A. & SMITH, R.I.L. 1988. Photosynthesis and respiration of *Colobanthus quitensis* and *Deschampsia antarctica* from the maritime Antarctic. *British Antarctic Survey Bulletin,* No. 81, 43–63.

ENGELSKJÖN, T. 1986. Zonality of climate and plant distributions in some Arctic and Antarctic regions. *Rapportserie Norsk Polarinstitutt,* **30**, 1–49.

FAHSELT, D., MAYCOCK, P.F. & SVOBODA, J. 1988. Initial establishment of saxicolous lichens following recent glacial recession in Sverdrup Pass, Ellesmere Island, Canada. *Lichenologist,* **20**, 253–268.

FRANZMANN, P.D., DOBSON, S.J., NICHOLS, P.D. & MCMEEKIN, T.A. 1997. Prokaryotic Antarctic biodiversity. *In* BATTAGLIA, B., VALENCIA, J. & WALTON, D.W.H., *eds. Antarctic communities - species, structure and survival.* Cambridge: Cambridge University Press, 51–56.

FRIEDMANN, E.I., KAPPEN, L., MEYER, M.A. & NIENOW, J.A. 1993. Long-term productivity in the cryptoendolithic microbial community of the Ross Desert, Antarctica. *Microbial Ecology,* **25**, 51–69.

FRIEDMANN, E.I. & WEED, R. 1987. Microbial trace-fossils formation, biogenous, and abiotic weathering in the antarctic cold desert. *Science,* **236**, 703–705.

GANNUTZ, T.P. 1970. Photosynthesis and respiration of plants in the Antarctic Peninsula area. *Antarctic Journal of the United States,* **5**(2), 49–51.

GREEN, T.G.A., SCHROETER, B. & SANCHO, L.G. 1999. Plant life in Antarctica. *In* PUGNAIRE, F.I. & VALLADARES, F., *eds. Handbook of functional plant ecology.* New York: Marcel Dekker, 495–543.

GREMMEN, N.J.M. 1997. Change in the vegetation of sub-Antarctic Marion Island resulting from introduced vascular plants. *In* BATTAGLIA, B., VALENCIA, J. & WALTON, D.W.H., *eds. Antarctic communities - species, structure and survival.* Cambridge: Cambridge University Press, 417–423.

GREMMEN, N.J.M. & SMITH, V.R. 1999. New records of alien vascular plants from Marion and Prince Edward Islands, sub-Antarctic. *Polar Biology,* **21**, 401–409.

GREUTER, W. 1979. The origin and evolution of island floras as exemplified by the Aegean Archipelago. *In* BRAMWELL, D., *ed. Plants and islands.* London: Academic Press, 87–106.

GROBE, C.W., RUHLAND, C.T. & DAY, T.A. 1997. A new population of *Colobanthus quitensis* near Arthur Harbour, Antarctica: correlating recruitment with warmer summer temperatures. *Arctic and Alpine Research,* **29**, 217–221.

HALE, M.E. 1973. Growth. *In* AHMADJIAN, V. & HALE, M.E., *eds. The lichens.* New York: Academic Press, 473–494.

HERTEL, H. 1987. Progress and problems in taxonomy of Antarctic saxicolous lecideoid lichens. *Bibliotheca Lichenologica,* **25**, 219–242.

HOVENDEN, M.J. & SEPPELT, R.D. 1995. Exposure and nutrients as delimiters of lichen communities in continental Antarctica. *Lichenologist,* **27**, 505–516.

IHLENFELDT, H.-D. 1994. Diversification in an arid world: the Mesembryanthemaceae. *Annual Review of Ecology and Systematics,* **25**, 521–546.

KAPPEN, L. 1973. Response to extreme environments. *In* AHMADJIAN, V. & HALE, M.E., *eds. The lichens.* New York: Academic Press, 311–380.

Kappen, L. 1983. Ecology and physiology of the Antarctic fruticose lichen *Usnea sulphurea* (Koenig) Th. Fries. *Polar Biology*, **1**, 249–255.

Kappen, L. 1984. Ecological aspects of exploitation of the nonliving resources of the Antarctic continent. *Veröffentlichungen des Instituts für Internationales Recht an der Universität Kiel* (Antarctic Challenge, Symposium 22-24-6-1983 in Kiel), **88**, 211–217.

Kappen, L. 1985a. Lichen-habitats as micro-oases in the Antarctic - the role of temperature. *Polarforschung*, **55**, 49–54.

Kappen, L. 1985b. Water relations and net photosynthesis of *Usnea*. A comparison. *In* Brown, D.H., *ed. Lichen physiology and cell biology*. New York: Plenum Publishing, 41–56

Kappen, L. 1988. Ecophysiological relationships in different climatic regions. *In* Galun, M., *ed. CRC Handbook of lichenology, Vol. II.* Boca Raton, FL: CRC Press, 37–100.

Kappen, L. 1989. Field measurements of carbon dioxide exchange of the Antarctic lichen *Usnea sphacelata* in the frozen state. *Antarctic Science*, **1**, 31–34.

Kappen, L. 1993a. Lichens in the Antarctic region. *In* Friedmann, E.I., *ed. Antarctic microbiology*. New York: Wiley-Liss, 433–490.

Kappen, L. 1993b. Plant activity under snow and ice, with particular reference to lichens. *Arctic*, **46**, 297–302.

Kappen, L. Bölter, M. & Kühn, A. 1987. Photosynthetic activity of lichens in natural habitats in the maritime Antarctic. *Bibliotheca Lichenologica*, **25**, 297–312.

Kappen, L. & Lange, O.L. 1970. The cold resistance of phycobionts from macrolichens of various habitats. *Lichenologist*, **4**, 289–293.

Kappen, L., Schroeter, B. & Sancho, L.G. 1990. Carbon dioxide exchange of Antarctic crustose lichens *in situ* measured with a CO_2/H_2O porometer. *Oecologia*, **82**, 311–316.

Kappen, L., Schroeter, B., Green, T.G.A. & Seppelt, R.D. 1998a. Microclimatic conditions, meltwater moistening, and the distributional pattern of *Buellia frigida* on rock in a southern continental Antarctic habitat. *Polar Biology*, **19**, 101–106.

Kappen, L., Schroeter, B., Green, T.G.A. & Seppelt, R.D. 1998b. Chlorophyll *a* fluorescence and CO_2 exchange of *Umbilicaria aprina* under extreme light stress in the cold. *Oecologia*, **113**, 325–331.

Kappen, L. & Straka, H. 1988. Pollen and spores transport into the Antarctic. *Polar Biology*, **8**, 173–180.

Körner, C. 1993. Scaling from species to vegetation: the usefulness of functional groups. *In* Schulze, E.-D. & Mooney, H.A., *eds. Biodiversity and ecosystem function*. Berlin: Springer Verlag, 117–140.

Lange, O.L. & Bertsch, A. 1965. Photosynthese der Wüstenflechte *Ramalina maciformis* nach Wasserdampfaufnahme aus dem Luftraum. *Die Naturwissenschaften*, **52**, 215–216.

Lange, O.L. & Kappen, L. 1972. Photosynthesis of lichens from Antarctica. *Antarctic Research Series*, **20**, 83–95.

Lange, O.L., Kilian, E. & Ziegler, H. 1986. Water vapor uptake and photosynthesis of lichens: performance differences in species with green and blue-green algae as phycobionts. *Oecologia*, **71**, 104–110.

Lechowicz, M.J. 1981. The effects of climatic pattern on lichen productivity: *Cetraria cucullata* (Bell.) Ach. in the Arctic tundra of northern Alaska. *Oecologia*, **50**, 210–216.

Longton, R.E. 1988. *Biology of polar bryophytes and lichens*. Cambridge: Cambridge University Press, 391 pp.

Lyons, W.B., Bartek, L.R., Mayewski, P.A. & Doran, P.T. 1997. Climate history of the McMurdo Dry Valleys since the last glacial maximum: a synthesis. *In* Lyons, W.B., Howard-Williams, C. & Hawes, I., *eds. Ecosystem processes in Arctic ice-free landscapes*. Rotterdam: Balkema, 15–22.

MacArthur, R.H. & Wilson, E.O. 1969. *The theory of island biogeography*, 2nd ed. Princeton, NJ: Princeton University Press, 203 pp.

Marshall, D.J. & Pugh, P.J.A. 1996. Origin of the inland Acari of continental Antarctica, with particular reference to Dronning Maud Land. *Zoological Journal of the Linnean Society*, **118**, 101–118.

Marshall, W.A. 1996. Biological particles over Antarctica. *Nature*, **383**, 680.

Melick, D.R., Hovenden, M.J. & Seppelt, R.D. 1994. Phytography of bryophyte and lichen vegetation in the Windmill Islands, Wilkes Land, continental Antarctica. *Vegetatio*, **111**, 71–87.

Melick, D.R. & Seppelt, R.D. 1997. Vegetation patterns in relation to climatic and endogenous changes in Wilkes Land, continental Antarctica. *Journal of Ecology*, **85**, 43–56.

Molau, U. 1993. Relationships between flowering phenology and life history strategies in Tundra plants. *Arctic and Alpine Research*, **25**, 391–402.

Nash III, T.H., Reiner, A., Demmig-Adams, B., Kilian, E., Kaiser, W.M. & Lange, O.L. 1990. The effect of atmospheric desiccation and osmotic water stress on photosynthesis and dark respiration of lichens. *New Phytologist*, **116**, 269–276.

Ochyra, R., Bednarek-Ochyra, H. & Smith, R.I.L. 1998. 170 years of research of the Antarctic moss flora. *Polish Polar Studies 25th International Polar Symposium*. Warszawa: Institute of Geophysics of the Polish Academy of Sciences, 159–177.

Peterson, G., Allen, C.R. & Holling, C.S. 1998. Ecological resilience, biodiversity, and scale. *Ecosystems*, **1**, 6–18.

Poelt, J. 1970. Das Konzept der Artenpaare bei den Flechten. *Berichte der Deutschen Botanischen Gesellschaft Neue Folge*, **4**, 187–198.

Quilty, P.G. 1990. Significance of evidence for changes in the Antarctic marine environment over the last 5 million years. *In* Kerry, K.R. & Hempel, G., *eds. Antarctic ecosystems: ecological change and conservation*. Berlin: Springer Verlag, 3–8.

Rudolph, E.D. 1966. Lichen ecology and microclimate studies at Cape Hallett, Antarctica. *In* Tromp, S.W. & Weihe, W.H., *eds. Proceedings International Biometeorological Congress*. Oxford: Pergamon Press, 900–910.

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.

Sancho, L.G. & Valladares, F. 1993. Lichen colonisation of recent moraines on Livingston Island (South Shetland Islands, Antarctica). *Polar Biology*, **13**, 227–233.

Sancho, L.G., Pintado, A., Valladares, F., Schroeter, B. & Schlensog, M. 1997. Photosynthetic performance of cosmopolitan lichens in the maritime Antarctic. *Bibliotheca Lichenologica*, **67**, 197–210.

Sancho, L.G., Valladares, F., Schroeter, B. & Kappen, L. In press. Ecophysiology of Antarctic versus temperate populations of a bipolar lichen: The key role of the photosynthetic partner. *In* Howard-Williams, C. & Davison, W., *eds. Antarctic ecosystems: models for a wider ecological understanding*. Christchurch: Caxton Press.

Schipperges, B., Kappen, L. & Sonesson, M. 1995. Intraspecific variations of morphology and physiology of temperate to Arctic populations of *Cetraria nivalis*. *Lichenologist*, **27**, 517–529.

Schlensog, M., Schroeter, B., Sancho, L.G., Pintado, A. & Kappen, L. 1997. Effect of strong light on photosynthetic performance of the melt-water dependent cyanobacterial lichen *Leptogium puberulum* (Collemataceae) Hue from the maritime Antarctic. *Bibliotheca Lichenologica*, **67**, 235–246.

Schroeter, B. 1997. *Grundlagen der Stoffproduktion von Kryptogamen unter besonderer Berücksichtigung der Flechten. Eine Synopse.* Habilitationsschrift, Math.-Nat. Fakultät Christian Albrechts Universität, Kiel, 130 pp.

Schroeter, B., Green, T.G.A., Kappen, L. & Seppelt, R.D. 1994. Carbon dioxide exchange at subzero temperatures: field measurements on *Umbilicaria aprina* in Antarctica. *Cryptogamic Botany*, **4**, 233–241.

Schroeter, B., Kappen, L., Green, T.G.A. & Seppelt, R.D. 1997a. Lichens and the Antarctic environment: effects of temperature and water availability on photosynthesis. *In* Lyons, W.B., Howard-Williams, C. & Hawes, I., *eds. Ecosystem processes in Arctic ice-free landscapes*. Rotterdam: Balkema, 103–117.

Schroeter, B., Schulz, F. & Kappen, L. 1997b. Hydration-related spatial and temporal variation of photosynthetic activity in Antarctic lichens. *In* Battaglia, B., Valencia, J. & Walton, D.W.H., *eds. Antarctic communities - species, structure and survival.* Cambridge: Cambridge University Press, 221–225.

Schroeter, B., Kappen, L., Schulz, F. & Sancho, L.G. In press. Seasonal variation in the carbon balance of lichens in the maritime Antarctic: long-term measurements of photosynthetic activity in *Usnea aurantiaco-atra*. In Howard-Williams, C., Davison, W., *eds. Antarctic ecosystems: models for wider ecological understanding.* Christchurch: Caxton Press.

Schroeter, B., Olech, M., Kappen, L. & 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.

Schroeter, B. & Scheidegger, C. 1995. Water relations in lichens at subzero temperatures: structural changes and carbon dioxide exchange in the lichen *Umbilicaria aprina* from continental Antarctica. *New Phytologist*, **131**, 273–285.

Selkirk, P.M., Skotnicki, M.L., Ninham, J., Connett, M.B. & Armstrong, J. 1998. Genetic variation and dispersal of *Bryum argenteum* and *Hennediella heimii* populations in the Garwood Valley, southern Victoria Land, Antarctica. *Antarctic Science*, **10**, 423–430.

Seppelt, R.D. 1995. Phytogeography of continental Antarctic lichens. *Lichenologist*, **27**, 417–431.

Seppelt, R.D., Smith, R.I.L. & Kanda, H. 1998. Antarctic bryology: past achievements and new perspectives. *Journal of the Hattori Botanical Laboratory*, **84**, 203–239.

Skotnicki, M.L., Selkirk, P.M. & Dale, T.M. 1997. RAPD profiling of genetic variation in Antarctic mosses. *In* Lyons, W.B., Howard-Williams, C. & Hawes, I., *eds. Ecosystem processes in Arctic ice-free landscapes*. Rotterdam: Balkema, 129–136.

Skotnicki, M.L., Selkirk, P.M. & Ninham, J.A. 1998. RAPD analysis of genetic variation and dispersal of the moss *Bryum pseudotriquetrum* from Southern Victoria Land, Antarctica. *Polar Biology*, **20**, 121–126.

Smathers, G. A. & Mueller-Dombois, D. 1974. Invasion and recovery of vegetation after a volcanic eruption in Hawaii. *U.S. National Park Service*, Monograph 5, 129 pp.

Smith, H.G. 1996. Diversity of Antarctic terrestrial protozoa. *Biodiversity and Conservation*, **5**, 1379–1394.

Smith, R.I.L. 1978. Summer and winter concentrations of sodium, potassium and calcium in some maritime Antarctic cryptogams. *Journal of Ecology*, **66**, 891–909.

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. 1985. Nutrient cycling in relation to biological productivity in Antarctic and sub-Antarctic terrestrial and freshwater ecosystems. *In* Siegfried, W.R., Condy, P.R. & Laws, R.M., *eds. Antarctic nutrient cycles and food webs*. Berlin: Springer Verlag, 138–155.

Smith, R.I.L. 1990a. Plant community dynamics in Wilkes Land, Antarctica. *Proceedings of the NIPR Symposium of Polar Biology*, **3**, 229–244.

Smith, R.I.L. 1990b. Signy Island as a paradigm of biological and environmental change in Antarctic terrestrial ecosystems. *In* Kerry, K.R. & Hempel, G., *eds. Antarctic ecosystems: ecological change and conservation*. Berlin: Springer Verlag, 32–50.

Smith, R.I.L. 1991. Exotic sporomorpha as indicators of potential immigrant colonists in Antarctica. *Grana*, **30**, 313–324.

Smith, R.I.L. 1993. The role of bryophyte propagule banks in primary succession: Case study of an Antarctic fellfield soil. *In* Miles, J. & Walton, D.W.H., *eds. Primary succession on land*. Oxford: Blackwell Scientific, 55–78.

Smith, R.I.L. 1994. Vascular plants as bioindicators of regional warming in Antarctica. *Oecologia*, **99**, 322–328.

Smith, R.I.L. 1995. Colonisation by lichens and the development of lichen-dominated communities in the maritime Antarctic. *Lichenologist*, **27**, 473–483.

Smith, R.I.L. 1996. Introduced plants in Antarctica: potential impacts and conservation issues. *Biological Conservation*, **76**, 135–146.

Smith, R.I.L. 1997a. Oases as centres of high plant diversity and dispersal in Antarctica. *In* Lyons, W.B., Howard-Williams, C. & Hawes, I., *eds. Ecosystem processes in Arctic ice-free landscapes*. Rotterdam: Balkema, 119–128.

Smith, R.I.L. 1997b. Impact of an increasing fur seal population on Antarctic plant communities: resilience and recovery. *In* Battaglia, B., Valencia, J. & Walton, D.W.H., *eds. Antarctic communities - species, structure and survival.* Cambridge: Cambridge University Press, 432–436.

Smith, R.I.L. 1999. Biological and environmental characteristics of three cosmopolitan mosses dominant in continental Antarctica. *Journal of Vegetation Science*, **10**, 231–242.

Stenroos, S. 1993. Taxonomy and distribution of the lichen family *Cladoniaceae* in the Antarctic and peri-Antarctic regions. *Cryptogamic Botany*, **3**, 310–344.

Valladares, F. & Sancho, L.G. 1995. Lichen colonisation and recolonisation of two recently deglaciated zones in the maritime Antarctic. *Lichenologist*, **27**, 485–494.

Valladares, F., Sancho, L.G., Chico, J.H. & Manrique, E. 1997. Diferencias en la utilizacion fotosintetica de radiaciones luminicas elevadas por lichenes y plantas vasculares en la Antártida marítima. *Bolétim de la Real Sociedad Española de Historia Natural, Sección Biológia*, **93**, 119–125.

Vestal, J.R. 1988. Carbon metabolism of the cryptoendolithic microbiota from the Antarctic desert. *Applied and Environmental Microbiology*, **54**, 960–965.

Vishniac, H.S. 1996. Biodiversity of yeasts and filamentous microfungi in terrestrial Antarctic ecosystems. *Biodiversity and Conservation*, **5**, 1365–1378.

Walker, F.J. 1985. The lichen genus *Usnea subgenus* Neuropogon. *Bulletin of the British Museum*, **B13**, 1–130.

Winkler, J.B., Kappen, L. & Schulz, F. In press. Snow and ice as an important ecological factor for the cryptogams in the maritime Antarctic. *In* Davison, W., *ed. Antarctic ecosystems: models for wider ecological understanding*. Christchurch, NZ: Caxton Press.

Woodward, F.I. 1993. How many species are required for a functional ecosystem? *In* Schulze, E.-D. & Mooney, H.A., *eds. Biodiversity and ecosystem function*. Berlin: Springer Verlag, 271–291.

Ye, H., & Mather, J.R. 1997. Polar snow cover changes and global warming. *International Journal of Climatology*, **17**, 155–162.