

REVIEW

Living on the edge – plants and global change in continental and maritime Antarctica

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Abstract

Antarctic terrestrial ecosystems experience some of the most extreme growth conditions on Earth and are characterized by extreme aridity and subzero temperatures. Antarctic vegetation is therefore at the physiological limits of survival and, as a consequence, even slight changes to growth conditions are likely to have a large impact, rendering Antarctic terrestrial communities sensitive to climate change.

Climate change is predicted to affect the high-latitude regions first and most severely. In recent decades, the Antarctic has undergone significant environmental change, including the largest increases in ultraviolet-B (UV-B; 290–320 nm) radiation levels in the world and, in the maritime region at least, significant temperature increases. This review describes the current evidence for environmental change in Antarctica, and the impacts of this change on the terrestrial vegetation. This is largely restricted to cryptogams, such as bryophytes, lichens and algae; only two vascular plant species occur in the Antarctic, both restricted to the maritime region. We review the range of ecological and physiological consequences of increasing UV-B radiation levels, and of changes in temperature, water relations and nutrient availability. It is clear that climate change is already affecting the Antarctic terrestrial vegetation, and significant impacts are likely to continue in the future. We conclude that, in order to gain a better understanding of the complex dynamics of this important system, there is a need for more manipulative, long-term field experiments designed to address the impacts of changes in multiple abiotic factors on the Antarctic flora.

Keywords: climate change, nutrients, ozone hole, temperature, UV-radiation, water relations

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Introduction

The Antarctic continent is the coldest, highest, driest, windiest and most isolated landmass on Earth. Growth conditions are therefore extreme, and plants exist at the physiological limits of survival. Plants are confined to the few ice-free areas, which constitute less than 2% of the continent. Characteristic of Antarctic growth conditions are low summer temperatures, a strongly seasonal climate, a very short growing season, continuous light in midsummer and frequent strong winds.

As a consequence of these severe conditions, the Antarctic flora is almost entirely cryptogamic, only two vascular species occur, both of which are restricted to the relatively mild Antarctic Peninsula.

Antarctica and the detection of climate change

Climate change is expected to impact first, and most severely, in the high latitudes (Callaghan *et al.*, 1992; Vincent, 1997; Walker, 1997), rendering Antarctica one of the most significant baseline environments for the study of global climate change (Lewis Smith, 1990b; Walton *et al.*, 1997). Vegetation characteristics, such as a simple community structure, and the geographic isolation of the Antarctic continent also contribute to

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the importance of this region in climate change research. The largely cryptogamic vegetation of continental Antarctica, dominated by bryophytes (mosses and liverworts) and lichens, constitutes one of the simplest ecosystems in the world, and therefore provides a biological study system with minimal associated ecosystem interactions (Lewis Smith, 1988a, b). In Antarctica, where vegetation grows at the physiological limit of survival, plants would be expected to show a more marked response to changes in growth conditions than those from less extreme climates (Adamson & Adamson, 1992; Callaghan *et al.*, 1997; Melick & Seppelt, 1997; Hansom & Gordon, 1998), thus enhancing the suitability of this system for the detection of environmental change. The life history characteristics of polar species (Callaghan *et al.*, 1992) and the precarious freeze–thaw balance, which influences many aspects of these ecosystems (Vincent, 1997), render high-latitude ecosystems vulnerable to change. In addition, the geographic isolation of the Antarctic continent further enhances the value of the vegetation of this region for climate change research, because it remains relatively free from the concurrent effects of anthropomorphic phenomena such as land use changes, weeds and pollution (Callaghan *et al.*, 1992). It is believed that, since polar regions have been relatively undisturbed, small climatic shifts may have a significant impact on biological habitats (Melick & Seppelt, 1997).

Vegetation and phytogeographic zones

Antarctica has been divided into three phytogeographic zones (continental, maritime and periantarctic; Fig. 1, Stonehouse, 1989). The high-latitude, Continental Antarctic, is the most climatically severe zone. The north-west coast of the Antarctic Peninsula and associated islands (including King George, South Shetlands, Sandwich and Orkney and Peter I Øy) make up the relatively mild Maritime Antarctic. The present review focuses on the continental and maritime zones.

Despite the severe growth conditions, plants are found on the Antarctic continent, although many species, including the two Angiosperms, are restricted to the relatively mild maritime zone (Table 1; Lewis Smith, 1984; Edwards & Smith, 1988; Hansom & Gordon, 1998; Longton, 1988). Outside the maritime zone, the remaining cryptogamic vegetation is primarily limited to a few small rocky outcrops along the coast, the dry valleys and inland nunataks (Hansom & Gordon, 1998). These continental areas are considered polar deserts, as the precipitation is less than 100 mm yr⁻¹ and is almost always delivered as snow (Kappen, 1985a). Exacerbating the extremely dry conditions are the subzero summer temperatures, which

lock most water away as snow and ice, significantly limiting plant productivity (Hansom & Gordon, 1998). Despite limitations to growth, mosses have been reported from as far south as 84°S and although bryophyte fruiting events are rare in the continental Antarctic zone (Wise & Gressitt, 1965; Filson & Willis, 1975), moss sporophytes have been reported as far south as 77°55'S (Seppelt *et al.*, 1992). In addition to the relatively conspicuous mosses and lichens, the continental Antarctic terrestrial vegetation includes groups that are often overlooked, including the chasmoendolithic algae, which occur only within rock fissures. These organisms are widespread in coastal regions of Antarctica and are believed to underlie up to 20% of the rock surface in some locations (Longton, 1985; Hansom & Gordon, 1998).

Adaptations to severe conditions

Cryptogams are poikilohydric, and as a result, during periods of low water availability or freezing temperatures, they possess the ability to enter a dormant state of physiological inactivity through controlled dehydration of their cells. Many Antarctic plants can therefore survive frozen and desiccated, beneath a cover of snow, over the long dark winter and rehydrate during the spring thaw for the short summer growing season of 1–4 months (Melick & Seppelt, 1997). Emerging from beneath the protective and insulating snow cover, these plants are exposed to the extreme conditions of the frigid Antarctic climate with frequent subzero temperatures, desiccating winds, intermittent water supply, a highly seasonal light regime and more recently, elevated ultraviolet-B (UV-B; 290–320 nm) radiation levels. Plant photosynthetic rates and consequently growth and productivity are greatly influenced by these environmental variables. Optimizing photosynthesis over the short growing season depends on the ability of these plants to acclimate to prevailing environmental conditions in this highly seasonal and variable climate (Melick & Seppelt, 1994b).

Distribution and community structure

Antarctic plant distributions are primarily determined by environmental factors such as temperature (Adamson & Adamson, 1992), moisture availability (Adamson & Adamson, 1992; Schwarz *et al.*, 1992; Melick & Seppelt, 1994a) and microtopography (Schwarz *et al.*, 1992; Melick & Seppelt, 1994a).

Most species occurring on continental Antarctica are restricted to either the continental or the maritime zone and only a few species are found in both (Table 1; Hansom & Gordon, 1998). For the cryptogamic species, lichens tend to predominate in drier, more exposed

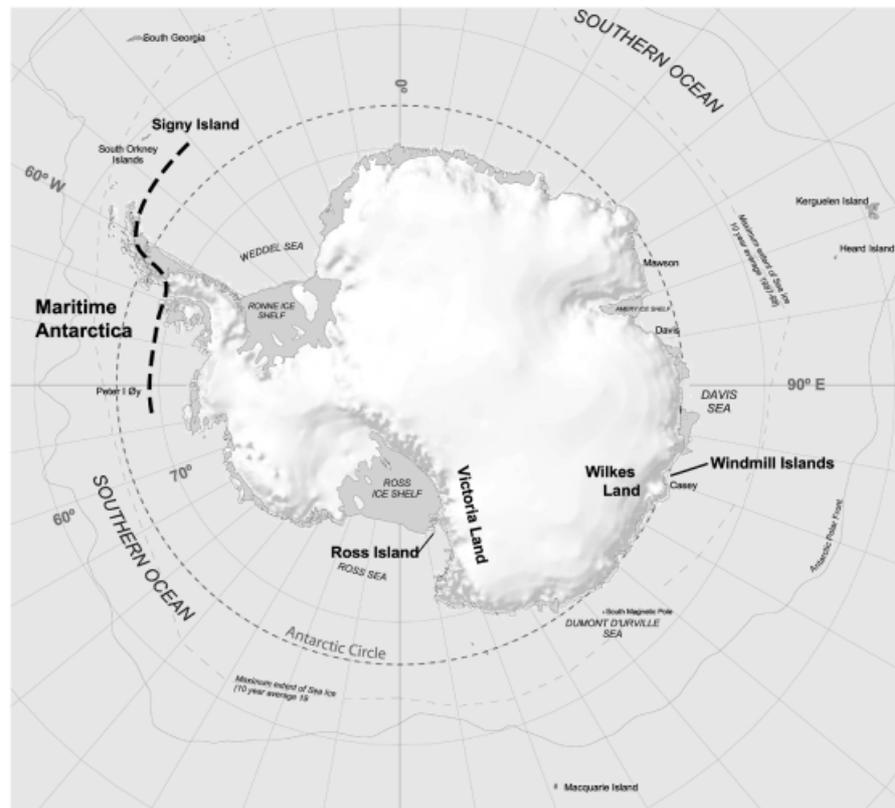


Fig. 1 Map of Antarctica. The Maritime Antarctic is the area to the left of the dashed line. The Periantarctic islands are found north of the limit of sea ice and bounded by the polar front. Locations where much of the research described in this review was conducted include Signy Island, Maritime Antarctic, Windmill Islands, Wilkes Land, Ross Island and Victoria Land.

Table 1 Estimated contribution of plant groups to the terrestrial plant biodiversity of Antarctica

Phytogeographic zone	Angiosperms	Mosses	Liverworts	Lichens	Macrofungi	References
Continental	–	30	1	125	2	Lewis Smith (1984)
Maritime	2	75	25	150	22 +	Lewis Smith (1984)
Total	2	85	25	200 +	28	Longton (1985)

locations, while bryophytes are restricted to moist, sheltered refuges (Lewis Smith, 1988). Of the two maritime Antarctic vascular species, the grass *Deschampsia antarctica*, which grows as dense tussocks, is relatively widespread compared with the cushion-forming pearlwort, *Colobanthus quitensis*, which is restricted to three localities (Corner, 1971; Komarkova *et al.*, 1985). The environmental conditions favourable to these latter species are found in sandy, mineral-rich, well-drained substrates that do not have a continuous supply of melt-water throughout the growing season, but do have some moisture-holding capacity (Komarkova *et al.*, 1985).

Antarctic terrestrial plant communities have small stature, low biomass, low productivity and low species diversity (Seppelt *et al.*, 1988). There is, however, a wide range of growth forms, including endolithic algae and

lichens (Broady, 1981b; Friedmann, 1982), and epiphytes (Seppelt & Ashton, 1978; Broady, 1981a), with communities containing multispecies assemblages that display both vertical and horizontal complexities (Seppelt *et al.*, 1988).

A small number of ice-free coastal areas in Antarctica support relatively rich and/or extensive floristic assemblages, and as a consequence these sites have been the focus of much research. These sites include the Windmill Islands Region, Wilkes Land, Ross Island, Victoria Land and Signy Island (see Fig. 1).

Antarctic research history and aims of this review

Early Antarctic terrestrial studies, prior to 1965, were limited to qualitative and taxonomic works, and are

reviewed in Lewis Smith (1984). Since the 1970s, research has become both more quantitative and directed towards species autecology and community and ecosystem processes (Lewis Smith, 1984). The research on vegetation patterns, life history attributes and ecosystem processes has been extensively reviewed (e.g. Lindsay, 1978; Longton, 1979; Pickard & Seppelt, 1984; Convey, 1996; Hansom & Gordon, 1998; Green *et al.*, 1999). Only a handful of review articles have been related to climate change, with topics including: Antarctic plants as indicators of climate change (Green *et al.*, 1999), polar desert ecosystems (Vincent, 1997), the ecological considerations of Antarctic ozone depletion (Karentz, 1991) and global change research strategies (Weller, 1992). The most relevant works are those discussing the potential effects of global climate change on Antarctic terrestrial ecosystems (Adamson & Adamson, 1992; Kennedy, 1995, 1996; Convey, 2001a,b). These reviews have all identified the need for greater research into the responses of Antarctic plants to climate change. We focus on research published in the last decade and indicate where research is still required. We address how terrestrial, photosynthetic eukaryotes are likely to cope with climate change. In doing this, we identify the major factors currently influencing plant distribution and productivity in Antarctica, discuss how these factors are likely to change and consider the potential impacts of such changes on the Antarctic flora.

UV and solar radiation

The Antarctic 'ozone hole'

Seasonal stratospheric ozone depletion over the Antarctic continent is evident in data collected since the 1970s (Kerr & McElroy, 1993; Frederick *et al.*, 1998). Prior to 1978, ozone layer thickness was generally >300 Dobson Units (DU) over Antarctica. The 'ozone hole', which is defined as the average area with an ozone thickness of <220 DU, develops during the austral spring (September–November) and is closely linked with the polar vortex (Roy *et al.*, 1994). Ozone depletion has recently extended into the mid-latitudes reaching South America and the south island of New Zealand (Stolarski *et al.*, 1986; McKenzie *et al.*, 1999). The largest 'ozone holes' were recorded between 1998 and 2001, with areas twice that of Antarctica (Fig. 2) and minimum ozone thickness reaching 90 DU at the south pole (NASA, 2002). Despite international efforts to reduce emissions of chlorofluorocarbons, substantial ozone depletion is expected to continue for several decades (Anderson *et al.*, 1991; Shindell *et al.*, 1998).

Ozone depletion results in elevated UV-B levels at the Earth's surface, with a spectral shift to the more



Fig. 2 Depth and area of the Antarctic ozone layer from 1980 to 2002 showing (a) minimum ozone concentration (Dobson Units) between 60°S and 90°S and (b) area of the springtime Antarctic ozone hole (ozone depth <220 DU, data represent 30 days mean with vertical lines showing minimum and maximum area). The area of the Antarctic Continent is shown for comparison. Data were collected from the following spacecraft; the Nimbus 7 Total ozone monitoring spectrophotometer (TOMS; 1979 and 1992), the Meteor 3 TOMS (1993 and 1994) and the Earth probe TOMS (1996–2000). No TOMS was in orbit in 1995. Figure redrawn from NASA (2002).

biologically damaging shorter wavelengths (Frederick & Snell, 1988). As a consequence, Antarctica now experiences high UV-B levels through much of the spring, caused by the combined effects of the dissipating ozone hole and the approach of the natural annual radiation peak, the summer solstice (Frederick & Snell, 1988; Karentz, 1991; Roy *et al.*, 1994). In Antarctic ecosystems, snow cover can offer protection from excess photosynthetically active radiation (PAR) and also damaging UV-B radiation (Marchand, 1984). Furthermore, the spectral composition of sunlight transmitted through snow is primarily between 450

and 600 nm, with shorter and longer wavelengths removed (Salisbury, 1984). However, these figures vary with the depth and density of snow cover. After snowmelt, submergence beneath water may reduce incident PAR. Water preferentially absorbs longer wavelengths and, although some attenuation of shorter wavelengths does occur, it offers only limited UV-B protection (Cockell & Knowland, 1999). In addition to changes in incident UV-B due to stratospheric ozone distribution and concentration, actual UV-B experienced on the ground is highly variable because it is strongly influenced by cloud cover, geometry and albedo (Bodeker, 1997).

Impact of UV-B on Antarctic plants

Damage by UV-B radiation

Absorption of UV-B radiation by plants can damage and disrupt key biological molecules, with an array of repercussions for the physiological functioning of the plant (reviewed by Greenberg *et al.*, 1997; Rozema *et al.*, 1997; Jansen *et al.*, 1998; Tobin, 2003). The first line of defence is to screen UV-B radiation before it reaches the cell, then to minimize damage within the cells through other protective strategies, and finally to repair damage once it has occurred (Fig. 3; reviewed by Stapleton, 1992; Jansen *et al.*, 1998). Since repair mechanisms are often incomplete, prevention of damage, through avoidance of UV-B absorption, should be more effective (Cockell & Knowland, 1999). Damage to biological molecules can occur through direct absorption of UV-B

or indirectly as a result of the production of reactive oxygen species (ROS; Fig. 3). Although such molecular effects of UV-B damage can manifest as reduced photosynthesis and growth of the plants, recent reviews have argued that photosynthetic productivity is unlikely to be significantly affected by increasing UV-B (Allen *et al.*, 1998), and direct effects on plant communities are likely to be subtle (Caldwell *et al.*, 1999).

Vulnerability to UV-B damage is likely to be greater in plants occurring at high latitudes due to the fact that they have evolved under lower UV-B conditions (Caldwell *et al.*, 1982; Barnes *et al.*, 1987; Marchant, 1997). Prior to ozone depletion, polar plants were growing under the lowest UV-B levels on earth, and in the last few decades they have been exposed to similar levels as temperate plants, having little time for evolutionary adjustment and acclimation (Karentz, 1991). Measurement of UV-B incident on similar altitude polar sites in 1991 showed that the Antarctic site was exposed to 150% greater UV-B than the Arctic site (Madronich *et al.*, 1995). The annual occurrence of the 'ozone hole' also coincides with time of emergence from winter dormancy beneath the protective snow cover (Karentz, 1991; Adamson & Adamson, 1992; Wynn-Williams, 1994), exposing plants to sudden elevations of UV-B radiation in combination with increased PAR and greater temperature fluctuations. Bryophytes may be particularly susceptible to UV-B damage because of their simple structure, with most having leaves that are only one cell thick and lacking protective cuticles or epidermal layers (Richardson, 1981; Gehrke, 1998; Gwynn-Jones *et al.*, 1999). The survival of Antarctic plants under 'ozone depletion' depends on their ability to acclimate, by employing photoprotective mechanisms to avoid and repair UV-B damage.

Studies investigating the impact of UV-B exposure on Antarctic vascular plants, bryophytes and terrestrial algae are summarized in Table 2 (photosynthetic parameters, growth and reproduction) and Table 3 (UV-B screening and photosynthetic pigments). The majority of studies to date have employed screens that reduce UV-B below the current levels. Such screens usually have confounding effects on temperature and water availability. The effect on precipitation may be less of a problem in Antarctica, since blowing snow can still accumulate under horizontal screens, reducing the negative effects (Robinson, 1999). However, screens with sides can elevate temperatures compared with those without sides, and have larger effects on water availability by reducing precipitation or increasing humidity (Huiskes *et al.*, 2000). These confounding factors must be considered when interpreting results, and in comparisons of screened with unscreened control treatments.

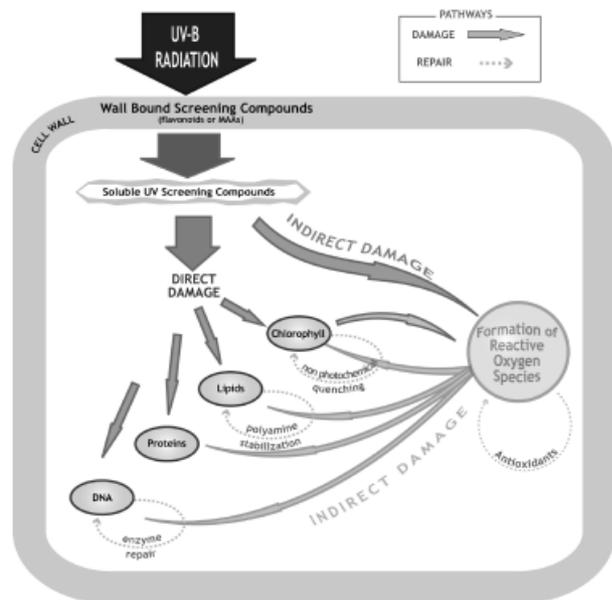


Fig. 3 Diagram to show potential effects of UV-B radiation on plant cells, showing screening, sites of damage and mechanisms of protection.

Table 2 Summary of effects of UV-B radiation on photosynthetic parameters, growth and reproduction in Antarctic plants and terrestrial algae

Plant group and species	Duration and type of study	Photosynthetic parameters	Growth	Reproduction	References
Vascular plants <i>Deschampsia antarctica</i>	2 m field screening study		Reducing UVR improved growth		Day <i>et al.</i> (1999)
	4 m field screening study		Leaves longer (cells elongated) under reduced UVR		Ruhland & Day (2000)
	4 m field screening study (pot grown)	O ₂ evolution not affected on area basis but higher on both chlorophyll and leaf mass basis under reduced UV-BR. Φ PSII higher under reduced UV-BR but F_v/F_m not affected	Total leaf area, tillar length and total biomass increased with reduced UV-BR. Leaves thinner under reduced UV-BR		Xiong & Day (2001)
	4 yr screening study		Leaf elongation faster with reduced UV	Overall no change per unit area. Slower development and reduced number of panicles under reduced UV-BR – offset by more spikelets. Larger seeds under reduced UV-BR but germination rates similar	Day <i>et al.</i> (2001)
<i>Colobanthus quitensis</i>	1 m and 2 yr screening studies	No effect of screening on Φ PSII or F_v/F_m			Huiskies <i>et al.</i> (2001), Lud <i>et al.</i> (2001b)
	7 d UV-BR field enhancement	No change in Φ PSII			Montiel <i>et al.</i> (1999)
	90 d enhanced UV-BR, controlled environment	No change in Φ PSII, A_{max} or dark respiration	Shoot length reduced, more branching of shoots and thicker leaves under increased UV-BR. Overall no effect on RGR		Rozema <i>et al.</i> (2001)
	2 m field screening study		Some indications of improved growth under reduced UV-BR		Day <i>et al.</i> (1999)
4 m field screening study (pot grown)	O ₂ evolution not affected on area basis but higher under reduced UV-BR on both chlorophyll and leaf mass basis. Midday Φ PSII slightly higher under reduced UV-BR but F_v/F_m not affected		Total leaf area, cushion diameter and total biomass increased with reduced UV-BR. Leaves thinner under reduced UV-BR		Xiong & Day (2001)

Similar 63 d study	RGR and NAR higher under reduced UV-BR. Higher shoot biomass, more branching and more leaves per shoot, larger leaves and greater leaf longevity under lower UV-BR. Leaf area higher, but total leaf biomass unchanged, due to lower SLM with reduced UV-BR	Higher reproductive biomass, capsules heavier under reduced UV-BR	Xiong <i>et al.</i> (2002)
Summer season screening	Seedlings produce more leaves and branches and have greater leaf area if grown under reduced UV-BR	No effect of UV-BR on seedling survival	Ruhland & Day (2001)
4 yr screening study	Increased leaf length, branching, cushion diameter, aboveground biomass and numbers of green leaves per shoot with reduced UV-BR	Overall no change per unit area. Slower development and reduced number of capsules with reduced UV-BR – offset by more seeds. Larger seeds under reduced UV-BR but germination rates similar	Day <i>et al.</i> (2001)
7 d UV-BR field enhancement	No change in Φ PSII		Montiel <i>et al.</i> (1999)
8 h screening study	No effect on P_n or F_v/F_m		Green <i>et al.</i> (2000)
1 m screening study	No effect on Φ PSII		Huisikies <i>et al.</i> (2001)
4–6 w study <i>in situ</i>	No effect of naturally increased UV-BR on F_v/F_m		Newsham <i>et al.</i> (2002)
7 d UV-BR field enhancement	Φ PSII reduced		Montiel <i>et al.</i> (1999)
2 d UV-BR field enhancement	No effect on P_{nr} , F_v/F_m or Φ PSII		Lud <i>et al.</i> (2002)
2 yr screening study	Density of thylakoids greater in shaded plants		Lud <i>et al.</i> (2002)
<i>Cephalozia exiliflora</i>	Reduced A_{max}		Post & Vesik (1992)
Algae	No effect on Φ PSII		
<i>Prasiola crispa</i>	No effect on gas exchange		Post & Larkum (1993)
			Huisikies <i>et al.</i> (2001)
			Lud <i>et al.</i> (2001a)

A_{max} , light saturated rate of photosynthesis; d, day; F_v/F_m , optimal efficiency of PSII; h, hour; m, month; NAR, net assimilation rate; Φ PSII, quantum yield of PSII; P_n , net photosynthesis; RGR, relative growth rate, UV-BR, ultraviolet-B radiation, w, week; yr, year.

Table 3 Summary of effects of UV-B radiation on UV-B screening and photosynthetic pigments in Antarctic plants and terrestrial algae

Plant group and species	Duration and type of study	UV-B absorbing pigments	Chlorophylls	Carotenoids	References
Vascular plants					
<i>D. antarctica</i>	2 and 4 m field screening study 4 m field screening study (pot grown) 2 yr screening study 90 d enhanced UV-B, controlled environment	No effect Lower under reduced UV-B No effect No effect	No change over 2 m Lower under reduced UV-B No effect	Total car. lower under reduced UV-B (methanol extract) No effect	Day <i>et al.</i> (1999) Ruhland & Day (2000), Xiong & Day (2001) Lud <i>et al.</i> (2001b) Rozema <i>et al.</i> (2001)
<i>C. quitensis</i>	2 m field screening study 63 d and 4 m field screening study (pot grown) Summer season screening	No effect Soluble pigments, measured on area basis, lower under reduced UV-B Trend for lower UV-B screening pigments in seedlings grown under reduced UV-B	No effect No change over 63 d Trend for higher chl. in seedlings grown under reduced UV-B	No effect Total car. reduced after 4 m (methanol extract)	Day <i>et al.</i> (1999) Ruhland & Day (2000), Xiong & Day (2001), Xiong <i>et al.</i> (2002) Ruhland & Day (2001)
Mosses					
<i>Bryum psuedotriquetrum</i>	6 m study <i>in situ</i>	High relative to other moss species and positively correlated with UV-B	High relative to other moss species. Negative correlation with TSR	VAZ positively correlated with TSR and WC. De-epoxidation status of VAZ negatively correlated with WC and air temp β -car positively correlated with WC and air temp (acetone extract)	Dunn (2000)
<i>B. argenteum</i>		Correlation between flavonoid concentration in herbarium specimens of plants collected from Ross Sea area and historic UV-B levels Generally show the ability to accumulate flavonoids			Markham <i>et al.</i> (1990)
<i>Bryum</i> spp.					Adamson & Adamson (1992), Markham & Given (1988) Dunn (2000)
<i>Ceratodon purpureus</i>	6 m study <i>in situ</i>	Low relative to other moss species, no correlation with TSR. Anthocyanin pigments high on chl. basis	Low relative to other moss species. No correlation with TSR	VAZ positively correlated with TSR and WC. De-epoxidation status negatively correlated with WC and air temp β -car. positively correlated with WC and air temp	Dunn (2000)

<i>Grimmia antarctici</i>	6 m study <i>in situ</i>	Low relative to other moss species, no correlation with TSR	Greatest range compared to other moss species Strong negative correlation with TSR and positive correlation with WC	VAZ positively correlated with TSR TSR negatively correlated with WC. De-epoxidation status negatively correlated with WC and air temp β -car. negatively correlated with WC, positively correlated with air temp	Dunn (2000)
<i>S. uncinata</i>	4–6 w study <i>in situ</i>	Increased pigments under naturally elevated UV-BR	Unaffected by ozone depletion	Increased total car. under naturally elevated UV-BR. Higher N and β -car (acetone extract)	Newsham <i>et al.</i> (2002)
<i>Cephalozia varians</i>	2 yr screening 4–6 w study <i>in situ</i>	Increased pigments under naturally elevated UV-BR	No effect Unaffected by ozone depletion	Increased total car. under naturally elevated UV-BR. Higher N and V but lower L and Z Increased total car. under naturally elevated UV-BR	Lud <i>et al.</i> (2002) Newsham <i>et al.</i> (2002)
<i>Andreaea regularis</i>	4–6 w study <i>in situ</i>	Increased pigments under naturally elevated UV-BR			Newsham (2003)
Algae <i>Prasiola crispa ssp antarctica</i>		Higher relative to chl. in summer vs. winter. Higher UV screening pigments in upper portions of thalli Reduced under UV-A or UV-B screens relative to unscreened controls. Pigments lowest under snow (Dec) increased until March then declined No effect No effect	Evidence of chl. bleaching in top layer of thalli	Tcar/chl increased under elevated UV-BR (methanol extract)	Post & Larkum (1993) Jackson & Seppelt (1997)
	4 w controlled chamber elevated UV-BR 1–2 d enhanced or reduced UV-BR	No effect No effect	Reduced under elevated UV-BR	Most car. did not change under screening treatments, V decreased under reduced UB-BR but no Z found (methanol extract)	Post & Larkum (1993) Lud <i>et al.</i> (2001a)

A, antheraxanthin; β -car, β -carotene; chl, chlorophyll; car, carotenoid; d, day; h, hour; L, lutein; m, month; N, neoxanthin; NAR, net assimilation rate; TSR, total solar radiation; UV, ultraviolet; UV-BR, ultraviolet-B radiation; V, violaxanthin; VAZ, xanthophyll cycle pigments; w, week; WC, water content; yr, year; Z, zeaxanthin.

There is also considerable variation in the duration of studies, with some performed over just 1 day and others over several years. Long-term studies in the Antarctic are difficult to maintain, but given the inter-season variability in Antarctica, they are very important in establishing real trends in growth. We focus mostly on field studies, given the problems associated with reproducing natural solar radiation in controlled environment studies. However, in relation to induction of UV-B screening pigments or establishment of maximum rates of DNA damage, laboratory studies can be informative.

Photosynthetic activity, growth and reproductive characteristics

A number of studies have found that photosynthetic activity (estimated by measuring gas exchange or chlorophyll fluorescence) does not appear to be strongly affected by either reduced or elevated UV-B treatments in the two Antarctic vascular species (Table 2). However, growth was affected in a number of ways by exposure to UV-B. The major impact was a reduction in cell length, leading to shorter leaves. Less branching and fewer leaves per shoot led to reduced plant size and biomass, with effects more pronounced in *C. quitensis* than *D. antarctica* (Table 2). Leaves were also thicker in plants exposed to UV-B. Perhaps the cost of producing and maintaining thicker leaves explains the reductions in growth that occur in the absence of effects on photosynthesis (Xiong & Day, 2001; Xiong *et al.*, 2002). Long-term field studies showed similar but less pronounced impacts of UV-B radiation compared with similar length pot studies (Xiong & Day, 2001), but the latter showed high inter-annual variation and provided evidence of cumulative UV-B effects (Day *et al.*, 2001).

Exposure to UV-B accelerated plant development and led to greater numbers of reproductive structures in both species, although the weight of *C. quitensis* seed capsules declined with higher UV-B exposure (Table 2; Xiong *et al.*, 2002). However, since these structures produced fewer spikelets and seeds, the overall reproductive effort was unchanged. In addition, although the final seeds produced under UV-B exposure were smaller, their germination rates were unaffected (Day *et al.*, 2001).

In two Antarctic bryophyte species (*Sanionia uncinata* and *Bryum argenteum*), no reductions of net photosynthesis or chlorophyll fluorescence parameters were observed under current levels of UV-B (Table 2). However, in the 7 day field UV-B enhancement study, effective photochemical quantum yield (Φ PSII) was reduced in *S. uncinata* (Table 2). *In situ* studies suggest

that increases in screening and protective pigments (see below) are sufficient to protect the photosynthetic apparatus from the damaging impacts of UV-B radiation in bryophytes (see Table 3; Newsham *et al.*, 2002).

Although exposure of the terrestrial alga *Prasiola crispa* to elevated UV-B for 1 month in controlled environment cabinets led to reductions in maximum rates of oxygen evolution (Post & Larkum, 1993), these experiments were performed at low PAR levels, and subsequent field studies have not supported these findings (Table 2).

Studies of lichens in Antarctica have concentrated on the impact of excess visible radiation on photosynthesis and have found that, while photoinhibition was evident when lichens were water stressed (Hovenden *et al.*, 1994), it was less likely to be a factor when lichens were fully hydrated (Kappen *et al.*, 1998a). No significant effects of either screening or supplementation of UV-B have been observed. As with the excess PAR studies, it appears that lichens are far more sensitive to moisture content and temperature. Perhaps these factors, which are hard to control under screening treatments, have tended to obscure any potential impact of UV-B (Huiskes *et al.*, 2001; Lud *et al.*, 2001b).

To date, few studies relating growth or reproduction to UV-B exposure have been reported for Antarctic bryophytes, lichens or algae. However, in one study of the moss *S. uncinata*, the shoot biomass and length were unaffected, but shoots had less branching, when turves were screened to reduce UV-B for 2 years (Lud *et al.*, 2002).

Studies of interactions between UV-B and other environmental factors (such as water availability and temperature) are particularly important because it is likely that there are interactive effects of these multiple stressors. In the Arctic, such studies have shown that soil microbial biota is more sensitive, than associated plants, to UV-B and CO₂ (Johnson *et al.*, 2002). These types of studies highlight the fact that the most profound effects of UV-B on plant communities may well be indirect (Caldwell *et al.*, 1999).

UV-B-absorbing compounds

Pigments that absorb biologically damaging UV-B while transmitting essential PAR are widespread across the plant kingdom (Cockell & Knowland, 1999). The primary UV-B-absorbing pigments found in higher plants are flavonoid compounds, providing a broad UV-B screen (Swain, 1976). UV-B-absorbing pigments such as flavonoids are wavelength-selective UV-B screens, which can accumulate rapidly in response to high UV-B radiation levels (Caldwell *et al.*, 1983). In addition to their UV-B-absorbing properties, some flavonoids (e.g. quercetin and luteolin) with additional

hydroxyl groups are thought to function as antioxidants, thus protecting plants against oxidative damage (see below; Bornmann *et al.*, 1997). Accumulation in higher plants is primarily in the epidermis, screening physiologically important molecules below (Fig. 3; Robberecht & Caldwell, 1978; Tevini *et al.*, 1991; Vogt *et al.*, 1991; Lois, 1994; Cuadra & Harborne, 1996; Bjerke *et al.*, 2002; Buffoni-Hall *et al.*, 2002). The accumulation of UV-B-absorbing pigments would be particularly useful in Antarctic plants because such passive screens could protect them from UV-B damage when physiological inactivity, due to desiccation or freezing, renders active repair mechanisms unavailable (Lovelock *et al.*, 1995a,b; Cockell & Knowland, 1999). UV-absorbing compounds have been investigated in a number of Antarctic terrestrial species from cyanobacteria to terrestrial plants. In general, cyanobacteria are protected by mycosporine-like amino acids (MAAs) and scytonemins, while terrestrial plants contain flavonoids (Fig. 3; Rozema *et al.*, 2002).

Several studies have investigated the effect of screening UV-B radiation on internal pigment concentrations in the two Antarctic vascular species, *D. antarctica* and *C. quitensis* (Table 3). These studies, performed over several years, have shown that in the short term (4 months), UV-B pigments may be higher under ambient rather than reduced UV-B radiation, but this trend was not found in longer term studies (Table 3; Lud *et al.*, 2001b). Elevated UV-B supplied in growth cabinets for 90 days also failed to produce an increase in UV screening pigments in *D. antarctica* (Rozema *et al.*, 2001). Leaves of both plants showed a low epidermal transmittance of UV-B (4% *D. antarctica*, 0.6% *C. quitensis*), suggesting that they may rely on wall-bound phenylpropanoids, which provide a spatially uniform filter, rather than on soluble UV-B pigments (Ruhland & Day, 2000). Levels of UV-B pigments were, however, higher in seedlings, suggesting that immature plants utilize soluble pigments, while developed leaves produce compounds bound to cell walls (Ruhland & Day, 2001).

Mosses are generally assumed to have a low capacity to produce flavonoids and tissue protection is usually less than in phanerogams and lichens (Callaghan *et al.*, 1992). In a survey of the response of plant functional types to enhanced UV-B radiation studies, mosses showed no stimulation of flavonoid production (Gwynn-Jones *et al.*, 1999). Most of the studies (total six globally) investigated arctic and periantarctic ecosystems, where bryophytes are among the dominant plants. Two of the five Antarctic bryophytes studied, *Grimmia antarctici* and *Ceratodon purpureus*, support this observation, showing low levels of UV-B-absorbing compounds and no evidence of stimulation in response

to elevated UV-B levels (Table 3). However, two recent studies of bryophytes *in situ*, which related concentrations of UV-B pigments to natural solar UV-B over a summer season (Dunn, 2000; Lovelock & Robinson, 2002; Newsham *et al.*, 2002), suggest that some bryophytes do produce screening pigments. Newsham *et al.* (2002) showed that UV-B-absorbing pigments were induced within 24 h under naturally elevated UV-B in the mosses *S. uncinata* and *Andreaea regularis* and the liverwort *Cephaloziella varians* on the Antarctic Peninsula (Newsham *et al.*, 2002; Newsham, 2003). Dunn (2000) showed that of the three dominant mosses found in the Windmill Islands, one (*B. pseudotriquetrum*) produced UV-absorbing pigments in response to increased UV-B radiation, while the other two (*C. purpureus* and *G. antarctici*) did not. In addition, Markham and coworkers (Table 3) demonstrated that flavonoid concentrations in herbarium specimens of Antarctic *Bryum* spp. were correlated with historical ozone levels (Markham & Given, 1988; Markham *et al.*, 1990). These latter studies show that at least for Antarctic bryophytes, the majority studied to date do produce sunscreens. Given the paucity of studies conducted worldwide, it is probably too early to conclude that this is not the case elsewhere.

Studies on the terrestrial alga, *P. crispa*, have also yielded contradictory results with higher levels of UV-B-absorbing pigments in summer than winter, but no response to increased UV-B in controlled environment studies, or in short-term UV supplementation studies (Table 3). Levels of UV-absorbing pigments appear to be constitutively higher than in most marine green algae, and screening treatments have generally resulted in reduced levels of all pigments rather than showing a specific effect on those absorbing UV-B (Lud *et al.*, 2001a). There is also evidence of chlorophyll bleaching in the uppermost, exposed layers of this sheet alga, and gradients of UV-absorbing pigments have been observed from exposed to self-shaded cell layers, suggesting that the upper thalli confer protection to the lower layers of cells (Table 3).

Most of the studies described above have been concerned with soluble UV-B pigments. However, not all pigments are soluble – some are bound to cell walls (Ruhland & Day, 2000). There is therefore a general need for further studies to investigate the role that such insoluble flavonoids might play in UV screening in Antarctic plants.

Photosynthetic and photoprotective pigments

Photo-oxidative damage can also occur as a result of UV-B radiation, with detrimental effects on DNA, photosynthetic pigments and membrane integrity (Fig. 3;

Murphy, 1983; Renger *et al.*, 1989; Tevini & Teramura, 1989; Middleton & Teramura, 1993; Tevini, 1993). Since any excess radiation (PAR or UV) can lead to the production of ROS, photosynthetic pigments adjust to optimize absorption of sunlight while avoiding photodamage. This acclimation of pigments involves changes in the relative concentration of light-harvesting pigments (especially chlorophylls), and antioxidant and photoprotective pigments that can reduce the likelihood of chlorophyll photo-oxidation (such as zeaxanthin and β -carotene; Young, 1991; Demmig-Adams *et al.*, 1996). If UV-screening compounds are unable to reduce UV penetration sufficiently, these carotenoids may be able to minimize the damage to macromolecules (Fig. 3). Comparison between studies of the levels of chloroplast pigments is complicated by variation in the extraction procedures used, and in the analytical techniques applied to separate and quantify these pigments. In studies of higher plants, sequential, and often multiple, extractions in 80% and 100% acetone are required to obtain accurate quantification of the various carotenoids and chlorophylls (Lovelock & Robinson, 2002). However, in phytoplankton studies, methanol extractions are more common (Wright *et al.*, 1991) and many studies of Antarctic bryophytes and vascular plants have utilized this extraction method (Table 3). Direct comparison of methanol and acetone extractions for various algae and plant species revealed that these solvents are equally efficient for extraction of xanthophylls and chlorophylls, but that acetone was more effective for extraction of the more hydrophobic carotenes (Dunn *et al.*, submitted). Some of the differences observed between studies may therefore be due to the different extraction methodologies employed.

For the two Antarctic vascular plants, studies have either shown a reduction in chlorophyll under reduced UV-B radiation or no effect on chlorophyll concentration (Table 3). The ratio of carotenoid to chlorophyll was higher in UV-B-exposed plants in some studies, but not in others (Table 3).

In continental Antarctica, low temperatures and low water availability often limit photosynthesis, while long summer days provide excess light, thus increasing the potential for photoinhibition and photodamage (Adamson *et al.*, 1988). Photoinhibition is reported to severely limit productivity in Antarctic bryophytes and photo-oxidative chlorophyll bleaching has been observed (Post *et al.*, 1990; Adamson & Adamson, 1992). High levels of photoprotective and antioxidant carotenoids have been observed in some Antarctic mosses, and it appears that species with low levels of UV-B-absorbing pigments accumulate higher levels of carotenoids, suggesting the possibility that bryophytes can

use alternative mechanisms of UV protection (Fig. 3; Robinson *et al.*, 2001; Lovelock & Robinson, 2002). Dunn (2000) found that, in all species studied, the xanthophyll cycle pigments increased with increasing radiation and the de-epoxidation status was negatively correlated with plant water content and air temperature, indicating strong stress responses. These increases cannot be attributed to UV-B radiation alone since high levels of xanthophylls might relate purely to combined stress from PAR, drought and temperature (Lovelock *et al.*, 1995a,b). However, Newsham *et al.* (2002) reported significant changes in carotenoid concentration in response to natural UV-B radiation for both *S. uncinata* and *C. varians*. An overall increase in total carotenoids in response to elevated UV-B was reported for both *S. uncinata* and *A. regularis*, but decreases in lutein and zeaxanthin were counteracted by increases in neoxanthin and violaxanthin in *C. varians*. Chlorophyll content showed a negative correlation with radiation for two moss species (*G. antarctica* and *B. pseudotriquetrum*), but no obvious relationship was seen for *C. purpureus*, *S. uncinata* or *C. varians* (Dunn, 2000; Lud *et al.*, 2002; Newsham *et al.*, 2002).

Studies of plants grown in controlled, elevated UV-B environments are needed to clarify the relationship between carotenoid concentrations and exposure to UV-B radiation, and to establish if these pigments have a role in UV-B protection. If carotenoids are found to be important in UV protection, it is likely to be as antioxidants since they are unlikely to have a direct screening role. Such studies could also be used to investigate if UV-B screening pigments can be induced in Antarctic bryophytes.

DNA damage and repair

Direct damage to DNA results from absorption of photons, with 98% of the resulting damage occurring in the form of pyrimidine dimers, which prevent replication and gene transcription and thus have the potential to be mutagenic and disrupt cellular metabolism (Mitchell & Karentz, 1993; Taylor *et al.*, 1997). Of these pyrimidine dimers, 75% of those produced under natural sunlight are in the form of cyclobutyl pyrimidine dimers (CPDs), with the remainder being (6 – 4) photoproducts (6 – 4PP; Mitchell & Nairn, 1989). Both forms of damage can be repaired in plants by either light-dependent (photorepair) reactions, catalysed by photolyases, or by excision repair, which is light-independent (Britt, 1999). Excision repair is 'error prone' in all systems, while photoreactivation cannot take place in the dark and is vulnerable to temperature extremes. Damage prevention is therefore a necessary part of UV-B protection (Murphy, 1983; Taylor *et al.*,

1997). The accumulation and repair of pyrimidine dimers have been studied in a number of plant species but there are few published studies of such experiments involving Antarctic plants. CPDs have been shown to accumulate in the Antarctic terrestrial alga, *P. crispa*, exposed to both natural and elevated UV-B radiation (Lud *et al.*, 2001a), while CPDs accumulated only in response to elevated UV-B radiation in *S. uncinata* (Lud *et al.*, 2002). Preliminary studies in our laboratories have found that *C. purpureus* accumulates both 6-4PP and CPDs over the course of a 24-h cycle in Antarctica. There was no direct correlation between the amount of DNA damage and incident UV-B levels, although there is evidence from both field and laboratory studies that desiccation may result in DNA photoproduct accumulation (Duncan & Tobin, 2002). There is also evidence of high somatic variation in Antarctic bryophytes (Skotnicki *et al.*, 2000), which suggests that DNA damage is sustained by these plants. However, it is not clear at this stage whether such damage is related to increased UV-B exposure or induced by other factors such as desiccation or freezing. Field studies such as those performed by Rousseaux *et al.* (1999), which have found increased accumulation of DNA photoproducts in South American species exposed to naturally elevated UV-B, would be highly appropriate.

Elevated CO₂

The atmospheric concentrations of greenhouse gases, such as carbon dioxide, have been rising over the last few decades (Houghton *et al.*, 2001). Despite considerable research effort being focussed on this issue worldwide (see for example, Drake *et al.*, 1997), no research appears to have been conducted to investigate the ecological impact of rising CO₂ levels in Antarctic terrestrial ecosystems.

The only relevant work to date is a study by Tarnawski *et al.* (1992) on the dominant moss species in the Windmill Islands, *G. antarctici*. This showed that, while small cushions growing in dry sites might be CO₂ limited for much of the summer, high CO₂ levels were achieved throughout the summer in the turf form common to moist sites and making up most of the biomass of this species. Although an increase in ambient CO₂ levels, as a result of global climate change, might alleviate CO₂ limitations in certain populations, a significant increase in overall productivity seems likely only if water availability increases (see below).

Evidence from a non-Antarctic system suggests that elevated CO₂ may increase the temperature optimum for photosynthesis in mosses (Silvola, 1985). The interactions of increased CO₂ with increasing and decreasing water and temperature therefore require

investigation before we can attempt to predict the effect of elevated CO₂ on these communities.

Temperature

Evidence

The most recent report by the Intergovernmental Panel on Climate Change (IPCC) estimates that the global surface temperature has increased 0.6 °C since the late 19th century, with a 95% confidence interval of 0.4–0.8 °C (Houghton *et al.*, 2001). Climate models predict a rise in global average surface temperatures of 1.5–4.5 °C in response to doubling of greenhouse gas concentrations (Tokioka, 1995). Temperature increases are predicted to impact predominately on the high latitudes in winter, largely due to sea ice-albedo and snow-albedo feedbacks (Tokioka, 1995). Other polar feedback loops, which contribute to the heightened sensitivity of the high-latitude regions, include those involving sea-ice extent and temperature, for which evidence is provided from the Antarctic Peninsula region (King, 1994; Smith *et al.*, 1996).

Predictions for escalating temperatures are supported by meteorological evidence from the Antarctic Peninsula region, where temperatures have increased over the last half-century by 1 °C in summer (Lewis Smith, 1990b, 1994; Fowbert & Lewis Smith, 1994) and 4–5 °C in winter (Smith *et al.*, 1996). These substantial temperature increases appear to have already triggered ice-albedo feedback loops, evidence for which is provided from Signy Island, where there has been a 35% reduction in ice cover (Lewis Smith, 1990b).

However, temperature trends for the Antarctic continent as a whole are not so clear. A recent, detailed analysis using meteorological data (1957–1998) from stations throughout the Antarctic region and satellite data (1979–1998) for the Antarctic continent found contrasting trends. The 45 years record in the meteorological data showed an overall increase of 0.012 ± 0.008 °C yr⁻¹, but a decline of 0.008 ± 0.025 °C yr⁻¹ over the past 20 years. The recent 20-year trend is supported by the satellite data for the same period, which showed a more severe decline in temperature of 0.042 ± 0.067 °C yr⁻¹ (Comiso, 2000). Similar fluctuations have been detected in the Windmill Islands region, East Antarctica; average temperatures increased 0.086 °C yr⁻¹ from 1960 to the mid-1980s and then declined 0.010 °C yr⁻¹ to the mid-1990s (Melick & Seppelt, 1997). Evidence of a cooling trend for continental Antarctica has also been provided in a recent study that analysed meteorological records throughout Antarctica for the period 1966–2000 (Doran *et al.*, 2002). Contrary to the predictions of increasing global

temperatures, and measured warming trends of the maritime Antarctic, these studies suggest a recent cooling trend for the Antarctic continent. However, since Antarctic temperature trends vary spatially, seasonally and interdecadally, we believe that it is impossible at this stage to confirm consistent warming or cooling of the continent and for the purposes of this review, we will concentrate on the likely impacts of increasing temperature (see also Turner *et al.*, 2002; Walsh *et al.*, 2002).

Alien invasion

The ameliorating growth conditions provided by rising maritime Antarctic temperatures increase the threat of invasion by alien species in this region. Evidence from Signy Island has shown that there is a continuous immigration of sporomorphia from South America (Lewis Smith, 1991) and exotic pollen and spores have also been detected on the continent (Kappen & Straka, 1988; Linskens *et al.*, 1993). Particular species (Melick *et al.*, 1994b) and sites (Selkirk *et al.*, 1997) have been identified as having greater potential for invasion. In addition to the potential for species from outside Antarctica to colonize the continent, expansion of species ranges within Antarctica is also a possibility, and five native Antarctic species (Table 4) have been identified as potential long-distance dispersers (Convey & Lewis Smith, 1993). Under ameliorating climatic conditions, alien species invasion to the Antarctic may cause detrimental disruptions to the current ecological balance in these sensitive communities (Green *et al.*, 1999; Walther *et al.*, 2002). Although not yet determined experimentally, sporophyte production in bryophytes is thought to be limited by the low Antarctic temperatures (Filson & Willis, 1975; Seppelt *et al.*, 1992), so an increase in temperature is likely to result in an increase in sexual reproduction events, and consequently, an increase in spore production and dispersal within continental Antarctica. Combined with ameliorating growth conditions, the likelihood of colonization by new populations of native and alien species is projected to increase under a warmer climate.

Ecological impacts

Substantial evidence is available to suggest that plant community dynamics are changing in response to recent warming for the maritime Antarctic (Table 4). On Signy Island, the steady rise in summer air temperatures since the late 1940s, and the consequent reduction in ice cover, have provided more favourable growth conditions and new areas for colonization, respectively (Lewis Smith, 1990b). There have been

changes in abundance and area of the Antarctic vascular species, *D. antarctica* and *C. quitensis* (Lewis Smith, 1990b, 1994; Fowbert & Lewis Smith, 1994). A 26-year survey in the Argentine Islands archipelago, western Antarctic Peninsula, found a species-specific correlation with warming; *D. antarctica* showed a considerable increase in colony numbers and a 25-fold increase in the area of each colony, while no additional *C. quitensis* colonies were recorded and only a five-fold increase in area was observed (Fowbert & Lewis Smith, 1994). Day *et al.* (1999) conducted a manipulative field experiment, increasing the ambient temperatures for these species over two consecutive growing seasons. They also detected species-specific responses, but the direction was opposite to that found in the field survey. When growth was measured in terms of leaf and shoot length, leaf production and foliar cover, warming improved the growth of *C. quitensis* and reduced growth in *D. antarctica* (Day *et al.*, 1999). Both species showed more advanced development of reproductive structures, at the time of census, as a result of the experimental warming treatment.

In the absence of long-term, field-based monitoring of plant communities on the continent, predictions for the impact of temperature change on the distribution of species can only be based on laboratory experiments and/or indirect evidence (Table 4). Perhaps the most direct evidence for the ecological impact of temperature on continental vegetation is provided by a manipulative growth experiment from the Windmill Islands, demonstrating the regeneration potential of continental Antarctic moribund moss. This study showed that in samples with up to 75% crustose lichen encrustation, moribund moss regeneration was faster at 18 °C than at 2 °C (Melick & Seppelt, 1997).

It is thought that the extremely low temperatures that are characteristic of the Antarctic environment are the primary factor limiting Antarctic terrestrial vegetation to predominantly cryptogams. Antarctic vegetation is often limited to sites maintaining relatively high temperatures, which tend to be sheltered from cold winds, have high levels of solar radiation, and consequently high levels of snow and ice melt (Shimizu, 1977; Seppelt & Ashton, 1978; Kappen, 1985a). Lichen vegetation, for example, tends to be particularly rich on north-facing rock sites (Kappen, 1985a), where temperatures are consistently warmer. Sheltered sites are also where fruiting events, which occur relatively rarely in Antarctica, have been observed (Filson & Willis, 1975). Increasing temperatures on the continent are likely to see an expansion of the area suitable for reproduction, vegetation colonization and survival. Long-term monitoring of continental Antarctic terrestrial vegetation is crucial for accurate measurement and

Table 4 Summary of effects of temperature on Antarctic vascular plants, bryophytes and terrestrial algae

Scenario	Impact	Nature of impact	Major results	Plant group	Location	Field/lab	References
Increased temperature	Increased risk of alien invasion	Physiological	Current, low, Antarctic temps limit sporophyte production	B	C	F	Filson & Willis (1975), Seppelt <i>et al.</i> (1992)
		Ecological	Sporophyte production higher at high latitudes than previously expected. Relatively high in micro-oases Supply of pollen and spores to Antarctica	B VB L F	M C M	F FC/L	Lewis Smith & Convey (2002) Lewis Smith (1991) Linskens <i>et al.</i> (1993) Kappen & Straka (1988) Selkirk <i>et al.</i> (1997)
Altered distribution	Ecological	Ecological	Vestfold Hills are at greater risk of alien invasion than the Ross Sea Region Some species have greater potential for invasion than others	B	C	FC/L	Melick <i>et al.</i> (1994b)
			Five native Antarctic species identified as potential long-distance colonists Species-specific response to increasing summer air temps (1944–1992): species distributions 1964–1990 – <i>D. antarctica</i> increased in area 25-fold + increased colony numbers, <i>C. quitensis</i> increased in area five-fold, no new colonies <i>D. antarctica</i> and <i>C. quitensis</i> : increased number of individuals and populations during 27-yr monitoring period	B V	M M	FC/L F	Convey & Lewis Smith (1993) Fowbert & Lewis Smith (1994)
			<i>D. antarctica</i> and <i>C. quitensis</i> : increased number of individuals and populations during 27-yr monitoring period Manipulative field experiment: warming increased <i>C. quitensis</i> growth (increased leaf production, shoot production and foliar cover). Warming decreased growth of <i>D. antarctica</i> (decreased leaf length, leaf production and foliar cover). Improved sexual reproduction in both species Antarctic veg often limited to sites maintaining relatively high temps, which tend to be sheltered from cold winds, have high levels of solar radiation, and consequently high levels of snow and ice melt With up to >75% crustose lichen encrustation, moribund moss regeneration faster at 18 °C than at 2 °C Lichen veg particularly rich on north facing rock sites, where temps are consistently warmer	V V	M M	F F	Lewis Smith (1994) Day <i>et al.</i> (1999)
			Antarctic veg often limited to sites maintaining relatively high temps, which tend to be sheltered from cold winds, have high levels of solar radiation, and consequently high levels of snow and ice melt With up to >75% crustose lichen encrustation, moribund moss regeneration faster at 18 °C than at 2 °C Lichen veg particularly rich on north facing rock sites, where temps are consistently warmer	B L	C	F	Kappen (1985a), Seppelt & Ashton (1978), Shimizu (1977) Melick & Seppelt (1997) Kappen (1985a)

(Continued)

Table 4 (Continued)

Scenario	Impact	Nature of impact	Major results	Plant group	Location	Field/lab	References
Increased productivity	Physiological	Physiological	<p><i>D. antarctica</i> and <i>C. quitensis</i> grown at 7 °C, 12 °C or 20 °C: despite P_n being highest in plants grown at 12 °C, all measures of growth (RGR, total biomass, leaf area, LAR and leaf mass ratio) were greatest in 20 °C grown plants</p> <p>P_n increased with increased temp (tested up to 20 °C). Species differences: <i>B. argenteum</i> > <i>B. pseudotriquetrum</i> > <i>C. purpureus</i></p>	V	M	L	Xiong <i>et al.</i> (2000)
				<p><i>D. antarctica</i> and <i>C. quitensis</i>: negligible midday field P_n at canopy air temp > 20 °C, but high P_n at temps < 10 °C. Lab tests show high temp, not visible irradiance, was responsible for P_n depression</p> <p><i>D. antarctica</i> pronounced decline in P_n at supra-optimal temps (> 12 °C), P_n negligible at 35 °C</p>	B	C	FC/L
Reduced productivity	Physiological	Physiological	<p><i>D. antarctica</i> and <i>C. quitensis</i>: negligible midday field P_n at canopy air temp > 20 °C, but high P_n at temps < 10 °C. Lab tests show high temp, not visible irradiance, was responsible for P_n depression</p> <p><i>D. antarctica</i> pronounced decline in P_n at supra-optimal temps (> 12 °C), P_n negligible at 35 °C</p>	V	M	F+L	Xiong <i>et al.</i> (1999)
				<p>Increased photoinhibition with increased temp</p> <p><i>S. uncinata</i>: dark respiration decreased as temp increased (tested range: 0–20 °C). Low temps important for positive carbon balance: climate warming may reduce carbon gain by increasing respiratory loss</p>	B	C	F
Morphological changes	Physiological	Physiological	<p><i>D. antarctica</i>: leaf anatomy shows plastic response to changes in growth conditions</p> <p><i>C. quitensis</i> optimal leaf temp for P_n 14 °C, <i>D. antarctica</i> 10 °C. Continued warming: increased frequency of supraoptimal temps, but canopy temps currently average 4.3 °C and remain < optimal for 86% of diurnal periods during the growing season. Continued warming will usually increase P_n</p> <p>Optimum temp for P_n: <i>D. antarctica</i> 13 °C, <i>C. quitensis</i> 19 °C</p>	V	M	FC/L	Romero <i>et al.</i> (1999)
				<p>Optimal temp regime (day/night) 22/15 °C for a moss species</p> <p>P_n highest at 15 °C for <i>B. argenteum</i> (measured over temp range –8 °C to 21 °C)</p>	B	C	FC/L
Physiological ranges	Physiological	Physiological	<p><i>P_n</i> highest at 15 °C for <i>B. argenteum</i> (measured over temp range –8 °C to 21 °C)</p>	B	C	L	Green <i>et al.</i> (2000)

Table 4 (Continued)

Scenario	Impact	Nature of impact	Major results	Plant group	Location	Field/lab	References
Increased temperature			Moss and lichen summer temps higher than, and fluctuate more than, air temps (measured over 5 d). Exposed lichen surface temp recorded to fluctuate > 30 °C during a 5 h period	B L E	C	F	Melick & Seppelt (1994b)
			Moss surface temp range (~17 °C to ~0 °C) greater than range of air temps (~4 °C to ~-2 °C), during 1 d of observation	B S A	C	F	Seppelt & Ashton (1978)
Increased freeze-thaw	Increased damage	Physiological	Lichen temp higher (with greater fluctuations) than the relatively stable air temp (~28 h diurnal plot). Air temp ~0 °C, lichen temp ~0–35 °C	L	C	F	Inoue (1989)
			Diurnal fluctuations greater at ground level than in air above or soil below	E	C	F	(Longton (1974)
			Surface temp (rock) greater, with greater fluctuations, than air temps	E	C	F	Rudolph (1966)
			Increased loss of soluble carbohydrates, species differences in % loss	B	C	FC/L	Melick & Seppelt (1992)
			<i>P. alpestris</i> : repeated freeze-thaw cycles caused a greater reduction in gross PS than constant freezing over the same time period. Frequency of freeze-thaw significant impact: 12 h cycles, more damage than 24 or 48 h cycles	B	M	L	Kennedy (1993)
		Environmental	Spring/summer (Nov–Mar) few freeze-thaw cycles, those that occurred were not severe. Authors suggest that freeze-thaw cycling is unlikely to currently limit organism survival during summer: if freeze-thaw increases in frequency or severity, this may change	S	M	F	Davey <i>et al.</i> (1992)

DR, dark respiration; d, day; LAR, leaf area ratio; Φ PSII, quantum yield of PSII; P_n , net photosynthesis; PS, photosynthesis; RGR, relative growth rate; temp, temperature; veg, vegetation yr. Plant group codes: V, vascular plants; B, bryophytes; M, moss; L, lichen; L(P), lichen phycobiont; A, algae; E, fungi; C, cyanobacteria; S, soil. Location codes: C, Continental Antarctic; M, Maritime Antarctic. Study type: F, field based; L, laboratory based; FC/L, field collected/laboratory analyses; R, review; M-FD model, based on field data; M-LD model, based on laboratory data.

predictions of vegetation dynamics in response to future temperature regimes.

Photosynthetic physiology

The response of vegetation to elevated temperatures varies across species and regions. There is evidence available to suggest that both increases and decreases to productivity may occur (Table 4). Since the prevailing low temperatures throughout the Antarctic biome are generally considered to limit net photosynthesis (P_n) for most of the growing season, warming conditions would therefore be expected to increase primary productivity (Xiong *et al.*, 1999). Increased P_n under elevated temperatures has been demonstrated, for example, in three continental moss species (Lewis Smith, 1999) and the two maritime vascular species (Xiong *et al.*, 2000). There is, however, a wealth of literature that suggests increasing temperatures may cause declines in P_n (Table 4). This has been demonstrated for both mosses and vascular plants. Laboratory experiments using the maritime moss, *S. uncinata*, showed that over a temperature range of 0–20 °C, net photosynthesis remains low but dark respiration steadily increases (Nakatsubo, 2002). Low temperatures thus appear to be important for positive net carbon balance in this species, and increasing temperatures may reduce carbon gain by increasing respiratory loss (Nakatsubo 2002). Declines in P_n with increasing temperatures also occur for those species exhibiting increased photoinhibition under conditions of increasing temperatures, as has been demonstrated by field measurements of some continental Antarctic moss species (Kappen *et al.*, 1989).

In addition, a rise in temperature will cause an increase in the duration and frequency of supra-optimal temperature events, during which photosynthesis is often depressed. Laboratory measurements of the maritime vascular species, *D. antarctica*, show a pronounced decline in photosynthetic rates at supra-optimal temperatures (> 12 °C), with negligible photosynthesis at 35 °C (Vining *et al.*, 1997). In the field, both *D. antarctica* and *C. quitensis* have negligible mid-day net photosynthetic rates at canopy air temperatures greater than 20 °C, while high rates of mid-day net photosynthesis are obtained at temperatures of less than 10 °C. Accompanying laboratory experiments verified that high temperatures, not visible irradiance, were responsible for the photosynthetic depression observed (Xiong *et al.*, 1999). Currently, canopy air temperatures exceed 20 °C for less than 1% of diurnal periods (Day *et al.*, 1999) and mid-day photosynthetic depression events are uncommon. The temperature at which conditions become supra-optimal for photosynthesis varies between species (Table 4). Cited values

of optimal temperatures range from 10 °C in *D. antarctica* (Xiong *et al.*, 1999) to 20–25 °C in a maritime moss species (Rastorfer, 1972).

The data available show that although plant surface temperatures may exceed 40 °C during the growing season (Lewis Smith, 1986, 1988b), these elevated temperatures are not sustained (Xiong *et al.*, 1999). A continental study recorded moss surface temperatures above 13 °C less than 5% of the time and below 2.5 °C approximately 60% of the time (Longton, 1974). Exceptionally high temperatures are often accompanied by large diel fluctuations, an extreme example of which exceeded 50 °C (–9.2 °C to 42.8 °C) in a continental Antarctic moss species (Lewis Smith, 1988b).

Despite the evidence of photosynthetic depression during elevated temperatures, it has been demonstrated that, at least in the two maritime vascular species, increasing vegetative growth outweighs declines in photosynthetic rates under these high growth temperatures (Xiong *et al.*, 2000).

The lack of experimental, field-based manipulation of temperature, due to the difficulty of performing such experiments in the severe Antarctic climate, limits our knowledge in this area. However, open-top chambers have been successfully used to increase soil temperatures by +2.2 °C at 10 cm depth and +5.2 °C at the surface (Marion *et al.*, 1997). In addition, experimental manipulation of growth conditions has shown that some species have a greater potential for plasticity of optimal temperatures in response to elevated temperatures. Collins (1977) demonstrated that the maritime moss species, *Drepanocladus uncinatus* and *Polytrichum alpestre*, showed optimal temperatures for net photosynthesis of 15 °C and 5–10 °C, respectively, when grown under a temperature regime similar to field conditions. When grown at warmer temperatures, the optimal temperature for *D. uncinatus* remained at 15 °C, while that for *P. alpestre* increased to 15 °C. Species such as *P. alpestre*, which show a relatively plastic response to increased temperatures, may be better equipped to cope with future field temperature increases (Collins, 1977).

Experimental manipulation of temperature in the field has been achieved as a side effect of UV-B screening experiments, thus providing an opportunity to investigate the effect of elevated temperature (e.g. Huiskies *et al.*, 2001). Despite the challenge of conducting this kind of work in the severe Antarctic environment, well-designed experiments of this type are possible and are badly needed.

Impact of increased freeze–thaw

Temperature fluctuations that cause plant tissues to freeze and thaw cyclically may be more damaging than

exposure to cold temperatures alone (Kennedy, 1993), and there is some evidence that these events are increasing in frequency (Lovelock *et al.*, 1995a, b).

Continental Antarctic species can survive repeated freeze–thaw events (Melick & Seppelt, 1992), while maritime species appear to be less tolerant (Davey, 1997b). Tolerance of freeze–thaw events involves interactions with other environmental parameters, such as water availability. For example, desiccation prior to freezing reduces damage to the photosynthetic apparatus and protection from freeze–thaw can be provided by snow cover, which acts as an insulator (Lovelock *et al.*, 1995a, b). If climate warming results in reductions in snow cover, Antarctic plants may be more exposed to damage by freeze–thaw events in the future. Since freeze–thaw cycles reduce plant productivity and survival (Table 4), increases in the frequency and/or magnitude of the temperature differential of freeze–thaw cycles on the Antarctic continent are likely to have negative impacts on the Antarctic flora.

Precipitation and water relations

The predominance of extreme cold across the Antarctic continent locks most water away in the form of snow and ice, resulting in the Antarctic being the largest desert on Earth. Biologically available water is in the form of melt water, and it is confined to the summer months. Melt water can be derived from freshly deposited snow, or from melting of permanent snow and ice banks. A fine balance between the snow regime and melt patterns is crucial in maintaining water availability to these exceedingly dry habitats. A discussion of precipitation and water relations must therefore also consider snow relations. Incorporating the variables of temperature, precipitation and melt, we suggest a model that predicts the impact of climate change on water availability in Antarctic ecosystems (Fig. 4). Three possible paths are suggested; two scenarios lead to increasing aridity, while the third results in either unchanged or increased water availability. If an increase in the area of permanent snow cover was the result of the final scenario, a concomitant loss of habitat for plants would occur.

Evidence

Climate warming is predicted to increase global precipitation and evaporation levels by 3–15% (Tokioka, 1995). Two types of precipitations occur: (1) from cumuli-form clouds, which will increase globally in response to climate change; and (2) from strati-form clouds, which will decrease with climate change. The effect of climate change on global precipitation patterns

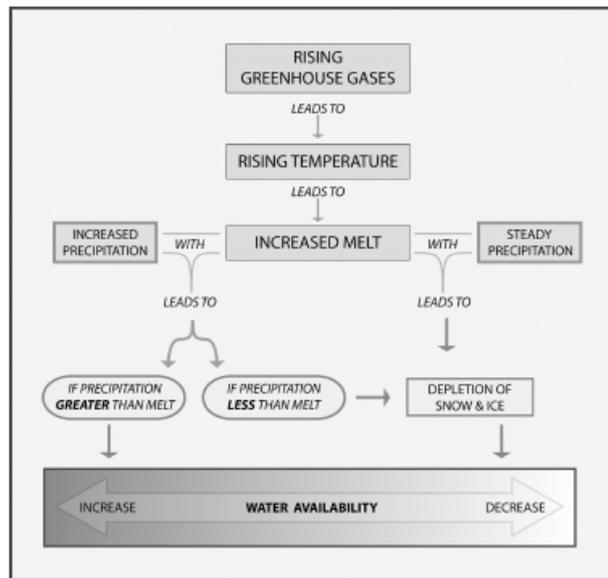


Fig. 4 Schematic model of impact of climate change on water availability in Antarctic ecosystems.

will therefore be a decrease in precipitation area, while precipitation amount will increase (Tokioka, 1995).

Under a global warming climate scenario, snow accumulation in Antarctica is predicted to increase (Ye & Mather, 1997). However, measurement of continental soil moisture levels shows that continental Antarctic moisture content is decreasing (Doran *et al.*, 2002). In the Windmill Islands, East Antarctica, the presence of moribund moss is considered indicative of a drying trend, which corresponds with glaciological and geomorphological evidence of isostatic uplift since the last glacial maximum (Melick & Seppelt, 1997).

Ecological impacts

Studies from across the Antarctic biome have established a correlation between water availability and species distributions (Table 5). The majority of these studies have investigated broad-scale patterns, covering large spatial scales and incorporating the majority of vegetation types or species (Rudolph, 1963; Nakanishi, 1977; Shimizu, 1977; Seppelt & Ashton, 1978; Lewis Smith, 1986, 1990a; Seppelt *et al.*, 1988; Broady, 1989; Melick *et al.*, 1994a; Melick & Seppelt, 1997; Bolter *et al.*, 2000). Examination of broad-scale patterns may be appropriate in regions undergoing rapid change, such as the Periantarctic (Adamson *et al.*, 1988; Smith & Steenkamp, 1990; Frenot *et al.*, 1997) and the Antarctic Peninsula (Lewis Smith, 1990b). On the continent, however, where growth rates are slow, fine-scale studies, working with selected vegetation components such as lichens (Kappen, 1985a; Inoue, 1989), bryophytes

Table 5 Summary of effects of precipitation and water relations on Antarctic vascular plants, bryophytes and terrestrial algae

Scenario	Impact	Nature of impact	Major results	Plant group	Location	Field/lab	References
Increased aridity	Changes to species distribution	Ecological	Presence of moribund moss is indicative of a drying trend: lichen-dominated veg. is expanding in area, while bryophyte communities are contracting to lower lying areas with reliable moisture supply	B L	C	F	Mellick & Seppelt (1997)
	Lichens most likely to survive: adapted to dry conditions	Physiological	ΦPSII highest at intermediate WC Capable of absorbing water from air. Modeled using field data Desiccated thalli able to reactivate P_n after uptake of water vapor from air Metabolic activity in thalli rehydrated from snow at subzero temps (-4°C)	L L L	C C C	F F + L FC/L	Hovenden <i>et al.</i> (1994) Hovenden & Seppelt (1995b) Lange & Kappen (1972)
Requires extreme tolerance of desiccation		Physiological	Three bryophyte species (Windmill Islands, East Antarctica) show species-specific responses to desiccation. <i>G. antarctica</i> (endemic to Antarctica) appears least tolerant of desiccation and is therefore likely to be adversely affected by an increase in frequency, duration and/or severity of desiccation events	L	C	L	Schroeter <i>et al.</i> (1997)
			Maritime species from a variety of habitats (hydric, mesic, xeric) showed differences in gross PS: hydric species are drought sensitive Recovery from desiccation faster in xeric than hydric species, but no correlation between habitat and final degree of recovery Maritime moss species from a variety of habitats (hydric, mesic, xeric) showed increased penetration of light into the moss as drying occurs, reducing loss of productivity during periods of desiccation Maritime liverwort (<i>Marchantia bertextana</i>) sensitive to desiccation, recovery of gross PS limited to approximately 10%	B B B	M M M	FC/L FC/L FC/L	Davey (1997a) Davey (1997c) Davey & Ellis-Evans (1996)
↑ Temperature fluctuations		Physiological	Continental Antarctic lichens were capable of tolerating, and recovering from, desiccation Exposed lichen thalli reached greater temps, with greater fluctuations, than moist moss bed. Measured temps only, no measurement of moisture	L B L	C C	FC/L F	Lange & Kappen (1972) Mellick & Seppelt (1994b)

(Continued)

Table 5 (Continued)

Scenario	Impact	Nature of impact	Major results	Plant group	Location	Field/lab	References
Increased aridity	Morphological impact	Physiological	<i>Bryum incomexum</i> : leaf size smaller and more diversified in dry habitats that in moist habitats. Leaf shape independent of water status	B	C	FC/L	Nakamishi (1979)
			<i>G. antarctici</i> : comparison of wet and dry sites – differences in turf and gametophyte morphology. Dry site: shorter shoots, leaves smaller and more tightly packed, cell size and number greater	B	C	FC/L	Wilson (1990)
			Growth form and water relations related to habitat occupied. <i>Andraea</i> and <i>Grimmia</i> species (small cushions) have low evaporation rates and take up water readily from any part of shoot: occupy dry sites. <i>Drepanocladus uncinatus</i> ranges in growth form and has a wide ecological amplitude in relation to water supply	B	M	FC/L	Gimingham & Lewis Smith (1971)
Increased water availability	Correlations with species distribution	Ecological	Distribution of moss species correlated with moisture availability. Quantification of % cover of species along hydrological gradient – no quantification of moisture content. Histograms of % cover along transects. Description of trends	B	C	F	Lewis Smith (1999)
			Distribution of moss species and <i>Nostoc</i> influenced by water level – e.g. <i>Pottia</i> shows significant correlation with the drier habitat of hummocks. Semi-quantitative, largely mapping of waterline on transects. Some statistical analysis performed	B	C	F	Schwarz <i>et al.</i> (1992)
			Moss community types correlated with nature of moisture supply	B	C	F	Shimizu (1977)
			Distribution of moss species correlated with moisture availability. Quantification of both species distribution and water availability	B	C	F + FC/L	Selkirk & Seppelt (1987)
			Windmill Islands: four major veg groups, correlated with water availability: pure bryophyte communities highest water availability, lichen communities lowest	B L	C	F	Melick & Seppelt (1997)
			Veg community types have different WCs. Quantitative measurements (moisture content in variety of community types), descriptive analysis	B L	C	F	Lewis Smith (1990a)

	Distribution of some moss sociations related to pattern of water supply (based on type of water supply: small, medium or large snow drift, lake-shore, seepage or stream). Quantification of veg patterns (development of sociations) + each veg quadrat assigned one of six water supply types. Veg + water data tabulated together – but analysis descriptive only	B L	C	F	Nakanishi (1977)
	Moss species diversity and abundance positively correlated with soil WC	B L	C	F + FC/L	Leishman & Wild (2001)
	Fine-scale (intra-transect) plant dispersion patterns determined primarily by physical factors affecting water availability (amount of drift snow available and the effects of shelter and shade on evaporation rates)	B L A	C	F	Ryan & Watkins (1989)
	Soil WC highest in areas with moss veg.	B L A	C	F + FC/L	Bolter <i>et al.</i> (2000)
	Quantitative measurements, no analysis of data	L	C	F	Kappen <i>et al.</i> (1998b)
Experimentally determined impact of water on species distributions	<i>Buellia frigida</i> (crustose lichen) distribution explained by frequency and duration of meltwater moistening, of rock surface. Qualitative observations and some quantification	B L	C	FC/L	Melick & Seppelt (1997)
	With up to 75% crustose lichen encrustation, moribund moss regeneration potential greatest in permanently moist samples. Regeneration potential reduced in samples irrigated weekly and non-existent in samples irrigated fortnightly	B	M	FC/L	Davey (1997a)
	14 bryophyte species (from hydric, mesic or xeric sites): broadscale community patterns explained by water availability, but other factors must be important in determining fine scale patterns of species distribution (within habitats of similar water availability)	B	M	L	Davey (1997b)
	Liverwort (<i>M. bertoana</i>), low tolerance of desiccation, therefore limited to relatively mild habitats. If conditions become wetter, might expand into new areas that are currently too severe	L A	M	FC/L	Huisnies <i>et al.</i> (1997a)
	Water availability determines the stability of lichen symbiosis: in wet habitats the free-living algal and intermediate forms became dominant				

(Continued)

Table 5 (Continued)

Scenario	Impact	Nature of impact	Major results	Plant group	Location	Field/lab	References
Increased water availability	↑ P_n and growth	Physiological	Increased P_n and larger temp range for P_n in mesic versus xeric moss	B	C	F + FC/L	Kappen <i>et al.</i> (1989)
			Mesic (compared with xeric) species showed largest growth increments under a range of WCs. Generally, species-specific responses to water availability (measured growth increments, lateral shoot production, leaf density and size, optimal WC etc.)	B	M	FC/L	Fowbert (1996)
	↓ P_n and growth	Physiological	13 moss species, 1 liverwort: Xeric species gross PS currently often water-limited.	B	M	FC/L	Davey (1997c)
			Liverwort (<i>M. berteroi</i>) desiccation had highly adverse effect on photosynthetic capacity, with only about 10% recovery after dehydration.	B	M	L	Davey (1997b)
			<i>Andreea gainii</i> and <i>Usnea antarctica</i> : xeric fellfield species, only water source precipitation, active only for about 40% and 31% of the time respectively.	B L	M	F	Schlensog & Schroeter (2000)
			Field manipulations (three lichen species):	L	C	F	Kappen & Breuer (1991)
			Depression of P_n at supra-optimal WC (optimum WC for P_n was 75–115% dwt). Current climate: conditions of supra-optimal WC relatively rare	B	C	FC/L	Wilson (1990)
			<i>G. antarctici</i> : no difference in photosynthetic physiology between wet and dry sites	B	M	FC/L	Convey (1994)
			14 moss species on Signy Is., no relationship between habitat (xeric versus hydric) and photosynthetic performance (rates of gross PS, P_n or DR)	B	M	FC/L	Fabiszewski & Wojtun (2000)
			Higher concentrations of nitrogen and potassium	V B L A	M	FC/L	Tarnawski <i>et al.</i> (1992)
			Higher turf CO ₂	B	C	FC/L	Robinson <i>et al.</i> (2000)
			Higher WCs at full hydration and at 50% photosynthetic efficiency	B	C	FC/L	Kappen <i>et al.</i> (1989), Melick & Seppelt (1994a)
Higher production rates and a wider temp range for P_n	B	C	F + FC/L	Kappen <i>et al.</i> (1989)			
Higher chlorophyll concentrations	B L	C	F + FC/L	Melick & Seppelt (1994a)			
Higher levels of soluble carbohydrates	B L	C	FC/L	Melick & Seppelt (1994a), Robinson <i>et al.</i> (2000)			

	Higher rates of nitrogen fixation		B C	C	F + FC/L	Davey (1982), Davey & Marchant (1983)
	Higher tissue freezing points		L	C	FC/L	Melick & Seppelt (1994a)
Signy Is., Maritime Antarctica	At some sites at least water was not limiting P_n		B	M	F	Collins (1977)
	P_n in xeric species, often water-limited		B	M	FC/L	Davey (1997c)
	Rates of P_n for a range of xeric and hydric species showed no difference between habitats		B	M	FC/L	Convey (1994)
	Differences in species tolerance of desiccation, <i>G. antarctici</i> was least tolerant, <i>C. purpureus</i> most tolerant and <i>B. pseudotriquetrum</i> intermediate	Physiological	B	C	L	Robinson <i>et al.</i> (2000)
	Lichen (<i>Mastodia tessellata</i>) and its free-living phycobiont (<i>Prasiola crispa</i>): when occurring in symbiosis as a lichen, decline in P_n measured when hydrated, no change in P_n in either the free-living algae, or an intermediate form of the lichen and alga		L A	M	FC/L	Huiskies <i>et al.</i> (1997a)
	Rates of uptake and loss of water measured for six lichen species. Differences between species detected and thought to be due to differences in thalli morphology and anatomy		L	M	F + L	Huiskies <i>et al.</i> (1997b)
Changes to snow regime	Permanent snow banks an important moisture source	Ecological	B	C	F + FC/L	Lewis Smith (1990)
	Snow cover positive impacts	Physiological	B, L	C	F	Kappen <i>et al.</i> (1990)
		Physiological	L	C	F	Hovenden <i>et al.</i> (1994)
			L	C	F	Kappen & Breuer (1991)
			L	C	F	Hovenden <i>et al.</i> (1994)
			L	C	F	Kappen & Breuer (1991)
			L	C	F + FC/L	Lange & Kappen (1972)
			Sn	M	F	Walton (1982)

DR, dark respiration; dwt, dry weight; Φ PSII, quantum yield of PSII; P_n , net photosynthesis; PS, photosynthesis; temp, temperature; WC, water content. ↑, increasing; ↓, decreasing. Plant group codes and Study type as in Table 4.

(Selkirk & Seppelt, 1987; Schwarz *et al.*, 1992; Lewis Smith, 1999) or single species (Kappen *et al.*, 1998b) will probably be required to detect community change.

Relatively few studies of the relationship between water availability and vegetation distribution have included modern, quantitative statistical analyses (Table 5). Studies from the continent that have employed such methods have generally found positive associations between fine-scale distribution patterns and water availability (Leishman & Wild, 2001) or factors affecting water availability (Ryan & Watkins, 1989).

Increasing aridity

Antarctic terrestrial ecosystems will suffer increasing aridity if temperatures increase, causing elevated melts but precipitation is insufficient to counteract the increased melt, resulting in net depletion of permanent snow and ice reserves (Fig. 4).

The ecological impact of increasing aridity in Antarctica has received very little attention (Table 5). One exception is the work by Melick & Seppelt (1997), who suggested that the drying trend evident in the Windmill Islands, East Antarctica, is driving an expansion of lichen-dominated vegetation in the region, while the bryophytes are contracting to lower-lying areas with more reliable moisture supply.

Increasing water availability

In Antarctic habitats, increases in water availability are likely to result if temperature increases are coupled with increased precipitation, equal to or exceeding the elevated melt, thus improving melt water availability and maintaining permanent snow and ice reserves (Fig. 4).

As is the case for increasing aridity, the ecological impacts of increasing water availability in Antarctica have received very little research attention. The regeneration potential of moribund moss (encrusted with up to 75% lichen cover) is greatest under permanently wet conditions, and regeneration potential is less under experimental irrigation regimes that provide reduced water availability (Melick & Seppelt, 1997).

It appears that no experimental tests of the influence of water availability on relative species distributions in Antarctica have yet been published.

Studies that have surveyed vegetation patterns in relation to water content have tended to be short term, with most conducted during only one summer season (Table 5). One ongoing study has employed a multivariate statistical approach, to test for differences in species distributions within bryophyte communities in the Windmill Islands and to correlate any differences to

environmental parameters such as water content (Wasley, unpublished).

Physiological impacts

Increasing aridity

Under a climate change scenario of increasing aridity, lichens may have a greater chance of survival than other groups of cryptogamic organisms, as they are particularly well adapted to dry conditions (Table 5). Uptake of water by lichen in Antarctica is largely from snow deposited on their surfaces (Schroeter *et al.*, 1994) which, even at subzero temperatures, is adequate for rehydration (Schroeter & Scheidegger, 1995; Schroeter *et al.*, 1997). The water relations of lichens under snow and ice have been reviewed by Kappen (1993, 2000).

Increasing aridity will subject vegetation to increasing frequency, severity and duration of desiccation events. Levels of tolerance of desiccation vary across the Antarctic biome and between species and vegetation types (Table 5). Some regions and species will therefore be more severely affected than others under conditions of increasing aridity. The maritime region appears to support some desiccation-sensitive species, particularly in hydric habitats, and these might be expected to be particularly vulnerable (Davey, 1997a–c). On the continent, lichens are likely to survive increasing aridity as they show extraordinarily high levels of tolerance of desiccation and are capable of reactivating photosynthetic activity via uptake of water vapour (Lange & Kappen, 1972; Hovenden & Seppelt, 1995b). Continental Antarctic bryophytes are not likely to be as tolerant of increasing aridity as lichens, but also have the ability to survive desiccation events. Species-specific differences in tolerance of desiccation have been detected for three moss species from the Windmill Islands, East Antarctica (Robinson *et al.*, 2000), with the endemic, *G. antarctici*, more likely to be adversely affected by drying climatic conditions than the cosmopolitan species tested.

Other impacts of increasing aridity include morphological changes such as reduced bryophyte leaf size (Table 5). In addition to the direct effects of increasing aridity, reductions in water availability may cause alterations to other environmental parameters. For example, it has been observed that dry habitats are characterized by higher temperatures and larger temperature fluctuations than moist habitats (Melick & Seppelt, 1994b).

Increasing water availability

Water is generally limiting in Antarctic terrestrial ecosystems and increases in water availability are likely

to induce significant biological effects. In general, the evidence suggests that net photosynthesis and growth are currently limited by water availability (Table 5). However, certain plant groups offer exceptions to this. As previously noted, lichens can achieve physiologically optimal water contents through contact with snow, but at water contents greater than optimal, a depression of net photosynthesis occurs (Kappen & Breuer, 1991; Hovenden *et al.*, 1994). Although it is clear that water uptake directly from melting snow is a very important source of water for lichens (Schroeter *et al.*, 1994, 1997), an increase in precipitation levels that cause more frequent periods of supra-optimal water contents may have a negative impact (Huiskes *et al.*, 2000).

In addition to altering rates of net photosynthesis, a range of morphological, physiological and biochemical changes are likely to occur if water availability increases, as is evident in the differences that have been measured between plants from wet and dry habitats in continental Antarctica (Table 5). Vegetation from wet sites, for example, has been found to have higher water contents at full hydration (Robinson *et al.*, 2000), higher chlorophyll concentrations (Kappen *et al.*, 1989; Melick & Seppelt, 1994a), higher concentrations of soluble carbohydrates (Melick & Seppelt, 1994a; Robinson *et al.*, 2000), nitrogen and potassium (Fabiszewski & Wojtun, 2000), higher turf CO₂ concentrations (Tarnawski *et al.*, 1992) higher rates of nitrogen fixation (Davey, 1982; Davey & Marchant, 1983), higher production rates, and a wider temperature range for maximal net photosynthesis (Kappen *et al.*, 1989). On the negative side, photosynthetic efficiency declines at higher tissue water contents (Robinson *et al.*, 2000) and tissues freeze at higher temperatures (Melick & Seppelt, 1994a) in samples collected from wet sites compared with those from dry sites.

Water may be less universally limiting in the relatively moist maritime Antarctic (Table 5). While some xeric species from Signy Island were occasionally water-limited (Davey, 1997c), there are several sites on Signy Island where photosynthesis was not water-limited (Collins, 1977). When the photosynthetic rates of a range of xeric and hydric species from this island were compared, under laboratory conditions, no difference between habitats was detected (Convey, 1994).

As is the case with the impact of changes to other environmental parameters, the impact of increasing water availability is likely to be species-specific and show variation across the Antarctic biome (Table 5). While many studies have compared sites with naturally occurring variations in water content, publications produced from field manipulations of water availability are lacking. The absence of such studies is probably

due to the associated difficulty of conducting field manipulations of this nature in the severe Antarctic environment.

One final point to consider with respect to the impact of increasing water availability in Antarctic terrestrial ecosystems is the interaction between water content and freezing. Evidence suggests that desiccation, prior to freezing, may improve plant survival at low temperatures (Kennedy, 1993; Lovelock *et al.*, 1995a,b). Increased damage during freezing events may therefore occur if Antarctic habitats receive an increase in water availability.

Changes to snow regime

A fine balance with respect to the snow regime may be particularly important to lichen survival in Antarctica. Although moisture from summer snowmelt is utilized by lichens (Kappen, 2000), a persistent summer snow cover can cause lichen mortality (Benedict, 1990; Lewis Smith, 1990b; Melick & Seppelt, 1997). Snow cover throughout winter, maintaining dark conditions with temperature close to zero, caused negative carbon balance in lichens (Kappen, 2000). This may mean that lichens would be particularly disadvantaged by an increase in snow cover as a result of climate change (Kappen, 2000).

Interactions between water, temperature and nutrients

Changes to environmental parameters, such as temperature, CO₂ and water availability, are likely to have a synergistic effect on productivity and nutrient cycling, resulting in alterations to the current balance of the nutrient cycle. Perhaps due to the difficulties associated with detecting environmental change of this nature, there are no published studies relating nutrient availability to climate change in Antarctica.

Nutrient cycling in the Antarctic is relatively slow, due to the restraints imposed on biological activity by low temperatures and extreme aridity. Antarctic terrestrial habitats often have low nutrient availability, but the communities that they support are generally not nutrient-limited (Table 6). Nutrient requirements for Antarctic vegetation are exceptionally low, such that nitrogen levels in precipitation (Greenfield, 1992a) are sufficient for growth of cryptogams, particularly lichens. However, nutrient availability does play a role in determining patterns of species distributions in Antarctica (Table 6). Nutrient availability in Antarctic terrestrial ecosystems is patchy with a high concentration of nutrients in the vicinity of bird and seal colonies, while elsewhere nutrients are limited to that deposited

Table 6 Summary of effects of nutrients on Antarctic vascular plants, bryophytes and terrestrial algae

Scenario	Impact	Nature of impact	Major results	Plant group	Location	Field/lab	References
Increased nutrient availability	Relative species distribution	Ecological	Field survey of broadscale veg patterns. Environmental influences observed and described. Crustose lichens: abundant at sites with nutrient input from skuas. Snow algae occurred in areas fertilized by birds. <i>P. crispata</i> (algae) is nitrophilous and common in the vicinity of bird colonies	B L A	C	F	Broady (1989)
			Coarse-scale (inter-transect) analysis of plant dispersal patterns showed significant responses along bird-influence gradients. Quantitative statistical analysis of veg and environmental data	B L A	C	F	Ryan & Watkins (1989)
			Field observations suggested that nitrogenous debris was a major factor in influencing the distribution of the veg components. Data presented as a veg map of the study area, no quantitative statistical analysis	B L A	C	F	Rudolph (1963)
			Determined distribution of veg (using 1 km grid squares). Description of field observations: nutrients (probably N & P) from bird nest sites have positive influence on distribution, biomass and species diversity of terrestrial lithic algae, mosses and lichens	B L A	C	F	Seppelt <i>et al.</i> (1988)
			Distribution of macroscopic terrestrial cryptogams determined by type of N compounds and the concentration of water-soluble salts	B L A	C	F + L	Schofield & Ahmadjian (1972)
			Positive relationship between lichens (diversity and abundance) and soil nutrients, P more influential than N. Soil nutrients not significantly associated with moss diversity or abundance. Quantitative statistical analysis of veg and environmental data	B L	C	FC/L + F	Leishman & Wild (2001)
			Field survey of veg patterns (aerial photography + ground truthing). Quantitative analysis of soil characteristics (conductivity, pH, total N and total P). Mosses and lichens absent, and terrestrial algae <i>P. crispata</i> dominant in eutrophic sites near bird colonies	B L	C	F + FC/L	Melick <i>et al.</i> (1994a)

	B A	C	FC/L + F	Yamanaka & Sato (1977)
Measured nutrient contents for a range of veg samples: description of relationship between moss communities and total N and C. <i>P. crispata</i> distribution influenced by P availability. Text in Japanese, figures suggest no quantitative statistical analysis	L	C	F	Nakamishi (1977)
Species composition and distribution of lichen communities influenced by organic nutrients supplied by sea bird excrement. Some quantification of veg patterns (determined sociations) Nutrient relations descriptive (related to observed vicinity of bird nests)	L	C	F	Kappen (1985b)
Suggests nutrient enrichment from birds explains relatively rich coastal communities	L	C	F	Inoue (1989)
Well-developed lichens around rookeries or nests of sea birds (except where wind-blown sea-spray is significant). Based on veg mapping and observations of environment	L	C	FC/L + F	Hovenden & Seppelt (1995a)
Quantitative measurement of substratum chemistry and veg cover along a transect. Lack of effect of nutrients on distribution of major lichen species, but several minor species restricted to nutrient-rich zones (nutrient source: ancient penguin rookery). Relationship between chemical and veg data descriptive	L	M	F	Gremmen <i>et al.</i> (1994)
Species distributions within veg complexes related to factors indicating nutrient status (Cl ⁻ and NH ₄ ⁺ concentration, distance from sea) as well as a range of microclimate variables. Although canonical correspondent analyses found a large amount of the variation could not be explained by these factors.	V	C	L	Rudolph (1966)
Concentration of Cl ⁻ , NH ₄ ⁺ and PO ₄ ³⁻ correlated with distribution of lichen complexes: <i>Usnea</i> complex with low, while <i>Mastodaria-Rinodina</i> complex with high salt concentration	V B	M	FC/L	Allen <i>et al.</i> (1967)
Soil nutrients not limiting to growth of alien vascular species	B S	C	FC/L	Cocks <i>et al.</i> (1998)
High mobility of plant nutrients in Signy Island ecosystem. K and Ca provided by rock weathering, Na and Mg from the ocean, phosphorous and N from fauna. Direct droppings and drainage particularly important for distribution of N				
Soils under moss favourable for soil respiration. Moss appears to act as a sink for nutrients originating from bird nests				

(Continued)

Table 6 (Continued)

Scenario	Impact	Nature of impact	Major results	Plant group	Location	Field/lab	References
No change to nutrient availability	Nutrients currently non-limiting	Physiological	Fellfield plants and soils obtain substantial quantities of N from atmospheric precipitation. In the absence of other limitations, precipitation N would allow an annual biomass increase for <i>U. antarctica</i> of 14% at Deception Is. and 7% at Ross Is. Precipitation N major N input to fellfield biota (Cape Bird and Signy Island)	B L S	CM	FC/L	Greenfield (1992a)
Changed nutrient availability	Species-specific differences in nutrient relations	Physiological	<i>U. sphacelata</i> highly efficient at scavenging inorganic N from snow meltwater, capturing 92% and 87% of NO_3^- and NH_4^+ , respectively Nutrients not limiting to veg: K, Mg and P values often extraordinarily high Measured differences in annual nitrogen content trends for two lichen species: <i>U. sphacelata</i> and <i>Umbilicaria decussata</i>	L	C	FC/L	Greenfield (1992b) Crittenden (1998)
				S	C	FC/L	Beyer <i>et al.</i> (2000)
				L	C	FC/L	Hovenden (2000)

Veg, vegetation. Plant group codes and study type as in Table 4.

in precipitation (Greenfield, 1992a,b). Two studies in particular have demonstrated positive correlations between vegetation patterns and nutrient availability associated with nutrient inputs from birds (Gremmen *et al.*, 1994; Leishman & Wild, 2001). Current nutrient availability can be determined by site history. Abandoned penguin rookeries, for example, can produce relatively nutrient-rich habitats, thus affecting local species compositions (Hovenden & Seppelt, 1995a). Knowledge of terrestrial site history can therefore be important in understanding current vegetation patterns.

In continental Antarctica, the release of nutrients from organic matter is primarily microbial and is relatively slow (Smith & Steenkamp, 1992). In the Periantarctic, rates of inorganic nutrient release from plant litter are enhanced by a suite of macroinvertebrates (Smith & Steenkamp, 1992), which are absent on the continent.

Nitrogen fixation by the cyanobacteria, *Nostoc commune*, occurs during the Antarctic summer. Fixation rates are dependent on water availability and temperature conditions; fixation ceases below -7°C (Davey & Marchant, 1983), with rates highest in areas of high water content (Davey, 1982). *N. commune* and moist associations of moss-*Nostoc* are estimated to contribute 52 and $119 \text{ mg N m}^{-2} \text{ yr}^{-1}$ to the terrestrial ecosystem, respectively (Davey & Marchant, 1983). These results suggest that warmer, wetter conditions are more favourable for nitrogen fixation.

If photosynthesis and growth rates of Antarctic plants increase, in response to greater water availability and/or temperature increases, the demand for nutrients will increase, leading to the development of a nutrient-limited system. Nutrient inputs through precipitation and biological fixation of nitrogen are known to be too small to meet the current demands of plants in Periantarctic ecosystems (Smith & Steenkamp, 1992). The capacity to increase nutrient availability under future climatic conditions might also be limited by low continental soil fauna diversity.

Conclusions

Climate change has already impacted on Antarctic plants. Temperature increases in the maritime Antarctic have led to changes in the distribution of native plants and increased the opportunities for alien species to invade. The current levels of UV-B have been shown to reduce growth of the two vascular species, suggesting that ozone depletion may be having a negative effect on these plants. Although negative effects of UV-B are ameliorated by UV-screening compounds in many

Antarctic plants, increased levels of these compounds may lead to indirect effects on nutrient cycling.

This review has suggested scenarios for the Antarctic flora under global climate change. Comprehensive predictions are complicated by both the lack of certainty in the prediction of changes to abiotic variables, and by the lack of long-term studies investigating recent changes to the flora. Although manipulative, long-term and quantitative research has been undertaken in recent years, there is a particular need for studies that address the impact of combinations of abiotic factors. Given the slow rate of change in these ecologically extreme communities, a commitment to long-term studies such as those planned and occurring as part of the Scientific Committee on Antarctic Research, Regional Sensitivity to Climate Change program are essential to investigate both the response of key species and of key assemblages.

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