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

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Antarctic terrestrial ecosystems experience some of the most extreme growth conditions on Earth and are characterised by extreme aridity and sub-zero 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; 290-320nm) 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 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, UV-radiation, ozone hole, temperature, water relations, nutrients

Disciplines

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

RUNNING TITLE: Global change and Antarctic plants

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Antarctic terrestrial ecosystems experience some of the most extreme growth conditions on Earth and are characterised by extreme aridity and sub-zero 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; 290-320nm) 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 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.

1. 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 simple community structure, and the geographic isolation of the Antarctic continent also contribute to 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 1988). 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; Hansom & Gordon 1998; Melick & Seppelt 1997) 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 northwest 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; Hansom & Gordon 1998; Lewis Smith 1984; Edwards and Smith, 1988; 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/year 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 (Filson & Willis 1975; Wise & Gressitt 1965), 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 (Hansom & Gordon 1998; Longton 1985).

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; 290-320nm) radiation levels. Plant photosynthetic rates and consequently, growth and productivity, are greatly influenced by these environmental variables. Optimising 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 & community structure

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

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 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 to 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 (Broady, 1981a; Seppelt and Ashton, 1978), 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 and Seppelt, 1984; Convey, 1996; Hansom and 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; Convey 2001a; b; Kennedy 1995; 1996). 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.

2. UV and solar radiation

The Antarctic 'Ozone Hole'

Seasonal stratospheric ozone depletion over the Antarctic continent is evident in data collected since the 1970s (Frederick *et al*. 1998; Kerr & McElroy 1993). 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 (McKenzie *et al.* 1999; Stolarski *et al.* 1986). The largest 'ozone holes' were recorded between 1998-2001 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 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 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; Jansen *et al*. 1998; Rozema *et al*. 1997; Tobin 2003). The first line of defence is to screen UV-B radiation before it reaches the cell, then to minimise damage within the cells through other protective strategies, and finally to repair damage once it has occurred (Fig. 3; reviewed by Jansen *et al.* 1998; Stapleton 1992). 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 (Barnes *et al.* 1987; Caldwell *et al.* 1982; 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 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 (Adamson & Adamson 1992; Karentz 1991; 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 which are only one cell thick and lacking protective cuticles or epidermal layers (Gehrke 1998; Gwynn-Jones *et al.* 1999; Richardson 1981). 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 which reduce UV-B below the current levels. Such screens usually have confounding effects on temperature and water availability. The effect on precipitation, maybe 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.

There is also considerable variation in the duration of studies, with some performed over just one 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 to 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 a 7 d field UV-B enhancement study, effective photochemical quantum yield (ΦPSII) 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, whilst 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*, 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 CO_2 (Johnson *et al.* 2002). These types of study 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). As well as their UV-B absorbing properties, some flavonoids (e.g. quercetin and lutonarin) 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; Bjerke *et al.* 2002; Buffoni-Hall *et al.* 2002; Cuadra & Harborne 1996; Lois 1994; Robberecht & Caldwell 1978; Tevini *et al.* 1991; Vogt *et al.* 1991). 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 (Cockell & Knowland 1999; Lovelock *et al*. 1995a; b). 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, whilst 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 d, also failed to produce an increase in UV screening pigments in *D. antarctica* (Rozema *et al*. 2001). Leaves of both plants showed 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 utilise soluble pigments, whilst 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 6 globally) investigated arctic and periantarctic ecosystems, where bryophytes are amongst 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*, that 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, whilst 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 *et al.* 1990; Markham & Given 1988). 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 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; Middleton & Teramura 1993; Murphy 1983; Renger *et al*. 1989; Tevini 1993; Tevini & Teramura 1989). Since any excess radiation (PAR or UV) can lead to the production of ROS, photosynthetic pigments adjust to optimise absorption of sunlight whilst 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 ß-carotene; Demmig-Adams *et al.* 1996; Young

1991). If UV-screening compounds are unable to sufficiently reduce UV penetration, these carotenoids may be able to minimise 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 utilised 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 and Robinson, *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 (Adamson & Adamson 1992; Post *et al.* 1990). 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; Lovelock & Robinson 2002; Robinson *et al*. 2001). 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 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). Accumulation and repair of pyrimidine dimers has been studied in a number of plant species but there are few published studies of such experiments involving Antarctic plants. Cyclobutyl pyrimidine dimers 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), whilst 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-hour 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.

3. Elevated CO_2

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 CO_2 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, whilst small cushions growing in dry sites might be CO_2 limited for much of the summer, high CO_2 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 CO_2 levels, as a result of global climate change, might alleviate CO_2 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 CO_2 may increase the temperature optimum for photosynthesis in mosses (Silvola 1985). The interactions of increased CO_2 with increasing and decreasing water and temperature therefore require investigation before we can attempt to predict the effect of elevated CO_2 on these communities.

4. 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 to 0.8°C (Houghton *et al*. 2001). Climate models predict a rise in global average surface temperatures of 1.5 to 4.5 ˚C in response to doubling of greenhouse gas concentrations (Tokioka 1995). Temperature increases are predicted to predominately impact 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 ºC in summer (Fowbert & Lewis Smith 1994; Lewis Smith 1990b; Lewis Smith 1994) and 4-5 ºC 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 y record in the meteorological data showed an overall increase of 0.012±0.008 ºC y^{-1} but a decline of 0.008±0.025 ºC y^{-1} over the past 20 y. The recent 20-y trend is supported by the satellite data for the same period, which showed a more severe decline in temperature of 0.042±0.067 ºC y^{-1} (Comiso 2000). Similar fluctuations have been detected in the Windmill Islands region, East Antarctica; average temperatures increased 0.086 ºC y^{-1} from 1960 to the mid-1980s and then declined 0.010 ºC y^{-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 analyzed 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 colonise 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 colonisation 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 colonisation, respectively (Lewis Smith 1990b). There have been changes in abundance and area of the Antarctic vascular species, *D. antarctica* and *C. quitensis* (Fowbert & Lewis Smith 1994; Lewis Smith 1990b; 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 area of each colony while no additional *C. quitensis* colonies were recorded and only a 5-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 ºC than at 2 ºC (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 (Kappen 1985a; Seppelt & Ashton 1978; Shimizu 1977). 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 colonisation and survival. Long-term monitoring of continental Antarctic terrestrial vegetation is crucial for accurate measurement and 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 to 20 ºC, 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 ºC), with negligible photosynthesis at 35 ºC (Vining *et al.* 1997). In the field, both *D. antarctica* and *C. quitensis* have negligible midday net photosynthetic rates at canopy air temperatures greater than 20 ºC, whilst high rates of midday net photosynthesis are obtained at temperatures of less than 10 ºC. 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 20ºC for less than 1% of diurnal periods (Day *et al.* 1999) and midday 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 ºC in *D. antarctica* (Xiong *et al.* 1999) to 20-25 ºC in a maritime moss species (Rastorfer 1972).

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

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 ºC at 10 cm depth and +5.2 ºC 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 ºC and 5-10 ºC, 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 ºC, whilst that for *P. alpestre* increased to 15 ºC. Species such as *P. alpestre* that 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.* Huskies *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 cyclically freeze and thaw 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 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 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.

5 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, whilst the third results in either unchanged or increased water availability. If an increase in the area of permanent snow cover were 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 to 15% (Tokioka 1995). Two types of precipitation 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 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 (Bolter *et al.* 2000; Broady 1989; Lewis Smith 1986; Lewis Smith 1990a; Melick *et al.* 1994a; Melick & Seppelt 1997; Nakanishi 1977; Rudolph 1963; Seppelt & Ashton 1978; Seppelt *et al.* 1988; Shimizu 1977). Examination of broad-scale patterns may be appropriate in regions undergoing rapid change, such as the Periantarctic (Adamson *et al.* 1988; Frenot *et al.* 1997; Smith and Steenkamp, 1990) 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 (Inoue 1989; Kappen 1985a), bryophytes (Lewis Smith 1999; Schwarz *et al.* 1992; Selkirk & Seppelt 1987) 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 and 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, whilst 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 *et al.* 1997; Schroeter & Scheidegger 1995). The water relations of lichens under snow and ice has 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; b; 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 (Hovenden & Seppelt 1995b; Lange & Kappen 1972). 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 characterised 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 (Hovenden *et al*. 1994; Kappen & Breuer 1991). Although it is clear that water uptake directly from melting snow is a very important source of water for lichens (Schroeter *et al.* 1994; Schroeter *et al.* 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 CO_2 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 to those from dry sites.

Water may be less universally limiting in the relatively moist maritime Antarctic (Table 5). Whilst 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). Whilst 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 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 utilised 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).

6. Interactions between water, temperature and nutrients

Changes to environmental parameters, such as temperature, CO_2 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 high concentration of nutrients in the vicinity of bird and seal colonies, whilst elsewhere nutrients are limited to that deposited 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, 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, *N. commune*, occurs during the Antarctic summer. Fixation rates are dependent on water availability and temperature conditions; fixation ceases below –7 ºC (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 mg N m^{-2} 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.

7. 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. 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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Table 1. Estimated contribution of plant groups to terrestrial plant biodiversity of Antarctica.

Phytogeographic zone	**Angiosperms**	**Mosses**	**Liverworts**	**Lichens**	**Macro-fungi**	**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)

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					
D. antarctica	2m field screening study		Reducing UVR improved growth.		(Day *et al.* 1999)
	4m field screening study		Leaves longer (cells elongated) under reduced UVR.		(Ruhland & Day 2000)
	4m 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. ΦPSII 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)
	4y 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 *et al.* 2001)
	1m and 2y screening studies	No effect of screening on ΦPSII or F_v/F_m.			(Huskies *et al.* 2001; Lud *et al.* 2001b)
	7d UV-BR field enhancement	No change in ΦPSII.			(Montiel *et al.* 1999)
	90d enhanced UV-BR, controlled environment	No change in ΦPSII, 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 *et al.* 2001)
C. quitensis	2m field		Some indications of improved growth under		(Day *et al.*

	screening study		reduced UV-BR.		1999)
	4m 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 ΦPSII 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 63d 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 *et al.* 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)
	4y 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 *et al.* 2001)
	7d UV-BR field enhancement	No change in ΦPSII.			(Montiel *et al.* 1999)
Bryophytes					
B. argenteum	8h screening study	No effect on P_n or F_v/F_m.			(Green *et al.* 2000)
S. uncinata	1m screening study	No effect on ΦPSII.			(Huskies *et al.* 2001)
	4-6w study *in situ*	No effect of naturally increased UV-BR on F_v/F_m.			(Newsham *et al.* 2002)
	7d UV-BR field enhancement	ΦPSII reduced.			(Montiel *et al.* 1999)
	2d UV-BR field	No effect on P_n, F_v/F_m or ΦPSII.			(Lud *et al.* 2002)

	enhancement				
	2y screening study		No effect on biomass or short length. Less branching under reduced UV-BR.		(Lud *et al.* 2002)
C. exiliflora		Density of thylakoids greater in shaded plants.			(Post & Vesk 1992)
Algae					
P. crispa	1m enhanced UV-BR, controlled environment	Reduced A_{max}.			(Post & Larkum 1993)
	1m screening study	No effect on ΦPSII.			(Huskies *et al.* 2001)
	2d enhanced UV-BR	No effect on gas exchange.			(Lud *et al.* 2001a)

Abbreviations: $\mathbf{A_{max}}$ light saturated rate of photosynthesis, **d** day, $\mathbf{F_v/F_m}$ optimal efficiency of PSII, **h** hour, **m** month, **NAR** net assimilation rate, **ΦPSII** quantum yield of PSII, $\mathbf{P_n}$ net photosynthesis, **RGR** relative growth rate, **UV-BR** ultraviolet-B radiation, **w** week, **y** 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					
D. antarctica	2 & 4 m field screening study	No effect.	No change over 2 m.		(Day *et al.* 1999)
	4 m field screening study (pot grown)	Lower under reduced UV-BR.	Lower under reduced UV-BR.	Total car. lower under reduced UV-BR (methanol extract).	(Ruhland & Day 2000; Xiong & Day 2001)
	2 y screening study	No effect.	No effect.	No effect.	(Lud *et al.* 2001b)
	90 d enhanced UV-BR, controlled environment	No effect.			(Rozema *et al.* 2001)
C. quitensis	2 m field screening study	No effect.	No effect.		(Day *et al.* 1999)
	63 d & 4 m field screening study (pot grown)	Soluble pigments, measured on area basis, lower under reduced UV-BR.	No change over 63 d.	Total car. reduced after 4 m (methanol extract).	(Ruhland & Day 2000; Xiong & Day 2001; Xiong *et al.* 2002)
	Summer season screening	Trend for lower UV-B screening pigments in seedlings grown under reduced UV-BR.	Trend for higher chl. in seedlings grown under reduced UV-BR.		(Ruhland & Day 2001)
Mosses					
B. psuedotriqetrum	6 m study *in situ*	High relative to other moss species and positively correlated with UV-BR.	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. B-car positively correlated with WC and air temp (acetone extract).	(Dunn 2000)
B. argenteum		Correlation between flavonoid concentration			(Markham *et*

		in herbarium specimens of plants collected from Ross Sea area and historic UV-BR levels.			*al.* 1990)
Bryum spp		Generally show ability to accumulate flavonoids.			(Adamson & Adamson 1992; Markham & Given 1988)
C. purpureus	6 m study *in situ*	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. B-car. positively correlated with WC and air temp.	(Dunn 2000)
G. antarctici	6 m study *in situ*	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 negatively correlated with WC. De-epoxidation status negatively correlated with WC and air temp. B-car. negatively correlated with WC, positively correlated with air temp.	(Dunn 2000)
S. uncinata	4-6 w study *in situ*	Increased pigments under naturally elevated UV-BR.	Unaffected by ozone depletion.	Increased total car. under naturally elevated UV-BR. Higher N and B-car (acetone extract).	(Newsham *et al.* 2002)
	2 y screening		No effect.		(Lud *et al.* 2002)
C. varians	4-6 w study *in situ*	Increased pigments under naturally elevated UV-BR.	Unaffected by ozone depletion.	Increased total car. under naturally elevated UV-BR. Higher N and V but lower L and Z.	(Newsham *et al.* 2002)
A. regularis	4-6 w study *in situ*	Increased pigments under naturally elevated UV-BR.		Increased total car. under naturally elevated UV-BR.	(Newsham 2003)
Algae					
P. crispa ssp *antarctica*		Higher relative to chl. in summer versus winter. Higher UV screening pigments in upper portions of thalli.	Evidence of chl. bleaching in top layer of thalli.	TCar/chl increased under elevated UV-BR (methanol extract).	(Post & Larkum 1993)
		Reduced under UV-A or UV-B screens relative to unscreened controls. Pigments lowest under snow (Dec) increased until March then declined.			(Jackson & Seppelt 1997)
	4 w controlled chamber	No effect.	Reduced under elevated UV-BR.		(Post & Larkum

	elevated UV-BR				1993)
	1-2 d enhanced or reduced UV-BR	No effect.		Most car. did not change under screening treatments, V decreased under reduced UB-BR but no Z found (methanol extract).	(Lud *et al.* 2001a)

Abbreviations: **A** antheraxanthin, **ß-car** ß-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, **y** year, **Z** zeaxanthin

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	Physiol-ogical	Current, low, Antarctic temps limit sporophyte production.	B	C	F	(Filson & Willis 1975; Seppelt *et al.* 1992)
			Sporophyte production higher at high latitudes than previously expected. Relatively high in micro-oases.	B	M	F	(Lewis Smith & Convey 2002)
		Ecological	Supply of pollen and spores to Antarctica.	V B L F	C M	FC/L	(Lewis Smith 1991; Linskens 1993; Kappen & Straka 1988)
			Vestfold Hills are at greater risk of alien invasion than the Ross Sea Region.	B	C	FC/L	(Selkirk *et al.* 1997)
			Some species have greater potential for invasion than others.	B	C	FC/L	(Melick *et al.* 1994b)
			5 native Antarctic species identified as potential long-distance colonists.	B	M	FC/L	(Convey & Lewis Smith 1993)
	Altered distribution	Ecological	Species-specific response to increasing summer air temps (1944-92): species distributions 1964-90 - *Deschampsia antarctica* increased in area 25-fold + increased colony numbers, *Colobanthus quitensis* increased in area 5-fold, no new colonies.	V	M	F	(Fowbert & Lewis Smith 1994)
			D. antarctica and *C. quitensis*: increased number of individuals and populations during 27-year monitoring period.	V	M	F	(Lewis Smith 1994)
			Manipulative field experiment: Warming increased *C. quitensis* growth (increased leaf production, shoot production and foliar cover). Warming decreased growth of *D. antarctica* (decreased leaf length, leaf production and foliar cover). Improved sexual reproduction in both species.	V	M	F	(Day *et al.* 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.	B L	C	F	(Kappen 1985a; Seppelt & Ashton 1978; Shimizu 1977)
			With up to >75% crustose lichen encrustation, moribund moss regeneration faster at 18 ˚C than at 2 ˚C.	B L	C	FC/L	(Melick & Seppelt 1997)
			Lichen veg particularly rich on north facing rock sites, where temps are consistently warmer.	L	C M	R	(Kappen 1985a)
	Increased productivity	Physiol-ogical	*D. antarctica* and *C. quitensis* grown at 7, 12 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	V	M	L	(Xiong *et al.* 2000)

			20 ˚C grown plants				
			P_n increased with increased temp (tested up to 20 ºC). Species differences: *Bryum argenteum* > *Bryum pseudotriquetrum* > *Ceratodon purpureus*.	B	C	FC/L	(Lewis Smith 1999)
	Reduced productivity	Physiological	*D. antarctica* and *C. quitensis*: 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.	V	M	F+L	(Xiong *et al.* 1999)
			D. antarctica pronounced decline in P_n at supra-optimal temps(>12 ˚C), P_n negligible at 35 ˚C.	V	M	L	(Vining *et al.* 1997)
			Increased photoinhibition with increased temp.	B	C	F	(Kappen *et al.* 1989)
			Sanionia uncinata: 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.	B	M	L	(Nakatsubo 2002)
	Morphological changes	Physiological	*D. antarctica*: leaf anatomy shows plastic response to changes in growth conditions.	V	M	FC/L	(Romero *et al.* 1999)
	Physiological ranges	Physiological	*C. quitensis* optimal leaf temp for P_n 14 ˚C, *D. antarctica* 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.	V	M	FC/L	(Xiong *et al.* 1999)
			Optimum temp for P_n: *D. antarctica* 13 ˚C, *C. quitensis* 19 ˚C.	V	M	L	(Edwards & Lewis Smith 1988)
			Optimal temp regime (day/night) 22/15 ºC for a moss species.	B	C	FC/L	(Longton 1981)
			P_n highest at 15 ˚C for *B. argenteum* (measured over temp range –8 to 21 ˚C).	B	C	L	(Green *et al.* 2000)
			Polytrichum alpestre: optimum temp 5-10 ˚C or 15 ˚C, depending on growth conditions. *Drepanocladus uncinatus*: 15 ˚C, regardless of growth conditions. Species-specific response to temp: *P. alpestre* showed ability to acclimate to changed temps.	B	M	L	(Collins 1977)
			4 species: differing responses to 5-25 ºC temp range. General trend: P_n increased with increasing temp. *D. uncinatus* shows 20-25 ºC optimum.	B	M	L	(Rastorfer 1972)
			P_n maximal at 20-25 ºC for *B. argenteum*: and 15-20 ºC for *Umbilicaria aprina*.	B L	C	FC/L	(Green *et al.* 1998)
			Lichen phycobionts (from 6 species of lichen): optimal temp 15 ºC.	L *P*	C	L	(Schofield & Ahmadjian 1972)
	Surface temps can reach relatively high levels, but are not sustained throughout the growing	Physiological	Moss surface temps measured over 13 d period) >10 ºC 44%, >20 ºC 24% of the time.	B	C	F	(Lewis Smith 1988)
			Moss surface temp reached 17 ºC (1 d observation).	B	C	F	(Seppelt & Ashton 1978)
			P. alpestre, 80% of summer: -5 to +5 ˚C.	B	M	F	(Collins 1977)
			B. pseudotriquetrum: field thallus temp up to 27 ˚C.	B	M	F	(Schlensog & Schroeter 2000)
			Hourly microclimate measurements 1972-4: *Polytrichum* surface temps >+5 ˚C and <-15 ˚C uncommon (<15% of measurements). Absolute max & min temps: +35 ˚C and –26.5 ˚C.	B	M	F	(Walton 1982)
			Andreaea gainii and Usnea antarctica: thallus temps in the range 0 ˚C – 15 ˚C, which is thought to	B	M	F	(Schlensog &

	season		be almost optimal for P_n in both species.	L			Schroeter 2000)
			When lichens were wet, and photosynthetically active, surface temps exceeded air temps but remained less than 10 ºC.	L	C	F	(Kappen 1985c)
			Measured surface and air temps + irradiance (5 weeks), showed lichen growth conditions to be relatively warm: rock surface & hydrated lichen up to 19 ˚C higher than air, overall rock surface temp averaged 5.5 ˚C warmer than air.	L R	C	F	(Kappen *et al.* 1998b)
			Within soil and plant habitats: spring/summer (Nov-Mar) minimum daily temps close to 0 ˚C.	S	M	L	(Davey *et al.* 1992)
	Surface temps and fluctuations are often greater than ambient	Physiol-ogical	Field moss surface temps (56 d measurement): >0 ºC >80% of the time, >10 ºC 25% of the time.	B	C	F	(Lewis Smith 1999)
			Field moss surface temps (27 d measurement): < 5% of readings >13 ºC, ~60% <2.5 ºC.	B	C	F	(Longton 1974)
			Extreme surface temp diurnal fluctuation of –9.2 to 42.8 ºC.	B	C	F	(Lewis Smith 1988)
			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 ºC during a 5 h period.	B L E	C	F	(Melick & Seppelt 1994b)
			Moss surface temp range (~17 ºC to ~0 ºC) greater than range of air temps (~4 ºC to ~-2 ºC), during 1 d of observation.	B S A	C	F	(Seppelt & Ashton 1978)
			Lichen temp higher (with greater fluctuations) than the relatively stable air temp (~28 h diurnal plot). Air temp ~0 ºC, lichen temp ~0-35 ºC.	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 freeze-thaw	Increased damage	Physiol-ogical	Increased loss of soluble carbohydrates, species differences in % loss.	B	C	FC/L	(Melick & Seppelt 1992)
			P. alpestre: 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: 12h cycles, more damage than 24 or 48h cycles.	B	M	L	(Kennedy 1993)
		Environ-mental	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 *et al.* 1992)

Abbreviations: DR dark respiration, **d** day, **LAR** Leaf area ration, **ΦPSII** quantum yield of PSII, $\mathbf{P_n}$ net photosynthesis, **PS** photosynthesis, **RGR** relative growth rate, **temp** temperature, **veg** Vegetation, **Plant group codes:** V vascular plants, B bryophytes, M moss, L lichen, L(P) lichen phycobiont, A algae, F 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

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, whilst bryophyte communities are contracting, to lower lying areas with reliable moisture supply.	B L	C	F	(Melick & Seppelt 1997)
	Lichens most likely to survive: adapted to dry conditions	Physiol-ogical	ΦPSII highest at intermediate WC.	L	C	F	(Hovenden *et al.* 1994)
			Capable of absorbing water from air. Modeled using field data.	L	C	F+L	(Hovenden & Seppelt 1995b)
			Desiccated thalli able to reactivate P_n after uptake of water vapor from air.	L	C	FC/L	(Lange & Kappen 1972)
			Metabolic activity in thalli rehydrated from snow at subzero temps (-4°C).	L	C	L	(Schroeter *et al.* 1997)
	Requires extreme tolerance of desiccation	Physiol-ogical	3 bryophyte species (Windmill Islands, East Antarctica) show species-specific responses to desiccation. *Grimmia antarctici* (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.	B	C	FC/L	(Robinson *et al.* 2000)
			Maritime species from a variety of habitats (hydric, mesic, xeric) showed differences in gross PS: hydric species are drought sensitive.	B	M	FC/L	(Davey 1997a)
			Recovery from desiccation faster in xeric than hydric species, but no correlation between habitat and final degree of recovery.	B	M	FC/L	(Davey 1997c)
			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.	B	M	FC/L	(Davey & Ellis-Evans 1996)
			Maritime liverwort (*Marchantia berteroana*) sensitive to desiccation, recovery of gross PS limited to approximately 10%.	B	M	FC/L	(Davey 1997b)
			Continental Antarctic lichens were capable of tolerating, and recovering from, desiccation	L	C	FC/L	(Lange & Kappen 1972)
	↑ Temperature fluctuations	Physiol-ogical	Exposed lichen thalli reached greater temps, with greater fluctuations, than moist moss bed. Measured temps only, no measurement of moisture.	B L	C	F	(Melick & Seppelt 1994b)
	Morphological impact	Physiol-ogical	*Bryum inconnexum*: Leaf size smaller and more diversified in dry habitats that in moist habitats. Leaf shape independent of water status.	B	C	FC/L	(Nakanishi 1979)
			G. antarctici: 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. *Andreaea* and *Grimmia* species (small cushions) have low evaporation rates and take up water readily from any part of shoot: occupy dry sites. *Drepanocladus uncinatus* 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 *Nostoc* influenced by water level - e.g. *Pottia* 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 *et al.* 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: 4 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 1990)
			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 1 of 6 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. Quantitative measurements, no analysis of data.	B L A	C	F + FC/L	(Bolter *et al.* 2000)
			Buellia frigida (crustose lichen) distribution explained by frequency and duration of meltwater moistening, of rock surface. Qualitative observations and some quantification.	L	C	F	(Kappen *et al.* 1998b)
	Experimentally determined impact of water on species distributions	Ecological	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 L	C	FC/L	(Melick & Seppelt 1997)
		Physiological	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	FC/L	(Davey 1997a)
			Liverwort (*M. berteroana*), low tolerance of desiccation, therefore limited to relatively mild habitats. If conditions become wetter, might expand into new areas that are currently too severe.	B	M	L	(Davey 1997b)
			Water availability determines the stability of lichen symbiosis: in wet habitats the free-living algal and intermediate forms became dominant.	L A	M	FC/L	(Huskies *et al.* 1997a)

	↑ P_n and growth	Physiol-ogical	Increased P_n and larger temp range for P_n in mesic versus xeric moss.	B	C	F + FC/L	(Kappen *et al.* 1989)
			Mesic (compared to 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)
			13 moss species, 1 liverwort: Xeric species gross PS currently often water-limited.	B	M	FC/L	(Davey 1997c)
			Liverwort (*M. berteroana*) desiccation had highly adverse effect on photosynthetic capacity, with only about 10% recovery after dehydration.	B	M	L	(Davey 1997b)
			Andreaea gainii and *Usnea antarctica*: 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)
	↓ P_n and growth	Physiol-ogical	Field manipulations (3 lichen species): 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.	L	C	F	(Kappen & Breuer 1991)
	No impact on P_n	Physiol-ogical	*G. antarctici*: No difference in photosynthetic physiology between wet and dry sites.	B	C	FC/L	(Wilson 1990)
			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	(Convey 1994)
	Characteristics of wet habitats (compared to dry habitats): *Continental Antarctica*	Physiol-ogical	Higher concentrations of nitrogen and potassium.	V B L A	M	FC/L	(Fabiszewski & Wojtun 2000)
			Higher turf CO_2.	B	C	FC/L	(Tarnawski *et al.* 1992)
			Higher WCs at full hydration and at 50% photosynthetic efficiency.	B	C	FC/L	(Robinson *et al.* 2000);
			Higher production rates and a wider temp range for P_n.	B	C	F + FC/L	(Kappen *et al.* 1989)
			Higher chlorophyll concentrations.	B L	C	F + FC/L	(Kappen *et al.* 1989; Melick & Seppelt 1994a)
			Higher levels of soluble carbohydrates.	B L	C	FC/L	(Melick & Seppelt 1994a; Robinson *et al.* 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)

	Species specific differences in physiological response	Physiological	Differences in species tolerance of desiccation:, *G. antarctici* was least tolerant, *Ceratodon purpureus* most tolerant and *B. pseudotriquetrum* intermediate.	B	C	L	(Robinson *et al.* 2000)
			Lichen (*Mastodia tesselata*) and its free-living phycobiont (*Prasiola crispa*): 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	(Huskies *et al.* 1997a)
			Rates of uptake and loss of water measured for 6 lichen species. Differences between species detected and thought to be due to differences in thalli morphology and anatomy.	L	M	F+L	(Huskies *et al.* 1997b)
Changes to snow regime	Permanent snow banks an important moisture source	Ecological	Steep decrease in moss moisture content as distance from snow patch increased.	B	C	F + FC/L	(Lewis Smith 1990)
			Positive correlation between veg cover and extension and duration of shallow snow cover.	B, L	C	F	(Kappen *et al.* 1990)
		Physiological	Lichens photosythetically active when moistened by snowfall or by run-off from snow melt.	L	C	F	(Hovenden *et al.* 1994)
	Snow cover positive impacts	Physiological	WC of lichens resulting from contact with snow was frequently near the optimum for P_n.	L	C	F	(Kappen & Breuer 1991)
			Lichens have total reliance on snow as a water supply.	L	C	F	(Hovenden *et al.* 1994)
			Quantum flux density under 15cm snow can reach light saturation for P_n of *U. sphacelata* at 0ºC.	L	C	F	(Kappen & Breuer 1991)
			Lichen productivity possible when snow covered: light compensation point low at low temps. Indirect quantification.	L	C	F + FC/L	(Lange & Kappen 1972)
			Up to 20% of the photosynthetically active radiation penetrates 20cm of winter snow.	Sn	M	F	(Walton 1982)

Abbreviations: DR dark respiration, **dwt** dry weight, **ΦPSII** quantum yield of PSII, **P_n** net photosynthesis, **PS** photosynthesis, **temp** temperature, **veg** Vegetation, **WC** water content. ↑ increasing, ↓ decreasing. Plant group codes and Study Type as in Table 4.

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. *Prasiola crispa* (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 1km 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 *et al.* 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 *P. crispa* dominant, in eutrophic sites near bird colonies.	B L	C	F + FC/L	(Melick *et al.* 1994a)
			Measured nutrient contents for a range of veg samples: description of relationship between moss communities and total N and C. *P. crispa* distribution influenced by P availability. Text in Japanese, figures suggest no quantitative statistical analysis.	B A	C	FC/L+F	(Yamanaka & Sato 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	(Nakanishi 1977)
			Suggests nutrient enrichment from birds explains relatively rich coastal communities.	L	C	F	(Kappen 1985b)
			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	F	(Inoue 1989)

			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	C	FC/L+F	(Hovenden & Seppelt 1995a)
			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. Concentration of Cl^-, NH_4^+ and PO_4^{2-} correlated with distribution of lichen complexes: *Usnea* complex – low whilst *Mastodia-Rinodina* complex – high salt concentration.	L	M	F	(Gremmen *et al.* 1994)
No change to nutrient availability	Nutrients currently non-limiting	Physiol-ogical	Soil nutrients not limiting to growth of alien vascular species.	V	C	L	(Rudolph 1966)
			High mobility of plant nutrients in Signy Island ecosystem. K and Ca provided by rock weathering, Na and Mg from the ocean, phosphorous and nitrogen from fauna. Direct droppings and drainage particularly important for distribution of N.	V B	M	FC/L	(Allen *et al.* 1967)
			Soils under moss favourable for soil respiration. Moss appears to act as a sink for nutrients originating from bird nests.	B S	C	FC/L	(Cocks *et al.* 1998)
			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 *U. antarctica* of 14% at Deception Is. and 7% at Ross Is.	B L S	C M	FC/L	(Greenfield 1992a)
			Precipitation N major N input to fellfield biota (Cape Bird and Signy Island).		C M	FC/L	(Greenfield 1992b)
			U. sphacelata highly efficient at scavenging inorganic N from snow meltwater, capturing 92 and 87% of NO_3^- and NH_4^+, respectively.	L	C	FC/L	(Crittenden 1998)
			Nutrients not limiting to veg: K, Mg and P values often extraordinarily high.	S	C	FC/L	(Beyer *et al.* 2000)
Changed nutrient availability	Species-specific differences in nutrient relations	Physiol-ogical	Measured differences in annual nitrogen content trends for two lichen species: *U. sphacelata* and *Umbilicaria decussata*.	L	C	FC/L	(Hovenden 2000)

Abbreviations: veg Vegetation, Plant group codes and Study Type as in Table 4

Figure legends

Figure 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 and Ross Island. Victoria Land.

Figure 2. Depth and area of the Antarctic ozone layer from 1980-2002 showing **(a)** minimum ozone concentration (Dobson Units) between 60-90 ˚S and **(b)** area of the springtime Antarctic ozone hole (ozone depth <220 DU, data represent 30 d 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).

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

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

Figure 1

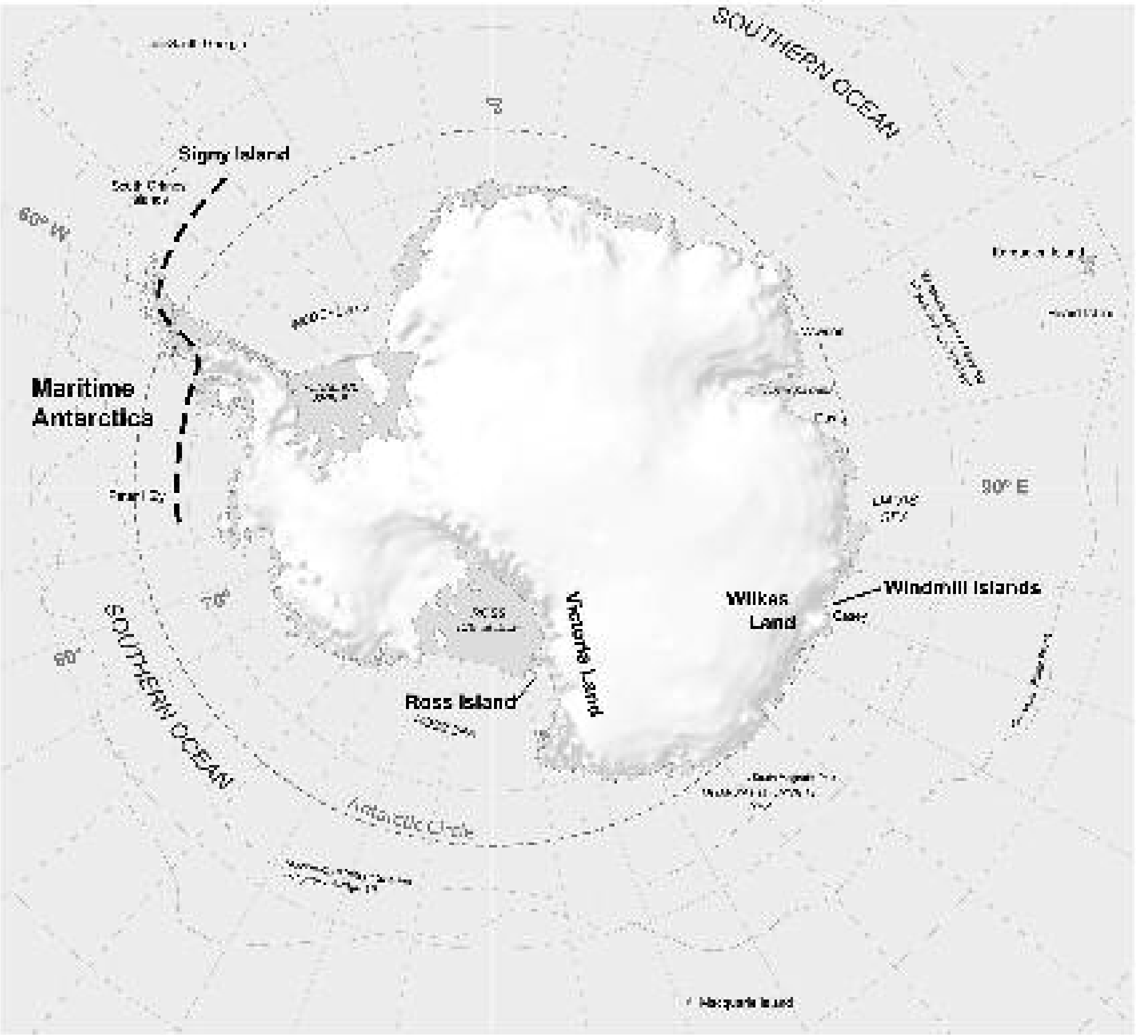

SOUTHERN OCEAN
0°
Signy Island
60° W
Maritime Antarctica
90° E
Wilkes Land
Windmill Islands
Casey
Victoria Land
70°
60°
Ross Island
SOUTHERN OCEAN
Antarctic Circle
Macquarie Island

Figure 2

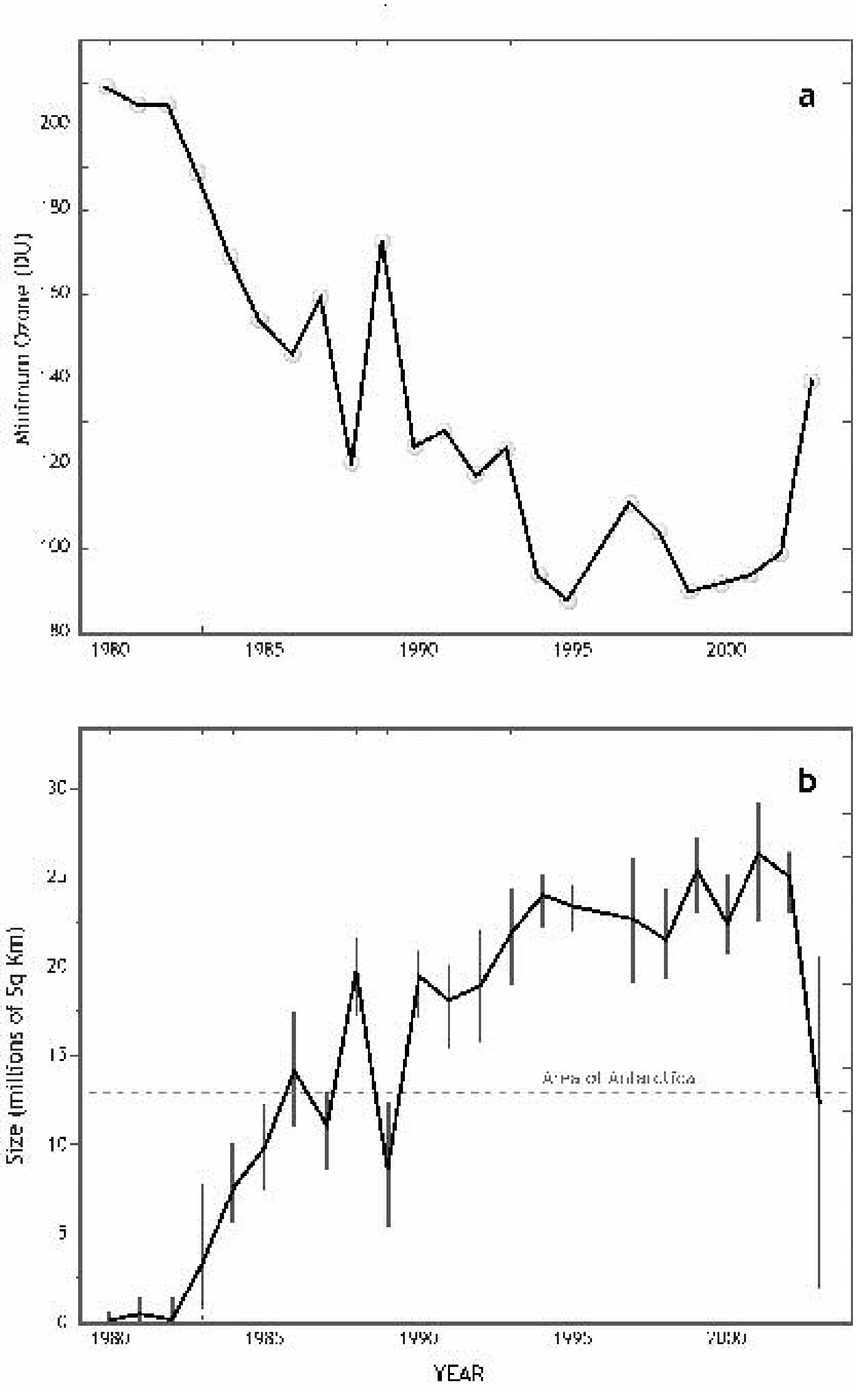

a
Minimum Ozone (DU)
80
100
120
140
160
180
200
1980
1985
1990
1995
2000
b
Size (millions of Sq Km)
0
5
10
15
20
25
30
Area of Antarctica
1980
1985
1990
1995
2000
YEAR

Figure 3

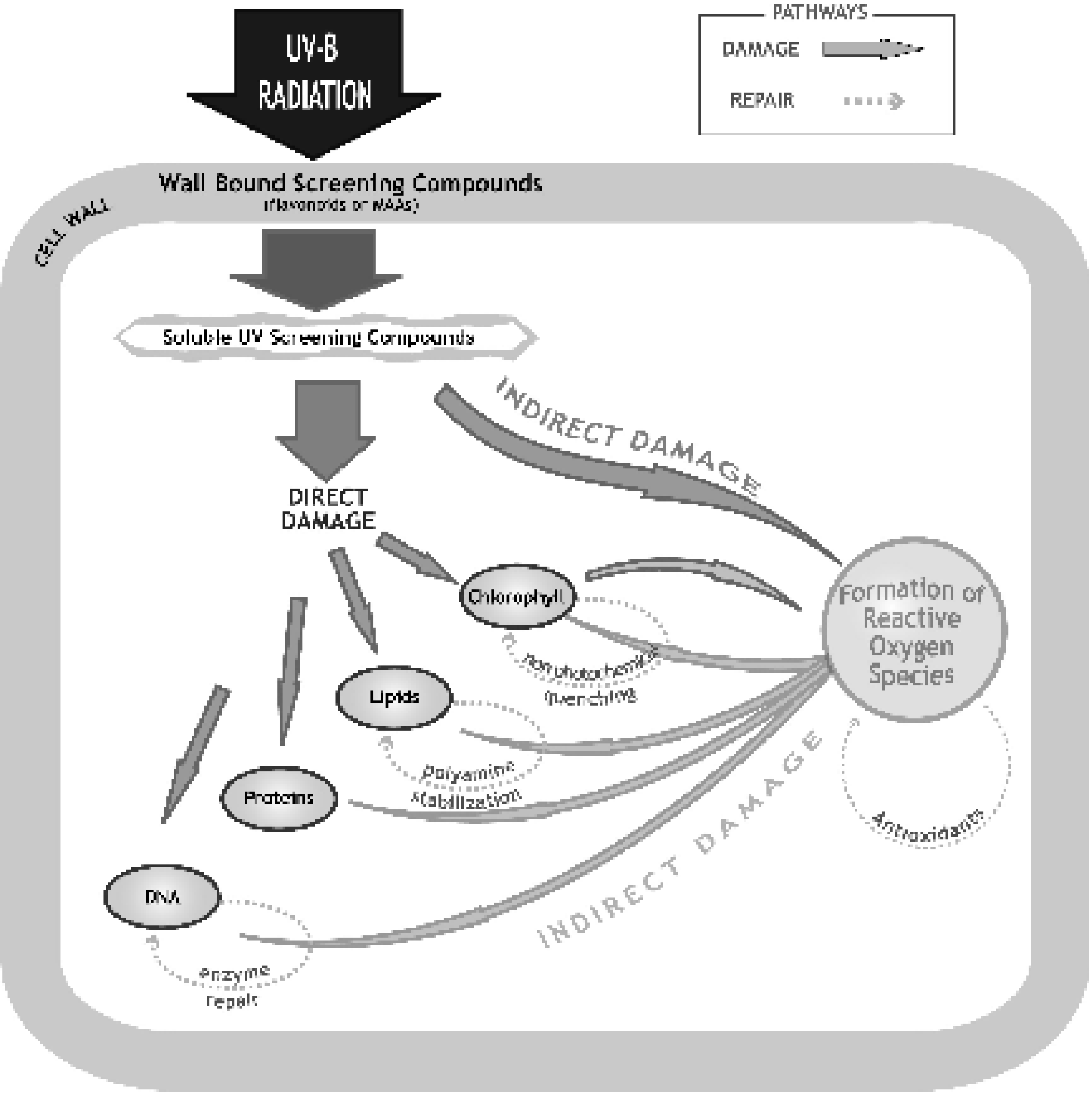
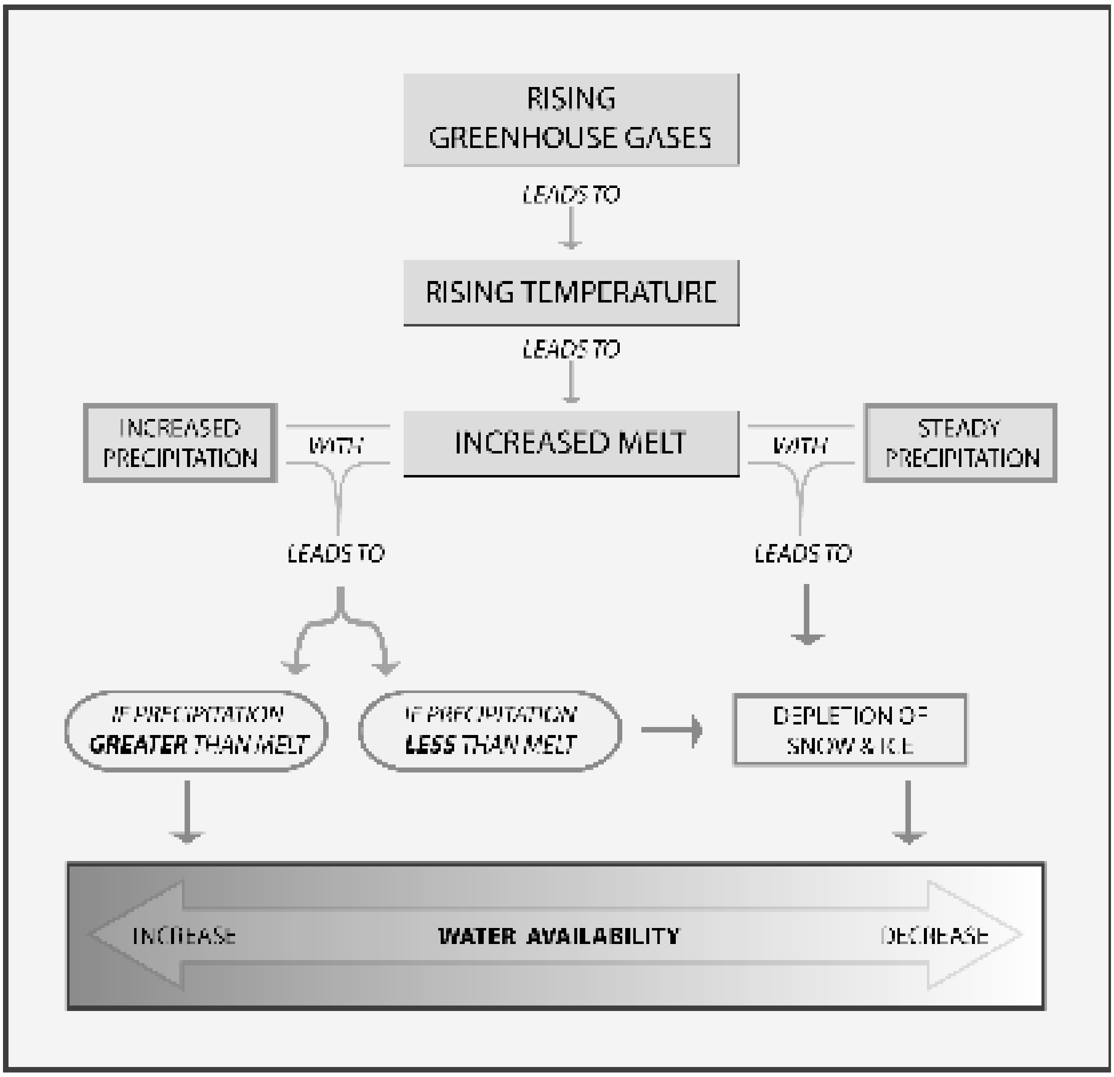

UV-B RADIATION
PATHWAYS
DAMAGE
REPAIR
CELL WALL
Wall Bound Screening Compounds
(flavonoids or MAAs)
Soluble UV Screening Compounds
INDIRECT DAMAGE
DIRECT DAMAGE
Chlorophyll
nonphotochemical quenching
Lipids
Polyamine stabilization
Proteins
DNA
enzyme repair
Formation of Reactive Oxygen Species
Antioxidants
INDIRECT DAMAGE

Figure 4


RISING GREENHOUSE GASES
LEADS TO
RISING TEMPERATURE
LEADS TO
INCREASED PRECIPITATION
WITH
INCREASED MELT
WITH
STEADY PRECIPITATION
LEADS TO
LEADS TO
IF PRECIPITATION GREATER THAN MELT
IF PRECIPITATION LESS THAN MELT
DEPLETION OF SNOW & ICE
INCREASE
WATER AVAILABILITY
DECREASE