

# Chapter 17

## Dominating the Antarctic Environment: Bryophytes in a Time of Change

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### Summary

Polar ecosystems, and particularly Antarctica, are one of the few environs in which bryophytes dominate the flora. Their success in these regions is due to bryophytes' ability to withstand an array of harsh conditions through their poikilohydric lifestyle. However, the unique conditions that allow bryophytes to proliferate over other forms of vegetation also create considerable limitations to growth and photosynthetic activity. High latitude areas are

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already experiencing some of the most pronounced and rapid climatic change, especially in the Arctic, the Sub-Antarctic Islands and Maritime Antarctica, and these are predicted to continue over the next century. This climatic change is already impacting the flora of the polar regions both via direct and/or indirect impacts on plant species. Water availability and temperature are undoubtedly the most influential factors that determine bryophyte productivity in the Antarctic, but the ozone hole is also having an impact either directly via increased ultraviolet-B radiation and/or indirectly through the increasing wind speeds associated with ozone depletion. In a time of shifting climate the dominance of bryophytes in these regions may be threatened.

## I. Introduction

### A. Antarctic Climate and Flora

Bound by the thermally isolating Antarctic Circumpolar Current, Antarctica sits in a frozen state between latitudes 60°S and 90°S (Fig. 17.1). The Antarctic continent is faced with large temperature extremes and seasonal fluctuations in water availability and solar radiation. It is, by definition, the driest and windiest continent in the world, making life in this frozen desert incredibly difficult (Robinson et al. 2003). Plants that inhabit Antarctica typical deal with subzero temperatures, limited ice free areas, moisture loss, due to high winds and little or no available water during winter months (Kappen 1993). In summer they have continuous light and in winter 24 h darkness. In addition over the past 30 years, anthropogenic ozone depletion has resulted in the continent experiencing a rapid increase in tropospheric ultraviolet-B (UV-B) radiation.

As a result of these harsh conditions and the extremely short summer growing season, the Antarctic flora is dominated by a diversity of cryptogams (bryophytes, lichens and algae), comprising more than 300 species. This diversity contrasts with the two vascular plants that are restricted to the comparatively

mild Antarctic Peninsula (Table 17.1; Lewis Smith 1984; Longton 1988; Bednarek-Ochyra et al. 2000; Øvstedal and Lewis Smith 2001, 2004; Ochyra et al. 2008). It is one of the few environs in which bryophytes predominate.

### B. Surviving the Freezer: Bryophytes Freeze Dry to Survive

The success of cryptogams in this region is undoubtedly due to their poikilohydric existence i.e. ability to equilibrate with the water status of their surroundings (Raven 1995; Schlensoeg et al. 2004). Due to morphological, biochemical and anatomical adaptations poikilohydric organisms can desiccate to a suspended metabolic state, where most of the protoplasmic water is lost and only a very small amount of tightly bound water remains in the cell. This typically occurs during times of adverse climatic conditions such as during the cold, dry Antarctic winter months (Proctor et al. 2007). In the desiccated state bryophytes can survive extremely cold conditions. In addition, their ability to freeze and thaw repeatedly is also essential during summer when temperatures are often below zero (e.g. Fig. 17.2). Surviving desiccation is made possible through the presence of compounds, including soluble carbohydrates (Smirnoff 1992) and lipids (Oliver et al. 2005), which protect membrane structure and function. When the environment becomes favorable poikilohydric organisms are able to then reactivate metabolism without major damage (Kappen and Valladares 1999).

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*Abbreviations:* DW – Dry weight; GRACE – Gravity Recovery and Climate Experiment; SAM – Southern Annular Mode; UV – ultraviolet; UVAC – ultraviolet absorbing compounds

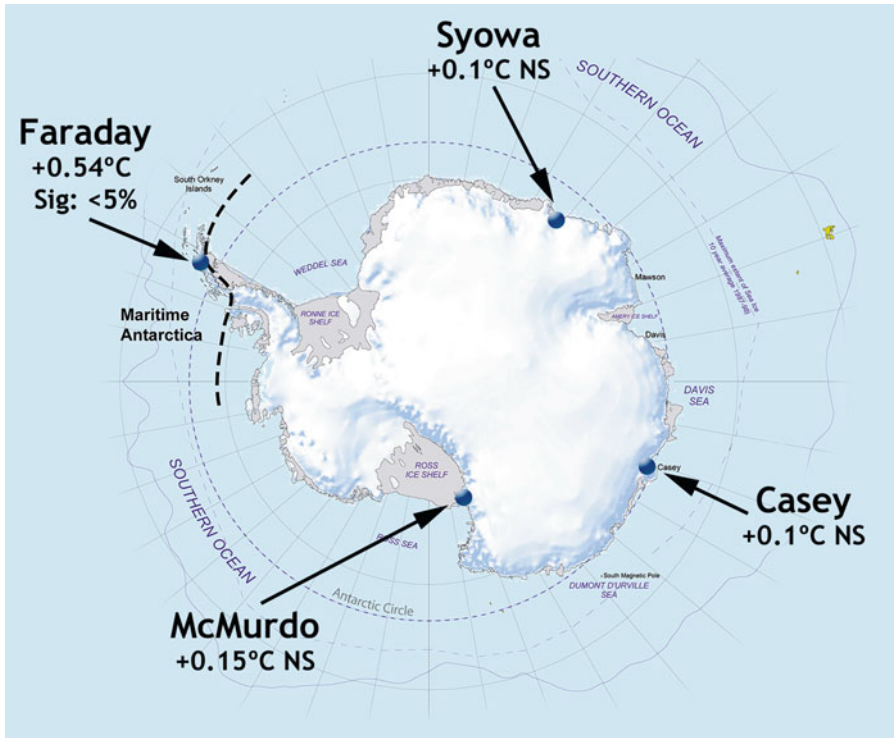


Fig. 17.1. Schematic map of Antarctica with the trends in mean annual air temperatures (degrees per decade) over the last 50 years (1951–2011 at selected research stations (Map adapted from Turner et al. (2013)). *Sig* significance value given, *NS* not significant.

Table 17.1. Estimated numbers of plant groups in Antarctica continental and maritime locations.

Region	Angiosperms	Mosses	Liverworts	Lichens
Continental	–	24	1	92
Peninsula	2	109	25	269
Total	2	111	27	393

Adapted from Lewis Smith (1984), Øvstedal and Lewis Smith (2001, 2004); Ochrya et al. (2008) and Bednarek-Ochrya et al. (2000)

This trait enables bryophytes to survive in a number of extreme habitats, ranging from the dry heat of deserts to the tops of mountains and the cold dry continent of Antarctica (Bewley 1979; Kappen 2000).

### C. Climate Change in Antarctica

High latitude areas are predicted to experience some of the most pronounced climatic changes over the next century (Anisimov et al. 2001; Turner et al. 2013) with major changes already clearly apparent for the sec-

ond half of the twentieth century, both on sub-Antarctic islands and across the Antarctic peninsula (Turner et al. 2013). Such changes include, rapid regional warming of the peninsula (Vaughan et al. 2003), increases in UV-B radiation (McKenzie et al. 2011) and associated increases in wind speeds (Marshall 2003; Turner et al. 2005; Hodgson et al. 2006; Perlwitz et al. 2008; Son et al. 2010; Ding et al. 2011), all of which are likely to have direct and/or indirect impacts on plant species in this area. Understanding current determinates of performance and

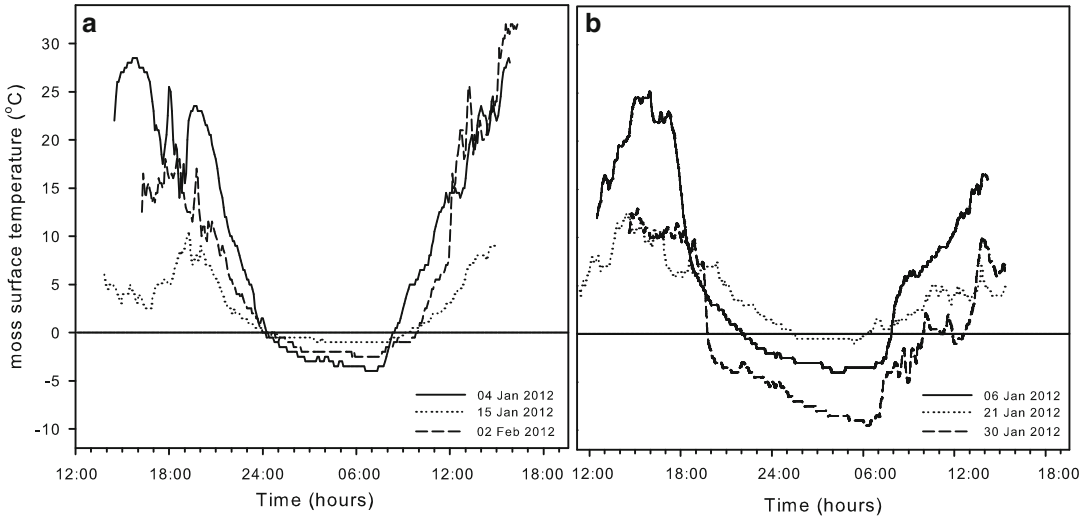


Fig. 17.2. Diurnal moss surface temperatures at two sites in the Windmill Islands, (a) Robinson's Ridge and (b) ASPA 135. At each site, temperatures were recorded at the same location over three 24 h periods, under varying weather conditions during the 2012 summer season. At Robinson's Ridge (a), two traces are for predominantly clear days (4–5 Jan, min/max air T:  $-4.0/1.7$  °C and 2–3 Feb, min/max air T:  $-6.0/1.3$  °C), and one is for an overcast day (15–16 Jan, min/max air T:  $-2.1/1.6$  °C). At the ASPA (b), again the least variation in moss surface T (range 13.5 °C) was recorded on an overcast day (20–21 Jan, min/max air T:  $-1.6/2.8$  °C), while despite different minima and maxima, moss surface temperatures ranged more widely over 21 and 29 °C, respectively, on two mostly clear days (30–31 Jan, min/max air T:  $-10.3/-1.1$  °C and 6–7 Jan, min/max air T:  $-6.3/0.7$  °C).

survival in Antarctic bryophytes is therefore important in order to predict how these ecosystems will respond to changes in the future.

## II. Water Availability

### A. Water Relations in a Frozen Desert

In climates that support extreme cold and/or dry conditions, water availability is one of the main factors determining plant growth and carbon gain (Melick and Seppelt 1994; Lenne et al. 2010). Antarctic mosses appear well adapted to high water availability and have relatively broad ranges of water content over which net photosynthesis is near maximal, for example 390–470 % for *Bryum subrotundifolium* and 245–1,400 % ( $\text{g H}_2\text{O g}^{-1}$  DW) for *Bryum pseudotriquetrum* (Pannowitz et al. 2005), 100–600 % for *Ceratodon purpureus* and 200–1,200 % ( $\text{g H}_2\text{O g}^{-1}$  DW) for *Schistidium antarctici* (Robinson et al. 2000).

Therefore areas that have access to regular melt water during the summer months (November to March; Fig. 17.3a, b, e) typically support greatest moss biomass. In some regions of Antarctica bryophytes form moss pillars in fresh water, summer lakes (Fig. 17.3c; Kudoh et al. 2009). Mosses are often found in conjunction with algae species and cyanobacteria that also rely heavily on available water (Fig. 17.3b, c; Melick et al. 1997) and the surface of moss turfs will sometimes support lichen growth (Fig. 17.3f). However lichens grow more readily on rock surfaces or by creating endolithic communities within rock crevices (Fig. 17.3g). In some of the driest regions hypolithic communities dominated by mosses flourish under opaque rocks (Fig. 17.3h; Cowan et al. 2011). Lake and hypolithic habits allow bryophytes to escape the worst stresses and extremes of the Antarctic environment, and to thrive in these relatively stable, lower radiation environments which probably reduce the



*Fig. 17.3.* Typical examples of Antarctic bryophyte flora. (a, b) Mosses thrive in areas with free water such as these turfs in and around melt lakes in the Windmill Islands East Antarctica and (c) moss pillars that occur in deeper freshwater lakes such as Hotoke-ike, Sōya Coast, East Antarctica. (d) In more exposed locations moss buttons are a common form (seen here with a bird quill). (f) Where areas are drying lichen grows above moss turfs and (g) endolithic lichen communities are commonly found in rock crevices. (h) Hypolithic communities where flora exists under or within rocks are common in Antarctica (*h2 is the underside of a rock which was originally above h1*) and such communities are often dominated by mosses. Mosses can photosynthesise at low temperatures in Antarctica; (e) the water surface is covered with a thin layer of ice but the moss is still producing O<sub>2</sub> bubbles; (i) moss lines an icy melt stream at Robinson Ridge, Windmill Island East Antarctica (taken at 0900 local solar time) (Photographs by Sharon Robinson and Satoshi Imura).

chance of freeze-thaw damage, desiccation, photobleaching and disturbance (Cowan et al. 2011).

On the Antarctic continent all species of moss display some degree of desiccation tolerance. The ability to desiccate enables moss to survive in Antarctica, although the process of desiccation itself directly affects metabolism, and as a result photosynthetic capacity is reduced when moss water content declines below the optimum for net photosynthesis (Van Gaalen et al. 2007). Desiccation tolerance was investigated in three East

Antarctic moss species (*S. antarctici*, *C. purpureus* and *B. pseudotriquetrum*) by Wasley et al. (2006b). The study showed that these species lost optimal photosynthetic efficiency (measured as the chlorophyll fluorescence parameter,  $F_v/F_m$ ) when the water content of the mosses reached between 50 and 200 % ( $\text{g H}_2\text{O g}^{-1} \text{DW}$ ), but that all three study species were able to survive desiccation and recover photosynthetic activity within an hour of rehydration (Wasley et al. 2006b). Within this broad desiccation tolerance, there were interspecific differences in regard

to photosynthetic functioning during desiccation, with *S. antarctici* showing the least tolerance of desiccation, *C. purpureus* the most and *B. pseudotriquetrum* intermediate tolerance (Robinson et al. 2000). This suggests that Antarctic bryophytes vary in their desiccation tolerance and shows that at least some species can acclimate to varying degrees of water availability.

Antarctic mosses appear to show plasticity in their response to desiccation depending on the moisture availability of their growth environment. This has been demonstrated for all three species of east Antarctic moss described above (Robinson et al. 2000). Similarly, Kappen and Schroeter (2002) showed that differences in the optimal water content for net photosynthesis were related to the water availability at the site of moss growth for Antarctic species. For example, xeric forms of the Antarctic moss species *Henediella heimii* displayed optimal net photosynthesis at relative water contents of 200–300 % compared to over 500 % ( $\text{g H}_2\text{O g}^{-1} \text{DW}$ ) in hydric forms. Furthermore, an earlier study by Kappen et al. (1989) found that the physiological response of the endemic species *S. antarctici* differed greatly between mesic and xeric environments, with a higher chlorophyll content, a lower light compensation point, a wider temperature range of positive net photosynthesis, and greater productivity in mesic rather than in xeric forms under similar conditions. Likewise, Davey (1997) found that regardless of other changing environmental factors (such as irradiance and temperature) there was a clear trend towards increasing photosynthetic performance in a range of Signy Island Antarctic bryophytes from xeric to mesic to hydric habitats. They concluded that water, rather than temperature, is the most important factor governing photosynthesis in this region. By contrast, an earlier study by Convey (1994), using a similar set of species from Signy Island, found no relationship between habitat wetness and productivity. It is also important to note that photosynthetic efficiency can decline at the highest tissue water contents (Robinson et al. 2000) and tolerance of complete submergence

depends on the species (see Fig. 17.3f and Wasley et al. 2006b). In addition, moss at wet sites tend to freeze at higher temperatures than that at dry sites (Melick and Seppelt 1994). Desiccation prior to exposure to freezing temperatures is an important factor in the survival of Antarctic bryophytes and there is probably a trade-off between optimum water availability for photosynthesis and risk of freezing damage. If climate change produces more freeze-thaw events in summer this is likely to have negative effects on bryophyte productivity in the Antarctic (Lovelock et al. 1995a, b).

### *B. Climate Change and Future Water Availability*

While it is not yet fully understood how climate change will affect biologically accessible water in Antarctic, rising temperatures are likely to augment melt, and therefore, have a short term positive effect on productivity, although if water becomes more available, nutrients may then become a more limiting factor (Robinson et al. 2003; Wasley et al. 2006a). Given that the summer growing season is so short it is probable that the length of availability of free water will be the critical factor. Thus a more rapid and extreme melt, accelerating run off, may potentially result in a shorter growing season. Studies of changes in the stable isotope ratio of carbon ( $\delta^{13}\text{C}$ ) along the length of moss shoots have shown that several sites in the Windmill Islands have become drier in recent decades (Clarke et al. 2012) supporting predictions of a drier future for this region (Hodgson and Sime 2010). Long-term predictions of water availability are complex but tend to point towards increased aridity across the continent, especially in the biologically rich coastal regions (Krunner et al. 2007). The long-term effects of losing previously permanent water sources, which are already receding due to increased melt (Vaughan et al. 2003; Chen et al. 2008, 2009), are assumed to be negative. Recent satellite studies known as the Gravity Recovery and Climate Experiment (GRACE) have detected a loss in the polar ice-sheet

mass balance of up to 19,077 Gt per year, with a rapid loss of ice mass in coastal regions of East Antarctica since 2006 (Chen et al. 2009). Future precipitation, although predicted to increase in areas of Antarctica in the twenty-first century (Krinner et al. 2007), will need to be substantially higher than average in order to replenish these reserves (Robinson et al. 2003; Wasley et al. 2006a; Christensen et al. 2007). Furthermore, an increase in wind speed, due to the positive phase of the dominant weather system over Antarctica, the Southern Annular Mode (SAM), is likely to cause shifts to a negative water balance through evaporation. Evidence of this is already apparent in a number of coastal East Antarctic lakes (Hodgson et al. 2006) and moss beds (Clarke et al. 2012), as well as in soil moisture content in the McMurdo dry valleys (Doran et al. 2002). Since these increased wind speeds and associated evaporative drying are linked to ozone depletion as well as increased greenhouse gases, they are likely to continue until at least mid century (Perlwitz et al. 2008; United Nations Environment Programme 2012).

The reduction of permanent water sources, coupled with the already observed drying effect of increased wind speeds, will subject Antarctic vegetation to longer periods of desiccation. This implies that a number of species are in danger of reduced distribution, with sensitive endemic species, such as *S. antarctici*, particularly threatened (Wasley et al. 2006a). Preliminary results from a recently developed State of the Environment Indicator for continental Antarctic vegetation (Robinson et al. 2009) suggested a remarkable decline in the dominant moss species between 2003 and 2008 with a simultaneous increase in dead moss (King 2009). The trend suggests the sensitive endemic species, *S. antarctici*, is being overgrown by more desiccation resilient species, such as *C. purpureus* (Robinson et al. 2000; Wasley et al. 2006b), with recent drying in the region the major driver of this change. If these drying trends outweigh extra water inputs from increased temperature and precipitation then the resulting decreased water availability is likely to

have a predominantly detrimental biological affect; however, this is clearly an area in which more research on both climate and resulting bryophyte carbon balance models is needed to predict the direction of change.

### III. Temperature

#### A. Temperature Relations

Temperature in Antarctica is undoubtedly challenging to life. The continent is cold and strongly seasonal with yearly temperatures in coastal regions ranging from below  $-40^{\circ}\text{C}$  during winter to over  $0^{\circ}\text{C}$  during summer months (Convey and Smith 2006). These low extremes are thought to be a primary limiting factor, both directly and through their influence on water availability to vascular plant growth in the region (Block et al. 2009). The shortness of the summer season, the few months when temperatures are close to or just above  $0^{\circ}\text{C}$ , is a major factor in determining the flora of the continent since the cumulative number of days where temperatures are above zero and water can melt are critical for bryophyte productivity. A study by Davey and Rothery (1997) found that in Signy Island moss species, *Andreaea depressinervis*, *Chorisodontium aciphyllum* and *Brachythecium austrosalebrosum*, there were significant seasonal changes in the maximum rates of photosynthesis, associated with differences in the summer maxima. Furthermore, field measurements of net photosynthesis in East Antarctic moss species, *C. purpureus* and *B. pseudotriquetrum*, found the maximum rate of net photosynthesis to be only  $4\ \mu\text{mol CO}_2\ \text{m}^{-2}\ \text{s}^{-1}$  at saturating radiation intensity and at an optimum temperature of  $10^{\circ}\text{C}$  (Ino 1990). The severity of the winter months restricts the growth of cryptogams, which congregate to sites that maintain a relatively high level of solar radiation (Seppelt and Ashton 1978) such as on North facing sides of rocks, sheltered from the wind.

Temperature at ground surface level is, however, strongly influenced by both radiative inputs and the boundary layer effect

(Geiger 1965). Moss cushions conform to black body solar radiation (Newsham 2010) and therefore have been found to reach temperatures above 40 °C during the summer months if situated in sun-exposed but wind-sheltered sites (Lewis Smith 1988). The button, turf and hypolith habits of Antarctic bryophyte communities (see Fig. 17.3d, b, h) are all effective at reducing wind chill as is their location in sheltered valleys, small depressions and upwind from rocks or in rock crevices. For example, studies by Schenker and Block (1986) recorded soil surface temperatures between 3.7 and 10.7 °C warmer than air temperature, and a study by Lewis Smith (1995) identified an increase in ground surface level temperature of between 5 and 25 °C compared to air temperatures. A study on the Antarctic Peninsula by Schlenzog and Schroeter (2000) reported the diurnal thermal cycle within a cushion of *Andreaea gainii* to range between -2 and 52 °C during the summer months. Whilst on the continent during a sunny day in January, Lewis Smith (1988) recorded a diurnal temperature cycle of between 9.2 and 42.8 °C just a few millimeters beneath the surface of a cushion of *S. antarctici*. At this same location in the Windmill Islands, moss surface temperatures were more than 30 °C above maximum air temperature on a sunny day, and even on an overcast day, the maximum moss surface temperature was more than 9 °C above the maximum air temperature (Fig. 17.2).

In summer, night-time temperatures can drop to -20 °C potentially exposing actively growing moss to a 40–60 °C daily range (Lovelock et al. 1995a, b). Such large ranges are most likely to occur on clear, sunny days, when maximum heating of moss turfs occurs through the day, but when cooling is more rapid during the cloudless low light night. For example, the surface temperature of the same moss ranged from -2.5 to 32 °C over a 24 h period with mostly clear skies in January in the Windmill Islands, but ranged from -1.0 to 10.5 °C on an overcast day the same month (Fig. 17.2). Fig. 17.3g shows a typical example of a moss lined icy melt stream taken on a sunny morning in the Windmill Islands

region of East Antarctica. Such conditions potentially expose moss to high photosynthetically active and UV radiation whilst the plants are cold, and would be expected to produce photoinhibition in less tolerant plants (see Chap. 7).

These large fluctuations between the extreme cold temperatures of winter to the warm temperatures of summer mean that Antarctic moss must possess a much greater range of temperature tolerance (~100 °C) than most equivalent species in other global biomes. Whilst the winter cold extremes will occur when the mosses are freeze dried and metabolically inactive, temperatures can rise above zero in mid winter potentially rehydrating moss and exposing it to freeze-thaw damage (Lenne et al. personal communication).

The two dangers of low temperatures for bryophyte growth and development are, firstly, a reduction in physiological activity due to cold, and secondly the more immediate danger of tissue freezing (Lovelock et al. 1995a, b; Lenne et al. 2010). For polar plants the ability to perform photosynthesis at low temperatures it is vital to compensate for the very short summer in which production is possible (Kennedy 1993) although as discussed above, it seems likely that the bulk of photosynthesis actually occurs when the bryophytes are warmed by solar radiation. Consistent with this, temperature optima for photosynthesis for the Antarctic mosses that have been measured are between 5 and 25 °C (Table 17.2). The more pressing danger is to avoid damage caused by ice formation in living tissue and to recover quickly from such damage in order to be able to respond opportunistically to the small window of production during the summer months (Lenne et al. 2010). Polar bryophytes have developed various biochemical, physiological and morphological mechanisms to limit such damage (e.g., Robinson et al. 2000; Wasley et al. 2006b; Block et al. 2009). Kappen (1993) demonstrated the ability of polar bryophytes to withstand prolonged periods of burial by snow and ice but resume normal photosynthesis within a few hours after exposure to extreme (and non physiologically



Table 17.2. Temperature optimum for photosynthesis for a range of Antarctic bryophytes measured under field and laboratory conditions.

Species	Temperature optimum for photosynthesis (°C)	Method and location of measurements (Field or laboratory)	References
<i>Bryum subrotundifolium</i>	13.7	Field laboratory NP	Pannewitz et al. (2005)
<i>Bryum pseudotriquetrum</i>	10–12.0	Field laboratory NP	Pannewitz et al. (2005), Ino (1990)
<i>Bryum argenteum</i>	≥20	Lab O <sub>2</sub> evolution	Lewis Smith (1999)
	15	Field laboratory NP	Green et al. (2000)
	≥20	Lab O <sub>2</sub> evolution	Lewis Smith (1999)
<i>Ceratodon purpureus</i>	25	Lab O <sub>2</sub> evolution	Rastorfer (1970)
	6.6	Field laboratory NP	Pannewitz et al. (2005)
	≥20	Lab O <sub>2</sub> evolution	Lewis Smith (1999)
<i>Schistidium antarctici</i>	5–10	Lab NP	Kappen et al. (1989)
<i>Cephaloziella varians</i>	≥20	Lab O <sub>2</sub> evolution	Newsham (2010)

Net photosynthesis (NP) was measured as CO<sub>2</sub> assimilation. Laboratory measurements were performed using an O<sub>2</sub> electrode system (Rastorfer 1970)

relevant cold; –196 °C) conditions. Several studies have demonstrated that continental Antarctic bryophyte species can survive repeat freeze-thaw events (Melick and Seppelt 1992; Lovelock et al. 1995a, b), but there are costs to such protection and increased frequency of such events in future could be detrimental (Lovelock et al. 1995a; Lenne et al. 2010).

### B. Climate Change and Future Temperature

Discerning recent temperature trends for the Antarctic continent as a whole is challenging, and much debated. Past studies by Raper et al. (1984) claimed that Antarctica, in its entirety, had been warming significantly by 0.29 °C per decade since the 1950s, whereas later studies by Doran et al. (2002) claimed a net cooling of the continent over this same period. More recent studies, such as by Turner et al. (2002), have exposed the invalidity of such studies due to limited data and overly large extrapolations, and since this time the Reference Antarctic Data for Environmental Research (READER) project has been implemented to provide an improved data set for use in climate change studies (Turner et al. 2013).

While the bulk of East Antarctica has experienced little significant change in temperature over the last 50 years (Fig. 17.1; Turner et al. 2013), recent studies suggest that West Antarctica has warmed by over 0.1 °C per decade (Steig et al. 2009b; Ding et al. 2011). The most significant change in temperature has occurred over the Antarctic Peninsula, where the accelerated rate of warming has seen this area classified as one of the fastest warming regions on Earth (Vaughan et al. 2003). Temperatures rose on the west and northern parts of the peninsula by 0.56 °C per decade from 1951 to 2000 (Turner et al. 2013) with the greatest rates of warming during the winter months (King and Harangozo 1998). The changing Southern Annular mode (SAM) has played a key role in driving warming in this region (Marshall et al. 2006, 2011; Fogt et al. 2009), mainly through generating stronger winds that bring relatively warm maritime air masses across the peninsula (Mayewski et al. 2009). In contrast, East Antarctica has shown regional differences, with Turner et al. (2005) proposing a gradual cooling to the area as a whole since the 1980s. Although there is no clear evidence of warming from station meteorological records in the region,

recent studies of ice-sheet mass balance have shown accelerated ice loss since 2006 from the East Antarctic sheet in the vicinity of Casey Station (Chen et al. 2009). Further, infrared satellite data suggest that contrary to previous reports, East Antarctica has warmed by 0.1 °C per decade since 1957 (Steig et al. 2009a, b).

Increasing temperature and precipitation in polar regions due to climate change (Chen et al. 2009) were predicted to result in increased bryophyte growth rates through increases in water availability and length of the growing season (Robinson et al. 2003). Even though temperature patterns in this region remain unclear, a shift to either warmer or cooler conditions could have serious consequences for Antarctic vegetation. The majority of bryophyte species respond positively to warmer temperatures, suggesting that a rise in temperatures would generate more productivity and vice versa. Studies on both vascular and non-vascular Antarctic plants have shown an increase in the maximum rate of gross photosynthesis in conjunction with temperature increases within the range of 0–20 °C (Xiong et al. 1999). Lewis Smith (1999) found net photosynthesis increased with temperature (tested up to 20 °C) for a range of Antarctic bryophytes including *Bryum argenteum*, *B. pseudotriquetrum* and *C. purpureus*. Likewise, a field study on vascular Antarctic tundra by Day et al. (2008) found that warming led to greater above-ground plant biomass, as well as greater mass of the litter layer and organic soil horizon.

On the other hand, too high a rise in temperature has been demonstrated to reduce bryophyte productivity. This is also apparent in Antarctic vascular plants as demonstrated by Xiong et al. (1999) who found that net photosynthesis was depressed above 20 °C in both *Deschampsia antarctica* and *Colobanthus quitensis*, but remained high at temperatures greater than 10 °C. This was consistent with the work of Vining et al. (1997), who found a pronounced decline in net photosynthesis in the same species at temperatures greater than 12 °C, with negligible photosynthesis at 35 °C. Furthermore, low temperatures

appear to be important for some species in order to achieve positive net carbon balance. For example, in the maritime moss *Sanionia uncinata* photosynthesis remains low over a temperature range of 0–20 °C but dark respiration steadily increases (Nakatsubo 2002) suggesting that increasing temperatures may reduce carbon gain through increasing respiratory losses.

#### IV. The Ozone Hole and Increased Ultraviolet Radiation

Stratospheric ozone depletion, resulting from anthropogenic, atmospheric pollution, has occurred since the 1980s, with an ozone hole (defined as the area with an ozone thickness of <220 DU) developing each austral spring (September–November) over Antarctica (Roy et al. 1994; NASA 2012). The largest ozone hole was recorded in September 2006 (NASA 2012) and full recovery of the ozone layer is not expected until 2050 (McKenzie et al. 2011). Depletion of stratospheric ozone, has led to increased ultraviolet (UV) radiation at the Earth's surface, as well as a spectral shift to the more biologically damaging shorter wavelengths, especially over Antarctica (Frederick and Snell 1988).

##### A. Protection from Ultraviolet Radiation in Antarctic Bryophytes

The ozone hole has resulted in Antarctic plant communities being exposed to a rapid change in UV-B exposure over the past four decades. A meta-analysis of the impact of this increase in UV-B suggests that Antarctic bryophytes respond to increasing UV-B radiation in a similar way to vascular plants, with increases in UV absorbing compounds (UVAC), reductions in aboveground biomass and plant height and increased accumulation of DNA damage (Searles et al. 2001; Newsham and Robinson 2009). There was little evidence of consistent impacts on photosynthesis, optimum photosynthetic efficiency ( $F_v/F_m$ ) or chlorophyll pigments

from this meta-analysis, but Antarctic plants responded to increased UV-B radiation by increasing their carotenoid concentrations by 17 % whilst Arctic plants did not show this response. As detailed in Chap. 7, UV-B radiation is implicated in direct damage to PSII, and photoprotective carotenoids, such as zeaxanthin and  $\beta$ -carotene, can mitigate against such damage through the dissipation of excess energy as heat thus reducing the formation of reactive oxygen species (ROS) as well as scavenging any ROS that are produced.

Studies have shown impacts on photosynthetic pigmentation for particular species; for example, decreases in chlorophyll and increases in zeaxanthin and  $\beta$ -carotene in *Schistidium antarctici* exposed to UV-B radiation (Robinson et al. 2005). Total carotenoids also increased with increasing UV-B/PAR in both the leafy liverwort, *Cephaloziella varians* and the mosses, *Sanionia uncinata* and *Andreaea regularis* (Newsham et al. 2002, 2005) but in contrast to *S. antarctici*, chlorophyll pigments were unaffected in these species. Acclimation of shade to sun forms of *C. purpureus* and *Bryum subrotundifolium* was achieved in as little as 6 days and sun forms of the two mosses exhibited enhanced UV-A shielding as measured using a UV-PAM fluorometer (Green et al. 2005).

Increasing UVAC in response to increasing UV-B radiation have been found in the liverwort, *Cephaloziella varians* and the mosses; *S. uncinata* (Newsham et al. 2002), *A. regularis* (Newsham 2003), *B. pseudotriquetrum* (Dunn and Robinson 2006) and *B. argenteum* (Ryan et al. 2009). In contrast two other Antarctic bryophyte species (*C. purpureus* and *S. antarctici*) have been shown to contain UVAC that are not particularly responsive to changes in UV-B radiation (Lovelock and Robinson 2002; Dunn and Robinson 2006). Both these mosses have since been shown to accumulate UVAC in their cell walls and it remains to be seen if these cell wall UVAC are responsive to changing UV-B radiation or produced constitutively (Clarke 2008; Chap. 7 this volume). Given that UV-B radiation dose has

only been measured around Antarctica for the last 30 years, bryophytes and bryophyte spores that contain UVAC that respond to UV-B radiation could be used to determine historic levels of UV-B radiation (Lomax et al. 2008; Ryan et al. 2009).

DNA damage has been detected in several Antarctic bryophyte species under naturally varying UV radiation (Turnbull and Robinson 2009) and was induced by UV supplementation in the lab (Turnbull et al. 2009) and the field (Lud et al. 2003). Desiccated bryophytes accumulated fewer DNA photo-products suggesting that either DNA is better stabilized in desiccated mosses or that screening is more effective (Turnbull et al. 2009). Most studies seem to suggest that DNA damage that accumulates under natural UV exposure is rapidly repaired (Lud et al. 2003).

### B. Climate Change and Future Ultraviolet Radiation

As a result of the Montreal Protocol, recovery of the ozone layer to pre 1980s levels is expected by mid century and climate models suggest that by 2100 UV-B radiation over Antarctica should be lower than it was prior to ozone depletion (Newman et al. 2007; McKenzie et al. 2011). With the closing of the ozone hole in coming decades, any additional UV-B radiation effects on Antarctic bryophytes should thus disappear.

Of more concern for the future is the influence of ozone depletion and increasing greenhouse gases on the jet stream. Ozone depletion has been implicated in a southwards shift of the jet stream, bringing stronger westerly winds to the Antarctic continent (Son et al. 2010; Perlwitz 2011). These winds are responsible for both warming of the Antarctic Peninsula and evaporative drying around the coast of East Antarctica (see sections above). Currently whilst both greenhouse gases and ozone depletion contribute to this jet stream shift, ozone depletion is the major driver. As the ozone hole recovers, the extent to which these winds continue to lash the Antarctic coast will depend on the levels of greenhouse gases in the atmosphere

(Perlwitz 2011). Since temperature and water appear to have more dramatic impacts on Antarctic bryophytes than increasing UV-B radiation (Clarke et al. 2012), these indirect changes are potentially of more concern for the future.

## V. Conclusions

Water availability and temperature are undoubtedly the most influential factors that determine current bryophyte productivity in the Antarctic and are likely to remain the major drivers in the future. Whilst mean temperatures are a key factor, extremes, especially those that initiate unseasonable freezing, can be particularly damaging. The extreme Antarctic climate explains the current success of poikilohydric organisms including bryophytes, but a changing climate could be threatening their dominance.

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## References

- Anisimov O, Fitzharris BB, Hagen JO, Jefferies B, Marchant H, Nelson F, Prowse T, Vaughan D (2001) Polar regions (Arctic and Antarctic). In: McCarthy JJ, Canziani OF, Leary NA, Dokken DJ, White KS (eds) *Climate change 2001: impacts, adaptation, and vulnerability*. Contribution of Working Group II to the third assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, pp 801–841
- Bednarek-Ochyra H, Vána J, Ochyra R, Lewis Smith RI (2000) *The liverwort flora of Antarctica*. Polish Academy of Sciences, Institute of Botany, Cracow
- Bewley J (1979) Physiological aspects of desiccation tolerance. *Annu Rev Plant Physiol* 30:195–238
- Block W, Smith RIL, Kennedy AD (2009) Strategies of survival and resource exploitation in the Antarctic fellfield ecosystem. *Biol Rev* 84:449–484
- Chen JL, Wilson CR, Tapley BD, Blankenship D, Young D (2008) Antarctic regional ice loss rates from GRACE. *Earth Planet Sci Lett* 266:140–148
- Chen JL, Wilson CR, Blankenship D, Tapley BD (2009) Accelerated Antarctic ice loss from satellite gravity measurements. *Nat Geosci* 2:859–862
- Christensen J, Hewitson B, Busuioc A, Chen A, Gao X, Held I, Jones R, Kolli R, Kwon W, Laprise R, Magaña Rueda V, Mearns L, Menéndez C, Räisänen J, Rinke A, Sarr A, Whetton P (eds) (2007) *Regional climate projections*. *Climate change 2007: the physical science basis*. Contribution of working group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge/New York
- Clarke L (2008) Resilience of the Antarctic moss *Ceratodon pupureus* to the effects of elevated UV-B radiation and climate change. Doctor of Philosophy thesis, Biological Sciences, University of Wollongong, Wollongong
- Clarke LJ, Robinson SA, Hua Q, Ayre DJ, Fink D (2012) Radiocarbon bomb spike reveals biological effects of Antarctic climate change. *Glob Change Biol* 18:301–310
- Convey P (1994) Photosynthesis and dark respiration in Antarctic mosses – an initial comparative study. *Polar Biol* 14:65–69
- Convey P, Smith RIL (2006) Responses of terrestrial Antarctic ecosystems to climate change. *Plant Ecol* 182:1–10
- Cowan D, Pointing S, Stevens M, Cary C, Stomeo F, Tuffin M (2011) Distribution and abiotic influences on hypolithic microbial communities in an Antarctic Dry Valley. *Polar Biol* 34:307–311
- Davey MC (1997) Effects of short-term dehydration and rehydration on photosynthesis and respiration by Antarctic bryophytes. *Environ Exp Bot* 37:187–198
- Davey MC, Rothery P (1997) Interspecific variation in respiratory and photosynthetic parameters in Antarctic bryophytes. *New Phytol* 137:231–240
- Day TA, Ruhland CT, Xiong FS (2008) Warming increases aboveground plant biomass and C stocks in vascular-plant-dominated Antarctic tundra. *Glob Change Biol* 14:1827–1843
- Ding QH, Steig EJ, Battisti DS, Kuttel M (2011) Winter warming in West Antarctica caused by central tropical Pacific warming. *Nat Geosci* 4:398–403
- Doran P, Prisco J, Lyons B, Walsh J (2002) Antarctic climate cooling and terrestrial ecosystem response. *Nature* 415:517–520
- Dunn JL, Robinson SA (2006) Ultraviolet B screening potential is higher in two cosmopolitan moss species than in a co-occurring Antarctic endemic moss: implications of continuing ozone depletion. *Glob Change Biol* 12:2282–2296

- Fogt RL, Perlwitz J, Monaghan AJ, Bromwich DH, Jones JM, Marshall GJ (2009) Historical SAM variability. Part II: Twentieth-century variability and trends from reconstructions, observations, and the IPCC AR4 models. *J Clim* 22:5346–5365
- Frederick JE, Snell HE (1988) Ultraviolet radiation levels during the Antarctic spring. *Science* 241:438–440
- Geiger R (1965) The climate near the ground. Harvard University Press, Cambridge, MA, US
- Green TGA, Schroeter B, Seppelt R (2000) Effect of temperature, light and ambient UV on the photosynthesis of the moss *Bryum argenteum* hedw. In: continental Antarctica. In: Davison W, Howard-Williams C, Broady P (eds) Antarctic ecosystems: models for wider ecological understanding. Canterbury University, Christchurch, pp 165–170
- Green TGA, Kulle D, Pannowitz S, Sancho LG, Schroeter B (2005) UV-A protection in mosses growing in continental Antarctica. *Polar Biol* 28:822–827
- Hodgson DA, Sime LC (2010) Palaeoclimate: Southern westerlies and CO<sub>2</sub>. *Nat Geosci* 3:666–667
- Hodgson D, Roberts D, McMinn A, Verleyen E, Terry B, Corbett C, Vyverman W (2006) Recent rapid salinity rise in three East Antarctic lakes. *J Paleolimnol* 36:385–406
- Ino Y (1990) Field measurement of net photosynthesis of mosses at Langhovde, East Antarctica. *Ecol Res* 5:195–205
- Kappen L (1993) Plant activity under snow and ice, with particular reference to lichens. *Arctic* 46:297–302
- Kappen L (2000) Some aspects of the great success of lichens in Antarctica. *Antarct Sci* 12:314–324
- Kappen L, Schroeter B (2002) Plants and lichens in the Antarctic, their way of life and their relevance to soil formation. In: Beyer L, Bölter M (eds) *Geocology of Antarctic ice-free coastal landscapes*. Springer, Berlin, pp 327–373
- Kappen L, Valladares F (1999) Opportunistic growth and desiccation tolerance: the ecological success of poikilohydrous autotrophs. In: Pugnaire F, Valladares F (eds) *Handbook of functional ecology*. Dekker, New York, pp 9–80
- Kappen L, Lewis Smith RI, Myer M (1989) Carbon dioxide exchange of two ecodomes of *Shistidium antarctici* in continental Antarctica. *Polar Biol* 9:415–422
- Kennedy A (1993) Photosynthetic response of the Antarctic moss *Polytrichum alpestre* Hoppe to low temperatures and freeze-thaw stress. *Polar Biol* 13:271–279
- King D (2009) Rapid change in continental Antarctic vegetation communities. BEnvSci Honours thesis, Environmental Science, University of Wollongong, Wollongong
- King J, Harangozo S (1998) Climate change in the western Antarctic Peninsula since 1945: observations and possible causes. *Ann Glaciol* 27:571–575
- Krinner G, Magand O, Simmonds I, Genthon C, Dufresne J (2007) Simulated Antarctic precipitation and surface mass balance at the end of the twentieth and twenty-first centuries. *Clim Dyn* 28:215–230
- Kudoh S, Tanabe Y, Matsuzaki M, Imura S (2009) In situ photochemical activity of the phytobenthic communities in two Antarctic lakes. *Polar Biol* 32:1617–1627
- Lenne T, Bryant G, Hocart C, Huang C, Ball M (2010) Freeze avoidance: a dehydrating moss gathers no ice. *Plant Cell Environ* 33:1731–1741
- Lewis Smith RI (1984) Terrestrial plant biology of the sub-Antarctic and the Antarctic. In: Laws RM (ed) *Antarctic ecology*. Academic, London
- Lewis Smith RI (1988) Recording bryophyte microclimate in remote and severe environments. In: Glime JM (ed) *Methods in bryology*. Hattori Botanical Laboratory, Nichinan, pp 275–284
- Lewis Smith RI (1995) Colonization by lichens and the development of lichen-dominated communities in the maritime Antarctic. *Lichenologist* 27:473–483
- Lewis Smith RI (1999) Biological and environmental characteristics of three cosmopolitan mosses dominant in continental Antarctica. *J Veg Sci* 10:231–242
- Lomax BH, Fraser WT, Sephton MA, Callaghan TV, Self S, Harfoot M, Pyle JA, Wellman CH, Beerling DJ (2008) Plant spore walls as a record of long-term changes in ultraviolet-B radiation. *Nat Geosci* 1:592–596
- Longton RE (1988) *Biology of polar bryophytes and lichens*. Cambridge University Press, Melbourne
- Lovelock CE, Robinson SA (2002) Surface reflectance properties of Antarctic moss and their relationship to plant species, pigment composition and photosynthetic function. *Plant Cell Environ* 25:1239–1250
- Lovelock CE, Osmond C, Seppelt RD (1995a) Photoinhibition in the Antarctic moss *Grimmia antarctici* card when exposed to cycles of freezing and thawing. *Plant Cell Environ* 18:1395–1402
- Lovelock CE, Jackson AE, Melick DR, Seppelt RD (1995b) Reversible photoinhibition in Antarctic moss during freezing and thawing. *Plant Physiol* 109:955–961
- Lud D, Buma AGJ, Moerdijk TCW, Huiskes AHL (2003) DNA damage and photosynthesis in *Prasiola crispa* ssp *antarctica* and *Sanionia uncinata* in response to manipulated UV-B radiation. In: Antarctic biology in a global context: proceedings of the VIIIth SCAR international biology symposium, Amsterdam, The Netherlands, pp 69–73

- Marshall G (2003) Trends in the southern annular mode from observations and reanalyses. *J Clim* 19:4134–4143
- Marshall GJ, Orr A, van Lipzig NPM, King JC (2006) The impact of a changing Southern Hemisphere annular mode on Antarctic Peninsula summer temperatures. *J Clim* 19:5388–5404
- Marshall G, Di Battista S, Naik S, Thamban M (2011) Analysis of a regional change in the sign of the SAM-temperature relationship in Antarctica. *Clim Dyn* 36:277–287
- Mayewski PA, Meredith MP, Summerhayes CP, Turner J, Worby A, Barrett PJ, Casassa G, Bertler NAN, Bracegirdle T, Naveira Garabato AC, Bromwich D, Campbell H, Hamilton GS, Lyons WB, Maasch KA, Aoki S, Xiao C, van Ommen T (2009) State of the Antarctic and Southern Ocean climate system. *Rev Geophys* 47:RG1003
- McKenzie RL, Aucamp P, Bais A, Björn L, Ilyas M, Madronich S (2011) Ozone depletion and climate change: impacts on UV radiation. *Photochem Photobiol Sci* 10:182–198
- Melick DR, Seppelt R (1992) Loss of soluble carbohydrates and changes in freezing point of Antarctic bryophytes after leaching and repeated freeze-thaw cycles. *Antarct Sci* 4:399–404
- Melick DR, Seppelt R (1994) The effect of hydration on carbohydrate levels, pigment content and freezing point of *Umbilicaria decussata* at a continental Antarctic locality. *Cryptogam Bot* 4:212–217
- Melick DR, Hovendon M, Seppelt R (1997) Vegetation patterns in relation to climatic and endogenous changes in Wilkes Land, continental Antarctica. *J Ecol* 85:43–56
- Nakatsubo T (2002) Predicting the impact of climatic warming on the carbon balance of the moss *Sanionia uncinata* on a maritime Antarctic island. *J Plant Res* 115:99–106
- NASA (2012) Ozone hole watch. <http://ozonewatch.gsfc.nasa.gov/>. 09 Jan 2012
- Newman PA, Daniel JS, Waugh DW, Nash ER (2007) A new formulation of equivalent effective stratospheric chlorine (EESC). *Atmos Chem Phys* 7:4537–4552
- Newsham KK (2003) UV-B radiation arising from stratospheric ozone depletion influences the pigmentation of the Antarctic moss *Andreaea regularis*. *Oecologia* 135:327–331
- Newsham KK (2010) The biology and ecology of the liverwort *Cephaloziella varians* in Antarctica. *Antarct Sci* 22:131–143
- Newsham KK, Robinson SA (2009) Responses of plants in polar regions to UV-B exposure: a meta-analysis. *Glob Change Biol* 15:2574–2589
- Newsham KK, Hodgson DA, Murray AWA, Peat HJ, Smith RIL (2002) Response of two Antarctic bryophytes to stratospheric ozone depletion. *Glob Change Biol* 8:972–983
- Newsham KK, Geissler P, Nicolson M, Peat HJ, Lewis Smith RI (2005) Sequential reduction of UV-B radiation in the field alters the pigmentation of an Antarctic leafy liverwort. *Environ Exp Bot* 54:22–32
- Ochyra R, Lewis Smith RI, Bednarek-Ochyra H (2008) The illustrated moss flora of Antarctica. Cambridge University Press, Cambridge
- Oliver MJ, Velten J, Mishler B (2005) Desiccation tolerance in bryophytes: a reflection of the primitive strategy for plant survival in dehydrating habitats? *Integr Comp Biol* 45:788–799
- Øvstedal DO, Lewis Smith RI (2001) Lichens of Antarctica and South Georgia: a guide to their identification and ecology. Cambridge University Press, Cambridge
- Øvstedal DO, Lewis Smith RI (2004) Additions and corrections to the lichens of Antarctica and South Georgia. *Cryptogam Mycol* 25:323–331
- Pannewitz S, Green TGA, Maysek K, Schlenzog M, Seppelt R, Sancho LG, Turk R, Schroeter B (2005) Photosynthetic responses of three common mosses from continental Antarctica. *Antarct Sci* 17:341–352
- Perlwitz J (2011) Atmospheric science: tug of war on the jet stream. *Nat Clim Change* 1:29–31
- Perlwitz J, Pawson S, Fogt RL, Nielsen JE, Neff WD (2008) Impact of stratospheric ozone hole recovery on Antarctic climate. *Geophys Res Lett* 35:L08714
- Proctor MCF, Oliver MJ, Wood AJ, Alpert P, Stark LR, Cleavitt NL, Mishler BD (2007) Desiccation-tolerance in bryophytes: a review. *Bryologist* 110:595–621
- Raper S, Wigley T, Mayes PR, Jones PD, Salinger MJ (1984) Variations in surface air temperature. Part 3. The Antarctic 1957–82. *Mon Weather Rev* 112:1341–1353
- Rastorfer JR (1970) Effects of light intensity and temperature on photosynthesis and respiration of two East Antarctic mosses, *Bryum argenteum* and *Bryum antarcticum*. *Bryologist* 73:544–556
- Raven J (1995) The early evolution of land plants: aquatic ancestors and atmospheric interactions. *Bot J Scotl* 47:151–175
- Robinson SA, Wasley J, Popp M, Lovelock CE (2000) Desiccation tolerance of three moss species from continental Antarctica. *Funct Plant Biol* 27:379–388
- Robinson SA, Wasley J, Tobin AK (2003) Living on the edge – plants and global change in continental and maritime Antarctica. *Glob Change Biol* 9:1681–1717

- Robinson SA, Turnbull JD, Lovelock CE (2005) Impact of changes in natural ultraviolet radiation on pigment composition, physiological and morphological characteristics of the Antarctic moss, *Grimmia antarctici*. *Glob Change Biol* 11:476–489
- Robinson S, Wasley J, King D (2009) Indicator 72 – windmill Islands terrestrial vegetation dynamics. [http://data.aad.gov.au/aadc/soe/display\\_indicator.cfm?soe\\_id=72](http://data.aad.gov.au/aadc/soe/display_indicator.cfm?soe_id=72) (Online database)
- Roy CR, Gies HP, Tomlinson DW (1994) Effects of ozone depletion on the ultraviolet radiation environment at the Australian stations in Antarctica. *Ultraviolet radiation in Antarctica: measurements and biological effects*. *Antarct Res Ser* 62:1–15
- Ryan KG, Burne A, Seppelt RD (2009) Historical ozone concentrations and flavonoid levels in herbarium specimens of the Antarctic moss *Bryum argenteum*. *Glob Change Biol* 15:1694–1702
- Schenker R, Block W (1986) Micro-arthropod activity in three contrasting terrestrial habitats on Signy Island, maritime Antarctic. *Br Antarct Surv Bull* 71:31–43
- Schlenosog M, Schroeter B (2000) Poikilohydry in Antarctic cryptogams and its influence on photosynthetic performance in mesic and xeric habitats. In: Davison W, Howard-Williams C, Broady P (eds) *Antarctic ecosystems: models for wider ecological understanding*. Caxton Press, Christchurch, pp 175–182
- Schlenosog M, Pannewitz S, Green TGA, Schroeter B (2004) Metabolic recovery of continental Antarctic cryptogams after winter. *Polar Biol* 27:399–408
- Searles PS, Flint SD, Caldwell MM (2001) A meta-analysis of plant field studies simulating stratospheric ozone depletion. *Oecologia* 127:1–10
- Seppelt R, Ashton D (1978) Studies on the ecology of the vegetation at Mawson Station, Antarctica. *Aust J Ecol* 3:373–388
- Smirnov N (1992) The carbohydrates of bryophytes in relation to desiccation tolerance. *J Bryol* 17:185–191
- Son SW, Gerber EP, Perlwitz J, Polvani LM, Gillett NP, Seo KH, Eyring V, Shepherd TG, Waugh D, Akiyoshi H, Austin J, Baumgaertner A, Bekki S, Braesicke P, Brühl C, Butchart N, Chipperfield MP, Cugnet D, Dameris M, Dhomse S, Frith S, Garny H, Garcia R, Hardiman SC, Jöckel P, Lamarque JF, Mancini E, Marchand M, Michou M, Nakamura T, Morgenstern O, Pitari G, Plummer DA, Pyle J, Rozanov E, Scinocca JF, Shibata K, Smale D, Teyssède H, Tian W, Yamashita Y (2010) Impact of stratospheric ozone on Southern Hemisphere circulation change: a multi-model assessment. *J Geophys Res* 115:D00M07
- Steig EJ, Schneider DP, Rutherford SD, Mann ME, Comiso JC, Shindell DT (2009a) Corrigendum: warming of the Antarctic ice-sheet surface since the 1957 International Geophysical Year. *Nature* 460:766
- Steig EJ, Schneider DP, Rutherford SD, Mann ME, Comiso JC, Shindell DT (2009b) Warming of the Antarctic ice-sheet surface since the 1957 International Geophysical Year. *Nature* 457:459–463
- Turnbull JD, Robinson SA (2009) Accumulation of DNA damage in Antarctic mosses: correlations with ultraviolet-B radiation, temperature and turf water content vary among species. *Glob Change Biol* 15:319–329
- Turnbull JD, Leslie SJ, Robinson SA (2009) Desiccation protects two Antarctic mosses from ultraviolet-B induced DNA damage. *Funct Plant Biol* 36:214–221
- Turner J, King J, Lachlan-Cope T, Jones P (2002) Climate change (communication arising): recent temperature trends in the Antarctic. *Nature* 418:291–292
- Turner J, Colwell SR, Marshall GJ, Lachlan-Cope TA, Carleton AM, Jones PD, Lagun V, Reid PA, Iagovkina S (2005) Antarctic climate change during the last 50 years. *Int J Clim* 25:279–294
- Turner J, Adams B, Arthern R, Atkinson A, Barbante C, Bargagli R, Bergstrom D, Bertler N, Bindschadler R, Bockheim J, Boutron C, Bromwich D, Chown S, Comiso J, Convey P, Cook A, Prisco GD, Fahrbach E, Fastook J, Forcarda J, Gili J-M, Gugliemin M, Gutt J, Hellmer H, Hennion F, Heywood K, Hodgson D, Holland D, Hong S, Huiskes A, Isla E, Jacobs S, Jones A, Lenton A, Marshall G, Mayewski P, Meredith M, Metzl N, Monaghan A, Naveira-Garabato A, Newsham K, Orejas C, Peck L, Pörtner H-O, Rintoul S, Robinson S, Roscoe H, Rossi S, Scambos T, Shanklin J, Smetacek V, Speer K, Stevens M, Summerhayes C, Trathan P, Veen KVD, Vaughan D, Verde C, Webb D, Wiencke C, Woodworth P, Worby T, Worland R, Yamanouchi T (2009) The instrumental period. In: Turner J, Bindschadler R, Convey P, Prisco G, Fahrbach E, Gutt J, Hodgson D, Mayewski P, Summerhayes C (eds) *Antarctic climate change and the environment*. Scientific Committee on Antarctic Research, Cambridge, pp 183–298
- Turner J, Barrand NE, Bracegirdle TJ, Convey P, Hodgson DA, Jarvis M, Jenkins A, Marshall G, Meredith MP, Roscoe H, Shanklin J, French J, Goosse H, Guglielmin M, Gutt J, Jacobs S, Kennicutt MIC, Masson-Delmotte V, Mayewski P, Navarro F, Robinson S, Scambos T, Sparrow M, Summerhayes C, Speer K, Klepikov A (2013) Antarctic climate change and the environment: an update. *Polar Record* FirstView:1–23
- United Nations Environment Programme EEAP (2012) Environmental effects of ozone depletion and its interactions with climate change: progress report, 2011. *Photochem Photobiol Sci* 11:113–127

- Van Gaalen E, Flanagan L, Peddle DR (2007) Photosynthesis, chlorophyll fluorescence and spectral reflectance in *Sphagnum* moss at varying water contents. *Oecologia* 153:19–28
- Vaughan DG, Marshall GJ, Connolley WM, Parkinson C, Mulvaney R, Hodgson DA, King JC, Pudsey CJ, Turner J (2003) Recent rapid regional climate warming on the Antarctic Peninsula. *Clim Change* 60:243–274
- Vining E, Crafts-Brandner S, Day TA (1997) Photosynthetic acclimation of Antarctic hair grass (*Deschampsia antarctica*) to contrasting temperature regimes. *Bull Ecol Soc Am* 78:327
- Wasley J, Robinson SA, Lovelock CE, Popp M (2006a) Climate change manipulations show Antarctic flora is more strongly affected by elevated nutrients than water. *Glob Change Biol* 12:1800–1812
- Wasley J, Robinson S, Lovelock C, Popp M (2006b) Some like it wet – an endemic Antarctic bryophyte likely to be threatened under climate change induced drying. *Funct Plant Biol* 33:443–455
- Xiong F, Ruhland C, Day TA (1999) Photosynthetic temperature response of the Antarctic vascular plants *Colobanthus quitensis* and *Deschampsia antarctica*. *Physiol Plant* 106:276–286