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Dominating the Antarctic environment: bryophytes in a time of change

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Abstract

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 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.

Keywords

change, environment, antarctic, bryophytes, dominating, time

Disciplines

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Dominating the Antarctic Environment: bryophytes in a time of change

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Running title: **Dominating the Antarctic Environment**

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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 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.

Abbreviations

DW	Dry weight
GRACE	Gravity Recovery and Climate Experiment
SAM	Southern Annular Mode
UV	ultraviolet
UVAC	ultraviolet absorbing compounds.

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. 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 typically 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 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.

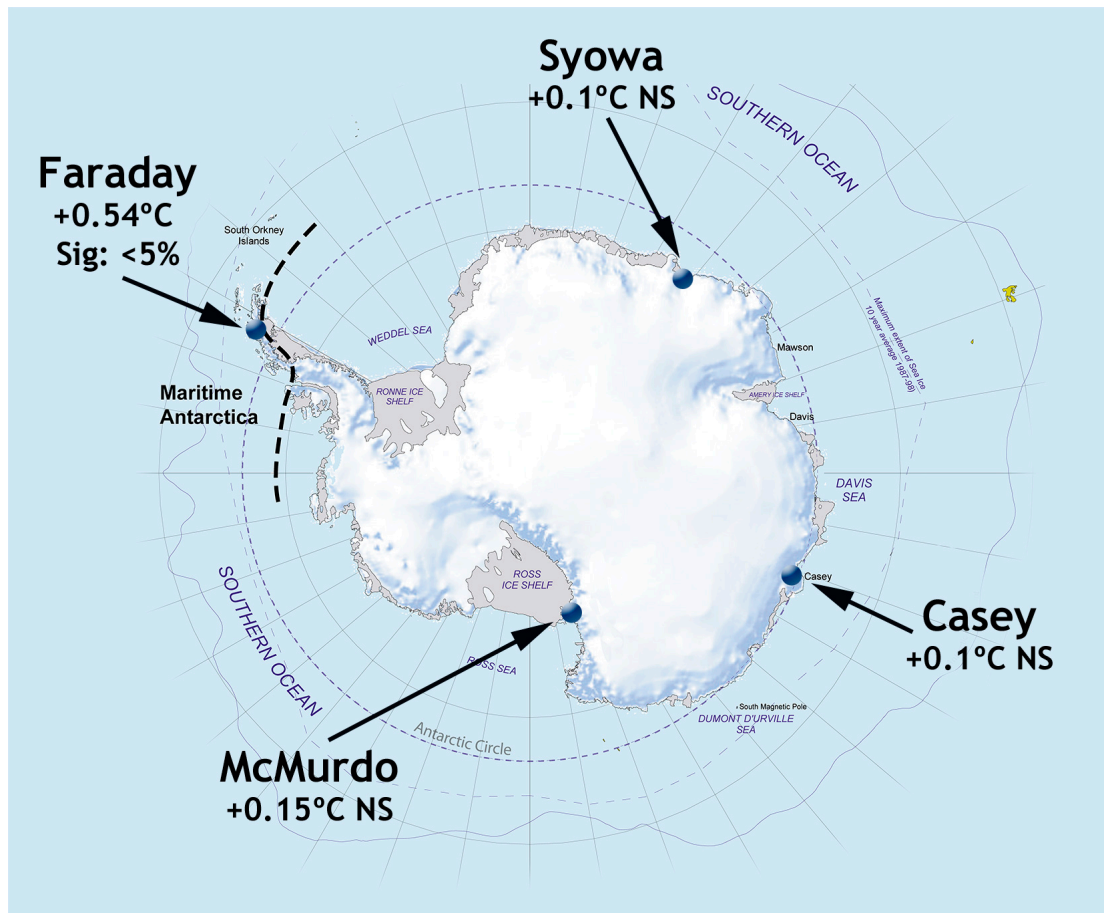


Figure 1. Schematic map of Antarctica with the trends in mean annual air temperatures (degrees per decade) over the last 50 years (1951–2011) at selected research stations. Map adapted from Turner and Overland (2009). Sig = significance value given, NS = not significant.

Table 1. Estimated numbers of plant groups in Antarctica continental and maritime locations adapted from Lewis Smith (1984), Øvstedal & Lewis Smith (2001, 2004); Ochrya *et al.* (2008) and Bednarek-Ochrya *et al.* (2000).

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

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; Schlenzog 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. 2). Surviving desiccation is made possible through the presence of compounds, including **soluble carbohydrates** (Smirnoff, 1992) and **lipids** (Oliver, 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). This trait enables bryophytes to survive in a number of extreme habitats, ranging from the dry heat of deserts, the tops of mountains and the cold dry continent of Antarctica (Bewley, 1979; Kappen, 2000).

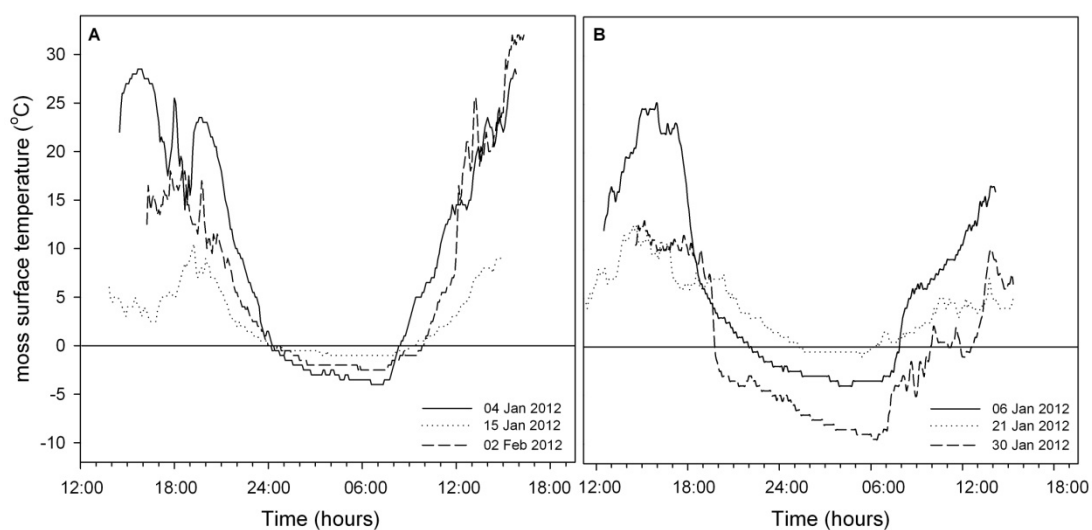


Figure 2. Diurnal moss surface temperatures at two sites in the Windmill Islands, (A) Robinson's Ridge and (B) ASPA 135. At each site, temperatures were recorded at the same location over three 24 h periods, under varying weather conditions during the 2012 summer season. At Robinson's Ridge (A),

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°C 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).

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 and Overland, 2009) with major changes already clearly apparent for the second half of the 20th century, both on sub-Antarctic islands and across the Antarctic peninsula (Turner et al., 2009). 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 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 245–1400% ($\text{g H}_2\text{O g}^{-1} \text{DW}$) for *Bryum pseudotriquetrum* (Pannewitz et al., 2005), 100–600% for *Ceratodon purpureus* and 200–1200% ($\text{g H}_2\text{O g}^{-1} \text{DW}$) for *Schistidium antarctici* (Robinson et al., 2000). Therefore areas that have access to regular melt water during the summer months (November to March; Fig. 3a, b, e) typically support greatest moss biomass. In some regions of Antarctica bryophytes form moss pillars in fresh water, summer lakes (Fig. 3c; Kudoh et al., 2009). Mosses are often found in conjunction with algae species and cyanobacteria that also rely heavily on available water (Fig. 3b, c; Melick et al., 1997) and the surface of moss turfs will sometimes support lichen growth (Fig. 3f). However lichens grow more readily on rock surfaces or by creating endolithic communities within rock crevices (Fig. 3g). In some of the driest regions hypolithic communities dominated by mosses flourish under opaque rocks (Fig. 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 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 (*Schistidium antarctici*, *Ceratodon purpureus* and *Bryum 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.

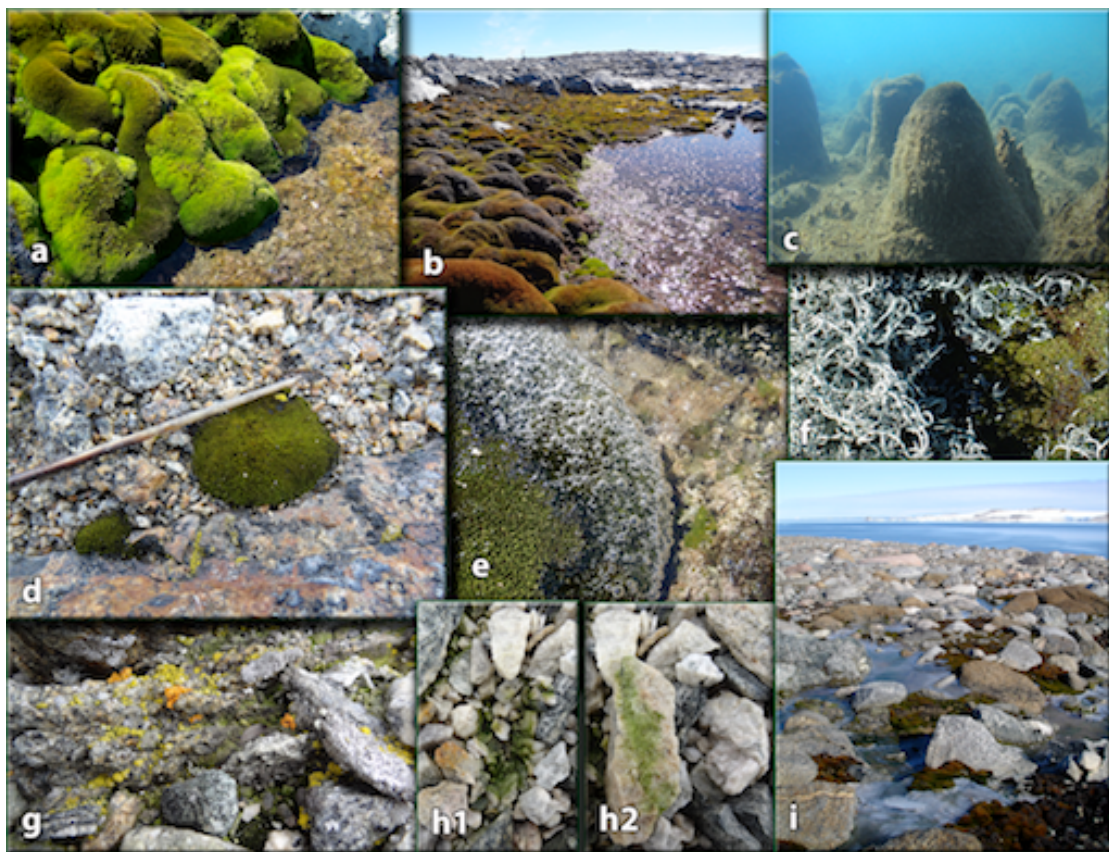


Figure 3. Typical examples of Antarctic bryophyte flora. (a, b) Mosses thrive in areas with free water such as these turfs in and around melt lakes in the Windmill Islands, East Antarctica and (c) moss pillars that occur in deeper freshwater lakes such as *Hotoke-ike*, Sôya Coast, East Antarctica. (d) In more exposed locations moss buttons are a common form (seen here with a bird quill). (f) Where areas

are drying, lichens grow above moss turfs and (g) endolithic lichens are commonly found in rock crevices. (h) Hypolithic communities where flora exists under or within rocks are common in Antarctica (N.B. h2 is the underside of a rock that 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 O₂ 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.

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 *Hennediella heimii* displayed optimal net photosynthesis at relative water contents of 200 – 300% compared to over 500% (g H₂O g⁻¹ DW) in **hydric** forms. Furthermore, an earlier study by Kappen (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 et al. (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. 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., 1995b; Lovelock et al., 1995a).

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 (Krinner 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; Chen et al., 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 19077 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 21st 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 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 $-40\text{ }^{\circ}\text{C}$ during winter to over $0\text{ }^{\circ}\text{C}$ 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 $0\text{ }^{\circ}\text{C}$, 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 austro-salebrosum*, 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 °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. 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 & Block (1986) recorded soil surface temperatures between 3.7 to 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 Schlensoeg & Schroeter (2000) reported the diurnal thermal cycle within a cushion of *Andreaea gainii* to range between -2 to 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. 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., 1995b; Lovelock et al., 1995a). 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. 2). Fig. 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 photoprotection chapter).

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 (Lenné et al.).

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., 1995b; Lovelock et al., 1995a;

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 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 (eg. 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 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., 1995b; Lovelock et al., 1995a), 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 and Overland, 2009).

Table 2. Temperature optimum for photosynthesis for a range of Antarctic bryophytes measured under field and laboratory conditions. Net photosynthesis (NP) was measured as CO₂ assimilation. Laboratory measurements were performed using an O₂ electrode system (Rastorfer, 1970).

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

While the bulk of East Antarctica has experienced little significant change in temperature over the last 50 years (Fig. 1; Turner and Overland, 2009), 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 and Overland, 2009) 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; Fogt et al., 2009; Marshall et al., 2011), 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 to 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 aboveground 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 Waterman & Robinson (this volume), UV-B radiation is implicated in direct damage to PSII, and photoprotective carotenoids, such as zeaxanthin and β -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 which have shown impacts on photosynthetic pigmentation for particular species; for example, decreases in chlorophyll and increases in zeaxanthin and β -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; Newsham et al., 2005) but in contrast to *S. antarctici*, chlorophyll pigments were unaffected in these species. Acclimation of shade to sun forms of *Ceratodon 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 flurometer (Green et al., 2005).

Increasing UVAC in response to increasing UV-B radiation have been found in the liverwort, *Cephaloziella varians* and the mosses; *Sanionia uncinata* (Newsham et al., 2002), *Andreaea regularis* (Newsham, 2003), *B. pseudotriquetrum* (Dunn and Robinson, 2006) and *Bryum 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; Robinson and Waterman, 2012). 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 photoproducts 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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