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# Ecophysiological traits of Antarctic vascular plants: their importance in the responses to climate change

Lohengrin A. Cavieres · Patricia Sáez · Carolina Sanhueza ·
Angela Sierra-Almeida · Claudia Rabert · Luis J. Corcuera ·
Miren Alberdi · León A. Bravo

**Abstract** Only two vascular plants have been able to colonize some of the ice and snow-free lands of the Antarctic Peninsula: the hair grass *Deschampsia antarctica* (Poaceae) and the pearlwort *Colobanthus quitensis* (Caryophyllaceae). This low species diversity may be due to the permanent low temperature even during summer time. Beside low temperature, Antarctic plants must be able to cope with other severe physiological stressors such as desiccation, low soil water availability, and high irradiance. However, these factors are found in other cold areas of the globe. Thus, what is so special about these two species that has enabled them to be the only successful flowering plants in the Antarctica? Although this question has been addressed in other articles, we still lack of an integrative ecophysiological framework that helps to disentangle what it is unique of these species in terms of adaptations to the Antarctic environments, and how these adaptations will help or preclude their responses to future climate change. Several adaptations seem to help to withstand the Antarctic climate: xerophytic anatomical characteristics, sufficient freezing tolerance, ability to maintain positive net photosynthesis at near 0 °C, adequate management of excess photosynthetic active radiation, resistance to photoinhibitory conditions, tolerance to water stress, and ability to form associations with endophytes that help in their mineral nutrition. Besides the very effective stress tolerance strategies, several ecophysiological traits show considerable response flexibility. The evidence reviewed here indicates that small increases in air

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L. A. Cavieres · C. Sanhueza · A. Sierra-Almeida ·
L. J. Corcuera
Departamento de Botánica, Facultad de Ciencias
Naturales y Oceanográficas, Universidad de Concepción,
Concepción, Chile

L. A. Cavieres (✉) · C. Sanhueza · A. Sierra-Almeida
Instituto de Ecología y Biodiversidad (IEB), Santiago,
Chile
e-mail: lcaviere@udec.cl

P. Sáez
Departamento de Silvicultura, Centro de Biotecnología,
Facultad de Ciencias Forestales, Universidad de
Concepción, Concepción, Chile

C. Rabert · M. Alberdi · L. A. Bravo
Laboratorio de Fisiología y Biología Molecular Vegetal,
Instituto de Agroindustria, Departamento de Ciencias
Agronómicas y Recursos Naturales, Facultad de Ciencias
Agropecuarias y Forestales & Center of Plant, Soil
Interaction and Natural Resources Biotechnology,
Scientific and Technological Bioresource Nucleus,
Universidad de La Frontera, Casilla 54-D, Temuco, Chile

temperature may be beneficial in terms of photosynthetic performance. However, increased frequency of leaf temperatures over 20 °C could be harmful affecting photosynthesis and reducing the ability of these plants to tolerate freezing temperatures and photoprotection at low temperatures, attributes by which they are able to colonize these very harsh environment.

## Introduction

Antarctica is the coldest region of the world and the great majority of its territory is covered by ice. Less than 1 % of the Antarctic territory is available for colonization of plants, where most of these ice- and snow-free lands are found along the Antarctic Peninsula, its associated islands, and coastal regions around the rest of the Antarctic continent (Fig. 1). This zone is known as the maritime Antarctic (Convey 2013), and has a relatively mild maritime climate that sharply contrasts with that of east Antarctica (Bargagli 2005). The mean annual temperature (−1.8 °C) is about 7 °C higher than that of the east coast at the same latitude, and present 1–4 months of positive values during the summer (Convey 2013). During summer, air temperatures range from −10 °C to +15 °C (op. cit.), and due to the great maritime influence there are few changes in temperature with latitude (Rakusa-Suszczewski 2002). Nonetheless, in the last decades air temperatures in the Antarctic Peninsula have increased at a faster rate than the rest of Antarctica and the globe (Turner et al. 2013). While global records indicate temperature increases of 0.6–1.0 °C century$^{-1}$ (IPCC 2007), the Antarctic Peninsula has warmed at 3.7 °C century$^{-1}$ (Vaughan et al. 2003).

Maritime Antarctic biota in general, and Antarctic plants in particular, are constantly dealing with low temperature. This contrasts to the Arctic where mean temperatures during summer, even in zones with strong maritime influence, are well above 0 °C (Hobbie 2007). For this reason, it has been suggested that cold stress has a greater influence in the Antarctic than in the Arctic, explaining in part the low plant species diversity of the Antarctic compared with the

Arctic (Green et al. 2007). Whereas ca. 2220 vascular plant species are found in the Arctic (Meltofte 2013), only two have been able to naturally colonize parts of the maritime Antarctic. These are the hair grass *Deschampsia antarctica* Desv. (Poaceae) and the pearlwort *Colobanthus quitensis* (Kunth) Bartl. (Caryophyllaceae) (Smith 2003) (Fig. 2).

These two species are found in most of the maritime Antarctic down to ca. 68°S, but do not extend into the continental Antarctic (Greene and Holtom 1971). *D. antarctica* has a remarkably ecological amplitude and competitive tolerance. It has colonized habitats ranging from mineral to organic soils, and from dry to waterlogged areas. In contrast, *C. quitensis* seems to be less tolerant to extreme conditions, preferring sparsely vegetated, sheltered, moist well-drained mineral soils (Smith 2003). In accordance with the former, the Antarctic hair grass is much more abundant and widely distributed in Antarctica than the pearlwort (Smith 2003). However, *C. quitensis* have a wider geographical distribution than *D. antarctica* (from Mexico down to Antarctica), although inhabiting sites with similar conditions along its distribution (i.e., cold and well-watered areas).

It is well known that of those species that arrive at a site, many lack the appropriate physiological traits to survive the physical environment (Lambers et al. 2008). Although Antarctica has remained isolated from other pieces of land during the last 10,000 years (Convey 2006), some studies report that either naturally or human-assisted dispersed propagules of several native and non-native species from sub-Antarctic habitats can arrive to Antarctica (e.g., Smith and Richardson 2011; Chown et al. 2012). Nonetheless, few of them can successfully establish new individuals that survive more than one season, and none has been able to establish populations that spread in natural habitats without human assistance (Hughes and Convey 2010; Chown et al. 2012). Thus, what is so special about these two species that has enabled them to be the only successful flowering plants in the Antarctica?

Although the former question has been addressed in other reviews (e.g., Alberdi et al. 2002; Smith 2003; Parnikoza et al. 2011), we still lack of an integrative ecophysiological view that helps to disentangle what it is unique of these species in terms of adaptations to the Antarctic environment, and how these adaptations will help or preclude their responses to future climate change. Besides low temperatures, Antarctic plants
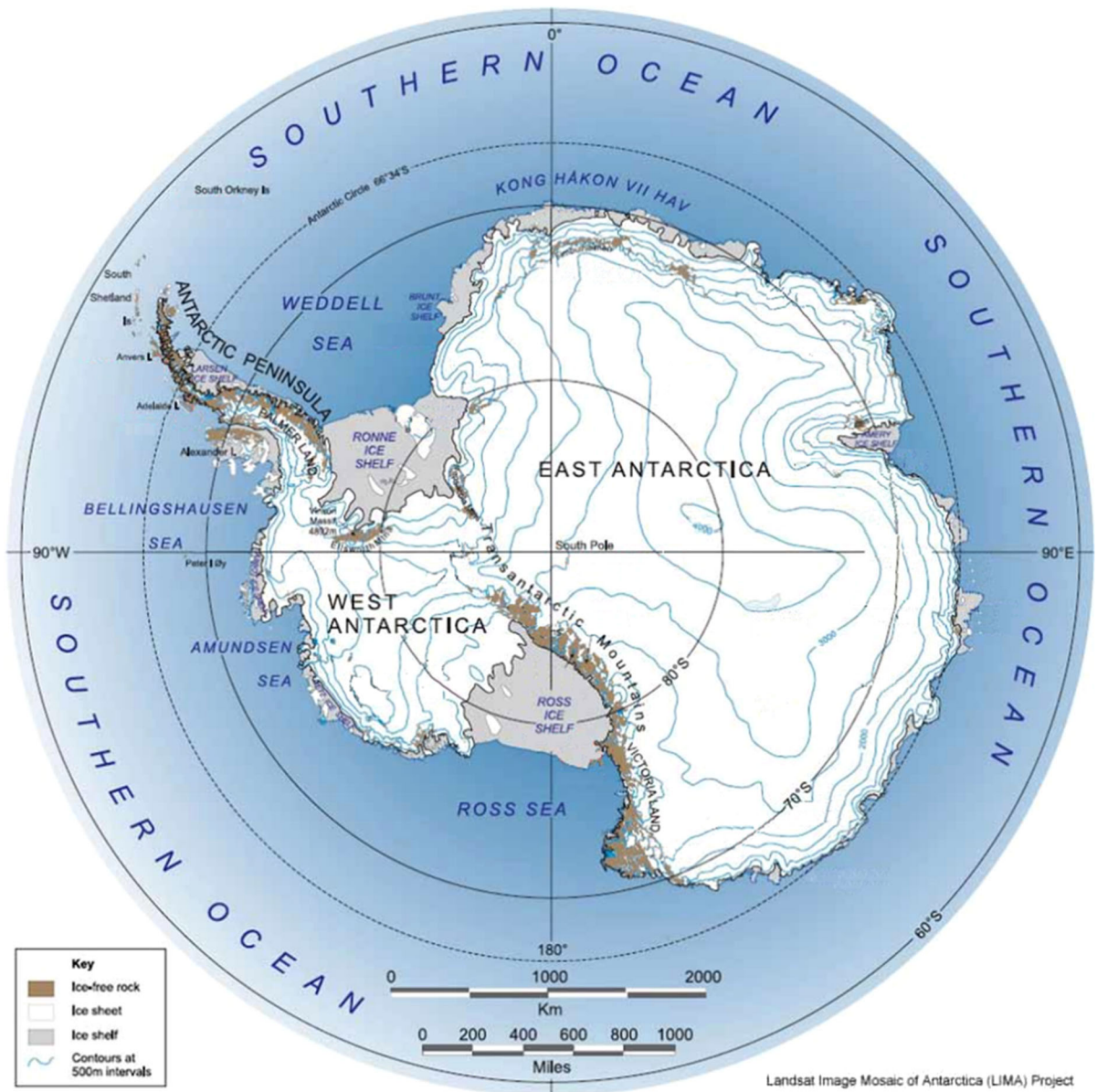
**Fig. 1** Map of Antarctica and main places mentioned in the *text*

must face other physiological stressors such as desiccation, low nutrient availability, and high irradiance. The chronically low temperatures of the Antarctica, even during the short summer season, are likely to be near the minimum thresholds for many physiological processes. This suggests that in the context of climate change, a small temperature increment experienced by plants in this environment will have a relatively greater biological impact than the same increment experienced in a less extreme environment (Convey 2001). However, many traits or adaptations to deal with chronically low temperatures, lose their functionality with small temperature increments (Convey 2000; Anderson et al. 2012), thereby decreasing the chance to positively respond to future climate change. Thus, the aim of this review is to present an updated revision of the Antarctic plant ecophysiological traits that allow them to survive in the harsh Antarctic
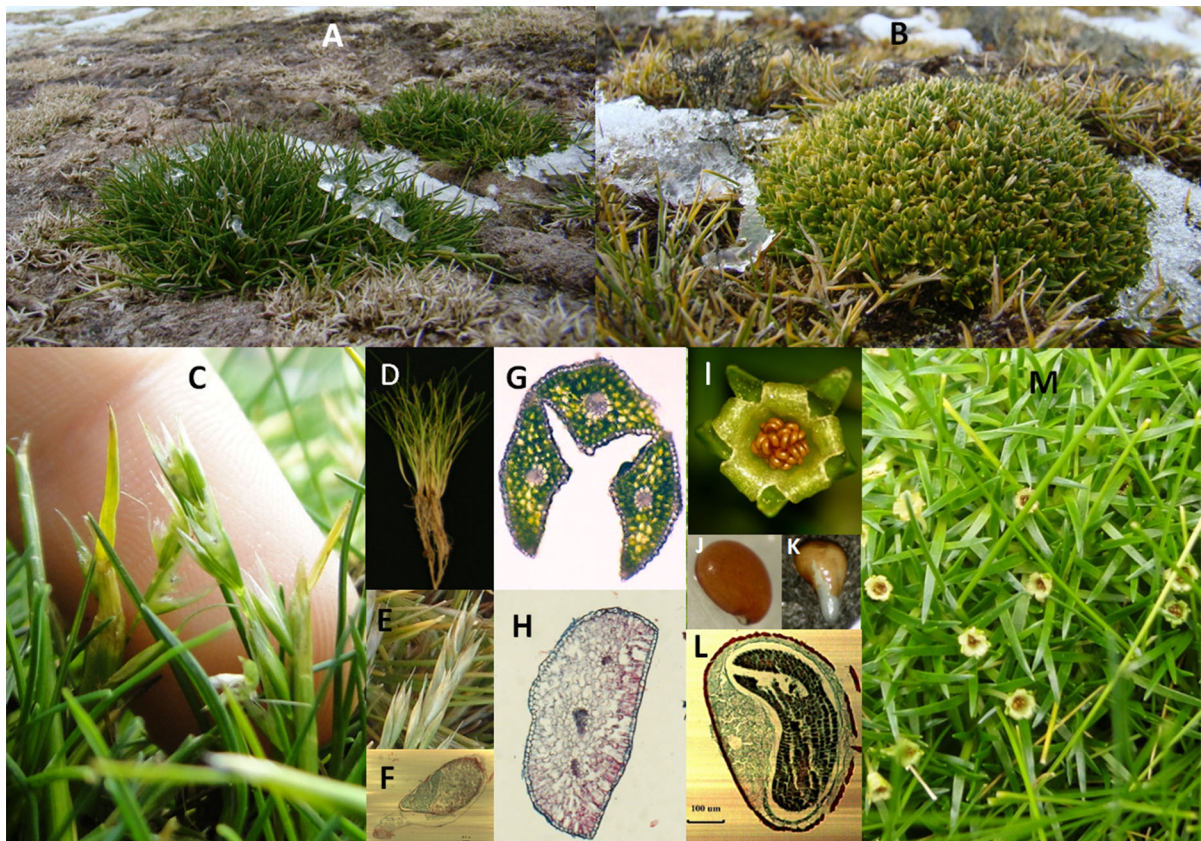
**Fig. 2** Antarctic vascular plant species *Deschampsia antarctica* (**A**) and *Colobanthus quitensis* (**B**) growing in the field near Arctowski research station, Admiralty Bay, King George Island (Lat: 62°9′49.62″S Long: 58°28′7.02″W). Plant details of *D. antarctica* (**C**) used for vegetative propagation by tillers (**D**) in growth chambers. Spikes observed in the field (**E**). Longitudinal sections in seeds of *D. antarctica* (**F**) and *C. quitensis* (**L**); dark shape area corresponded to the embryos and a more clear material corresponded to endosperm. Leaf cross sections of *D. antarctica* (**G**) and *C. quitensis* (**H**). *C. quitensis* with its numerous tiny flowers (**M**) and each capsule (**I**) contains about 35 viable seeds. Imbibed seed (**J**) and germinating seed (**K**)

conditions in view of the likely consequences of climate change.

## Climate change footprints in the Antarctic vascular plants

Several studies have shown that climate change have increased the availability of areas susceptible to be colonized by plants as a result of the reduction of ice and snow cover, and the recession of glaciers along the Antarctic Peninsula (Fox and Cooper 1998; Cook et al. 2005). Associated with these changes, Smith (1994) and Day et al. (1999) reported increases in both the size and number of *D. antarctica* and *C. quitensis* populations along the Antarctic Peninsula. These changes were associated to increases in the reproductive capacity of both species as result of longer and warmer growing seasons (Fowbert and Smith 1994). Nonetheless, Day et al. (1999) in a short-term field study found that while the vegetative growth of *C. quitensis* increased with warming, in *D. antarctica* it decreased. This suggests that future warming along the Antarctic Peninsula may benefit *C. quitensis*, but restrict *D. antarctica*. This, however, disagrees with other reports. For example, Hughes (2000) reported that in Galindez Island, *D. antarctica* increased from 500 individuals in 1964 to 12,030 individuals in 1990, and that similar increases have been found at many other locations. Torres-Mellado et al. (2011) reported

that while in general both species have colonized new sites and have increased their abundance in some localities, in other sites they have disappeared. Thus, it seems important to know when changes in climate are positive for these plants, and when are unfavorable. This certainly depends on a thorough understanding of the ecophysiological characteristics of these species, not only on those aspects directly governing plant metabolism, but also considering indirect effects of warming on other aspects such as those associated to soil nutrient availability and plant nutrition.

## Habitat and spatial distribution of Antarctic vascular plants

It has been suggested that factors such as temperature, moisture availability, nutrients, salinity, and microtopography influence the distribution of the Antarctic vegetation (Kennedy 1993; Leishman and Wild 2001; Kappen and Schroeter 2002). However, most of these studies dealing with factors related with the distribution and abundance of Antarctic plants have focused on bryophytes and lichens with few studies related with the vascular plants (Edwards 1972; Vera 2011; Park et al. 2012, 2013).

The first studies focused on the ecology and distribution of the Antarctic vascular plants were mostly descriptions of the localities and general habitats conditions where the two species were found (Holtom and Greene 1967; Lindsay 1971; Greene and Holtom 1971). From these studies stands out that although both species are present along the same geographical range in Antarctica (62°–67°S latitude), *C. quitensis* is more restricted in its habitats distribution than *D. antarctica*. This last species can be found in different habitats (e.g., sandy beaches, rocky outcrops, moss carpets, etc.), showing a remarkable morphological variation with different growth forms in dry and moist habitats: small discrete tufts in dry areas and more luxuriant tufts, sometime forming small closed sward in wetter areas (Greene and Holtom 1971; Lindsay 1971). In contrast, *C. quitensis* is found in fewer localities, showing a more exacting habitat requirement, being restricted to the more favorable *D. antarctica* sites. Indeed, with the exceptions of Deception and Robert Islands, it is usually found in coexistence with *D. antarctica* or in its immediate vicinity (Greene and Holtom 1971; Lindsay 1971).

In relation to microhabitat requirements, some information is available only for *D. antarctica*. In recent studies, Park et al. (2012, 2013) found that the density of *D. antarctica* mature individuals was positively associated with moss cover, organic matter, and available phosphorus, meanwhile it was negatively associated with clay, water content, and snow. Kim et al. (2007) and Park et al. (2012) observed that most grass tufts were formed on ground covered by the moss *Sanionia* spp. This association may occur due to an overlap in the environment preference of *D. antarctica* and the mosses, or that the moss cover could improve the microenvironmental conditions for the vascular species. In an extensive sampling across the maritime Antarctic, Casanova-Katny and Cavieres (2012) found that *D. antarctica* showed a significant association with moss carpets, with higher frequencies as well as more and larger individuals than on bare ground areas. Moss removal and *D. antarctica* seedlings transplant experiments showed that and found that while survival was not affected by the presence of moss carpet, growth rate was significantly lower in those individuals with the moss carpets removed (Casanova-Katny and Cavieres 2012). Thus, the presence of mosses resulted to be a key factor for the growth and expansion of *D. antarctica* populations (see also Park et al. 2012, 2013). Mosses modify soil properties that are critical for *D. antarctica* by maintaining optimal water levels and supplying organic matter (Park et al. 2012, 2013).

The importance of organic matter for the distribution of seedlings and adults of *D. antarctica* is also highlighted by Park et al. (2012, 2013) who showed a strong positive association of both seedlings and adults distribution with organic matter. Although the origin of organic matter in Antarctic soil is complex, Park et al. (2012) suggested that mosses could serve as one of the principal sources of organic matter at productive sites.

Animals (seabirds and mammals) are regarded as important determinants of the distribution of the plants due to their role in nutrient transfer from and the dispersal of propagules (Edwards 1972; Parnikoza et al. 2007; Vera et al. 2013). Smykla et al. (2007) described zonation patterns in vegetation influenced by penguin rookeries in King George Island, and showed that the abundance of *D. antarctica* decreased with low nutrient availability. Tatur et al. (1997) also found that nutrient-rich soils at abandoned rookeries

served as optimum habitats for *D. antarctica* growth. Nonetheless, Lindsay (1971) noted that although the most luxuriant growth of *D. antarctica* occurred at the edge of penguin rookeries, plants there were sterile, whereas stunted plants in areas not nitrogen enriched can be fertile. *C. quitensis* seems to be not influenced by nitrogen enrichment (Lindsay 1971).

Drainage is also an important environmental feature that influences the distribution of *D. antarctica*, as mentioned by Edwards (1972) and Kim and Chung (2004). Soil drainage conditions, which are determined by water and sand clay content, greatly affect root growth. All studies point out the preference of *D. antarctica* for fertile soils and that poor drainage, low pH, and snow accumulation during the growing season are critical factors for its survival in Antarctica (Lindsay 1971; Park et al. 2013). For *C. quitensis*, there is a lack of more detailed information, but since it is restricted to more favorable *D. antarctica* sites, fertile soils and good drainage might be important positive factors. However, much research is needed for this species, particularly in assessing at what extent colonization and establishment are limiting process in population growth.

## Anatomical adaptations

Morphological changes are considered as one of the main manifestations of adaptation to the environment, and can also influence other processes such as net $CO_2$ assimilation and water use efficiency (Vieira and Mantovani 1995). Both Antarctic species have developed several morphological and anatomical modifications, although the majority of these modifications have been described for *D. antarctica* but not as so for *C. quitensis*.

Detailed anatomical adaptations in *D. antarctica* have been reported in Romero et al. (1999), Gielwanowska and Szczuka (2005) and Gielwanowska et al. (2005). These authors have shown that this grass species have several xerophytic characteristics: small leaf and epidermal cells, thick leaves, high stomata density and number of cells per area, thick cuticle, etc. Examinations of the adaxial epidermis of leaves show the presence of turgid papillae, that have been interpreted as a storage mechanism of carbohydrates involved in freezing point depression (Romero et al. 1999, see below). In leaf transverse sections, it is

possible to observe an inner sheath with thick lignified walls (mestome), which has been regarded as an adaptation to high irradiance (Pyykkö 1966). The mestome can function as an endodermis, limiting apoplastic movement of water to the mesophyll, allowing *D. antarctica*, in addition to the stomata, a high capacity to control water loss (Vieira and Mantovani 1995; Alberdi et al. 2002).

At a first glance, the leaf anatomy of *D. antarctica* leaves does not differ considerably from that of other plant species growing in cold regions (Körner and Larcher 1988). However, certain anatomical and ultrastructural particularities have been found in the leaf organelles. For example, some of the chloroplasts in the mesophyll cells differ from the rest in having small vesicles or pockets (Gielwanowska and Szczuka 2005). Both, vesicles and pockets increase the surface of chloroplasts, thus increasing the amount of substances exchanged between chloroplasts and the cytoplasm. Mitochondria or peroxisomes adhere very tightly to chloroplasts, and this can facilitate $CO_2$ exchange between the respiration and the photosynthesis processes (Gielwanowska and Szczuka 2005).

Much of these anatomical modifications seem to be highly plastic and connected with the environmental conditions experienced by the individuals in their current conditions (e.g., Romero et al. 1999; Gielwanowska et al. 2005), although the existence of specialization by genetic differentiation cannot be ruled out (Parnikoza et al. 2011). Thus, future warmer temperatures may affect plant growth in this species inducing morphological and anatomical changes that probably maximize light capture and growth, but at the same time may also compromise plant freezing tolerance and photoprotection strategies (see below).

Although *C. quitensis* is less exposed to reduced water availability and wind abrasion than *D. antarctica* due to their lower stature and cushion-like habit (Larcher 2003), leaf thickness and mesophyll surface area values of *C. quitensis* fall on those typical of xeric plants. Mantovani and Vieira (2000) reported the parallel occurrence of palisade and stomata in the leaves of this species, which generate a higher cellular surface area for $CO_2$ exchange. The presence of the bundle-sheath found in *D. antarctica* has also been reported in *C. quitensis* (Vieira and Mantovani 1995). In addition, this species shows a thick mesophyll without fibers (Edwards and Smith 1988). Recent morphological leaf analyses of three provenances of

*C. quitensis* from a latitudinal gradient (Pta. Arenas: 58° Lat S, King George Island: 62° Lat S, Lagotellerie Island: 67.5° Lat S) showed that toward higher latitudes there are smaller and thicker leaves, evidenced by a lower cross section, with higher mesophyll thickness, narrower adaxial surface, and reduction of epidermis thickness (Table 1). The lower leaf plasticity exposed by *C. quitensis* compared to that of *D. antarctica*, suggests that plant morphology of *C. quitensis* would change to a lesser extent due to the regional warming. Nonetheless, further studies are needed because anatomical and morphological changes may have profound influences on plant functioning and growth. The genetic base for these morphological changes also needs to be addressed in more detail (Parnikoza et al. 2011).

## Freezing resistance

Antarctic plants have to withstand the freezing temperatures that occur during the summer. Bravo et al. (2001) reported the first study dealing with the freezing resistance of Antarctic vascular plants, and found that *D. antarctica* and *C. quitensis* have different strategies to cope with freezing temperatures. While non-acclimated *D. antarctica* plants (i.e., plants growing at constant 15 °C) exhibited a lethal temperature for 50 % of leaf tissues ($LT_{50}$) of −12 °C, after cold acclimation (14 days at 4 °C) $LT_{50}$ decreased to −26.6 °C. Although, this species was able to supercool, it was classified as a freezing-tolerant species (Bravo et al. 2001). In contrast, *C. quitensis* experienced freezing injury ($LT_{50}$) in non-acclimated plants at −4.8 °C and a cold-acclimation period slightly affected $LT_{50}$ (−5.8 °C); the mechanism of freezing resistance for *C. quitensis* was avoidance by moderate supercooling (Bravo et al. 2001).

Subsequent studies, however, showed some discrepancies with those of Bravo et al. (2001). For example, Chew et al. (2012) reported that cold-acclimated plants of *D. antarctica* increased their freezing tolerance from −12 to −17 °C after the same period of acclimation but at 5 °C. A likely explanation for these discrepancies arises from the different methods used to assess freezing injury (Bravo et al. (2001) estimated $LT_{50}$ from electrolyte leakage by freezing-induced cell lysis, whereas Chew et al. (2012) $LT_{50}$ estimation was based on tiller survival

from re-growth). For *C. quitensis*, Gianoli et al. (2004) found that $LT_{50}$ of *C. quitensis* decreased from −7 to −14 °C after 21 days of cold-acclimation period, indicating that this species has a high ability to cold acclimate. Gianoli et al. (2004) calculated $LT_{50}$ with plant survival percentage, and plants were allowed to supercool (i.e., no ice nucleators were added). Estimations of $LT_{50}$ using chlorophyll fluorescence indicated that *D. antarctica* exhibited a $LT_{50}$ of −16.5 and −18.4 °C in non- and cold-acclimated plants (21 days of cold acclimation), respectively (Reyes-Bahamonde 2013). These results indicated a low ability for cold acclimation in *D. antarctica* because $LT_{50}$ decreased only 1.9 °C after cold acclimation which contrast with the 14.6 °C found in Bravo et al. (2001), and the 5 °C reported by Chew et al. (2012). Nonetheless, the freezing resistance mechanism is tolerance in all cases. On the other hand, *C. quitensis* exhibited $LT_{50}$ of −7 and −14.9 °C in non- and cold-acclimated plants, respectively (Reyes-Bahamonde 2013), which are in line with $LT_{50}$ values reported by Gianoli et al. (2004). However, *C. quitensis* was considered a freezing-tolerant species by Reyes-Bahamonde (2013).

An important factor that must be considered in freezing resistance determinations is the time that plants are maintained in greenhouse and/or growth chambers. It is well known that the ambient temperatures experienced by plants affect their ability to resist freezing temperatures (Beck et al. 2004). Bravo et al. (2001) collected adult plants from Antarctica that were vegetative propagated at 15 °C for a couple of years before the determinations. Chew et al. (2012) obtained adult plants from seeds collected in the field, while Reyes-Bahamonde (2013) used plants grown at constant 11 °C during 2 months after their collection in the field. Thus, in situ determinations are required to unveil the real freezing resistance of the Antarctic vascular plants. Nonetheless, although field determinations are required, $LT_{50}$ values obtained under laboratory conditions (and despite the methodological discrepancies), indicate that these species are able to cope with the summer freezing events in the maritime Antarctic.

Several biochemical and physiological mechanisms of freezing resistance are present in these plants during the growing season. However, most of them have been studied in *D. antarctica* but not yet in *C. quitensis*. Among them, we highlight the presence in *D. antarctica* of a high percentage of saturated fatty

**Table 1** Foliar anatomy of *C. quitensis* from different populations along an Antarctic–sub-antarctic latitudinal gradient

| Populations | Pta. Arenas | King George I. | Lagotellerie I. |
|---|---|---|---|
| Cross-sectional area (cm$^2$) | 0.44 ± 0.02a | 0.32 ± 0.02b | 0.23 ± 0.02c |
| Adaxial surface length (μm) | 1415.09 ± 31.2a | 1073.36 ± 41.9b | 749.36 ± 17.4c |
| Mesophyll width (μm) | 378.73 ± 7.56a | 400.41 ± 20.2ab | 440.37 ± 16.0b |
| Palisade mesophyll width (μm) | 89.67 ± 4.21a | 90.94 ± 3.48ab | 93.02 ± 3.12a |
| Lower epidermis width (μm) | 19.81 ± 0.53a | 17.51 ± 0.57b | 13.54 ± 0.83c |
| Upper epidermis width (μm) | 18.39 ± 0.71a | 18.43 ± 0.70a | 12.98 ± 0.67b |
| Lower epidermis cells length (μm) | 21.88 ± 1.03a | 16.67 ± 0.57b | 14.73 ± 1.58b |
| Upper epidermis cells length (μm) | 21.40 ± 1.33ab | 23.52 ± .56a | 14.77 ± 2.18b |

Media ± SE ($n = 20$). Different letters indicates significant differences among population ($P < 0.05$). Right: transversal leaf section of *C. quitensis* from Punta Arenas (A–B), King George (C–D) and Lagotellerie Island (E–F). Bars represent 30 μm (left) y 50 μm (right)
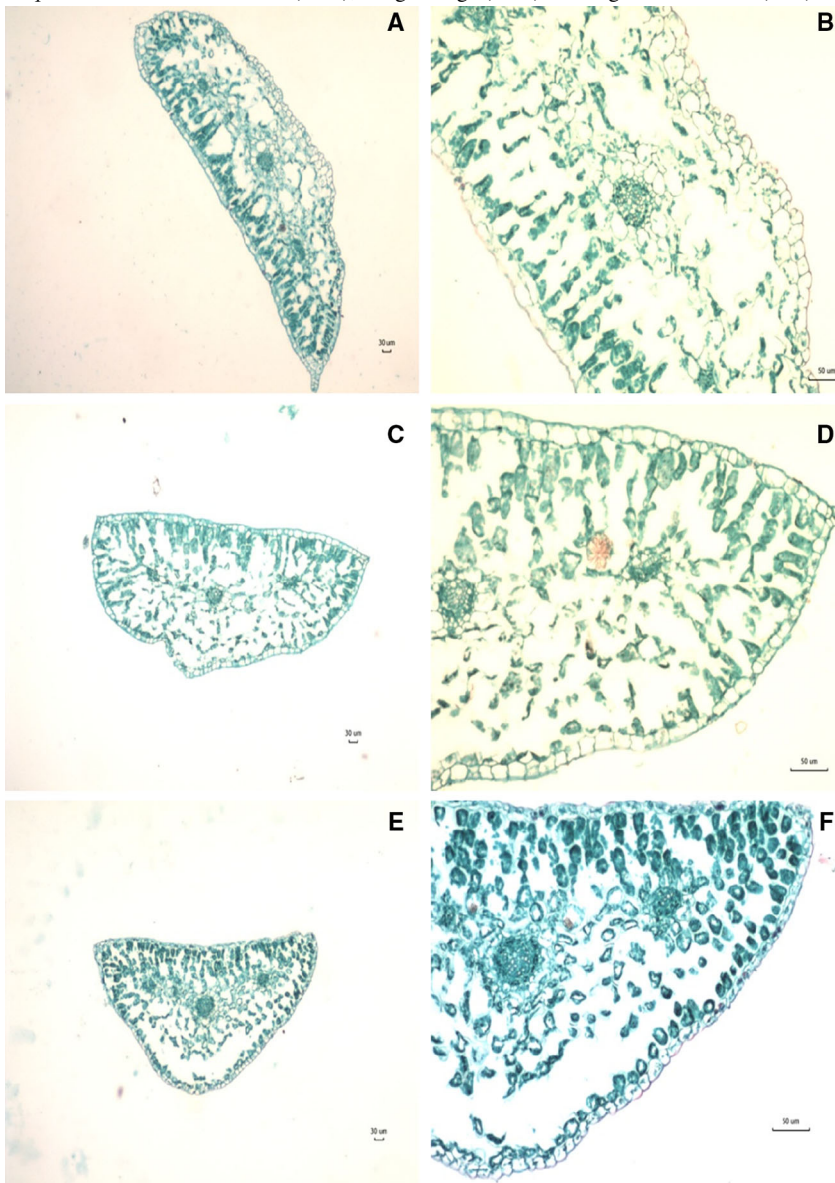
acids in the cell membranes of leaves (Zúñiga et al. 1994), a constitutive high activity of antifreeze proteins in the apoplast (Bravo and Griffith 2005) as well as other stress-induced proteins such as dehydrins (Olave-Concha et al. 2005), and the high concentration of different non-structural carbohydrates (Chatterton et al. 1989; Zúñiga et al. 1996; Zúñiga-Feest et al. 2003, 2009; Piotrowicz-Cieslak et al. 2005). For details and insights of these mechanisms, readers must refer to more specific reviews (e.g., Alberdi et al. 2002; Bravo et al. 2009).

How global warming may affect the freezing resistance of *D. antarctica* and *C. quitensis* is an interesting question that should be addressed in the near future. Antarctic plants are covered by snow during winter, which protects them from exposure to extremely low air temperatures that occur in the coldest season (Smith 2003). Warmer temperatures will reduce snow cover duration, increasing their exposure to sudden freezing events during the growing season (Easterling et al. 2000). Warming could also reduce the current ability to survive freezing temperatures because of effects on deacclimation processes (Pagter and Arora 2013), as it has been shown for alpine plant species exposed to warmer conditions (Sierra-Almeida and Cavieres 2010).

# Photosynthesis

Antarctic plants have to photosynthesize when the snow and ice covers disappear in summer. As mentioned, in contrast to the Arctic or alpine areas, in Antarctic plants photosynthesis has to occur with the low temperatures and highly variable irradiance levels that characterize the summers.

## Photosynthetic responses to light

The highly variable irradiance level of the Antarctic summer is an important feature that plants have to face (Casanova-Katny et al. 2010). Thus, the ability to photosynthesize under different irradiance levels is expected. Edward and Smith (1988) found that net photosynthesis in *D. antarctica* was largely independent of irradiance levels above 150 µmol photon m$^{-2}$ s$^{-1}$ (i.e., saturation). In contrast, Xiong et al. (1999) reported that in both *D. antarctica* and *C. quitensis* net photosynthesis saturated at high

irradiance (750–800 µmol photon m$^{-2}$ s$^{-1}$). However, Montiel et al. (1999) revealed lack of saturation of photosynthesis at high irradiance in *D. antarctica* (1500 µmol photon m$^{-2}$ s$^{-1}$), even in plants from shaded habitats. These authors argued that the absence of saturation in *D. antarctica* allow a complete exploitation of the irradiance levels experienced during the growing season, and can also serve as a photoprotective mechanisms against photoinhibition.

## Photosynthetic response to temperature

The rate of photosynthesis in Antarctic plants is mainly regulated by temperature. Gannutz (1970) reported that *D. antarctica* ceased photosynthesis below 0 °C. Edwards and Smith (1988) grew individuals of both species from different localities and reported that both species achieved around 30 % of their maximum photosynthesis at 0 °C. Xiong et al. (1999) also demonstrated that both species were able to maintain substantial positive net photosynthesis at near-freezing temperatures (see also Montiel et al. 1999).

Edward and Smith (1988) reported optimal temperatures for photosynthesis of 13° and 19 °C for *D. antarctica* and *C. quitensis*; respectively. Interestingly, despite differences among species, they did not find differences among populations within species. Xiong et al. (1999) assessed the optimal temperatures for photosynthesis in the field, near Palmer Station in the Antarctic Peninsula (64°47′S, 64°0′W), reporting 10° and 14 °C for the *D. antarctica* and *C. quitensis*, respectively. Although both, Edward and Smith (1988) and Xiong et al. (1999) reported higher optimum temperatures for *C. quitensis* than *D. antarctica*, Montiel et al. (1999) showed that *D. antarctica* had a broader temperature optimum range (approximately 90 % of the maximum) between 10 and 25 °C. In all these studies, both species maintained substantial photosynthetic rates at temperatures around 20 °C. Thus, both species have the ability to photosynthesize over a relatively wide range of temperatures. The fact that optimal temperatures for net photosynthesis are higher than the average diurnal canopy air temperature (irrespective of field or controlled conditions) suggest that photosynthesis of Antarctic plants is often limited by low temperatures (Xiong et al. 1999). This suggests that future warming would improve vegetative growth of these species due to greater biomass allocation to leaf-area production.

However, while temperatures between 14 and 19 °C may improve the photosynthetic performance in both Antarctic species, long-term exposure to temperatures over 20 °C may result in plant death (Edward and Smith 1988). Xiong et al. (1999) reported that the high-temperature compensation point for photosynthesis was 22 °C in *D. antarctica* and 26 °C in *C. quitensis*, suggesting a high sensitivity to high temperatures. Edward and Smith (1988) indicate high-temperature compensation points around 30 °C. When leaves reach temperatures above their thermal optimum for photosynthesis they potentially suffer negative effects on electron transport or associated enzymes. For instance, Xiong et al. (1999) found that carboxylation efficiencies are lower at higher temperatures (>20 °C) suggesting reduced activity of Rubisco. Likewise, *D. antarctica* showed inactivation of Rubisco activase when leaf temperature exceeded 20 °C (Salvucci and Crafts-Brandner 2004). Therefore, if supra-optimal temperatures (over 20 °C) become more prevalent in the future, the photosynthetic performance of *C. quitensis* and *D. antarctica* might be seriously affected.

Xiong et al. (2000) studied the photosynthetic acclimation and growth to contrasting temperature regimes, and found that *C. quitensis* exhibited a slight ability for acclimation of its net photosynthesis (optimal temperature of photosynthesis increased from 8.4 to 11.5 °C as the daytime growth temperatures increased from 7° to 20 °C). Similar results were reported by Sierra-Almeida et al. (2007) where the optimum temperature for photosynthesis slightly increased with an increase of growing temperature (17 °C when plants were grown at 4 and 18 °C when plants were grown at 15 °C). In contrast, *D. antarctica* does not seem to acclimate photosynthesis because plants growing at three different temperatures had a similar optimal temperature for photosynthesis (10 °C) (Xiong et al. 2000, see also Bystrzejewska-Piotrowska and Urban 2009). Xiong et al. (2000) argued that the poor ability for photosynthetic acclimation may be associated with the relatively stable temperatures experienced by these species along the maritime Antarctic. This poor ability for photosynthetic acclimation suggests that future warming would generate that these plants will be exposed to harmful conditions for photosynthesis. However, more research is needed on this topic, especially under field conditions.

## Photoprotection

During the day, when plants are actively harvesting light, low temperature may have significant effects in terms of energy balance, because absorbed energy might be greater than that used or dissipated, causing photo-oxidative stress (Huner et al. 1998). Luccini et al. (2005) reported average daily irradiation of 27.4 MJ m$^{-2}$ in December in the Antarctic Peninsula, indicating that irradiation levels in Antarctica are among the highest values reported worldwide. Thus, Antarctic plants usually have to cope with simultaneous episodes of high irradiance and low temperature, suggesting that both species should have the ability to deal with this stress factor. Although there are no experimental data assessing the capacity of these species to cope with photoinhibition under field conditions (but see Casanova-Katny et al. 2010), both species have shown a high capacity to deal with photoinhibition under laboratory conditions (Pérez-Torres et al. 2007; Bravo et al. 2007; Bascuñan-Godoy et al. 2010, 2012). Nonetheless, the two species showed slightly different photoprotective strategies. While *C. quitensis* regulates its electron transport pathway avoiding reduction of oxygen, *D. antarctica* actively use O$_2$ as an electron alternative sink through the water–water cycle to protect PSII from excessive light (see Pérez-Torrez et al. 2004a and 2007 for details of the physiological mechanisms). In addition, *C. quitensis* has lower levels of antioxidant enzymes compared to *D. antarctica*, suggesting a low contribution of the water–water cycle to the modulation of redox state of the photosynthetic electron transport chain (Pérez-Torres et al. 2004b).

Thermal dissipation of excess energy (NPQ) is considered a safe and fast alternative to balance energy in plants (Demmig-Adams and Adams 1992). Both Antarctic plants increase NPQ with light intensity at low temperature (4 °C). However, only *C. quitensis* exhibited a substantial increase in its heat dissipation capacity (max NPQ) with low temperatures (Pérez-Torres et al. 2007). In particular, the thermal dissipation in *C. quitensis* is mostly due to dynamic and reversible processes (i.e., xanthophyll cycle), indicating the adaptability of this species to a changing light and temperature environment (Bravo et al. 2007).

The fact that both species have positive photosynthetic rates at 0 °C indicates that key enzymes of the Calvin

cycle remain active at low temperature (Pérez-Torres et al. 2006; Bascuñan-Godoy et al. 2006), suggesting that $CO_2$ remains as the main electron sink (Xiong et al. 1999). Photochemical quenching (qP) in both Antarctic plants increased with temperature, but it decreased at supra-optimal temperatures, with this decrease being correlated with increases in qNP, especially in *C. quitensis* (Xiong et al. 1999). Therefore, warmer temperatures in Antarctica could favor the partition of energy toward the photochemical component, but within a limited range of temperature increment (0–10 °C).

Several studies have shown that the exposure to low temperature (cold acclimation) is the main the factor inducing some of the photoprotective mechanism mentioned above (e.g., the water–water cycle) (Pérez-Torrez et al. 2004b, 2006; Bravo et al. 2007; Bascuñan-Godoy et al. 2006, 2012). Cold acclimation also favors photoinhibition recovery, probably by inducing repairing mechanisms (Bascuñan-Godoy et al. 2012). Therefore, long-term warming may limit the acquisition of fully functional photoprotective mechanisms, which in turn may result in a reduction in plant performance.

## Plant nutrition

The soil nutrient status in cold ecosystems is highly relevant because it may directly limit plant responses to increases in temperature (Klanderud 2008). Broadly speaking, Antarctic soils are characterized by a high content of coarse mineral particles and total organic carbon, scarcity of nutrients, low C/N ratio, and acidic pH (Beyer et al. 2000). However, the formation of organic soils by debris of mosses, lichens, and algae is widespread (Campbell and Claridge 1987; Beyer et al. 1999). Further, these soils are frequently rich in nutrients due to an input from seabirds (Beyer et al. 2000; Bölter 2011).

In cold habitats, soil nitrogen is usually present in organic form due to the inhibition of organic matter decomposition at low temperatures (Kielland 1994). At Signy Islands in the South Orkneys, Roberts et al. (2009) analyzed the different forms of nitrogen in the rhizospheres of *D. antarctica* and *C. quitensis*, and found that concentrations of dissolved organic nitrogen were ca. sevenfold higher than those of the inorganic forms of the element. Recently, Hill et al. (2011) demonstrated that *D. antarctica* has the ability

to avoid N limitation from slow N mineralization in the soil by directly using N from free amino acids and short-chain peptides present in the soil.

The presence of other organisms that generate mutualistic relations with plants (e.g., $N_2$-fixing bacteria, mycorrhizas) affect the way in which plants obtain nutrients in cold habitats (Lambers et al. 2008). So far, no nitrogen fixing organisms have been described in the rhizosphere of Antarctic vascular plants. In addition, neither *C. quitensis* or *D. antarctica* have been found to form any arbuscular mycorrhiza in the Palmer Station area (DeMars and Boerner 1995), although *D. antarctica* has been induced to form arbuscular mycorrhizas in greenhouse experiments (Cabello et al. 1994). From this last evidence, the possibility of finding mycorrhizas associated to *D. antarctica* should not be ruled out.

Arbuscular mycorrhizal fungi are either not found or are found only sporadically (Upson et al. 2008; Newsham et al. 2009). In the absence of arbuscular mycorrhizas, it has been suggested that dark septate endophytes (DSE) might act as root mutualists (Bledsoe et al. 1990). DSE have been frequently found associated to *D. antarctica* and *C. quitensis* roots (Upson et al. 2008) and Upson et al. (2009) have showed that DSE isolated from roots of *D. antarctica* play an important role in plant nutrition, especially when organic nitrogen sources was applied to plants. Thus, the presence of this kind of mutualistic relationship seems to be important, but as far as we know, no studies have assessed its presence and importance in the field.

In cold ecosystems not limited by water, warming tends to increase nutrient availability for plants due to increases in soil enzyme activities, nutrient mineralization, and organic matter decomposition (Von Lützow and Kögel-Knabner 2009). Thus, an important indirect effect of warming is the release of more nutrients that become available for plant uptake and growth (Schmidt et al. 2002). Although the expansion of the Antarctic plant populations during the last decades has been associated to direct effects of temperature on the increases of growth and reproduction of both species, indirect effects of temperature on soil nutrients availability cannot be ruled out. In glasshouse experiments, we have found that addition of nitrogen to *D. antarctica* increased dry biomass production in 645 % with ammonium and 403 % with nitrate compared to control plants without nitrogen

**Table 2** Some open questions related with the ecophysiology of the Antarctic vascular plants that need to be addressed to gain insights about the adaptations of these plants to the peculiar Antarctic environment and how they will respond to the future climate changes

| |
| --- |
| What factors promote/restrict *Colobanthus quitensis* distribution at different spatial scales? |
| Are there micro-anatomical changes/adaptations that allow Antarctic vascular plants face the harsh climatic conditions of the summer? |
| Are these morphological changes/adaptations plastics? |
| What is the genetic base for these changes? |
| How these micro anatomical adaptations will respond to climate change? |
| How global warming may affect the freezing resistance? |
| Can acclimation of photosynthesis occur under field conditions? |
| How will photosynthesis be affected under warmer conditions in the field? |
| Will photoprotective mechanisms be affected by warming? |
| Will *Deschampsia antarctica* and *Colobanthus quitensis* respond in different way to warming? |
| How the morphophysiological adaptations of these plants will contribute to resist change in climate conditions? |

addition. For *C. quitensis*, these figures were 162 and 178 % for ammonium and nitrate, respectively. These results suggest differential responses of the two species to increased availability of different form of inorganic nitrogen. Thus, the effect of warming on the rates of nitrification in Antarctic soils will certainly modulate plant responses to future warming and may at least partially explain the different levels of population expansion detected in recent time for both species (Torres-Mellado et al. 2011).

## Concluding remarks

The Antarctic vascular plants have ecophysiological adaptations related to cold and desiccation tolerance, and display an array of traits to survive under these conditions. Evidence reviewed here indicates that what really distinguishes Antarctic plants from other cold-resistant plants is that they must cope with low temperatures year-round. This imposes a major constraint: they must grow and reproduce under continuous low temperature conditions. This is a big challenge because temperatures between 5 and 7 °C have often been treated as zero points of life in the sense of growth and development, although leaf photosynthesis is active at sub-zero temperatures (Körner 2015). Several adaptations seem to help with this major constrain. Among these are xerophytic anatomical characteristics, sufficient freezing tolerance, ability to maintain positive net photosynthesis at near 0 °C (low temperature compensation point),

adequate management of excess PAR radiation, resistance to photoinhibitory conditions, tolerance to water stress, and ability to form associations with endophytes that help in their mineral nutrition. Further, several of these ecophysiological traits show considerable response flexibility. The wide degree of environmental variability experienced throughout the Antarctic Peninsula sites inhabited by these vascular plant species, suggest that predicted levels of change in environmental variables (particularly temperature and water availability) are often small relative to the range already experienced.

Nonetheless, it seems that global warming has generated increases in population size and reproduction of the Antarctic vascular plants leading to an increase in the expansion range of both species. The evidence reviewed here indicates that small increases in air temperature may be beneficial in terms of photosynthetic performance considering that both species are highly efficient in their light capture at low temperatures. However, more frequent leaf temperatures over 20 °C could be harmful affecting photosynthesis and reducing the ability of these plants to tolerate freezing temperatures, key attributes by which they are able to colonize these very harsh environment. Moreover, the wide range of ecophysiological responses showed here indicates that both species are being differentially affected by the warming in the maritime Antarctic. These interspecific responses will depend on the different sites where these species are developing along the Antarctic Peninsula and related islands, which as it has been

described here, are highly variable in availability of nutrients and water, and associations with other organisms. There are still many questions that should be answered to elucidate the real effect of warming on *C. quitensis* and *D. antarctica* (see Table 2 for examples of questions that remain elusive). Here, we indicate that climate change may have significant effects on indirect processes facilitating the growth and reproduction of these plant species such as soil nutrient availability, plant nutrient uptake, and metabolism. Significant effects on other processes different to photosynthesis which are also influencing the carbon balance such as growth per se (i.e., cellular expansion and division) cannot be ruled out. Many responses to climate change are likely to be subtle and multifactorial. However, it is fundamental to recognize that integrating these subtle responses can result in considerable and unexpected impacts for these plant species and the ecosystems they belong to. Given the importance of understanding biological responses to climate change in the Antarctica, it is clear that such an understanding requires that we continue to unveil the entire life history traits of the Antarctic vascular plants and their responses to changes in both their biotic and abiotic environment.

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