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Minireview

Ecophysiology of Antarctic vascular plants

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Most of the ice and snow-free land in the Antarctic summer is found along the Antarctic Peninsula and adjacent islands and coastal areas of the continent. This is the area where most of the Antarctic vegetation is found. Mean air temperature tends to be above zero during the summer in parts of the Maritime Antarctic. The most commonly found photosynthetic organisms in the Maritime Antarctic and continental edge are lichens (around 380 species) and bryophytes (130 species). Only two vascular plants, *Deschampsia antarctica* Desv. and *Colobanthus quitensis* (Kunth) Bartl., have been able to colonize some of the coastal areas. This low species diversity, compared with the Arctic, may be due to permanent low temperature and isolation from continental sources of propagules. The existence of these plants in such a permanent harsh environment makes them of particular interest for the study of adaptations to cold environments and mechanisms of cold resistance in plants. Among these adaptations are high freezing resistance, high resistance to light stress and high photosynthetic capacity at low temperature. In this paper, the ecophysiology of the two vascular plants is reviewed, including habitat characteristics, photosynthetic properties, cold resistance, and biochemical adaptations to cold.

Introduction

General characteristics of the Antarctic environment

Polar areas are the coldest regions of the world, containing 99% of the ice in the planet (about 13% in the Arctic and 86% in the Antarctic). The majority of the Antarctic continent is covered by permanent ice and snow, with only 2% available for colonization by plants and animals. Most of the ice and snow-free land is found along the Antarctic Peninsula, its associated islands, and in the coastal region around the rest of the Antarctic continent (Fig. 1). In the proximity of the coast (Maritime Antarctic) temperatures ameliorate. Summer (January) maximum daily air temperatures are usually between 0°C and 6°C, and minima are between 2°C and 4°C (Edwards and Smith 1988, Zúñiga et al. 1996). The mean summer air temperature is about 2.8°C on Robert Island (Zúñiga et al. 1996). In winter, temperatures range between −10°C and −20°C, as reported at the Casey Station by Jackson and Seppelt (1995). From the interior to the coast of the continent (especially westward towards the coast of the Peninsula), temperature and precipitation increase, resulting in increased presence of liquid water. In the past 50 years, along the west coast of the Antarctic Peninsula, the mean annual temperature rose by about 2.6°C and mean summer air temperatures have risen by 1.5°C (Day et al. 1999, Xiong et al. 2000). More evidence of regional warming comes from the dramatic retreat of ice shelves along the west coast of the Peninsula over this period (Sympson 2000). Summer fogs are frequent in the South Shetland Islands. Precipitation in the Maritime Antarctic falls mainly as snow, although rain is also frequent in summer. In the South Shetland Islands, precipitation in form of snow and rain is around 400 mm year^{-1}; while in Margarita Bay, it is 100 mm. Thus, in many areas of the Antarctic, conditions vary from arid to semiarid.

Antarctic soils, especially those of the coastal areas, are characterized by a high content of coarse mineral particles and total organic carbon, a low C/N ratio, acidic pH, and are frequently enriched in nutrients due to the influence of sea spray and an input of seabirds (Beyer et al. 2000). Permafrost conditions and high soil water-content may be important constraints for plant growth in Antarctic regions. Following thermal changes, soil moisture can pass from a saturation state in summer to physiological aridity in winter. Little is known on the effect of nutrients on the performance of Antarctic vegetation (Kappen 2000), whereas the microclimate, including factors such as moisture availability, low temperature and ground-level wind speed, has a major influence on plant growth (Beyer et al. 2000). Snow cover in the Antarctic is an important microclimatic factor in protecting plants from wind, windblown ice, and sand particles and extreme temperature.

Other important microclimatic factors for plant growth in this habitat are day length and irradiance. Due to the high latitude of the continent, considerable differences in the levels of solar radiation and day length between summer and winter occur. In summer, day length at the northern end of the Antarctic Peninsula is shorter than at the southern end. In mid-summer plants growing within the Antarctic circle receive 24 h of daylight, while those further north receive 3–4 h of darkness a day. During the growing season (December to February), day length is about 20 h in the Antarctic Peninsula. Irradiance can reach up to $>2000\ \mu\text{M m}^{-2}\ \text{s}^{-1}$ in summer and around $50\ \mu\text{M m}^{-2}\ \text{s}^{-1}$ in winter in the Maritime Antarctic (Schroeter et al. 1995). The conjunction of high irradiance and low temperature may damage the photosynthetic apparatus, causing a reduction in photosynthesis known as photoinhibition (Demmig-Adams and Adams 1992).

Cold stress is a greater influence in the Antarctic than in the Arctic (Kappen 2000). This unfavourable climatic condition could explain the low plant species diversity of the Antarctic in comparison with the Arctic (Kappen 1999). Subantarctic islands are richer in life diversity, mostly because of milder climatic conditions. For example, the Kerguelen Archipelago (49°20′S, 70°20′E) has 36 vascular plant species. This archipelago is located on the convergence where upwelling cold water from the Antarctic mixes with the warmer water from the Indian Ocean (Clark and Dingwall 1985). On the other hand, the Antarctic continent is much further to the south and is spatially and climatically isolated from the other continents of the Southern Hemisphere because the characteristic ring of cyclonic air circulation around the Antarctic limits the import of plant diaspores. It is well

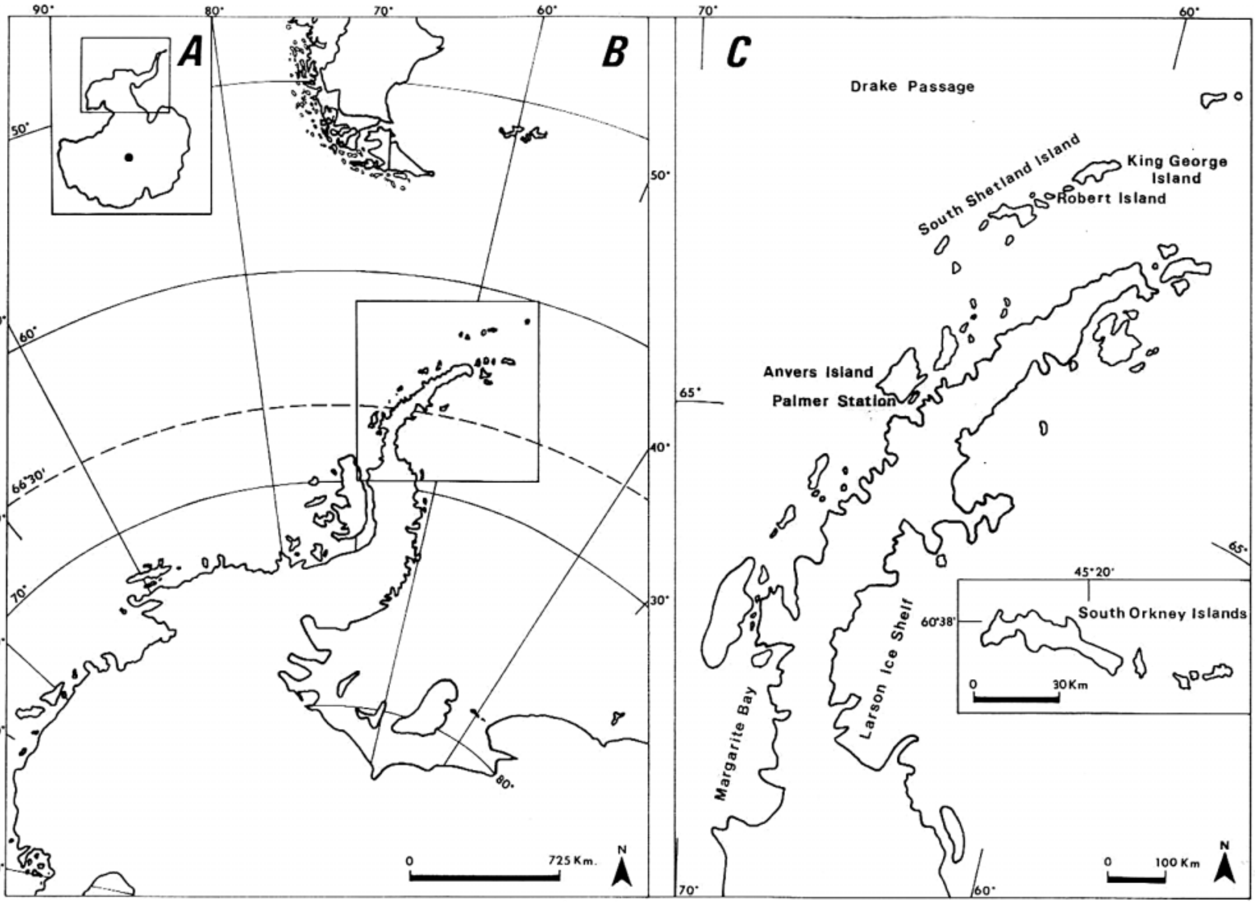

Fig. 1. Distribution of plants in the Antarctic. Plants are widely distributed along the ice-free coastal areas of the Antarctic Peninsula and associated islands. The Antarctic continent (A). The Antarctic Peninsula (B, inset from A). The South Shetland Islands and botanical area of the peninsula (C, inset from B). Vascular plants can be found as far south as Marguerite Bay (Grobe et al. 1997). A comprehensive review on the precise location of these plants is available (Green and Holtom 1971). Lichen dominance increases with increasing latitude up to 86°S, competing with mosses and vascular plants in the milder parts of the Maritime Antarctic (Kappen 2000).

known that islands or isolated areas are poorer in species than comparable continental areas (MacArthur and Wilson 1969). Moreover, glaciations in the Arctic commenced about 2–3 million years ago, while the Antarctic glaciations are believed to have commenced in the early Oligocene (Barker et al. 1998). Thus, to survive in the Antarctic, plants must be able to cope with severe physiological stresses, especially during the growing season (Antarctic summer), caused by low temperature, repeated freezing and thawing, desiccation, low availability of water and high irradiance. Many plant species are regarded to be salt tolerant, often in combination with ornitocoprophily (Gremmen et al. 1994).

Antarctic flora

The Antarctic vegetation is predominantly composed of about 130 cryptogams (mosses, liverworts and lichens, with a poikilohydrous behaviour) and two flowering plants with homeohydrous behaviour, the hair grass *Deschampsia antarctica* Desv. (Poaceae) and the pearlwort *Colobanthus quitensis* (Kunth) Bartl. (Caryophyllaceae) (Kappen 1999). These two plant species are found in the South Orkney Islands and in most of the Maritime Antarctic down to approximately 68°S (Fig. 1), but do not extend into the continental Antarctic (Greene and Holtom 1971). In contrast, lichens, have been found as far south as 86°S (Schroeter et al. 2000). Both vascular plants are thought to be post-glacial immigrants and are often found in association with one another (Holtom and Greene 1967). The populations of these vascular species are expanding in the Maritime Antarctic (Casaretto et al. 1994, Smith 1994, Day et al. 1999). Terrestrial algae, growing in the snow banks or soils, are also present (Kappen 1999). A comprehensive database on Antarctic plants, linked to a geographical information system, has been developed (Peat 1998).

Under the present climatic conditions, lichens co-exist with bryophytes and vascular plants as equal partners in the vegetation in the most favourable areas of the Maritime Antarctic (Kappen 2000). In areas with more extreme environmental conditions, lichens, after microorganisms and unicellular algae, are pioneers in occupying terrestrial habitats (Smith 1993). Any significant climatic change, such as warming, would favour growth of vascular plants (Smith 1994, Bravo et al. 2001), altering the composition of the vegetation. Susceptibility of lichen vegetation to climatic changes, air pollution, and animal activities, has raised concern over its future as a component of the Antarctic vegetation (Kappen 2000).

Ecophysiology of vascular Antarctic plants

Anatomical features

Since *D. antarctica* has been present in the Antarctic for at least five millennia (Smith 1994), it could be postulated that its leaf anatomy might show constitutive adaptations to this environment. This appears not to be the case. Romero et al. (1999) studied the leaf anatomical features of this plant growing in Robert Island, and in clones cultivated in the laboratory for 2 years at 13 ± 1.5°C and 180 μM m^{-2} s^{-1} irradiance. Antarctic samples showed more xerophytic characteristics (smaller leaf surface and epidermal cells, higher leaf thickness, higher stomata density and number of cells per area, thicker cuticle) than the leaves of plants cultivated at 13°C. Adaxial epidermis of leaves of plants growing in the field showed turgid papillae, which were absent in the leaves growing at 13°C. As reported for other plants, these papillae could be interpreted as a storage mechanism of carbohydrates involved in freezing point depression. In the leaf transverse section, the vascular bundles of the Antarctic samples appeared surrounded by two bundle sheaths (Mantovani and Vieira 2000): an outer sheath, with parenchymatous cells with small chloroplasts visible only with electronic microscopy (Romero et al. 1999) and an inner sheath with thick lignified walls (mestome). The outer bundle sheath was absent in the laboratory samples. The presence of two bundle sheaths in vascular bundles of leaves of other Poaceae has been associated with an adaptation to high radiation destined to optimise photosynthesis and water use efficiency (Pyykkö 1966). In fact, *D. antarctica* has a high water use efficiency, with values ranging between 62 and 123 mol H_2O per mol CO_2; in most C_3 species these values range from 300 to 500 mol H_2O per mol CO_2 (Montiel et al. 1999). Evert et al. (1985) suggested that the mestome functions as endodermis, limiting apoplastic movement of water to the mesophyll. A diminution of water supply to the mesophyll could be advantageous to *D. antarctica* since the water control could take place in the vascular bundles, in addition to the stomata with a high control capacity to water loss (Mantovani and Vieira 2000). Resistance to transpiration avoids heat loss in cold environments, being an important adaptation for these habitats. The outer bundle sheath was absent in leaves of plants growing at 13°C. Thus, the leaf anatomical features of *D. antarctica* do not correspond to a constitutive adaptation produced by natural selection under harsh Antarctic conditions, but rather to a plastic response to these conditions. In *C. quitensis*, the bundle sheath lacks a mestome, although leaf thickness and mesophyll surface area values are typical of xeric plants (Mantovani and Vieira 2000). The xeromorphic leaf characteristics of plants growing in the Antarctic could be principally explained by disturbances in water balance due to low temperature, low rainfall and water availability (Smith 1993).

In cold soils the water and root membrane viscosities are increased, producing disturbances in water absorption. Thus, leaf xeromorphic features should be higher in colder soils. Although low N and P content in soils may also induce xeromorphic characteristics, the organic input by sea birds is likely to attenuate its importance. Future ecophysiological studies in this habitat should consider not only air temperature measurements, but also soil temperatures and nutrient composition in the root region. The ability to incorporate organic nitrogen is widespread in tropical and subantarctic plant communities (Schmidt and Stewart 1999). It is unclear where most of the biologically available nitrogen comes from. No nitrogen fixing organisms have been described in the rhizosphere of Antarctic vascular plants. Neither *C. quitensis* nor *D. antarctica* have been found to form arbuscular mycorrhizae in the Palmer Station area, but *D. antarctica* has been induced to form arbuscular mycorrhizae in greenhouse experiments (DeMars and Boerner 1995).

Photosynthesis

Little was published earlier than 1970 on the physiology under field or laboratory conditions of the two unique vascular plants (*D. antarctica* and *C. quitensis*) that have naturally colonized the Antarctic (Fig. 2). Holtom and Greene (1967) demonstrated that alternating high and low temperature conditions were more favourable for the growth of both species than continuous temperatures above 20°C, which may be fatal. Gannutz (1970) reported that the grass ceases to photosynthesise below 0°C and can maintain the respiration down to −10°C. The optimum temperature for net photosynthesis is around 13 and 19°C for the grass and the pearlwort, respectively, as shown under controlled laboratory conditions by Edwards and Smith (1988). Both species maintain around 30% of their maximum photosynthetic rates at 0°C. Measurements of whole-canopy CO_2 gas exchange and chlorophyll *a* fluorescence of both plant species growing near Palmer Station in the Antarctic Peninsula showed negligible midday net photosynthetic rates on warm, usually sunny days (canopy air temperature >20°C), but relatively high rates on cool days (canopy air temperature <10°C) (Xiong et al. 1999). Laboratory measurements of photosynthetic responses to light and temperature show that high temperature, not PPF, is responsible for depressions of net photosynthesis on warm sunny days, due to high rates of temperature-enhanced respiration and possibly impairment of the photosynthetic apparatus. Additionally, carboxylation efficiencies are lower at higher temperatures (>20°C), suggesting reduced activity of ribulose-1,5-biphosphate carboxylase-oxygenase (Rubisco).

D. antarctica and *C. quitensis* show no photoinhibition on clear and cold days in the Antarctic and in the laboratory at low temperature and high irradiance (Xiong et al. 1999). Photoprotective mechanisms associated with carotenoids through the xanthophyll cycle could function in these plants when conditions are photoinhibitory. Total chlorophylls and carotenoids were higher in plants of *D. antarctica* from the field (18 μg cm^{-2} and 4.6 μg cm^{-2}, respectively) than those growing in the laboratory at 13°C (11 μg cm^{-2} chlorophyll and 2.1 μg cm^{-2} carotenoids) (M. A. Casanova 1997. Thesis, University Austral de Chile, Valdivia, Chile).

Day length and growth

Day length is an important environmental factor in the Maritime Antarctic, and ranges from about 21 h at the beginning of summer to about 3 h in winter in the northern part of the Antarctic Peninsula. The effect of day length (LD, long day = 21/3 h light/dark; MD, medium day = 16/8 h light/dark and SD, short day 8/16) on cold acclimation responses in *D. antarctica* growing in the laboratory was determined by Bravo et al. (2001). The main effects of cold were observed with the MD and LD treatments. This is understandable because plants are

Fig. 2. The Antarctic vascular plants. *D. antarctica* (left) and *Colobanthus quitensis* (right) were grown in the laboratory at 15°C, with an irradiance of 150 μM m^{-2} s^{-1}. Plants in the Antarctic are smaller in size, forming compact tussocks. *C. quitensis* flowers after cold treatment. This has not been observed in *D. antarctica*.

usually covered with snow during most of the autumn, winter and spring in the Maritime Antarctic, when the shortest days occur. The longer the day length treatment, the faster the growth rates for both cold-acclimated and non-acclimated plants. Similarly, the longer the day treatment during cold acclimation, the higher the sucrose (up to 7-fold) and proline (up to 77-fold) contents, with respect to non-acclimated control values. Total fructans accumulated significantly (339 mg g^{-1} DW) during cold acclimation only in the MD treatment, which occurs in the field by the end of summer. They were higher than fructan contents in leaves of *D. antarctica* growing in the Antarctic during the summer (112 mg g^{-1} DW) (Zúñiga et al. 1996) and slightly lower than the higher values found in cool season grasses (Chatterton et al. 1989). Oligofructans accounted for more than 80% of total fructans. The degrees of polymerization were mostly between 3 and 10. Since sucrose, but not glucose and fructose, was significantly higher in the LD than in the other day lengths during exposure to cold, a depolymerization of fructans to fructose through the activity of a fructan-exohydrolase may occur, as in other plants (Morvan et al. 1997). The released fructose could be converted by fructose kinase, sucrose phosphate synthase (SPS) and sucrose phosphatase to sucrose. This is consistent with the augmented SPS activity of this species during the light period. Alternatively, as in some temperate zone grasses, fructans may not be synthesized significantly at long day length, so the plants accumulate sucrose. *D. antarctica* and *C. quitensis* accumulated little starch under different day length during cold acclimation (Bravo et al. 2001).

With respect to the association of growth and fructans, it is generally accepted that fructans accumulate under conditions that favour photosynthesis but not growth, as demonstrated in *Poa pratensis* growing under SD with respect to LD conditions, where growth rates are higher and fructan contents lower (Solhaug 1991). According to this author, the increases in growth of this species in the long day treatment, compared with the short day treatments, is associated with allocation of more assimilates to leaf blade growth in LD and to storage as fructans in the SD. The growth analysis in *D. antarctica* also shows higher growth rates under LD (32 mg^{-1} d^{-1}) than under SD (4.8 mg g^{-1} d^{-1}) and MD (10 mg g^{-1} d^{-1}) conditions (Bravo et al. 2001). Because the PPFs of these three treatments were the same, the higher total carbohydrate content achieved during the cold acclimation in the MD and LD treatments was attributed to a prolonged time for photosynthesis, thus more assimilates are available to divert for growth than in SD treated plants. This behaviour is also observed in grasses of maritime environments from 52°N northwards when they are exposed to cool long days without increasing the supply of PPF (Hay 1990). This author suggests that this response is not a specific adaptation to the cool long days of the high latitude summer. Instead, the short day depression of growth, which facilitates cold hardening of these grasses in autumn, is likely to be more important. Grasses and cereals from lower latitudes are equipped to grow well during summer at high latitudes. However, they are subject to winterkill because they do not recognize the correct photoperiodic cue in autumn. Some plants seem to have a critical photoperiod for stimulation of growth. Probably, a 21-h day length is above the critical photoperiod for growth stimulation of *D. antarctica* (Bravo et al. 2001). The accumulation of sucrose and fructans in cold acclimated *D. antarctica* and sucrose in *C. quitensis* reflects an efficient carbon metabolism under these conditions (Bravo et al. 2001), which corresponds well with the positive carbon balance of these plants at 0°C (Edwards and Smith 1988, Xiong et al. 1999).

The factors required for inflorescence initiation and development of these Antarctic plants are unknown. Most arctic and alpine plants require a dual flower induction, as it has been shown for *Phleum alpinum* from South Georgia (54°S) and Norway (61°N). This plant has an obligatory low temperature and short day requirement for inflorescence initiation, while inflorescence development is enhanced by long days (Heide and Solhaug 2001)

Regional warming and increased UV-B

Associated with the warming trend over the past 50 years along the Antarctic Peninsula, Smith (1994) and Day et al. (1999) reported increases in both the size and number of populations of the hair grass and the pearlwort along the Antarctic Peninsula, suggesting an improvement in their reproductive capacity as the result of longer and warmer growing seasons. Day et al. (1999) also found in a short-term field study that while vegetative growth of *C. quitensis* improved under warming, in *D. antarctica* it decreased. This implies that continued regional warming along the Antarctic Peninsula might benefit the pearlwort, but impair the performance of the grass. This evidence represents a discrepancy with other reports, where an improvement of vegetative growth with warming is found for both species (Holtom and Greene 1967, Xiong et al. 2000). Both research groups assessed vegetative growth of *D. antarctica* and *C. quitensis* grown separately in growth chambers at different temperature regimes. Holtom and Greene (1967) used 5°C (constant), 20°C (constant) and 20°C day/5°C night, and found more vegetative growth at the higher temperature in both species. They also suspect that with the predicted regional warming of about 3°C in summer air temperatures over the next 30 years (see Smith 1994) vegetative growth of both species along the Antarctic Peninsula should improve. As Day et al. (1999) pointed, the discrepancy between growth chamber conditions and field results underscores the difficulties of extrapolating from controlled-environments to field situations. A likely explanation for this discrepancy is that the warming treatments in the field of Day et al. (1999) might have temporarily raised temperatures on sunny days above the 20°C daytime optima for growth found in the growth chamber study.

Xiong et al. (2000) studied how Antarctic vascular plants might respond to strong warming along the Antarctic Peninsula. They assayed the photosynthetic and respiratory acclimation and growth response of *D. antarctica* and *C. quitensis* to contrasting temperature regimes (7°C day/7°C night, 12°C day/7°C night and 20°C day/7°C night, 18 h/6 h photoperiod) in the laboratory. Plants of both species growing at a daytime temperature of 20°C had greater relative growth rates and produced 2.2–3.3 times as much biomass and leaf area as plants growing at daytime temperatures of 12° or 7°C. Rates of whole canopy net photosynthesis (per plant) were highest in plants at 20°C and were well correlated with differences in relative growth rates and total biomass. On a leaf area basis *D. antarctica* and *C. quitensis* plants growing at 12°C had the highest rates of net photosynthesis when measured at their respective daytime growth temperature, while on a whole canopy basis, plants growing at 20°C had the highest rates of net photosynthesis. The pearlwort exhibited a slight ability for acclimation of its net photosynthesis (leaf area basis), as the optimal temperature increased from 8.4 to 10.3–11.5, as the daytime growth temperatures increased from 7° to 12° and 20°C, respectively. *D. antarctica* does not appear to acclimate photosynthetically, because plants growing at the three treatment temperatures had a similar optimal temperature (10°C). This behaviour may be associated with the relatively stable maritime temperature during the growing season in the Antarctic Peninsula. From these results, Xiong et al. (2000) suggested that, in the absence of interspecific competition, continued warming along the Antarctic Peninsula would lead to improved vegetative growth of these species due to greater biomass allocation to leaf-area production and their ability to acclimate their dark respiration; such respiratory loss per leaf area does not increase under higher temperature regimes. For example, on a leaf area basis, the dark respiration of plants of *C. quitensis* grown at 7°C when measured at 7°C (6 μM m^{-2} s^{-1}) was very similar to that of plants grown at 12°C when measured at 12°C (6.3 μM m^{-2} s^{-1}) and to that of plants grown at 20°C when measured at 20°C (5.8 μM m^{-2} s^{-1}). A similar result was found in *D. antarctica*, in which the rates of dark respiration among plants from different temperature regimes were similar when measured at their respective day time temperatures (about 7 μmol m^{-2} s^{-1}). In both species, rates of dark respiration on a whole canopy basis (per plant) were higher in plants grown at 20°C than at 7°C and 12°C. Xiong et al. (1999) suggested that warming would improve the rates of net photosynthesis, because the air temperatures of the sites where these species grow (an average of 4.3°C) are below their temperature optima for net photosynthesis. These findings may support the proposition of Smith (1994) to use these two vascular plants as bioindicators of regional warming in the Antarctic.

While warming seems to benefit the growth of these plant species, it is unclear what effects are produced by higher UV-B levels in the Antarctic. Generally, enhanced UV-B levels can decrease growth and alter the morphology of plants (Barnes et al. 1990), reduce their photosynthesis (Teramura and Sullivan 1994), and damage DNA (Pang and Hays 1991). Day et al. (1999) and Ruhland and Day (2000) found that ambient UV-B levels reduced the vegetative growth of *C. quitensis* and *D. antarctica* near Palmer Station in Anvers Island. These reductions did not appear to be associated with reductions in photosynthesis per se, when expressed on a leaf area basis. Leaves exposed to UV-B were thicker and had higher concentrations of UV-B absorbing pigments (Montiel et al. 1999, Xiong and Day 2001). Increased levels of flavonoids are found in the tussock during the Antarctic mid-summer over the levels measured in early and late summer (Webby and Markham 1994). Therefore, these species appear to be well adapted to current levels of solar irradiance and UV-B radiation (Montiel et al. 1999).

Freezing resistance

D. antarctica may cope with low air temperature by occupying the most favourable habitats. It has been suggested that it has developed metabolic adaptations to survive under low temperatures, especially during the growing season, when plants are normally very sensitive to cold. In this season, the mean temperature is above 2°C, with temperatures usually ranging between 6° and −4°C (Zúñiga et al. 1994). Under these conditions, *D. antarctica* is highly frost-tolerant (LT$_{50}$ around −27°C). To operate under relatively low temperature, plant membranes must be sufficiently fluid to allow metabolic reactions. Fluidity is determined by fatty acid composition and unsaturation in lipid fractions, which may play a role in cryoprotection of plants (Alberdi and Corcuera 1991). The contents in polar lipids and the degree of unsaturation of fatty acids of most membrane lipid fractions of leaves and roots of *D. antarctica* growing in the Maritime Antarctic were not unusual when compared with other Gramineae (Zúñiga et al. 1994). The phosphatidylglycerol fraction rich in saturated fatty acids (16:0 + 18:0 + *t*16:1) has been associated with chilling sensitivity in various plants (Roughan 1985). The content of this fraction in leaves of *D. antarctica* is about 25% of the normal content of chilling sensitive plants. (Roughan 1985, Zúñiga et al. 1994). Non-structural carbohydrates in *D. antarctica* are higher compared with some cultivated cereals (Zúñiga et al. 1996). Sucrose and fructan contents were higher in leaves than in roots. These compounds fluctuated during the summer, being lowest in January and highest in February. This appears to be associated with a decrease in air temperature in February. Carbohydrate accumulation may be involved in increasing freezing resistance of *D. antarctica*. These substances would enhance its survival because they are readily accessible reserves during growth periods with a negative carbon balance.

Since *D. antarctica* and *C. quitensis* live in a harsh cold environment, the study of cold resistance mechanisms is highly relevant. Both plants have different strategies to resist cold temperatures (Bravo et al. 2001). Because the ice nucleating temperature, measured by thermal analysis, of the grass leaves was −5.3°C in non-acclimated and −10.4°C in cold-acclimated plants and the LT_{50} reached −26.6°C, we concluded that *D. antarctica* is mainly a freezing-tolerant species. In contrast, the pearlwort had higher LT_{50} values than the ice nucleation temperature; thus, this plant species supercools and avoids freezing. It was also demonstrated that the grass had a remarkable cold acclimation capacity (TL_{50} from −12 to −26.6°C) whereas *C. quitensis* does not cold acclimate (from TL_{50} −4.8 to −5.8°C) under laboratory conditions. Nevertheless, this plant supercools down to −9.4°C in plants grown at 4°C in the laboratory, which may be sufficient to withstand Antarctic temperatures before the snow covered period begins. The LT_{50} of *C. quitensis* growing in the Antarctic has not been determined. It is likely that acclimation at a lower temperature and under harsher environmental conditions in the field may, as in *D. antarctica*, reduce its TL_{50} or increase supercooling capacity.

Freezing tolerance results from several cryoprotective mechanisms operating concurrently. Since soluble and membrane bound proteins increase during cold acclimation, it is thought that accumulation of some proteins is one of these protective mechanisms (Alberdi and Corcuera 1991). Most studies on cryoprotection in the Antarctic terrestrial organisms have been concerned with invertebrates and have usually focused on polyhydric alcohols and sugars as cryoprotectants (Jackson and Seppelt 1995). The first study on the role of proteins as cryoprotective substances in Antarctic plants (*D. antarctica*) was undertaken. Compared with bovine serum albumin (BSA), protein leaf extracts from plants growing in the field (Robert Island, Maritime Antarctic) cryoprotected thylakoids of *Hordeum vulgare* subjected to −20°C efficiently in vitro. Ninety percent of the total thylakoid activity (measured as O_2 evolution in the presence of $MgCl_2$) was recovered when frozen thylakoids were incubated with protein extracts from Robert Island, while BSA recovered only 60%. This cryoprotective activity is similar to that provided by 250 m*M* sucrose (Bravo et al. 1997). Additionally, a transport system for fructose similar to humans (GLUTs) was found in cold-acclimated *D. antarctica* leaves (C. P. Triviño 1998, PhD Thesis, University Austral de Chile, Valdivia, Chile). Doucet et al. (2000) reported that all Antarctic species show an ability to inhibit recrystallization of ice when exposed to low temperature.

Differential expression of genes occurs in *D. antarctica* when cultivated under cold conditions (L. Mujica 1999, PhD Thesis, University Austral de Chile, Valdivia, Chile). In vivo labelling proteins separated in two-dimensional electrophoresis showed qualitative (de novo synthesis) and quantitative changes in polypeptide synthesis induced by cold in leaves and roots. The identity and cryoprotective activity of the various differentially expressed peptides remains to be studied. Recently, our group has isolated several cDNA clones using mRNAs differential display during cold acclimation, such as a glutaredoxin like sequence (Genbank accession No. AF374461), a putative pyruvate kinase (Genbank accession No. AY090539) and several unknown differential ESTs.

Future perspectives

Many ecophysiological features of cold resistance of Antarctic plants have already been studied, but beyond the accumulation of several metabolites, little is known about the genes that control this resistance and their regulation. The molecules and genes responsible for the high freezing resistance of *D. antarctica* remain to be identified. Characteristics and regulation of the enzymes involved in provoking the unusually high contents of soluble carbohydrates are features that need to be understood. Similarly, the supercooling capacity of Antarctic angiosperms needs further characterization to elucidate the cellular structures and molecules involved. The flowering of both vascular plants has been observed in the Antarctic, but it is unknown to what extent cold and day length are required for inflorescence initiation and development. Because nutrient effects on the Antarctic vegetation are not well characterized, studying nutrient acquisition by these plants is of high interest. The positive carbon balance of vascular plants at low temperature and the ability to photosynthesise at low temperature offer the possibility of further characterizing the functioning of biological membrane systems under extreme conditions. The low amount of material available and its low rate of growth in the Antarctic are great barriers for these types of studies in the field. Nevertheless, the Antarctic angiosperms rapidly acclimate to laboratory conditions, providing the opportunity for more in-depth molecular studies. Global warming may have a deep impact on the size and rate of expansion of the population of the vascular plants in the Antarctic. Monitoring these populations may be useful to evaluate biological effects of warming in the Antarctic.

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