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ORIGINAL PAPER

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# Robustness of activity of Calvin cycle enzymes after high light and low temperature conditions in Antarctic vascular plants

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**Abstract** Only two vascular plants have naturally colonized the Maritime Antarctic: *Colobanthus quitensis* and *Deschampsia antarctica*. We propose that one of the reasons of their success in this environment is the robustness of their $CO_2$ assimilation machinery. In order to understand the mechanisms involved in the positive photosynthetic rates under stressful conditions, we analyzed changes in the activity of two key Calvin cycle enzymes: Ribulose bisphosphate carboxylase oxygenase (Rubisco) and stromal Fructose-1,6-bisphosphatase after high light and low temperature treatments. Our results show that the activity of both enzymes does not decrease after 48 h high light/low temperature treatments, a feature usually observed in plants adapted to harsh environments. The activation state of both enzymes remained high throughout the treatments. This feature has been related to the redox state of the chloroplast, suggesting that both plants maintain their redox balance under high light and/or low temperature conditions assayed. Both plants differed in their responsiveness to cold acclimation as observed by gas exchange and enzymatic measurements. We propose that these differences may be related to microclimate adaptations to the environment they naturally develop in the Maritime Antarctic.

**Abbreviations** FBPase: Fructose-1,6-bisphosphatase Rubisco: Ribulose bisphosphate carboxylase oxygenase · AOS: Active oxygen species · PFD: Photon flux density · DTT: Dithiothreitol · Pn: Net photosynthesis

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## Introduction

Plants are continuously exposed to changes in temperature, light intensity, humidity, water availability and other environmental factors, which are known to affect their capability to use the energy absorbed from the sun. Environmental conditions that cause plants to absorb more energy than they can use result in a higher risk of over-reduction of the electron transport chain and, consequently, damage to the photosynthetic apparatus by active oxygen species (AOS) (Aro et al. 1993; Alscher et al. 1997). Plants rely on non-photochemical and photochemical protections, among other mechanisms, in order to withstand this energy imbalance (Horton and Ruban 2005). Non-photochemical protection is a fast response mechanism that involves dissipation of light energy as heat before photochemistry occurs (Muller et al. 2001; Niyogi et al. 2005; Zsabo et al. 2005). On the other hand, photochemical protection involves reactions related to the allocation of electrons from the photosynthetic electron transport chain and includes: photorespiration, the water–water cycle, cyclic electron transport around PSI and $CO_2$ assimilation (Niyogi 1999; Asada 2000; Badger et al. 2000; Wingler et al. 2000; Heber 2002; Johnson 2005).

Stressful environmental conditions often lead to a decrease in $CO_2$ assimilation and, consequently, to a higher risk of over-reduction of the photosynthetic electron transport. $CO_2$ assimilation in plants that develop under extremely harsh environments should be positive enough to sustain growth and, therefore, continue to be an important electron sink in conditions that are lethal to other plants. Among the most extreme environments are the Polar Regions, especially the Antarctic. This region has been colonized only by two

vascular plants, *Deschampsia antarctica* and *Colobanthus quitensis* (Xiong et al. 1999, 2000; Bravo et al. 2001; Alberdi et al. 2002; Smith 2003). They have been shown to survive and grow under conditions that promote an over-reduction of the electron transport chain such as low temperature and/or high light and maintain about 30% of their maximum photosynthetic rate at 0°C (Edwards and Smith 1988; Xiong et al. 1999). In order to explore the possible mechanisms responsible for this robust $CO_2$ assimilation machinery, changes in Ribulose bisphosphate carboxylase oxygenase (Rubisco) and fructose-1,6-bisphosphatase (FBPase) activities have been determined after high light and/or low temperature treatments and related to changes in $CO_2$ assimilation in these plants.

## Materials and methods

### Plant material and growth conditions

*Colobanthus quitensis* (Kunth) Bartl. (Caryophyllaceae) was collected in the vicinity of Artowsky Base in King George Island, Maritime Antarctic (62°14′S; 58°48′W) and *D. antarctica* (Poaceae) was collected in the Coppermine Peninsula on Robert Island, Maritime Antarctic (62°22′S; 59°43′W). Plants were reproduced vegetatively in plastic pots using a soil–peat mixture (3:1) and were fertilized with 0.12 g/l Phostrogen® (Solaris, Buckinghamshire, UK) once a week. Growth conditions were a photosynthetic photon flux density (PFD) of 100 μmol $m^{-2}$ $s^{-1}$ (cool-white fluorescent tubes F40CW, General Electric, Charlotte, NC, USA) at 15°C (100/15) at 18/6 h light/dark photoperiod. Plants were cold acclimated by exposure to 4°C for 21 days at 100 μmol $m^{-2}$ $s^{-1}$.

### Gas exchange measurements

Changes in $CO_2$ assimilation were measured with an IRGA (CIRAS-2 PP systems Hitchin, England). Photosynthetic light response curves were recorded every 5 min at 15 and 4°C between 0 and 1,600 μmol $m^{-2}$ $s^{-1}$ at a $CO_2$ concentration of 360 ppm. Photosynthetic $CO_2$ response curves were recorded every 10 min at 800 μmol $m^{-2}$ $s^{-1}$ and 15°C with $CO_2$ between 0 and 2,000 ppm for *D. antarctica* and 0 and 1,000 ppm for *C. quitensis*.

### Plant treatments

Samples were taken from non-acclimated plants exposed to low temperature (4°C) and/or high light (1,600 μmol $m^{-2}$ $s^{-1}$) for 0, 1, 3, 6, 12, 24 and 48 h and frozen in liquid nitrogen for later use. Cold-acclimated plants were exposed to high light and low temperature and samples were taken as above.

### Enzyme measurements

Rubisco activity was extracted and assayed according to Hurry et al. (1994). This assay follows NADPH oxidation measured spectrophotometrically at 340 nm. Total activity was achieved after incubation in 20 mM $MgCl_2$ and 10 mM $NaHCO_3$ for 10 min.

Stromal Fructose 1,6 bisphosphatase was extracted and assayed according to Holaday et al. (1992). This assay is coupled to NADP reduction measured spectrophotometrically at 340 nm. Total activity was achieved by incubation in 4 mM fructose-1,6-bisphosphate and 10 mM DTT for 10 min.

### Statistical analysis

Values reported correspond to the mean of three assays. Differences between values were determined by ANOVA analysis ($P < 0.05$). Three-way ANOVA was applied for light response curves with factors: PFD, temperature and acclimation treatment. Two-way ANOVA was used for $CO_2$ response curves with factors: $CO_2$ concentration and acclimation treatment. Three-way ANOVA was applied for Rubisco and sFBPase activities with factors: time, activation treatment and species.

## Results

Light response curves indicated that light compensation points for *C. quitensis* were very similar in non-acclimated and cold-acclimated plants at 15° and 4°C. On the other hand, *D. antarctica* showed higher light compensation points for non-acclimated plants at 15°C and very similar values at 4°C for plants before and after exposure to low temperature for 21 days (Table 1). Cold acclimation reduced $CO_2$ assimilation in *D. antarctica* up to 35% at light intensities higher than 400 μmol $m^{-2}$ $s^{-1}$ at 15°C ($P < 0.05$), meanwhile in *C. quitensis* differences were not statistically significant between 0 and 1,600 μmol $m^{-2}$ $s^{-1}$ ($P < 0.05$) (Table 1). Higher dark respiration rates were observed for *C. quitensis* after cold acclimation measured at 15°C, meanwhile *D. antarctica* showed lower or similar values ($P < 0.05$). Cold acclimation did not change the apparent quantum yield for *D. antarctica* measured at 4 and 15°C; on the other hand, apparent quantum yield for *C. quitensis* was consistently lower for cold-acclimated plants.

A versus Ci response curve showed higher photosynthetic rates in cold acclimated versus non-acclimated *D. antarctica* from 700 ppm onward ($P < 0.05$), meanwhile *C. quitensis* presented very similar values after cold acclimation (Fig. 1). The initial slope of A versus Ci curve in *D. antarctica* decreased about 50% after cold acclimation, meanwhile it was not statistically different for *C. quitensis* after the same conditions ($P < 0.05$).

**Table 1** Photosynthetic parameters of light reponse curves in Antarctic vascular plants

| Plant | Treatment | AQY | $A_{max}$ (μmol $m^{-2}$ $s^{-1}$) | DR (μmol $m^{-2}$ $s^{-1}$) | LCP (μmol $m^{-2}$ $s^{-1}$) |
|---|---|---|---|---|---|
| *D. antarctica* | 15 NA | 0.035 ± 0.003 | 6.1 ± 0.5 | 3.4 ± 0.2 | 40 ± 4 |
| | 15 CA | 0.034 ± 0.002 | 4.0 ± 0.4 | 0.7 ± 0.4 | 10 ± 3 |
| | 4 NA | 0.040 ± 0.002 | 4.6 ± 0.2 | 3.3 ± 0.5 | 50 ± 5 |
| | 4 CA | 0.038 ± 0.007 | 2.9 ± 0.4 | 2.3 ± 0.8 | 50 ± 3 |
| *C. quitensis* | 15 NA | 0.034 ± 0.003 | 8.9 ± 1.8 | 1.1 ± 0.2 | 45 ± 4 |
| | 15 CA | 0.051 ± 0.004 | 10.4 ± 2.1 | 3.4 ± 0.4 | 48 ± 3 |
| | 4 NA | 0.041 ± 0.002 | 2.3 ± 0.2 | 7.5 ± 0.3 | 200 ± 7 |
| | 4 CA | 0.056 ± 0.005 | 2.5 ± 0.1 | 11.0 ± 1.2 | 200 ± 5 |

Values reported correspond to the mean of 3 measurements ± their SE
*AQY* apparent quantum yield, $A_{max}$ maximum $CO_2$ assimilation rate, *DR* dark respiration rate, *LCP* light compensation point, *15 NA* 15°C non-acclimated, *15 CA* 15°C cold acclimated, *4 NA* 4°C non-acclimated, *4 CA* 4°C cold acclimated

Rubisco activity proved to be higher in *D. antarctica* than in *C. quitensis* at low temperature and high light conditions ($P < 0.05$) (Fig. 2). In both plants, Rubisco activity increased in response to high light intensity at 15°C ($P < 0.05$) (Fig. 2c, d). However, this effect was suppressed by low temperature (Fig. 2e, f). Although values obtained at high light and low temperature were similar in both plants, they represented an increase of 54 and 350% for *D. antarctica* and *C. quitensis,* respectively. In general, maximum activity obtained after carbamylation in vitro with $CO_2$ and $Mg^{2+}$ was very close to untreated values, which indicates conservation of a high activation state throughout most conditions. High light and 15°C treatments increased potential Rubisco activity in both plants and resulted in an actual activity increase within 48 h ($P < 0.05$).

Cold acclimation did not change Rubisco activity significantly in *C. quitensis*. In contrast, *D. antarctica* showed a 60% diminishment under the same conditions. Control values of Rubisco activity and its activation state remained similar for 48 h in non-acclimated and cold-acclimated plants exposed to low light intensity (data not shown).

sFBPase activity proved to be relatively stable in both plants throughout high light and/or low temperature treatments (Fig. 3). In *D. antarctica*, exposure to low temperature and low light was the only condition that resulted in a non-transient increase in sFBPase activity after 48 h ($P < 0.05$) (Fig. 3a), meanwhile in *C. quitensis* it remained virtually constant at all conditions (Fig. 3b, d, f, h). Activity measured after incubation with 4 mM fructose-1,6-bisphosphate and 10 mM DTT corresponds to the potential activity of this enzyme (100% activation) and it is used to calculate its activation state. High light and low temperature caused a drop in the sFBPase activity after full activation in both plants ($P < 0.05$). However, actual sFBPase values remained stable by increasing the activation state of the enzyme from around 50 to 100% within 48 h. In general, sFBPase activity was higher in *D. antarctica* than in *C. quitensis* except after cold acclimation when both plants had similar values.

## Discussion

Positive photosynthetic rates under harsh environmental conditions are considered one of the features that allow *C. quitensis* and *D. antarctica* to survive in the Antarctic environment (Edwards and Smith 1988; Xiong et al. 1999). In order to understand the mechanisms involved in the robust photosynthetic performance of these plants under stress, we analyzed changes in Pn, activity and activation state of two regulatory enzymes of the Calvin

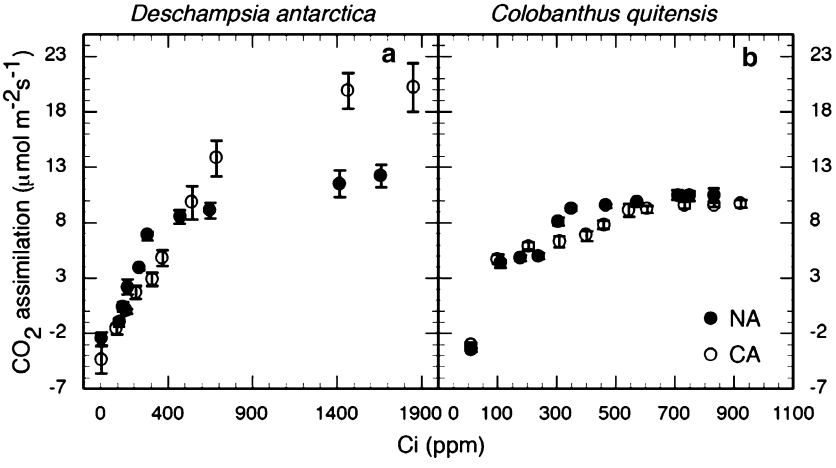


**Fig. 1** $CO_2$ response curves in non-acclimated (*NA*) and cold acclimated (*CA*) Antarctic vascular plants at 15°C and 800 μmol $m^{-2}$ $s^{-1}$ PFD. *Symbols* equal the mean of three measurements and *bars* correspond to the standard error

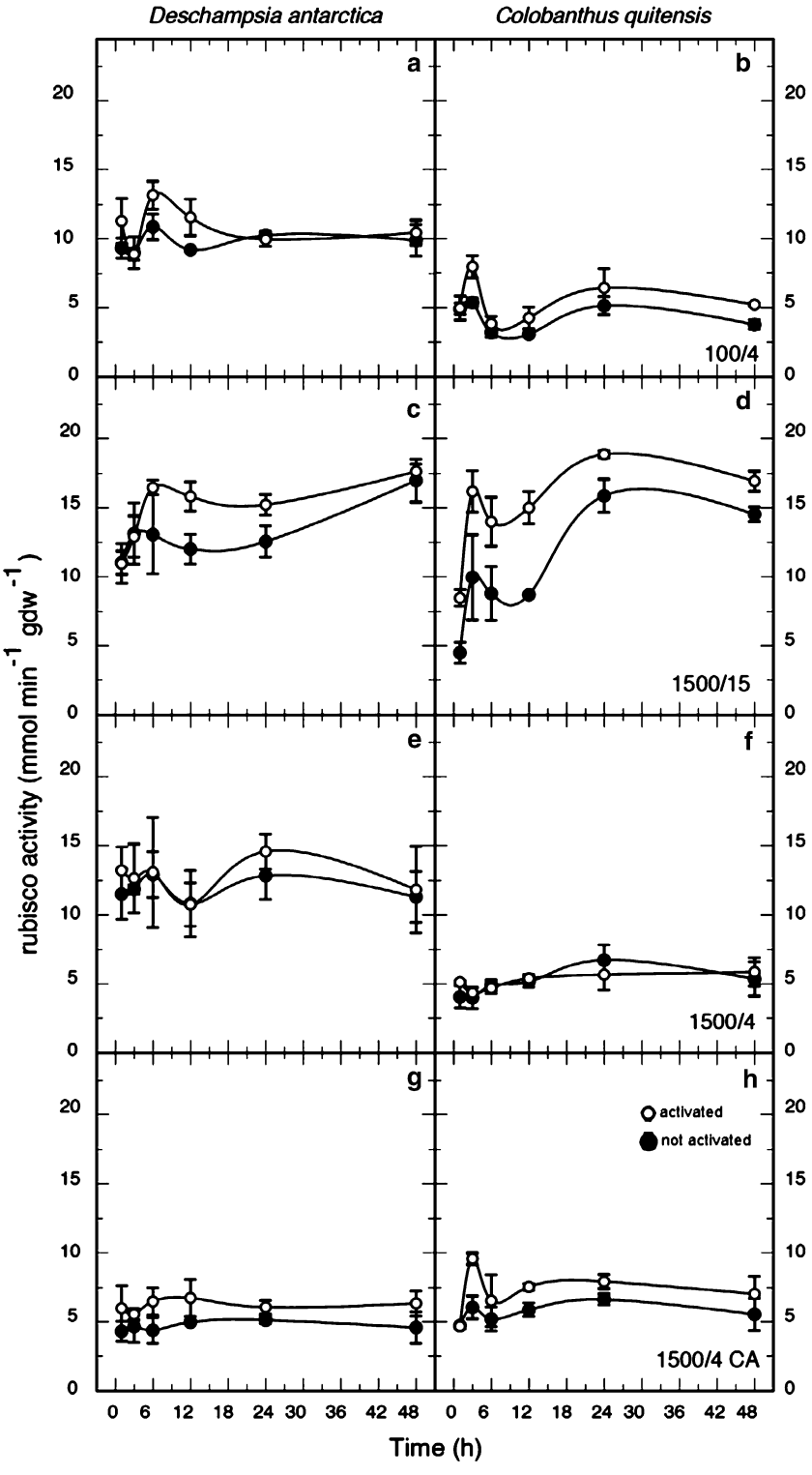


**Fig. 2** Rubisco activity in Antarctic vascular plants. Graphs **a** and **b** correspond to values after low light and low temperature treatment (100/4). Graphs **c** and **d** correspond to values after high light and 15°C (1,500/15). Graphs **e** and **f** correspond to values after high light and low temperature treatment (1,500/15). Graphs **g** and **h** correspond to values for cold-acclimated plants after high light and low temperature treatment (1,500/4 CA). Activated values correspond to activity measured after incubation with 20 mM $MgCl_2$ and 10 mM $NaHCO_3$ for 10 min. *Symbols* equal the mean of three measurements and *bars* correspond to the standard error

cycle: Rubisco and stromal FBPase under high light and/or low temperature conditions. Light and A versus Ci response curves were determined in order to get a general overview of photosynthetic changes induced by cold acclimation and high light/low temperature stress in these plants. Cold acclimation changed light response curves in both plants. In general, dark respiration rates in *C. quitensis* were higher than *D. antarctica* suggesting a greater demand for respiratory energy in the caryophyllaceae, specially when acclimated to low temperature. Apparent quantum yield was consistently higher in *C. quitensis* after cold acclimation, suggesting changes in the efficiency of light utilization for carbon fixation. However, since apparent quantum yield is based on

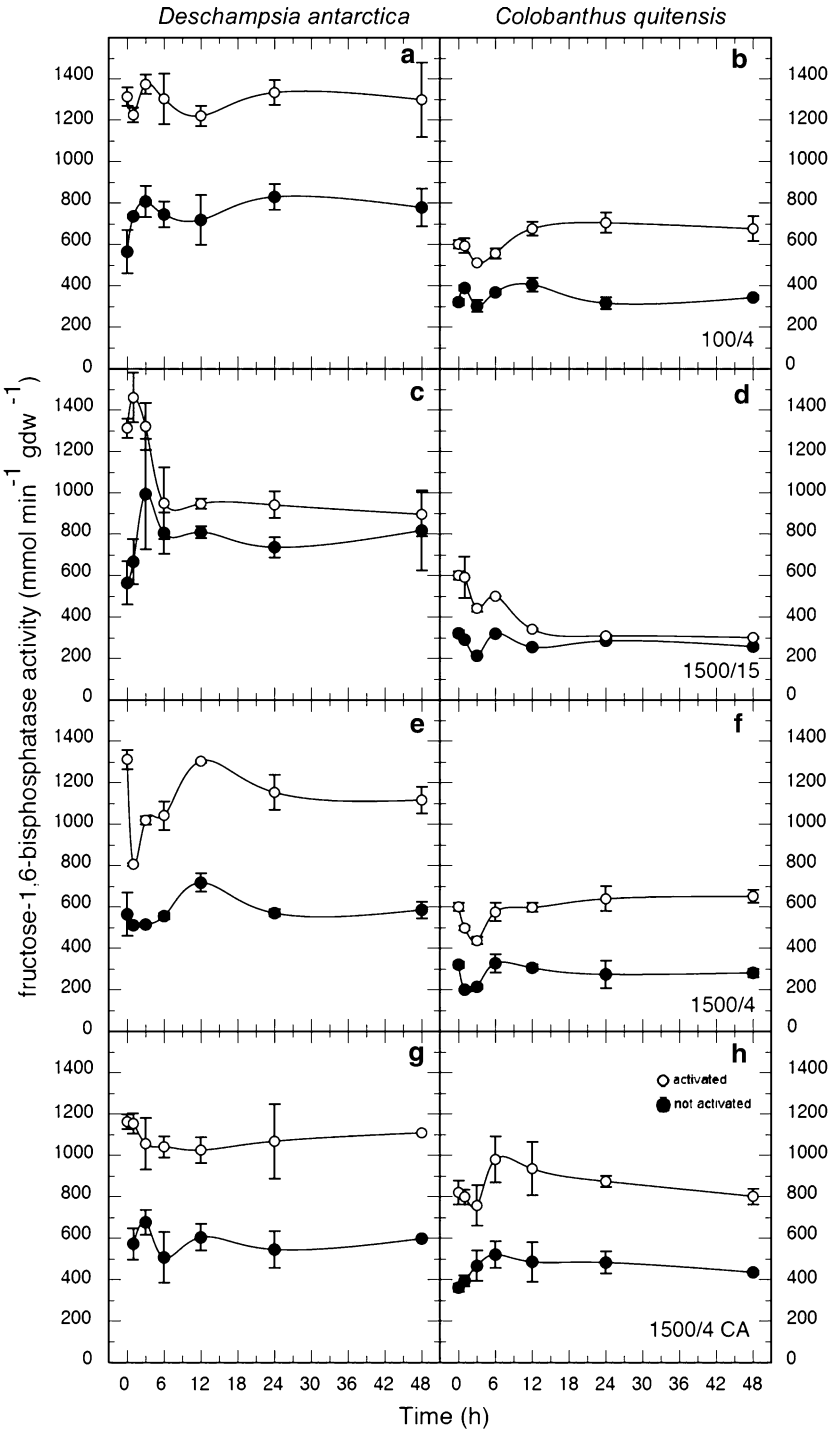


**Fig. 3** Stromal fructose-1,6-bisphosphatase activity in Antarctic vascular plants. Graphs **a** and **b** correspond to values after low light and low temperature treatment (100/4). Graphs **c** and **d** correspond to values after high light and 15°C (1,500/15). Graphs **e** and **f** correspond to values after high light and low temperature treatment (1,500/4). Graphs **g** and **h** correspond to values for cold-acclimated plants after high light and low temperature treatment (1,500/4 CA). Activated values correspond to activity measured after incubation in 4 mM fructose-1,6-bisphosphate and 10 mM DTT for 10 min. *Symbols* equal the mean of three measurements and *bars* correspond to the standard error

incident light, changes in chlorophyll concentration may be responsible for this observation. Light compensation points between non-acclimated and cold-acclimated plants were dissimilar only for *D. antarctica* at 15°C, which is probably related to the very low dark respiration rates observed after cold acclimation in this plant at 15°C. In general, *C. quitensis* showed higher Pn values than *D. antarctica* at 15°C, meanwhile at 4°C values they were similar in both plants. Cold-resistant plants grown at low temperature may increase or decrease their maximum photosynthetic rates compared to plants grown at their optimum temperature. Consequently, this phenomenon has been reported to be cultivar and species dependent (Boese and Huner 1990; Hurry and Huner 1991; Öquist and Huner 1993).

Cold acclimation resulted in higher photosynthetic rates above 700 ppm internal $CO_2$ in *D. antarctica*. It is known that assimilation rates at high $CO_2$ levels may be limited by sucrose synthesis, linear electron transport and Rubisco activity among other factors. Sucrose

phosphate synthase (SPS), an important regulatory enzyme of the sucrose biosynthetic pathway, increases its activity along with sucrose content in *D. antarctica* after cold acclimation (Zuñiga-Feest et al. 2005). It is likely that sucrose synthesis is less limiting in *D. antarctica* after cold acclimation and allows a better use of high $CO_2$ levels, as it has been proposed for other plants (Badger et al. 1982; Huner et al. 1986; Maruyama et al. 1990). This may explain higher assimilation rates observed for *D. antarctica* even though Rubisco activity decreased after cold acclimation.

Salvucci and Crafts-Brandner (2004) reported that the activation state of Rubisco in *D. antarctica* is around 100% within moderate to low temperature. This observation is in agreement with our results. We additionally show that this activation state is maintained throughout high light and/or low temperature conditions. Similar results were observed in *C. quitensis* suggesting that a high activation state of Rubisco is a common feature among Antarctic vascular plants. Activation state of Rubisco has been reported to be the function of light intensity, temperature and other environmental factors. Values reported for other plants in control conditions are: 90% in tobacco and cotton (Crafts-Brandner and Salvucci 2000); from 44 to 75% in pea under 100 and 1,000 μmol $m^{-2}$ $s^{-1}$, respectively (Harbinson et al. 1990); from 60 to 80% in barley under 280 and 1,400 μmol $m^{-2}$ $s^{-1}$, respectively (Dujardyn and Foyer 1989); 100% in creosote bush leaves at 1,800 μmol $m^{-2}$ $s^{-1}$ (Salvucci and Crafts-Brandner 2004); 80% in tobacco at 1,000 μmol $m^{-2}$ $s^{-1}$ (Ruuska et al. 2000). Rubisco activase, an enzyme involved in Rubisco activation, is known to have a relatively low temperature optimum and is considered very labile to moderate–high temperatures (Robinson and Portis 1989; Crafts-Brandner et al. 1997). On the other hand, in vitro Rubisco deactivation has been shown to increase with temperature (Crafts-Brandner and Salvucci 2000). Both affirmations may partially explain the high activation state observed by Antarctic vascular plants in our experiments.

Rubisco activity was responsive to high light at 15°C in both plants by increasing its maximum and actual activity within 48 h. However, this process seemed to be inhibited by low temperature. Differences between potential and actual Rubisco activities were only observed during the first hours of high light and 15°C treatments, probably reflecting a time lag of adjustment to this new condition.

Cold acclimation has been shown to cause variable effects in Rubisco activity (Morris and Farrel 1971; Chabot et al. 1972; Markus et al. 1981; Lawlor et al. 1987a, b; Hahn and Walbot 1989; Maruyama et al. 1990; Holaday et al. 1992). Antarctic plants are no exception as Rubisco activity lowered after 21 days at 4°C in *D. antarctica*, meanwhile it remained unaltered in *C. quitensis*. The initial slope of A versus Ci curves is considered an indicator of Rubisco activity in vivo (Long and Bernacchi 2003) and was in agreement with changes in Rubisco activity by enzyme kinetics in both Antarctic vascular plants after cold acclimation.

Stromal FBPase catalyzes the irreversible reaction of fructose-1,6-bisphosphate to fructose-6-phosphate and Pi and constitutes a key regulation point in the $CO_2$ assimilation pathway (Chueca et al. 2002). In Antarctic vascular plants, non-transient variations in the activation state of sFBPase were observed only at high light and 15°C and involved a drop in the potential activity, meanwhile actual activity remained stable. sFBPase has been shown to be susceptible to $H_2O_2$ as stated by Charles and Halliwell (1981); however, it is unlikely that it is responsible for our results because both plants, especially *D. antarctica*, have been previously shown to have a high antioxidant activity in these conditions (Pérez-Torres et al. 2004a, b). Besides, similar or more intense changes would have been observed after high light and low temperature treatments, since they are known to impose a greater oxidative stress.

*D. antarctica* presented higher sFBPase activity than *C. quitensis* in non-acclimated conditions, meanwhile values were very similar in cold-acclimated plants. As observed with cold acclimation effects on Rubisco activity, sFBPase activity in *D. antarctica* seems to be more responsive than *C. quitensis*. The fact that cold acclimation does not increase sFBPase activity in *D. antarctica* may be related to the key regulatory role of this enzyme in the destination of photoassimilated carbon either to starch or to sucrose synthesis. This plant is known to accumulate high levels of sucrose (Zuñiga-Feest et al. 2005) and higher stromal FBPase levels may involve lower exportation of triosesphosphate to the cytosol and consequently affect sucrose synthesis.

Low temperature for 48 h did not cause important changes in sFBPase activity as has been shown in chilling susceptible plants (Sassenrath et al. 1990). The stability of sFBPase activity in Antarctic vascular plants subjected to high light and low temperature treatments might be partially responsible for positive $CO_2$ assimilation rates observed even at 0°C (Xiong et al. 1999). Stromal FBPase activity is regulated by thioredoxins (Trxs), specifically Trx f, which is also involved in the regulation of other photosynthetic enzymes (Kamo et al. 1989; Lepiniec et al. 1992; Jacquot et al. 1997). The stability demonstrated by stromal FBPase activity throughout most conditions suggests that the redox state of the chloroplast remains mostly unaltered under these circumstances. However, further measurements of chloroplast of NADP–MDH activity and its activation state would be necessary to sustain this hypothesis because of its important role in the transport of reducing equivalents between the chloroplast and the cytosol (Scheibe 2004).

Higher Rubisco and sFBPase activity in *D. antarctica* than in *C. quitensis* did not imply higher Pn values at 15°C, which indicates that there are other limiting steps for $CO_2$ assimilation.

In general, it was observed a higher responsiveness at the level of Calvin cycle activity in *D. antarctica*

compared to *C. quitensis*. This may be related to different microclimate adaptations of these plants. It is known that, in the Maritime Antarctic, *C. quitensis* grows in more protected areas than *D. antarctica* (Alberdi et al. 2002). Plants adapted to grow in more stable environments are suggested to be less responsive to changes in growing conditions. Our results suggest that the robustness of photosynthesis reported for Antarctic vascular plants is related to the stability of the Calvin cycle to high light and low temperature conditions.

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