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ORIGINAL PAPER

Deschampsia antarctica Desv. primary photochemistry performs differently in plants grown in the field and laboratory

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Abstract Primary photochemistry of photosystem II (F_v/F_m) of the Antarctic hair grass *Deschampsia antarctica* growing in the field (Robert Island, Maritime Antarctic) and in the laboratory was studied. Laboratory plants were grown at a photosynthetic photon flux density (PPFD) of 180 μmol m^{-2} s^{-1} and an optimal temperature (13 ± 1.5°C) for net photosynthesis. Subsequently, two groups of plants were exposed to low temperature (4 ± 1.5°C day/night) under two levels of PPFD (180 and 800 μmol m^{-2} s^{-1}) and a control group was kept at 13 ± 1.5°C and PPFD of 800 μmol m^{-2} s^{-1}. Chlorophyll fluorescence was measured during several days in field plants and weekly in the laboratory plants. Statistically significant differences were found in F_v/F_m (=0.75–0.83), F_0 and F_m values of field plants over the measurement period between days with contrasting irradiances and temperature levels, suggesting that plants in the field show high photosynthetic efficiency. Laboratory plants under controlled conditions and exposed to low temperature under two light conditions showed significantly lower F_v/F_m and F_m. Moreover, they presented significantly less chlorophyll and carotenoid content than field plants. The differences in the performance of the photosynthetic apparatus between field- and laboratory-grown plants indicate that measurements performed in ex situ plants should be interpreted with caution.

Keywords Antarctic plants · Chlorophyll *a* fluorescence · Quantum yield of PSII primary photochemistry · Photoinhibition · Pigments · OJIP-test

Abbreviations

F_v/F_m	Primary photochemical efficiency of PS II
F_m	Maximum fluorescence
F_v	Variable fluorescence
F_0	Minimum fluorescence
PS II	Photosystem II
LT	Low temperature treatments
LT-180	Low temperature + PPFD of 180 μmol m^{-2} s^{-1}
LT-800	Low temperature + PPFD of 800 μmol m^{-2} s^{-1}
FP	Field plants
CO-180	13°C + PPFD of 180 μmol m^{-2} s^{-1}

Introduction

The Antarctic continent offers extreme environmental conditions to all forms of life; 98% of its total surface is covered by ice. The limited ice-free zones available for the establishment of plant communities are characterized by adverse factors such as low temperatures, aridity, short day

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length, repeated freezing–thawing cycles, turbulent winds, cryoturbation of soils and low nutrient availability. Despite these harsh abiotic conditions, certain fauna and flora have established and developed the capacity to cope with the limits set to their biological activities. Along the latitudinal gradient, there is a marked difference in richness and abundance of plants and lichens between the Maritime and Continental Antarctic (Kennedy 1993, 1999). Dominant groups are lichens and mosses (Ochyra 1998). Only two vascular plant species are currently known to grow in the Maritime Antarctic, viz.: *Deschampsia antarctica* Desv. and *Colobanthus quitensis* (Kunth) Bartl. (Moore 1970; Komárková et al. 1985, 1990). Since access to the Antarctic is limited, few ecological and physiological studies of these plants have been performed in situ. Changes in distribution and size structure of tussocks of a population of *D. antarctica* show that this species is still expanding in the Maritime Antarctic (Smith 1994; Casaretto et al. 1994; Geringhausen et al. 2003; Smith 2003). These authors found that on King George Island, the number of individuals and populations has been increasing during the last two decades and suggest that this phenomenon is a response to global warming. Most of the physiological information on the photosynthetic performance of this species at low temperature has been obtained from laboratory experiments (Bravo et al. 2001; Alberdi et al. 2002). It has been shown that *D. antarctica* is able to maintain about 30% of the maximum photosynthesis at 0°C (Xiong et al. 1999), exhibiting a very robust carbon assimilation capacity at low temperature and high irradiance (Perez-Torres et al. 2006). It can also maintain high levels of primary photochemistry even at low temperature and high irradiance, probably due to an efficient water cycle and ROS scavenging system (Perez-Torres et al. 2004). Whether *D. antarctica* is also able to maintain its photosynthetic performance in the field has not yet been clearly shown.

Performing ecophysiological experiments with plants from extreme environments in the laboratory guarantees their long-term availability and allows precise adjustment of the variables to be tested. This applies especially to Antarctic plants, the natural locations of which are of limited access due to logistic and climatic restrictions. Although it seems trivial to state that results obtained from laboratory experiments may not faithfully reflect the performance of the same organism in situ, very few studies of plants in polar environments have compared the same species under laboratory and field conditions. Therefore, we analyzed the photochemical response of *D. antartica* in situ and compared it with data obtained from plants growing under controlled growth conditions and after low temperature treatments in the laboratory.

Materials and methods

Study area and sampling

Field work was carried out during the XXXII Research Expedition of the Instituto Antártico Chileno (INACH) during January 1996, and the subsequent laboratory studies were performed in Valdivia, Chile during the same year. The study area was located on Robert Island (South Shetland Islands, Maritime Antarctic, 62°22′S, 59°43′W), where the presence of *D. antarctica* had been reported by Casaretto et al. (1994). Plants usually grow in isolated small tussocks, less than 10 cm in diameter. Individuals were randomly selected from tussocks in January for in situ measurements of fluorescence parameters and pigment contents, as described below. Another group of plants was extracted and transported by air in plastic bags to the Plant Physiology Laboratory at the Universidad Austral de Chile, Valdivia (Chile), for cultivation in climate chambers at different temperatures (see below). Photosynthetic photon flux density (PPFD) and air temperatures at Robert Island were measured during January (1996) with a data logger (LICOR, Lincoln, USA). Microclimatic conditions on Coppermine Peninsula on Robert Island during January are shown in Fig. 1. Maximum air temperatures were above 5°C during the warmer months when only on few days temperatures sank below 0°C (Fig. 1). Average monthly air temperature was ca. 4.3°C. Maximum PPFD varied between ca. 1,800 μmol photons m^{-2} s^{-1} on a clear day (14 January 1996) to ca. 130 μmol m^{-2} s^{-1} on a cloudy day (29 January 1996) (Fig. 1a). At least on 14 days, radiation was over 500 μmol m^{-2} s^{-1}.

Growth conditions of laboratory plants

Plants of *D. antarctica* from Robert Island were pot-cultured immediately after extraction. After transport to the laboratory, they were grown in a Sigma Scientific growth chamber at 13 ± 1.5°C, the optimal temperature for net photosynthesis according to Edwards and Smith (1988), and a PPFD of ca. 180 μmol photons m^{-2} s^{-1} at the upper plant canopy, provided by cool white fluorescent tubes (Sylvania/GTE, Danvers, MA, USA). Plants grew at 16/8 h light/dark periods and 65–70% relative humidity. The substrate was a mixture of organic soil and peat (3:2 w/w) simulating the natural substrate. Plants were irrigated every 3 days at 80% field capacity with water or nutrient solution (Phostrogen 0.12 g/l). The experiments were started after 2 months when plants had reached a height of about 10 cm. Plants under these growing conditions are referred to as controls.

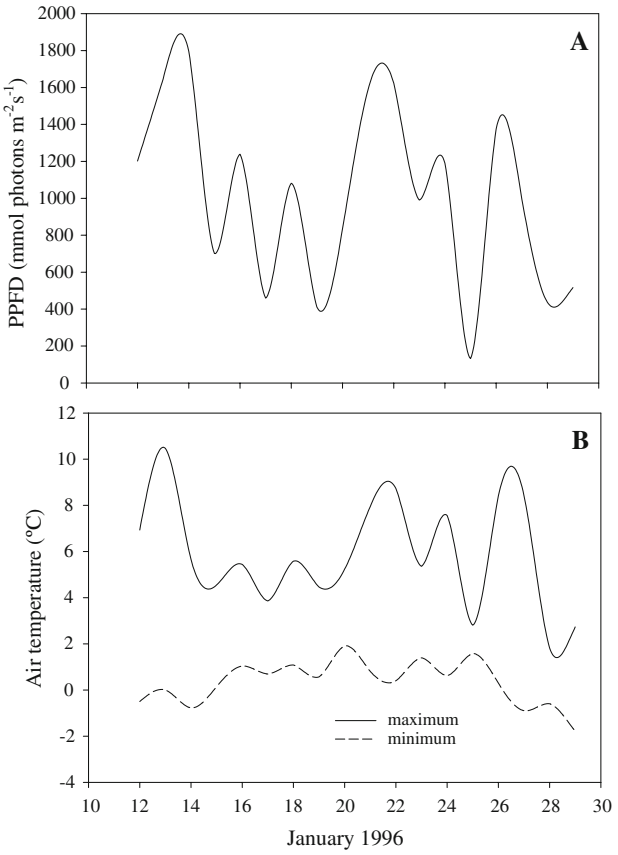

Fig. 1 Daily course of light and temperature at the study site (Robert Island, Maritime Antarctic) during January 1996. **a** Photosynthetic photon flux density (PPFD, µmol photons m^{-2} s^{-1}). **b** Air temperatures (°C)

Low temperature exposure of laboratory plants at two different light levels

Two groups of 30 plants, grown at control conditions, were transferred to another growth chamber for a long-term low temperature (LT) treatment at 4 ± 1.5°C under 180 µmol photons m^{-2} s^{-1} (LT-180) and 800 µmol photons m^{-2} s^{-1} (LT-800); control plants were left to grow under their original conditions. Long-term exposure to high light intensity was carried out with a halogen lamp (1000 W-halogen, General Electric Co., Fairfield, CT) mounted above a cooling chamber, which was conditioned to maintain leaf temperature at 4 ± 1.5°C. To avoid excessive warming on the system, a water filter was placed between the lamp and the chamber. Light intensity was measured with a PAR sensor. Another group of plants was kept at 13 ± 1.5°C and with 800 µmol photons m^{-2} s^{-1} (CO-800) as control for the LT-800 plants. All other conditions were the same as mentioned above for control plants. During this treatment, which lasted for 21 days, chlorophyll *a* fluorescence curves were measured every week in all groups. At the end of the treatment, leaves were removed for measurement of photosynthetic pigment content.

Chlorophyll *a* fluorescence measurements

In the field, Chlorophyll *a* fluorescence parameters were measured at noon during several days in January 1996. In laboratory plants (control and cold-exposed plants), the measurements were performed 2 h after the start of the photoperiod. During the dark adaptation of leaves, plants were kept inside the climate chamber. In the field, fluorescence was measured daily in intact attached leaves after dark adaptation (15 min) of four different tussocks, whereas in the laboratory, four pots with one tussock each (2.5-cm diameter; 10-cm high) were used. Measurements were carried out with a portable Plant Efficiency Analyzer (PEA, Hansatech Instrument Ltd., Norfolk, UK) with a light intensity of about 3,000 µmol m^{-2} s^{-1} provided by an array of six light-emitting diodes (peak at 650 nm) focused onto the sample (4 mm diameter) to provide homogeneous illumination over the exposed area. The fluorescence signal was detected by a PIN-photodiode associated with an amplifier circuit. Fluorescence transients were recorded at a time span of 2 s with a data acquisition rate of 10 µs for the first 2 ms and with 12 bits of resolution. Maximum (F_m) and minimum (F_0) fluorescence, and the primary photochemical efficiency of PS II (F_v/F_m) were recorded.

Chlorophyll and carotenoid determination

Chlorophyll (Chl) and carotenoid (car) contents were determined from extracts in 80% acetone at 0°C. The extracted pigments were spectrophotometrically measured at 663, 646 and 470 nm (Lichtenthaler and Wellburn 1983).

Statistics

One-way ANOVA was applied to test for significant differences between the fluorescence parameters measured in the field. Three-way ANOVA was applied for the comparison between the laboratory plants grown at different light and temperature levels. Dependent variables were the fluorescence parameters versus three independent variables (light levels, time of exposure and temperature treatments). For the pigment analysis, one-way ANOVA was used; when ANOVA indicated a significant effect at $P \leq 0.05$, a Tukey a posteriori test was applied.

Results

In the field, significant differences in the maximum quantum yield of PS II (F_v/F_m) were observed in leaves of *D. antarctica* between days with values within the physiological range (0.7–0.85) (Björkman and Demmig 1987). During the daily cycle, no significant differences among

morning, noon and afternoon were measured (inset Fig. 2c).

According to the fluctuation of F_v/F_m between days, we registered changes in light intensity, which oscillated daily with values over 1,000 µmol photons m^{-2} s^{-1} (Fig. 2a). Concomitantly, high values of maximum canopy temperature were registered at 14:30 hours when fluorescence measurements were carried out (Fig. 2b). The canopy temperature fluctuated from 5°C to about 18°C during the study (Fig. 2b), and values were frequently decoupled from air temperature (Figs. 1, 2b). Both, minimum and maximum fluorescence levels, showed significant differences in field plants (Fig. 2d; Table 1). F_0 levels were high at increased levels of PPFD, and fluorescence intensity values fluctuated between 480 and 730 (relative units), being negatively correlated with F_v/F_m ($r^{-2} = -0.745$, $P < 0.013$).

After long-term growth under controlled conditions, control plants (CO-180) showed a low level of total chlorophyll and carotenoid contents compared to field plants, with the total chlorophyll levels being 11.7 µg cm^{-2} in CO-180 and 18.0 µg cm^{-2} in FP, respectively (Fig. 3). Moreover, between the laboratory-grown plants, the lowest values (about 40–60%) of total chlorophyll content were found in plants exposed to low temperature during 3 weeks in LT-180 (9.6 ± 0.3 µg cm^{-2}) and LT-800 (7.2 ± 0.4 µg cm^{-2}). Accordingly, the carotenoid content fluctuated between 1.7 and 2.7 µg cm^{-2} in plants growing under control and LT conditions, with the highest ratios of Chl/car in the CO-180 and LT-180 groups. Interestingly, in field plants, Chl *a*/*b* ratios were the lowest in all plants groups (Fig. 3).

Photosynthetic efficiency expressed as F_v/F_m values in dark-adapted control plants (CO-180) showed similar values as in field plants (Figs. 2c, 4a). After transferring plants from control conditions (CO-180) to high light intensity (CO-800) and to long-term low-temperature treatment (4 ± 1.5°C), either at 180 or 800 µmol m^{-2} s^{-1} of PPFD, a slight, but significant ($P \leq 0.041$), decrease of F_v/F_m was found also for the factors light level ($P \leq 0.001$) and for the combined effect of light and low temperature ($P \leq 0.001$) (Fig. 3a), with 4% of variation in F_v/F_m between LT-180 and LT-800 plants. Moreover, the strongest significant decrease of F_m values was observed in plants under saturating light conditions (800 µmol m^{-2} s^{-1} of PPFD) both at 13 ± 1.5 and 4 ± 1.5°C. However, no marked changes were observed in F_0 values in these groups.

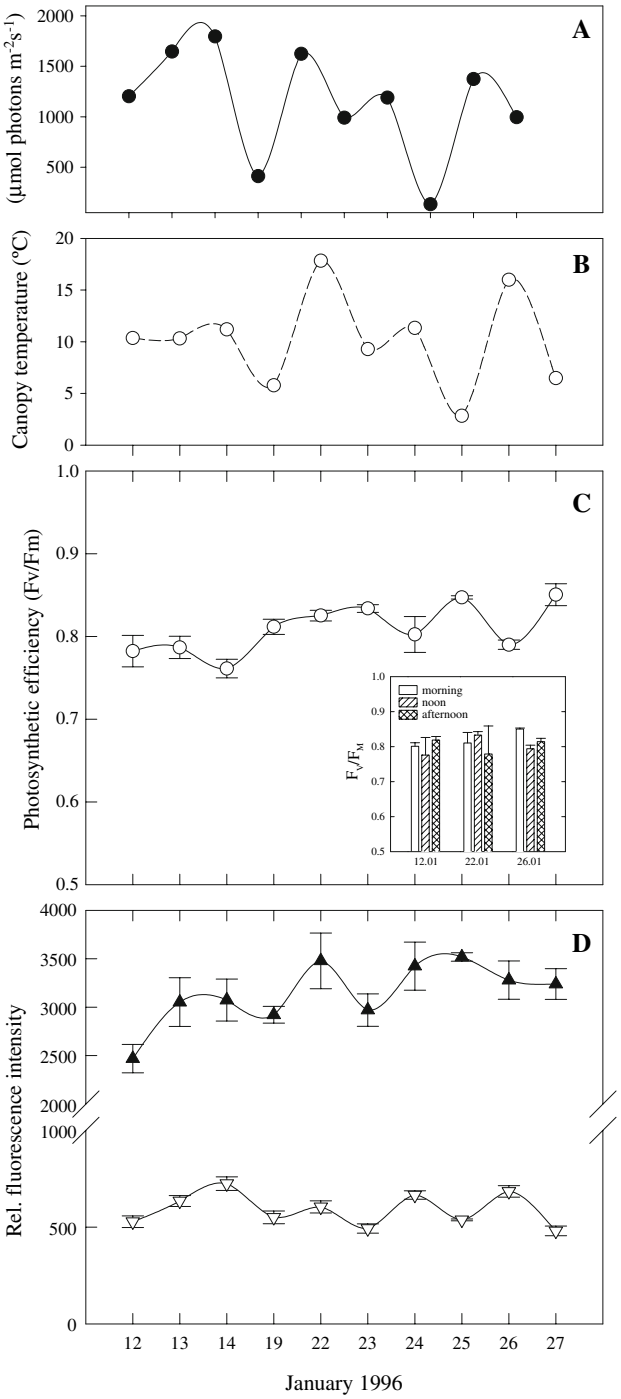

Fig. 2 Photosynthetic efficiency of *D. antarctica* in the field during different days in January 1996 in relation to microclimatic parameters. Chl fluorescence was measured in dark-adapted leaves. **a** Photosynthetic photon flux density (PPFD, µmol photons m^{-2} s^{-1}). **b** Maximum canopy temperatures (°C). **c** Maximum quantum yield of primary photochemistry of PSII (F_v/F_m). **d** Maximum (F_m) and minimum (F_0) fluorescence intensity. Values are means of four different individual tussocks ($n = 4$ + SE) measured daily

Discussion

We found high photosynthetic efficiency at a stable level in *D. antarctica* growing in the field during the relatively good weather conditions of the Antarctic summer (January 1996), not only between days but also throughout the daily cycle (Fig. 2c). Canopy temperature was not correlated with the efficiency of photosystem II in the field, as temperature is not a limiting factor for photosynthetic activity

Table 1 Results of ANOVA for the fluorescence parameters measured during different days in field plants of *D. antarctica*

Source	*df*	*F*	*P* values
F_0			
Between groups	9	7.28	0.0001
Within groups	33		
F_m			
Between groups	9	2.35	0.0359
Within groups	33		
F_v/F_m			
Between groups	9	4.54	0.0006
Within groups	33		

F_0 minimum fluorescence, F_m maximum fluorescence, F_v/F_m photosynthetic effciciency

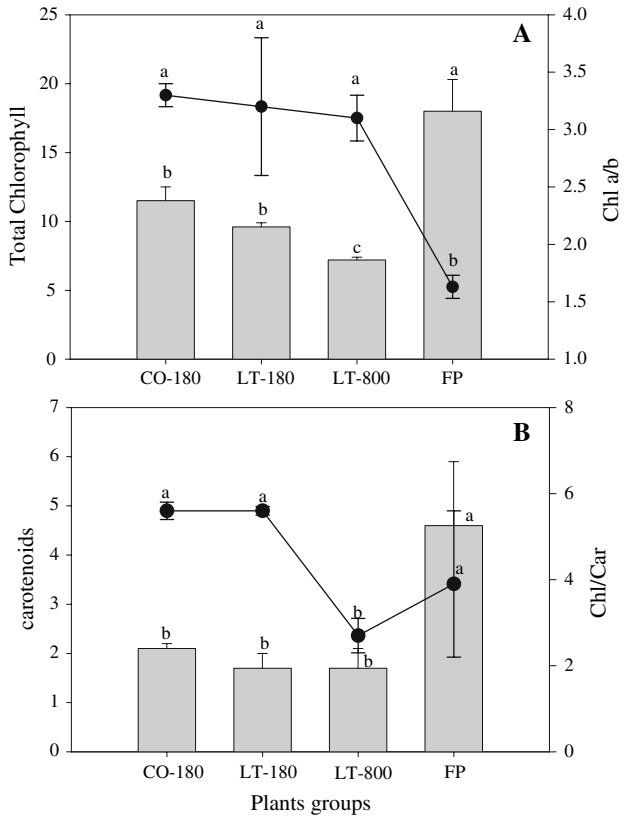

Fig. 3 Pigment contents in plants growing in the field and in the laboratory. **a** Total chlorophyll contents (mg cm^{-2}) and chlorophyll *a*/*b* ratio. **b** Carotenoid contents (mg cm^{-2}) and carotenoids/total chlorophyll ratios. *CO-180* control plants grown at 13 ± 1.5°C and 180 µmol m^{-2} s^{-1}, *LT-180* and *LT-800* after 3 weeks exposure to low temperature (4 ± 1.5°C) at two PPFD levels, 180 and 800 µmol m^{-2} s^{-1}. *FP* field plants. Values are means of different plants ($n = 4 \pm$ ES) in three independent experiments in the case of laboratory plants and for 3 days in field plants. *Different letters* indicate significant differences according to Tukey test

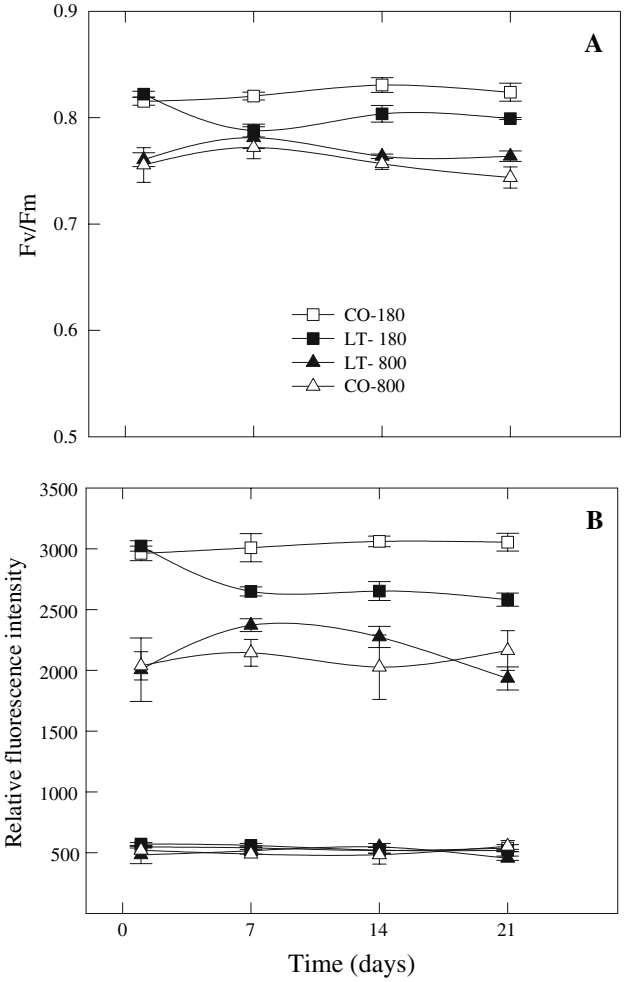

Fig. 4 Fluorescence parameters in *D. antarctica* growing under controlled conditions. **a** Maximum quantum yield of primary photochemistry of PSII (F_v/F_m) of dark-adapted plants. **b** Minimum (F_0) and maximum (F_m) fluorescence intensity. *CO-180* grown at 13 ± 1.5°C and 180 µmol m^{-2} s^{-1}, *CO-800* grown at 13 ± 1.5°C and 800 µmol m^{-2} s^{-1}, *LT-180/LT-800* after 3 weeks exposure to low temperatures (4 ± 1.5°C) under two PPFD levels: 180 and 800 µmol m^{-2} s^{-1}. *FP* field plants. Values are means of $n = 4 \pm$ ES

according to several authors (Edwards and Smith 1988; Montiel et al. 1999; Xiong et al. 1999). Few field studies have shown canopy temperature under Antarctic conditions, although it can be considerably higher than air temperature. We measured maxima up to 18°C (Figs. 1b, 2b). Edwards and Smith (1988) found even higher values and demonstrated that canopy temperatures can be strongly dependent on water conditions, being higher at dry sites (30–40°C) than at moist sites (10–20°C). It is therefore not surprising that canopy temperatures may also deviate considerably from the minimum temperatures registered at weather stations (Edwards and Smith 1988; Larcher 1995),

which may lead to the erroneous conclusion that *D. antarctica* is not photoinhibited under low air temperature and high irradiation.

F_v/F_m was negatively correlated with high light intensity (PPFD >1,000 μmol photons m^{-2} s^{-1}, Fig. 2a), a condition which often prevailed during those days when weather conditions allowed fluorescence measurements. Slight decreases in F_v/F_m were correlated with the increase in minimum fluorescence (F_0), which was higher during days with high light intensity (Fig. 2d). Even more, considering the 3 days when the canopy temperature was near 5°C (19, 25 and 27 June), F_v/F_m showed the highest values, even at light intensity of ca. 1,000 μmol photons m^{-2} s^{-1} (Fig. 2c). This finding is in concordance with several reports on other plant species exposed to extreme environments, for example in alpine ecosystems (Lütz 1996; Körner 1999; Casanova-Katny et al. 2007), where neither photodamage at high PPFD nor significant declines of F_v/F_m ratios were observed in the field (Streb et al. 1998; Pittermann and Sage 2000), adding evidence that high irradiance does not necessarily lead to chronic photoinhibition.

Our results support the finding that *D. antarctica* has a broad temperature optimum for photosynthesis, fluctuating between 10 and 25°C, with optimum temperature for net photosynthesis rate at 13°C (Edwards and Smith 1988; Xiong et al. 1999). Correspondingly, Montiel et al. (1999) show a high light saturation point for net photosynthesis, which may allow more complete exploitation of the high irradiance levels experienced in the region during the short growing season and may also serve as a protective mechanism against photoinhibition (Long and Humpries 1994), as has been also reported for *Geum montanum* from the Alps (Manuel et al. 1999).

Another important result of our experiments is that *D. antarctica* growing under controlled conditions and in the field shows clear differences in some properties of the photosynthetic apparatus: pigment contents (chlorophyll and carotenoids) were much lower after long-term growth under controlled conditions compared with plants in situ. The low total chlorophyll content could be a response to the low light intensity in laboratory plants (CO-180 and LT-180 Fig. 3); correspondingly, the low maximum fluorescence values (Fig. 4b) suggest a decreased photochemical activity. Moreover, after long-term growth under saturating light intensity (LT-800), plants show the lowest chlorophyll content, which could be related to a photoprotection mechanism, where loss of chlorophyll content decreases the excitation pressure of the combined effect of high light and low temperature, as has been reported for other plants. Lütz (1996) observed a decrease in chlorophyll of *Eriophorum* leaves under field conditions during cold days with high light intensity. Chl *a*/*b* ratios in the laboratory-grown plants were similar, but lower in field plants, which suggests differences in the light harvesting systems. We could not find published data on the content of chlorophyll and carotenoids in field plants of *D. antarctica*; however, Xiong et al. (2000), showed a higher chlorophyll content in laboratory plants at 12°C than in plants grown at 7 or 20°C and suggest that growth temperature has no effect on carotenoid concentrations after 90 days of saturating light intensity (400 μmol m^{-2} s^{-1}).

Our results contradict the report of Perez-Torres et al. (2004), who, working with plants growing under controlled conditions, observed a decrease of 35% in F_v/F_m values after a short-term exposure of *D. antarctica* to high PPFD level (24 h, at 1,600 μmol m^{-2} s^{-1}) at low temperature. The author postulated a possible photoinhibition in plants growing in the field under similar high light conditions. An explanation for these contrasting results may be that the PPFD level at which *D. antartica* was grown in the mentioned experiment was too low (100 μmol m^{-2} s^{-1}). No information was given on the chlorophyll contents in plants under these conditions. Earlier studies on photosynthetic capacity of *D. antarctica* showed no differences in net photosynthesis rate after cultivation under different temperature treatments (Edwards and Smith 1988). No details about the growing conditions has been provided in the mentioned studies.

In conclusion, plants growing in the field maintained a high quantum yield of primary photochemistry of PSII during the short growing season under high light conditions. Clearly, laboratory plants performed differently from in situ ones, showing a marked decrease of pigments under variable light and temperature conditions. It should also be mentioned that leaf anatomy of *D. antarctica* was markedly different in laboratory-grown plants compared to field plants (Romero et al. 1999). Consequently, the results of the laboratory experiments should be interpreted with caution and may not explain the PSII behavior of *D. antarctica* in the field. Necessarily, more ecophysiological studies in situ are needed to understand the complexity of the photosynthetic activity of vascular plants in the Antarctic under different microclimatic conditions.

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