

Adaptive phenotypic plasticity and competitive ability deployed under a climate change scenario may promote the invasion of *Poa annua* in Antarctica

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Abstract Antarctica is one of the less prone environments for plant invasions, nevertheless a growing number of non-native species have been registered in the last decades with negative effects on native flora. Here we assessed adaptive phenotypic plasticity in three photoprotective traits (non-photochemical quenching, total soluble sugars, and de-epoxidation state of xanthophylls cycle), and fitness-related traits (maximum quantum yield, photosynthetic rate and total biomass) in the invasive species *Poa annua* and *Deschampsia antarctica* under current conditions of water availability and those projected by climate change models. In addition, two manipulative experiments in controlled and field conditions were conducted to evaluate the competitive ability and survival

of both species under current and climate change conditions. Moreover, we performed an experiment with different water availabilities to assess cell damage as a potential mechanism involved in the competitive ability deployed in both species. Finally, was assessed the plasticity and biomass of both species subject to factorial abiotic scenarios (water × temperature, and water × nutrients) ranging from current to climate change condition. Overall, results showed that *P. annua* had greater phenotypic plasticity in photoprotective strategies, higher performance, and greater competitive ability and survival than *D. antarctica* under current and climate change conditions. Also, cell damage, assessed by lipid peroxidation, was significantly greater in *D. antarctica* when

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grown in presence of *P. annua* compared when grown alone. Finally, *P. annua* showed a greater plasticity and biomass than *D. antarctica* under the factorial abiotic scenarios, being more evident under a climate change scenario (i.e., higher soil moisture). Our study suggests that the high adaptive plasticity and competitive ability deployed by *P. annua* under current and climate change conditions allows it to cope with harsh abiotic conditions and could help explain its successful invasion in the Antarctica.

Keywords Alien species · Climate change · *Deschampsia antarctica* · Ecophysiological traits · *Poa annua* · Survival

Introduction

Phenotypic plasticity has long been suggested to facilitate biological invasions across changing environments in which species can maintain a good ecophysiological performance (Hulme 2008; Molina-Montenegro and Cavieres 2010; Molina-Montenegro et al. 2013a). Understanding how and why certain biological traits promote invasiveness is a very important ecological and management tool. For this reason, several attempts have been conducted to find differences in biological traits of invasive and non-invasive taxa (Vilà and Weiner 2004; Pyšek and Richardson 2007; van Kleunen et al. 2010; Molina-Montenegro et al. 2012a).

Invasion biologists suggest that invasive species may be more plastic than non-invasive or native ones, enhancing their performance, and hence, their invasion success (Durand and Goldstein 2001; McDowell 2002; but see Palacio-López and Gianoli 2011). Because adaptive plasticity in physiological and morphological traits can provide greater access to limiting resources or improve their use-efficiency, invasive species may benefit from plasticity in limited resources or harsh environments. For instance, drought can induce oxidative stress and photoinhibition, decreasing the maximum quantum yield (Fv/Fm) and photosynthetic rate (Ogaya et al. 2011; Pinheiro and Chaves 2011), lowering growth (Heres et al. 2012), and modifying the competitive ability of plants (Wurzburger and Ford-Miniat 2014). In addition, has been shown that under severe drought plant species

can suffer cell damage by the oxidative degradation of lipids (see Miller et al. 2010). However, plant species should have several mechanisms to cope with changing water availability along their distributional range. For instance, several studies have shown that variation in the amounts of pigments, particularly those involved in the xanthophyll cycle (non-photochemical quenching), and total soluble sugars (osmotic protection) are efficient mechanisms of energy dissipation and drought tolerance in plants, respectively (García-Plazaola et al. 2007; Molina-Montenegro et al. 2012d; Pintó-Marijuan and Munné-Bosch 2013). Thus, those species deploying greater plasticity in traits related to coping with unfavorable conditions or to taking advantage of resources under most favorable conditions, could improve their survival, competition ability, and establishment.

High plasticity may be advantageous to cope with spatio-temporal fluctuations of resources in different environments (Godoy et al. 2011; Molina-Montenegro and Naya 2012). Because physiological performance may be impaired in low-resources environments (Davis et al. 2000), phenotypic plasticity can help maintain plant fitness under such stressful conditions (fitness homeostasis); on the other hand, may contribute to better capitalize temporal pulses of high-resource availability experienced by plants (see Sultan 2001). Richards et al. (2006) summarized these concepts in three possible strategies by which invasive plant species can thrive in changing environments: (1) plasticity in morphological or physiological traits; the invasive plant is able to maintain its fitness in a range of environments, including stressful habitats, a “Jack-of-all-trades” strategy. (2) phenotypic plasticity allows the invader to better exploit high resource availability in favorable environments; a “Master-of-some” strategy. (3) combination of these abilities; the “Jack-and-Master” strategy (see Muth and Pigliucci 2007).

The Antarctic continent is one of the most extreme environments for plant life worldwide. As for many Arctic plants, the establishment and survival of Antarctic plants is determined or modulated by harsh abiotic conditions, particularly during the short growing seasons (Ellis-Evans and Walton 1990; Robinson et al. 2003). This environment is characterized by low temperatures, repeated events of freezing and thawing, desiccation (due to high wind speeds), high irradiance, and low availability of liquid water and nutrients (Robinson et al. 2003; Wasley et al. 2006). Low water

availability has been suggested as the main constraint to successful establishment of plant species, because it adversely affects the reproductive and physiological responses of plants (Nobel 2005). For example, water has been indicated as a pivotal factor to maintain an optimal physiological performance, flower production, and survival in some Antarctic plants (Molina-Montenegro et al. 2012b, 2013b). Several morphological and physiological strategies that enable different plants to reduce the negative effects of water shortage have been well documented, where the physiological strategies are the more widely studied (see Nobel 2005; Flexas et al. 2006). However, ecophysiological approaches to the high performance of invasive plant species in the Antarctica are seldom found in the literature (e.g., Molina-Montenegro et al. 2012c). This is somewhat surprising because it is considered that the abiotic filter to plant establishment precedes the biotic filter (Lambers et al. 1998). To the best of our knowledge, the present study is the first to test under controlled and in situ conditions if the mechanisms employed by alien species provide an advantage over a native Antarctic plant, as well as improve its survival in the Antarctic.

Most of the Antarctic continent is covered by permanent ice and snow, and only 0.33 % of its surface is free of ice and available for colonization by plants (see Fox and Cooper 1998). Most of the ice-free lands are found along the Antarctic Peninsula, their associated islands, and on the coastal shores around the rest of the Antarctic continent (Alberdi et al. 2002; Convey 2008). Although the expected impact of global change on Antarctica is thought to be lower than that expected for the Arctic (Kennedy 1995; IPCC 2013), its effect on all terrestrial ecosystem are undisputable. Recent studies suggest that the effects of major changes (e.g., climate change and/or biological invasions) on the Antarctic Peninsula and Antarctic islands have been underestimated (Moline et al. 2004; IPCC 2013). Current climatic models for polar latitudes of the southern hemisphere, in particular for coastal zones of mainland Antarctica, predict a temperature increase, which should cause an increase in cloudiness and precipitation (IPCC 2013). In fact, it has been suggested that in the next years the water availability in the Antarctica will be increased in ca. 20–25 % (Turner et al. 2005; Bokhorst et al. 2011), ameliorating the harsh abiotic condition currently prevailing. It is thought that increased nitrogen deposition should enhance the

ecophysiological performance and productivity in the Antarctic environment (Wasley et al. 2006). Thus, since nitrogen is essential for plant performance and survival, its increase will affect the establishment and spread of native and invader species. Despite the impact on plants of the increased availability of nitrogen in the Antarctica, studies that have evaluated the effects of such driver of global change together with other components of climate change (e.g., water) are seldom found in the literature. The Antarctic vegetation is mostly composed by cryptogams (lichens, mosses, and liverworts) and only two native flowering plants: *Colobanthus quitensis* (Caryophyllaceae) and *Deschampsia antarctica* (Poaceae) (Smith 2003; Convey 2008). Both flowering plant species inhabit in the majority of the Maritime Antarctic islands down to approximately 68°S, being unable to extend into the continental Antarctic (Komárková et al. 1985; Robinson et al. 2003). Nevertheless, several alien species have been found inhabiting the South Shetland Islands as well as the Antarctic Peninsula (Frenot et al. 2005; Olech and Chwedorzewska 2011; Molina-Montenegro et al. 2012c). *Poa annua* (Poaceae) is the most widespread alien species in the maritime Antarctica, colonizing anthropogenically-influenced and natural habitats on most of the sub-Antarctic islands (Frenot et al. 1997; Chwedorzewska et al. 2015). Nevertheless, in Antarctica *P. annua* has occurred sparsely in places strongly disturbed by human activity (e.g. Smith 1996; Chwedorzewska 2009; Molina-Montenegro et al. 2014) with negative effects on the native flora (Molina-Montenegro et al. 2012c).

Here, we assessed whether the adaptive plasticity in several ecophysiological traits and great competitive ability showed by *P. annua* promote its invasion process in the Antarctica. Specifically, we compare the plasticity by the reaction norms of the invasive *P. annua* and the native *D. antarctica* under two different water conditions (current and simulated climate change) performed in growth chambers. In addition, we evaluated through a manipulative experiment in growth chambers the change in biomass as a proxy of competitive ability in both *P. annua* and *D. antarctica* growing in monoculture and together. Furthermore, we compared the survival percentage of both plant species from a transplant experiment conducted in the field (South Shetland Island). Finally, we undertook two factorial experimental approaches to test the greater plasticity and performance of *P. annua* compared with *D. antarctica* under current and climate

change scenario conditions. In order to do this, we set up a factorial array in growth chambers with two levels of water and two different temperatures, and two levels of water and two concentrations of nitrogen.

Methodology

Plant sampling and establishment of watering treatments

Individuals of the invasive *P. annua* and the native *D. antarctica* were collected in King George Island. The study site was located at 62°09'S; 50°28'W, in the vicinity of the Polish Antarctic Station "Henryk Arctowski". All plants were collected during the 2010–2011 growing season close to the coastline (50–60 m). Each individual plant (tussock) was excavated together with the soil around the roots (ca. 250 g) and kept well-watered in a plastic box under natural conditions of light and temperature for 3 h until the transplant experiment in situ or for its transportation to be used in growth chambers experiments at the Centro de Estudios Avanzados en Zonas Áridas (CEAZA), La Serena, Chile (29°S). Plants transported to CEAZA were replicated by vegetative reproduction in order to increase the biological material for the plasticity and competitive ability experiments conducted in the growth chambers. Plants used in the experiments with controlled condition (CEAZA) were generated from an initial pool of plants separated between 1 and 200 m from each other, in the hopes of obtaining greater genetic variability. Since the effect of treatment can be affected by the identity of the growth chamber, different treatments were conducted in both chambers to avoid this factor (see Potvin and Tardif 1988). To do it, each chamber was turned off, individuals were transferred to the other chamber and new environmental conditions were calibrated again.

To establish the current and future (climate change scenario) water availability we sampled soil moisture at the study site at the beginning of the growing season (January 2010). Using a tensiometer (2725 Series Jet Fill, CO, USA) we determined matric water potential of the soil at 5–7 cm in ten points. Points were randomly selected and separated by 2–3 m. Soil moisture (kPa) recorded in the field was -29 ± 0.51

(mean \pm SE). Given that under a climate change scenario is suggested an increase in the water availability of soil ca. ≈ 20 –25 %, we estimated a matric water potential of -20 kPa for the future climatic scenario. Then, we calibrated in the field the volume of water needed to attain these soil moisture levels. Considering the evaporative demand in the walk in growth chambers (20 m²), and in the field it was determined that supplying 30 and 45 cc of tap-water (growth chambers) and, 35 and 50 of tap-water (field) every 4 days per pot would roughly mimic soil moisture for current and climate change- conditions, respectively. Water addition lasted for the entire period of the experiment. Matric water potential was measured five times during the experiment to verify that differences between watering treatments were maintained (mean ranges obtained during the experiment: current condition: -27 to -31 kPa; climate change scenario: -18 to -20 kPa).

Since the effects of a treatment can be affected by the characteristics of the growth chamber (see Potvin and Tardif 1988), different treatments were conducted in both chambers and individuals were transferred between chambers, changing the settings in the abiotic conditions. In each chamber, plants of both species were randomly assigned to one of the two levels of water. For each plant species, 20 individuals were assigned to the growth chambers with current water condition and other 20 individuals were assigned to future water condition. Therefore, 40 plants were grown in each chamber. Plastic pots positions were randomized within the growth chambers every week. Plasticity in ecophysiological traits was measured after 5 months. At the end of each month, the chambers were switched off, cleaned, and individuals were transferred between chambers, and growth conditions were re-established.

Experiment 1

Plasticity in ecophysiological traits of *P. annua* and *D. antarctica*

In order to assess if greater adaptive plasticity may promote the invasiveness of *P. annua*, we compared the reaction norms of *P. annua* and *D. antarctica* growing in two water conditions. The reaction norm is

the graphical expression of plasticity where is observed in a given genotype, the contribution of environmental variation to observed phenotypic variation. Specifically, we compared the plasticity in the non-photochemical quenching (NPQ), total soluble sugars (TSS) and de-epoxidation state, as photoprotective strategies, and net photosynthesis, water use efficiency (WUE), maximum quantum yield (Fv/Fm) and total biomass as measurements of plant performance. Each individual clump (10 cm of diameter) was transferred to growth chambers and planted in 300-ml plastic pots filled with soil taken from the South Shetland Islands. To accomplish the main goal of this experiment we used two growth chambers, one to mimic the current water condition, and the other to mimic future water condition. Both growth chambers were set at 20/4 h light/dark photoperiod and 4 °C, in order to maintain fixed other abiotic factors. For each plant species, 20 individuals were assigned to the growth chamber with current water condition and other 20 individuals were assigned to future water condition. Plastic pots positions were randomized within the growth chambers every week.

Experimental treatments lasted for 5 months, emulating the duration of the growing season at the study site. At the end of experiment, we measured the ecophysiological and fitness-related traits on 12 individuals of each species exposed to current and future water condition (*total n* = 24 per species). The de-epoxidation state of the pigments involved in the xanthophyll cycle was quantified as $Z + (0.5 \times A) / (V + A + Z)$, where the Violaxanthin (V), Antheraxanthin (A) and Zeaxanthin (Z) were determined according to Munné-Bosch and Alegre (2000). The non-photochemical quenching (NPQ) and maximum quantum yield (Fv/Fm) were measured with a pulse-amplitude modulated fluorometer (FMS 2, Hansatech, Instruments Ltd, Norfolk, UK). Green and visually healthy leaves from each individual were placed in the dark for 30 min, carefully avoiding leaf detachment. We placed the leaves in the dark for 20–30 min to ensure maximum photochemical efficiency. We measured maximum quantum yield of the photosystem II (Fv/Fm; where $F_v = [F_m - F_0]$, F_m = maximum fluorescence yield, and F_0 = minimum fluorescence yield) as the photosynthetic performance parameter (for further details see Maxwell and Johnson 2000). To assess the total soluble sugar concentration, three to four leaves from 12 individuals, both in current and

future water condition, were collected. Each sample was cut into small pieces and kept in ethanol (86 %) for a period of 24 h, and then centrifuged at 1200 g for 10 min. the supernatant was de-pigmented and the aqueous fraction was dried in cold for 12 h. The total soluble sugar content was determined spectrophotometrically using the resorcinol method (Roe 1934) with a reading at 520 nm, using sucrose as standard. The net photosynthetic rate was measured on a visually healthy leaf from 12 individuals of each species both in current and climate condition. The measurements were made at room temperature (4 °C), with a photosynthetically active radiation of 1000 $\mu\text{mol}, \text{m}^{-2} \text{s}^{-1}$, and a CO₂ concentration of 360 ppm using an infrared gas analyzer (IRGA, Infra Red Gas Analyser, CIRAS-1, PP-Systems Haverhill, USA). Finally, total dry biomass was obtained after whole plants, including fallen leaves, were oven-dried at 70 °C for 72 h, at the end of experiment.

Competitive ability

To assess the competitive ability, we calculated the relative competition intensity index (RCI; Grace 1995) between *P. annua* (Pa) and *D. antarctica* (Da) under the two water conditions described above (current and climate change scenario). We focused on the outcome of competition between both species with final biomass (BSp) as response variable. To conduct this assay, two individuals of each species were grown alone (monoculture) and one individuals of each species were grown together (1 pair of species per pot; 5 replicates per treatment and 15 individuals per species). Hence, we evaluated the relative competitive impact of *P. annua* on *D. antarctica* ($\text{RCI-Da} = [\text{BDa monoculture} - \text{BDaPa}] / \text{BDa monoculture}$), and the resistance to invasion by the native species testing its effect on *P. annua* ($\text{RCI-Pa} = [\text{BPa monoculture} - \text{BPaDa}] / \text{BPa monoculture}$).

Cell damage as potential mechanism of competitive ability

In order to assess some parameter related with the potential mechanisms involved in the competitive ability, was measured cell damage by the oxidative degradation of lipids in *D. antarctica* and *P. annua*. The lipid peroxidation is considered as an indicator of cell damage, and was estimated by measuring the

concentration of malondialdehyde (MDA) by thiobarbituric acid (TBA) assay (Egert and Tevini 2002). Ten individuals of each species were grown alone (monoculture) and 5 individuals of each species (*total n* = 10 individuals) were grown together (1 pair per pot). Plant individuals were subjected to three water availability conditions: -10 , -20 , and -30 kPa. Thus, we evaluated one of the potential mechanisms underlying the competitive impact of *P. annua* on *D. antarctica*, and the resistance to invasion by the native species testing its effect on *P. annua*. Considering the evaporative demand in the walk-in growth chambers, the water availability conditions (-10 , -20 and -30 kPa) were determined supplying 55, 45 and 30 cc of tap-water every 4 days per pot, respectively. Water addition lasted for the entire period of the experiment. Matric water potential was measured seven times during the experiment to verify that differences between watering treatments were maintained throughout the experimental period.

At the end of experiment, fresh tissue (0.1 g) of each species growing in monoculture and together were homogenized with 2 ml of TCA (1 %) and centrifuged at 10.000 g for 5 min. 250 ml of the supernatant was mixed with 1 ml of TBA (0.5 %) in TCA (20 %). Mixtures were incubated in boiling water for 30 min, and then cooled to room temperature. Absorbance was determined at 532 nm and non-specific absorbance at 600 nm (Hodges et al. 1999). The MDA content was determined using a molar extinction coefficient of $155 \text{ mol}^{-1} \text{ cm}^{-1}$.

Experiment 2

Survival experiments

To assess if the plasticity in ecophysiological traits can enhance the survival percentage and invasion success of *P. annua* we performed a transplant experiment with adult individuals of *P. annua* and *D. antarctica* collected at the study site. All plants used ranged from 4 to 5 and 6 to 7 cm height for *P. annua* and *D. antarctica*, respectively, appeared healthy, and were collected close to the coastline. Plant status was visually assessed just before the transplant (plants showing foliar and/or root damage were excluded). We selected 3 patches separated by at least 20 m from each other where *P. annua* and *D. antarctica*

individuals were grown alone or with individuals of the other target species. Each experimental unit (patch) consisted of 10 individuals of *P. annua*, 10 individuals of *D. antarctica* (control treatments), and 5 individuals of *P. annua* plus 5 individuals of *D. antarctica* (competition treatment) (*total n* = 90 individuals). Each individual was planted 2 cm apart from each other to maximize the interaction among them (e.g., competition). Transplants were carried out during the 2010–2011 growing season during 10 weeks, and survival was recorded every 2 weeks. At the end of the experiment, all surviving *P. annua* individuals were removed and destroyed in order to avoid its spread.

Experiment 3

Plasticity in ecophysiological and fitness traits between *P. annua* and *D. antarctica* under factorial climate change scenarios

We experimentally generated two abiotic gradients, each with four levels ranging from unfavorable (S1) to favorable scenarios (S4). The first abiotic gradient resulted from a factorial combination of two watering levels (irrigation every 4 days with 30 and 45 cc of tap water; current and climate change, respectively), and two temperatures (4 and 7 °C; current and climate change, respectively). The scenarios were 30 cc + 4 °C (scenario 1, S1), 30 cc + 7 °C (scenario 2, S2), 45 cc + 4 °C (scenario 3, S3), and 45 cc + 7 °C (scenario 4, S4). The second abiotic gradient arose from a factorial combination of two watering levels (same as above) and two nitrogen levels (20 and 25 mg kg⁻¹; current and climate change, respectively). The scenarios were 30 cc + 20 mg kg⁻¹ (S1), 30 cc + 25 mg kg⁻¹ (S2), 45 cc + 20 mg kg⁻¹ (S3), and 45 cc + 25 mg kg⁻¹ (S4). Current condition for nitrogen levels was based on the average of 15 soil samples taken from the study site ($20.1 \pm 1.2 \text{ mg kg}^{-1}$). In all cases, ten individuals from each plant species were subject to each of the abiotic scenarios along the favorable-unfavorable axis. All combinations of abiotic conditions that gave rise to the experimental gradients are likely to be experienced by both plant species under current and climate change scenarios. Each abiotic scenario was performed in a separated growth chamber (*n* = 4 per each abiotic gradient) for water × temperature

treatment as well as for water \times nitrogen treatment. All combinations of abiotic conditions in the second abiotic gradient (W \times N) were performed with the temperature set at 4 °C. The unfavorable-favorable hierarchy of scenarios was defined a priori based on previous experience with the study species. Pot positions were randomized within the growth-chamber every 5 days. Inter-pot distances were sufficient to prevent mutual shading. After 5 months, we recorded in *P. annua* and *D. antarctica* individuals the following ecophysiological traits: maximum photosynthesis (A_{max}), and instantaneous water use efficiency (WUE). An infrared gas analyzer (CIRAS-1; PP-Systems, Haverhill, MA, USA) was used to measure gas exchange traits. We measured maximum photosynthetic rate (A_{max} , $\mu\text{mol m}^{-2} \text{s}^{-1}$) and evapotranspiration rate (E, $\text{mmol m}^{-2} \text{s}^{-1}$) on ten individual of both tested species. From gas exchange values, WUE was calculated as the ratio between photosynthesis and transpiration rate (A/E , Nobel 2005). At the end of the experiment (5 months) we recorded fitness-related traits, the survival percentage, and total dry biomass of all plants. Dry biomass was obtained by oven-drying plant tissues at 70 °C for 72 h.

Statistical analysis

Ecophysiological traits (non-photochemical quenching, total soluble sugar, and de-epoxidation state of the xanthophyll cycle) and performance traits (maximum quantum yield of PSII (Fv/Fm), net photosynthesis and total biomass) in the plasticity experiments were compared by two-way analysis of variance (two-way ANOVA), where water condition and different species were the independent variables (Zar 1999). Differences between competitive ability under current and climate change water condition were analysed considering the differences in total biomass at the end of the experiment. This was done also using a two-way ANOVA. Differences in cell damage were also evaluated by two-way ANOVA, where water availability and competition (*D. antarctica* and *P. annua* growing in monoculture and together) were the independent variables. Survival percentage both in native and alien species was evaluated in situ every 2 weeks and estimated by mean of the Kaplan–Meier method, and statistical differences were assessed with the Cox–Mantel test (see Fox 1993). Survival percentage was assessed separately for each irrigation

condition. Finally, the comparison of reaction norms between *P. annua* and *D. antarctica* in ecophysiological and fitness-related traits was conducted with a factorial ANOVA for each of the two environmental gradients separately. We considered the origin (native and invasive), and abiotic scenarios (S1 to S4) as main factor, and ecophysiological or fitness trait as dependent variable. For all analyses, the assumptions of normality and homogeneity of variances were tested using the Shapiro–Wilks and Bartlett tests, respectively (Zar 1999).

Results

Experiment 1

Plasticity in ecophysiological traits between P. annua and D. antarctica

P. annua individuals showed significantly greater values of non-photochemical quenching (NPQ) than *D. antarctica* (Table 1; Fig. 1a). In addition, the water condition \times species interaction was significant (Table 1), since NPQ decreased in both origins with greater water content, but in *P. annua* the decrease was greater (Fig. 1a). The total soluble sugar content was significantly greater in the driest condition for both species (Table 1; Fig. 1b). Water condition \times species interaction was also significant (Table 1), because the magnitude of increase was greater in *P. annua* than in *D. antarctica* (Fig. 1b). De-epoxidation state of the xanthophyll cycle did not differ between species (Table 1; Fig. 1c), and the water condition \times species interaction was not statistically significant (Table 1; Fig. 1c).

The maximum quantum yield of the PSII (Fv/Fm) was significantly greater (Table 1) under climate change condition than under current water status (Fig. 2a). In addition, the interaction factor (water condition \times species) was significant (Table 1) because *P. annua* increased its Fv/Fm more than *D. antarctica* under a climate change scenario (Fig. 2a). In the same way, net photosynthesis was significantly greater (Table 1; Fig. 2b) in *P. annua* than in *D. antarctica*, as well as the interaction between water condition and species (Table 1). Under climate change condition, both plant species increased their net photosynthesis, but the increase was greater in *P.*

Table 1 Factorial ANOVA of the effect of species (*D. antarctica* vs. *P. annua*), climate (current vs. future) and interaction (S × C) on non-photochemical quenching (NPQ), total soluble sugars (TSS), de-epoxidation state of xanthophyll cycle (EPS), maximum quantum yield (Fv/Fm), net photosynthesis and total biomass

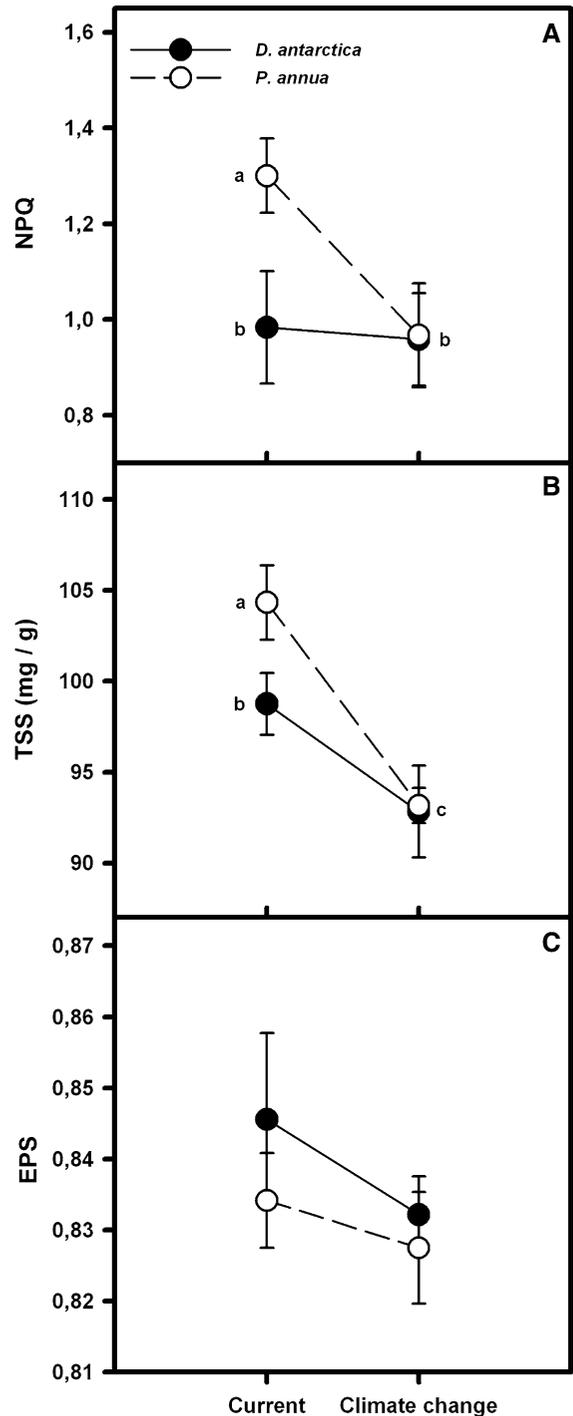
Trait	fd	F	P
NPQ			
Species	1, 44	12.31	0.001
Climate	1, 44	3.23	0.079
S × C	1, 44	9.11	0.031
TSS			
Species	1, 44	5.33	0.064
Climate	1, 44	6.35	0.032
S × C	1, 44	8.16	0.038
EPS			
Species	1, 44	1.21	0.074
Climate	1, 44	1.01	0.122
S × C	1, 44	1.08	0.084
Fv/Fm			
Species	1, 44	2.45	0.154
Climate	1, 44	9.55	0.033
S × C	1, 44	8.38	0.029
Photosynthesis			
Species	1, 44	5.54	0.044
Climate	1, 44	10.03	0.001
S × C	1, 44	9.82	0.021
Biomass			
Species	1, 44	6.77	0.032
Climate	1, 44	14.21	0.001
S × C	1, 44	10.08	0.021

Significant differences are denoted in bold

annua (Fig. 2b). Similarly, total biomass was significantly greater in climate change treatment than in current water condition (Table 1; Fig. 2c), also with a significant water condition × species interaction (Table 1). Although, both species increased their total biomass with greater water availability, this increase was more evident in the invasive *P. annua* than that of the native *D. antarctica* (Fig. 2c).

Competitive ability

Overall, the invasive *P. annua* showed greater competitive ability than native *D. antarctica* ($F_{1, 44} = 13.21$; $p = 0.012$), and this effect was slightly greater under climate change than under current water condition



($F_{1, 44} = 1.08$; $p = 0.084$). The relative competition intensity index (RCI) showed that *P. annua* exerted a significant competitive effects on *D. antarctica*, mainly under higher water condition, depressing its biomass by

◀ **Fig. 1** Reaction norm of photoprotective mechanisms. Non-photochemical quenching (a), total soluble sugars (b), and de-epoxidation state of the xanthophyll cycle (c), in the native *D. antarctica* (closed circles) and the invasive *P. annua* (open circles) grown under current condition and future climate change scenario. Mean values \pm SE are shown. Significant differences are denoted with *different letters* (a posteriori Tukey test $\alpha = 0.05$)

22 and 39 % under current and future water condition, respectively (Fig. 3). Contrarily, *D. antarctica* showed a weaker effect on *P. annua* under current water condition, decreasing the biomass of *P. annua* only by 4 % (Fig. 3). Under climate change scenario, the competition intensity between *P. annua* and *D. antarctica* was lower than between individuals of *P. annua* alone, since total biomass of *P. annua* increased significantly by 7 % (Fig. 3).

Cell damage as potential mechanism of competitive ability

The TBARS concentration was similar ($F_{2, 6} = 1.22$; $p = 0.65$) between different water availability conditions (Fig. 4). Moreover, TBARS concentration was significantly higher ($F_{3, 6} = 11.91$; $p = 0.011$) in *D. antarctica* individuals when grown associated to *P. annua* (*Da + Pa*) than alone (*Da*). In fact, TBARS concentration in *D. antarctica* growing in association with *P. annua* was more than two times greater than in monoculture (Fig. 4). The TBARS concentration in *P. annua* growing in monoculture (*Pa*) was not statistically different to the levels measured when grown with *D. antarctica* (*Pa + Da*) ($F_{3, 6} = 2.02$; $p = 0.53$; Fig. 4). There was no significant competition treatment \times water interaction.

Experiment 2

Survival experiments

Under current water condition, the survival percentage of *P. annua* when grown with *D. antarctica* (*Pa + Da*) was significantly greater, followed by *P. annua* (*Pa*) and *D. antarctica* (*Da*) growing in monoculture, and finally by *D. antarctica* growing with *P. annua* (*Da + Pa*) (value of Cox–Mantel test = 16.73; $p = 0.032$; Fig. 5a). When grown with *D. antarctica*, *P. annua* showed a smooth decrease in

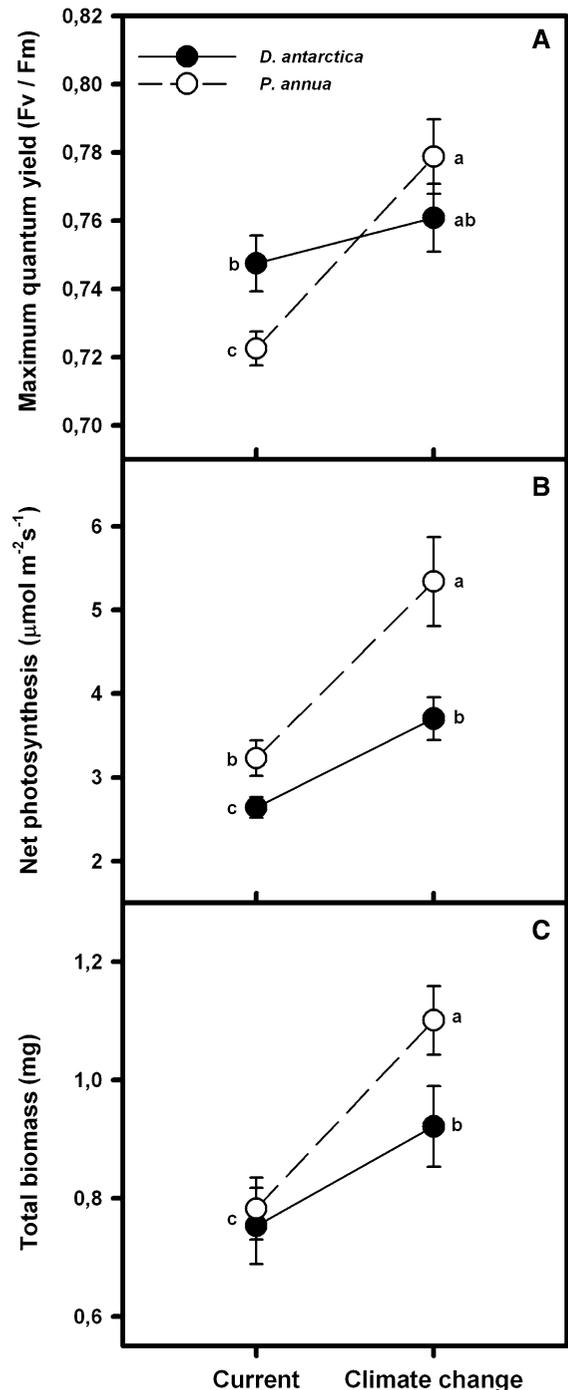


Fig. 2 Reaction norm of ecophysiological performance. Maximum quantum yield (a), net photosynthesis (b) and total biomass (c), in the native *D. antarctica* (closed circles) and the invasive *P. annua* (open circles) grown under current condition and future climate change scenario. Mean values \pm SE are shown. Significant differences are denoted with *different letters* (a posteriori Tukey test $\alpha = 0.05$)

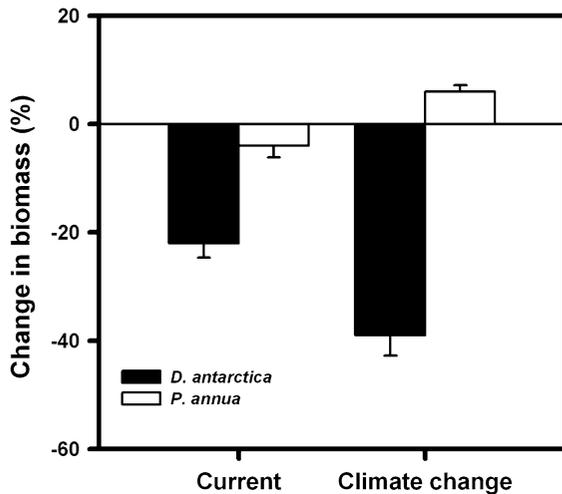


Fig. 3 Manipulative experiment of competition among the native *D. antarctica* (black bars) and the individuals of the invasive *P. annua* (white bars). It is shown the average of change in biomass (\pm SE) in the invasive and native species subject to current and simulated climate change conditions. Negative values indicate that growth associated (both species together) negatively affects the accumulation of biomass compared with growth alone (monoculture)

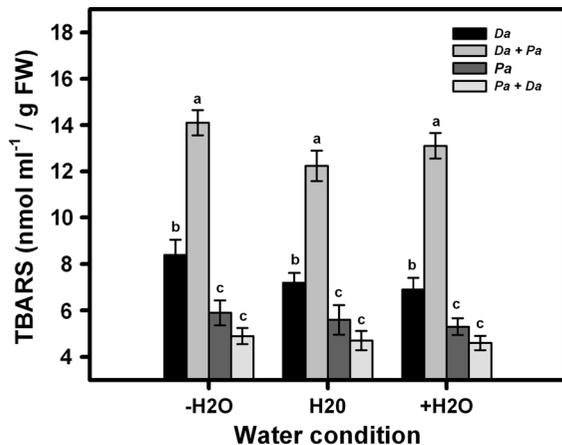


Fig. 4 Mean values (\pm SE) of peroxidation of lipids (TBARS) in the native *D. antarctica* growing alone (*Da*) or associated to *P. annua* (*Da + Pa*), and the invasive *P. annua* growing alone (*Pa*) or associated to *D. antarctica* (*Pa + Da*). Individuals of both species were subject to different water availability conditions. Significant differences within each water condition are denoted with different letters ($\alpha = 0.05$)

survival reaching a $\sim 50\%$ after 8 weeks. When *D. antarctica* was grown with *P. annua* it showed a sharp decrease in survival reaching a $\sim 50\%$ after 2 weeks and $<20\%$ after 8 weeks (Fig. 5a). Under simulated

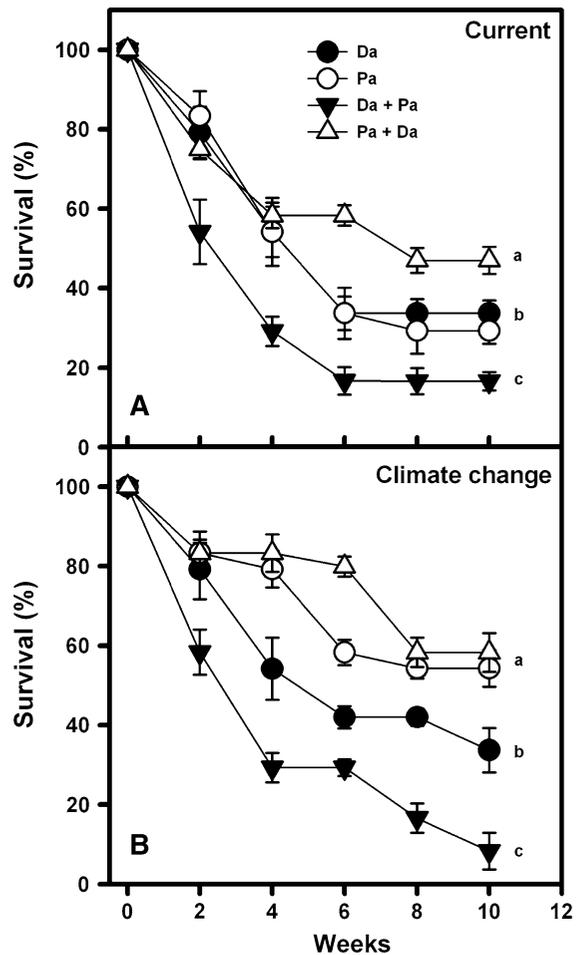


Fig. 5 Survival percentage along the time in the native *D. antarctica* (*Da*) and the invasive *P. annua* (*Pa*) growing in monoculture and associated in both current condition (a) and future climate change scenario (b). Mean values \pm SE are shown. Significant differences are denoted with different letters (Cox–Mantel test $\alpha = 0.05$)

climate change condition, the individuals of *P. annua*, growing with *D. antarctica* and growing alone, showed significantly higher survival percentage than *D. antarctica* individuals from all treatments (Fig. 5b, Cox–Mantel test = 19.56; $p = 0.019$). In addition, *D. antarctica* individuals grown alone showed a higher final survival than those individuals grown together with *P. annua* (Fig. 5b). Although, the trends in mortality of *D. antarctica* were similar when were grown with and without *P. annua*, when grown in competition, the decrease in survival was sharper, reaching a mortality of ~ 70 and 90% after four and 8 weeks, respectively (Fig. 5b).

Experiment 3

Plasticity in ecophysiological and fitness traits between P. annua and D. antarctica under factorial climate change scenarios

Under the water and temperature gradient, the invasive *P. annua* showed a significantly higher maximum photosynthesis and water use efficiency ($F_{1, 72} = 17.34$; $p = 0.011$ and $F_{1, 72} = 136.53$; $p < 0.001$, respectively) than the native *D. antarctica* considering all scenarios (S1 to S4; Fig. 6a, b). On the other hand, under more favorable conditions (climate change scenario) both species increased their photosynthesis, but *P. annua* showed a significantly higher increase, as evidenced by the significant Origin (O) \times Scenario (S) interaction ($F_{3, 72} = 7.07$; $p < 0.01$; Fig. 1a). Additionally, the O \times S interaction was also significant for WUE. Although in both plant species the WUE was higher under water shortage conditions compared with well watered treatments, this increase was greater in *P. annua* than *D. antarctica* ($F_{3, 72} = 11.13$; $p < 0.01$; Fig. 1b). At the end of the experiment, biomass was significantly higher in *P. annua* than in *D. antarctica*, and higher in climate change (more favorable) compared to current conditions ($F_{1, 72} = 26.66$; $p < 0.001$ and $F_{3, 72} = 63.87$; $p < 0.001$, respectively). Although biomass increased in both species under more favorable condition, it was not in the same fashion, being this increase significantly greater in *P. annua* than *D. antarctica* ($F_{3, 72} = 21.04$; $p = 0.021$; Fig. 6c).

Under the water and nutrient gradient, the invasive *P. annua* showed significantly higher maximum photosynthesis and water use efficiency ($F_{1, 72} = 23.82$; $p < 0.001$ and $F_{3, 72} = 193.65$; $p < 0.001$, respectively) than the native *D. antarctica* (Fig. 6d, e). Under more favorable conditions (climate change scenario) both species increased the photosynthesis, but *P. annua* showed a significantly higher increase, as evidenced by the significant O \times S interaction ($F_{3, 72} = 11.03$; $p < 0.001$; Fig. 6d). Additionally, the O \times S interaction was also significant for WUE. Although in both plant species WUE increased under water shortage, this increase was significantly higher in *P. annua* than *D. antarctica* ($F_{3, 72} = 20.25$; $p < 0.001$; Fig. 6e). Regarding the fitness-related traits, *P. annua* showed a significantly higher biomass accumulation than *D. antarctica* ($F_{1, 72} = 44.30$; $p < 0.001$;

Fig. 6f). Similar to the previous gradient, biomass accumulation increased with more favorable conditions (climate change scenario) in *P. annua* and *D. antarctica* both ($F_{3, 72} = 80.09$; $p < 0.001$, respectively). Contrary to the previous results, this increase in biomass showed a similar trend in both species along all abiotic scenarios (interaction O \times S = $F_{3, 72} = 0.71$; $p = 0.54$; Fig. 6f).

Discussion

Plasticity seems to be a successful strategy for plant invasiveness in many environments (McDowell 2002; Davidson et al. 2011; Molina-Montenegro et al. 2013a). In our study, we found that *P. annua* can deploy a high adaptive plasticity in response to increased watering, temperature, and nutrient in key photoprotective and fitness-related traits. In addition, this high plasticity could be translated in higher use efficiency of some resources or higher environmental tolerance, and in turn a greater competitive ability and invasion potential. Maintaining a high physiological performance and efficient photoprotective mechanisms under current and future water conditions could result in an overall higher growth and competitiveness, and higher environmental tolerance of this invasive species. The high ecophysiological plasticity showed by *P. annua* can confer it a high potential to avoid photoinhibition and increase resource up-take under the current abiotic conditions prevailing in Antarctica. It may also improve its competitive abilities under more suitable future climate scenarios.

Phenotypic plasticity and polyploidy are among the main factors that can increase the environmental tolerance of plant species and, thus, have the potential of expanding the distributional range of native and alien species (Rejmánek et al. 2005; Richards et al. 2006; Pyšek and Richardson 2007; Molina-Montenegro et al. 2013a). High phenotypic plasticity has been previously reported for sub-Antarctic populations of *P. annua*, along with allotetraploidy and low genetic diversity, the latter possibly due to founder effect (Frenot et al. 1999). These characteristics may have helped *P. annua* to form permanent populations in the Maritime Antarctica. Thus, plasticity may initially allow introduced species to become naturalized across a range of environments (Sexton et al. 2002; Palacio-López and Gianoli 2011) and then heritable phenotypes

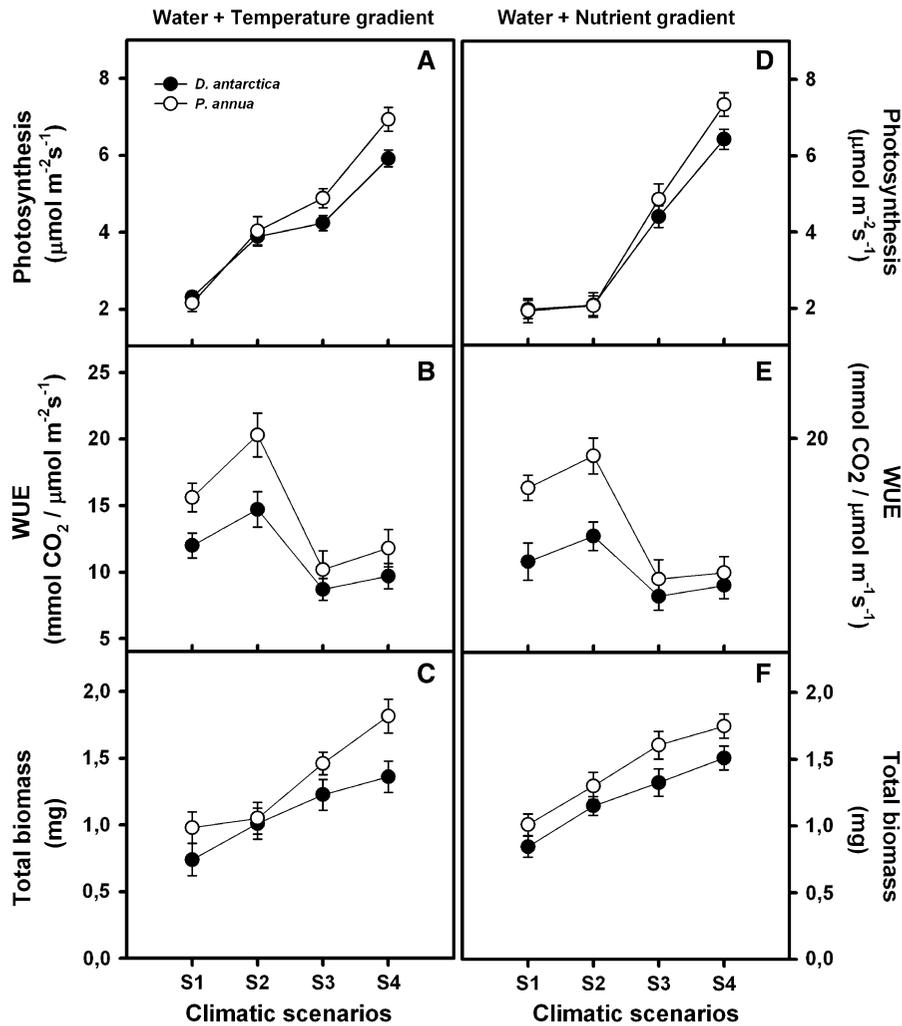


Fig. 6 Maximum photosynthesis (a, d), water use efficiency (WUE) (b, e), and biomass accumulation (c, f), in the invasive *P. annua* (open circles) and in the native *D. antarctica* (closed circles) exposed to two different environmental gradients

(water + temperature and water + nutrient, respectively). Each environmental gradient is comprised by four stress levels ranging from unfavorable scenario (S1, current condition) to favorable scenario (S4, climate change condition)

may respond to local selection pressures, thus forming ecotypes, better adjusted to local conditions (Sexton et al. 2002).

In addition, the native *D. antarctica* showed low plasticity in response to increased water supply, possibly due to ecotypic differentiation of Antarctic populations (Chwedorzewska et al. 2008). These populations could be adapted to current water conditions and display several traits or mechanisms to cope with drought and cold, such as sugars accumulation (Zúñiga-Feest et al. 2009) and anatomical adaptations (Chwedorzewska et al. 2008). These climatic tolerance

mechanisms are costly, and could reduce growth and competitiveness in less stressful environments such as those predicted for Antarctica in the next 50–100 years (IPCC 2013). Then, a “successful” phenotype resulting from trait adjustment by plasticity becomes genetically fixed following directional selection on the optimum phenotype in a determined habitat after several generations (Pigliucci et al. 2006). The significant plasticity in photoprotective mechanisms, eco-physiological performance, and fitness-related traits found in *D. antarctica* under current climatic conditions are consistent with the genetic assimilation

hypothesis (Pigliucci et al. 2006), which predicts the selection of an optimum phenotype. Nevertheless, this high performance in a stressful environment could be reduced under the milder conditions predicted by climatic models (IPCC 2013), due to the lack of adaptive plasticity like that evidenced for *P. annua*.

We demonstrated that, under current climate conditions, the competitive effects of *P. annua* on *D. antarctica* is lower than that found under a climate change scenario. This probably because *D. antarctica* has a set of ecophysiological traits that allows higher performance and competitive ability, making this species more efficient in the current environment. Nevertheless, under the future climate change scenario, in which resource availability will be higher (e.g., soil moisture), *P. annua* will exert a stronger negative effect on *D. antarctica*. This increase in the competitive impacts exerted by *P. annua* may be explained by an increase in the competitive ability as well as by an increase in the overlapping of niches among *P. annua* and *D. antarctica* for a specific set of resources (sensu Hutchinson 1957). *P. annua* might possess higher resource up-take ability through its greater plasticity. Although these hypotheses cannot be ruled out, more studies should be conducted to unravel the mechanisms underlying the competitive interaction between the invasive *P. annua* and the native *D. antarctica* under current and future climate change scenarios. In addition, cell damage by peroxidation of lipids could be considered as a potential mechanism explaining the greater competitive ability of *P. annua* over *D. antarctica*. It has been shown that *D. antarctica* has high capacity to scavenge free radicals when this species is subjected to drought (Zamora et al. 2010). Our results are in agreement with previous studies since *D. antarctica* showed low (and not different) TBARS production along the water availability gradient. However, when *D. antarctica* was grown together with *P. annua*, the TBARS production significantly increased in all water conditions, suggesting that presence of *P. annua* induce more cell damage than drought. It has been suggested that cell damage induced by peroxidation of lipids can reduce the growth in plant species (Tian and Lei 2007) as was found in *D. antarctica* when grown in presence of *P. annua*. Thus, our results suggest that *P. annua* has greater competitive ability and exert a negative effect on *D. antarctica* as assessed by reduction in the physiological performance and fitness-related traits, likely modulated by cell damage.

Fifty years ago, Baker (1965) described the combination of the “jack-of-all-trades” and “master-of-some” strategies (now referred to as the “Jack-and-Master” strategy). This strategy consists in maintaining fitness in resource-poor environments and maximizing fitness in favorable conditions. This type of response may be accountable for successful and quick invasions (Mozdzer and Megonigal 2012; Pichancourt and van Klinken 2012). Here we have shown that the invasive *P. annua* exhibits this type of strategy, as suggested by its ability to; (a) maintain fitness-related traits and biomass accumulation in unfavorable scenarios (current condition) and also (b) a greater ability to increase its performance when conditions are favorable (climate change condition), compared with the native *D. antarctica*. Hence, we suggest that it is this combination of strategies in different ecophysiological and fitness-related traits that contribute to the invasiveness of this species under current and climate change scenarios. There are few examples of clear “Jack-and-Masters” in the invasion literature (but see Mozdzer and Megonigal 2012). Nevertheless, the lack of clear evidence may be due to the difficulties in correctly assessing “Jack-and-Master” invaders. Although a few articles have showed the potential importance of Jack-and-Master phenotypic plasticity in plant invasions (Mozdzer and Megonigal 2012; Pichancourt and van Klinken 2012), to our knowledge, our study is the first that has empirically demonstrated the Jack-and-Master strategy displayed for a plant species in Antarctica. Additionally, we suggest that water is hierarchically more relevant for the ecophysiological performance in both plant species than other drivers of climate change such as temperature and/or nutrients. In fact, only in presence of higher water availability, the photosynthesis and biomass increased notoriously with temperature and nutrients, being this effect more evident in the invader *P. annua*. Thus, under a complex climate change scenario with higher water availability and higher temperatures, *P. annua* will likely increase its ecophysiological performance and invasion success in Antarctica.

In the last 20–30 years *P. annua* (Frenot et al. 1997, 2005; Chwedorzewska 2008, 2009; Olech and Chwedorzewska 2011; Molina-Montenegro et al. 2014; Chwedorzewska et al. 2015), and other non-native species (Pertierra et al. 2013; Hughes et al. 2015), have been found growing naturally in Antarctica. In current climate conditions, *P. annua* is restricted to a few sites

subjected to high human influence where soil disturbance increase nutrient availability, germination and survival (Molina-Montenegro et al. 2014). If climate (precipitation and temperature) change as predicted by recent models (IPCC 2013), *P. annua* populations could spread toward natural communities and outcompete local *D. antarctica* populations, increasing in number, range, and impact. In fact, a first appearance and establishment of *P. annua* in natural habitats on the forefield of a retreating glacier in Antarctica, where the availability of resources are increased (water and nutrients), has been recently recorded (Olech and Chwedorzewska 2011). Thus, in the future climate change scenario, functional plasticity may help *P. annua* tolerate the harsh condition and subsequently spreading into natural communities. Although this prediction is difficult to test, previous experimental evidence obtained under controlled conditions (see, Molina-Montenegro et al. 2012c) support it.

Final remarks

It is well known that the cost of controlling an invasive species increase with time (Mack et al. 2000). Considering the maintenance and increase of *P. annua* populations in space and time, eradication seem practically impossible. We suggest that control measurements for *P. annua* should be taken now to avoid future ecological problems. We also suggest that preventive measurements should also be taken to avoid the spread of *P. annua* to currently unoccupied sites (see, Hughes et al. 2015). *P. annua* is capable to tolerate the harsh conditions of Antarctica through its plasticity in photoprotective mechanisms. However, under the future climate change, the high plasticity of this species will result in stronger negative impacts on the native flora, further increasing the costs and difficult of its control.

Antarctica is one of the less anthropized continents, but the recent increases in research and touristic activities have increased the human impact on the Antarctic biota, especially in the Antarctic Peninsula and South Shetland Islands (Chown et al. 2012; Molina-Montenegro et al. 2014). Surprisingly, nowadays there is no clear strategy for control of established exotic species in Antarctica (but see Hughes et al. 2015). Our study (together with other such as, Moline et al. 2004; Chown et al. 2012; Molina-Montenegro

et al. 2014) provides evidence that in Antarctic environments could be severely impacted in the near future (and also in the long-term) and there may be unsuspected consequences for the Antarctic diversity. Although, some efforts have been made to accomplish this goal (see Huiskes et al. 2014), they are still insufficient to mitigate the negative impacts of human activities on Antarctic biodiversity. Thus, we strongly suggest establishing a concerted collaboration to assess the current and future impacts of the presence and spreading of the non-native plants that have been already established in Antarctica.

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