

# The importance of facilitative interactions on the performance of *Colobanthus quitensis* in an Antarctic tundra

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## Abstract

**Aims:** The sign of interactions among plants in very harsh environments is under debate. The Antarctic tundra is one of the harshest environments on Earth and only two vascular plants (*Deschampsia antarctica* and *Colobanthus quitensis*) have successfully established natural populations. *D. antarctica* mostly establishes facilitative interactions with other species (mosses), but there is no information about the inter-specific interactions established by *C. quitensis*. We assessed whether *C. quitensis* grows frequently associated with *D. antarctica*, and if *D. antarctica* neighbours have a positive effect on the survival, growth and photochemical efficiency of *C. quitensis* individuals.

**Location:** King George Island, Antarctic Peninsula.

**Methods:** To assess the spatial association among the two Antarctic vascular plants fifty 50 m × 50 cm quadrats were sampled on each of four different substrates: moss carpet areas; dead moss carpet areas dominated by *D. antarctica*; a transition zone between dead moss carpets and fellfields; and fellfields characterized by very poor vegetation cover. Infrared thermal images were taken to estimate whether growth associated with *D. antarctica* affected the foliar temperature of *C. quitensis*. The importance of *D. antarctica* neighbours on the growth, survival and photochemical efficiency of *C. quitensis* was evaluated with a neighbour removal experiment.

**Results:** The number of *C. quitensis* individuals associated with *D. antarctica* was significantly higher than when growing alone in the moss carpet and the dead moss carpet, while in the transition zone there was a trend in that direction. *C. quitensis* individuals growing associated with *D. antarctica* were bigger than those growing alone in these three substrate types. In the fellfield site there were no significant differences, neither in the number nor the size of individuals when growing alone or associated with *D. antarctica*. Foliar temperature of *C. quitensis* individuals associated with *D. antarctica* was slightly (1.1°C) but significantly higher than in those growing alone. The growth, survival and photochemical efficiency of *C. quitensis* individuals with neighbours were higher than in individuals with neighbours removed.

**Conclusions:** Our results indicate that *D. antarctica* has a facilitative effect on the growth, survival and photochemical efficiency of *C. quitensis*. Thus, facilitative interactions are present and are important in one of the harshest environments on Earth, although results from the fellfield site indicate that further research is needed.

## KEY WORDS

Antarctic plants, Facilitation, positive interactions, tundra

## 1 | INTRODUCTION

Positive interactions among species are important factors affecting the structure and diversity of plant communities (Brooker et al., 2008; McIntire & Fajardo, 2014; Michalet et al., 2006). Although positive (i.e., facilitation) and negative (i.e., interference) interactions occur simultaneously between neighbouring plants (Armas & Pugnaire, 2005; Callaway, Nadkarni, & Mahall, 1991), several studies support that facilitative interactions prevail over negative interactions as the environment becomes harsher (Bertness & Callaway, 1994; Brooker & Callaghan, 1998; He & Bertness, 2014). Nonetheless, from a theoretical point of view it has been suggested that facilitative interactions might wane under highly stressful conditions (Holmgren & Scheffer, 2010; Michalet et al., 2006), whilst other studies suggest no decreases or even increases in the importance of facilitative interactions under highly stressful conditions (Kawai & Tokeshi, 2007; leRoux & McGeoch, 2010). Field studies assessing the presence and importance of facilitative interactions among plants have also found contrasting results. For instance, de Bello et al. (2011) and Dvorský et al. (2013) reported that facilitation was negligible at very high elevation (>5,000 m a.s.l.) in the Himalayas, whilst Pugnaire, Zhang, Li, and Luo (2015) reported no collapse of facilitation, even under the most stressful conditions, also at >5,000 m elevation in the Himalayas. Thus, field studies assessing whether facilitative interactions are present and are important in very harsh environments are needed.

The Antarctic tundra is among the harshest environments on Earth, where only mosses, lichens and two vascular plant species have been able to successfully establish permanent natural populations. These vascular plants are *Deschampsia antarctica* Desv. (Poaceae) and *Colobanthus quitensis* (Kunth) Bartl. (Caryophyllaceae), which grow naturally along the west coast of the Antarctic Peninsula (Komárková, Poncet, & Poncet, 1985). Although several studies have been conducted to reveal the morphological and physiological adaptations that enable *D. antarctica* and *C. quitensis* to withstand the adverse abiotic conditions of Antarctica (Alberdi, Bravo, Gutiérrez, Gidekel, & Corcuera, 2002; Cavieres et al., 2016; Smith, 2003), little is known about their regeneration ecology, particularly on processes relevant to their growth and survival.

Regarding species interactions, most of the scarce available information for the Antarctic tundra has focused on *D. antarctica*. For instance, Krna, Day, and Ruhland (2009) reported that neighbouring plants have negative effects on the growth of *D. antarctica* in two communities located on one of the Stepping Stone Islands. However, these negative effects were of lower intensity when the neighbour plant was a moss, and in some cases the effects were even positive (Krna et al., 2009). In an extensive sampling across the Maritime Antarctic, Casanova-Katny and Cavieres (2012) found that *D.*

*antarctica* showed a positive spatial association with moss carpets, where individual mats were larger and more abundant than on bare ground areas. The removal of the moss carpet around *D. antarctica* individuals as well as seedling transplant experiments showed that while survival was not affected by the presence of a moss carpet, the growth rate of *D. antarctica* was significantly higher inside moss carpets (Casanova-Katny & Cavieres, 2012). Thus, the presence of mosses was a key factor for the growth and expansion of *D. antarctica* populations (see also Park, Ahn, & Lee, 2012, 2013). However, little is known about *C. quitensis*. Throughout its remarkably wide latitudinal distribution (see below), this perennial herb forms loosely compact small cushions (0.5–10.0-cm diameter) that always grow surrounded by other forbs or grasses in bogs occurring at high elevations along the Andes (Aguirre, Rangel, Cleef, & Hooghiemstra, 1982; Méndez, 2007; Ruthsatz, 2012). Thus, we might suspect that growing associated with other plant species is beneficial for *C. quitensis*.

In this study we assessed the sign of the spatial association of *C. quitensis* with *D. antarctica* in an Antarctic tundra, and through a removal experiment in the field we assessed the importance of neighbours for the survival, growth and photochemical efficiency of *C. quitensis* individuals. Foliar temperatures of *C. quitensis* individuals growing alone or associated with *D. antarctica* were measured to assess the importance of neighbours in providing milder temperatures. We expect that the presence of neighbours would have a positive effect on *C. quitensis*, suggesting that positive interactions are important in a very stressful environment such as the Antarctic tundra.

## 2 | METHODS

### 2.1 | Study site

Fieldwork was carried out during the Antarctic Scientific Expedition (ECA) of the Chilean Antarctic Institute, INACH. The study was conducted in the King George Island near the H. Arctowski Polish Station (62°09'S, 58°28' W), where *D. antarctica* and *C. quitensis* co-exist and are abundant (Kozeretska et al., 2010). According to Angiel, Potocki, and Biszczuk-Jakubowska (2010) and Arażny, Kejna, and Sobota (2013), who analysed climatic data for 2006/2007 and 2012/2013, respectively, the mean air temperature during summer months (Jan to Mar) in this area is ca. 3°C, with maximum and minimum of 12°C and -5°C, respectively. Most days are characterized by overcast conditions, with short periods of high irradiance (Angiel et al., 2010). For instance, during Dec 2006–Jan 2007 there was only one clear day, 17 partly cloudy days and 44 overcast days (Kejna, 2008). Ground-level temperatures, which are relevant for Antarctic plants, are around 2–4°C higher than air temperatures and are importantly affected by wind speed (Arażny et al., 2013). Average wind speed during summer at 2 m a.s.l. is 5.0 m/s (18 km/hr; Kejna, 2008),

although winds of storm (>17 m/s) and hurricane (>30 m/s) strengths are observed during each month (Angiel et al., 2010). For instance, on 11 Feb 2007 wind velocity reached 33.3 m/s (120 km/hr; Kejna, 2008). Another important characteristic of the climate in the vicinity of the H. Arctowski Station is the large number of days with precipitation (Angiel et al., 2010), generating substrates that remain humid all summer. For instance, in 2006 there were 220 days with precipitation: 90 days with rainfall, 139 days with snowfall, and 2 days with hail, reaching a total precipitation of 610.4 mm (Angiel et al., 2010).

The selected area for this study corresponded with the intermediate vegetation zone after deglaciation described by Kozeretska et al. (2010), which is characterized by high vegetation cover, the presence of bare ground areas or fellfields and considerable soil water availability due to the high precipitation levels. Vegetation is dominated by bryophyte species forming a compact and continuous moss carpet where the two vascular plant species grow interspaced. The most abundant moss species in the carpet are *Sanionia georgico-uncinata*, *Polytrichum piliferum* and *P. alpinum*, and an analysis of the age structure of the *D. antarctica* and *C. quitensis* populations indicated that they were numerically dominated by mature plants (Kozeretska et al., 2010).

## 2.2 | Target species

*Colobanthus quitensis* is a perennial herb forming loosely compact small cushions of 0.5–10.0-cm diameter. Leaves are linear to linear-triangular, and gradually or abruptly contract to a short mucronate apex, herbaceous or rarely sub-coriaceous (Moore, 1983). Although it occurs from Mexico until the northern continental edge of the Antarctic Peninsula, as well as in several Antarctic and sub-Antarctic islands (Moore, 1979), the majority of its distribution is associated with the high Andes where it grows within local bogs dominated by knit sedges and grasses known as “Vegas” or “Bofedales” (Ruthsatz, 2012). In Antarctica, *C. quitensis* distribution is more limited than that of *D. antarctica*; it prefers drier, mineral-rich soils and occurs alone only in 3% of all localities where vascular plant presence has been described (Komárková et al., 1985).

## 2.3 | Vegetation sampling

To examine the abundances, individual size and spatial association of the two Antarctic vascular plants, we sampled different substrate types in the surroundings of our study area (see Appendix S1: Figure S1). The sampled substrates were:

1. Moss carpet areas: dominated by *Sanionia georgico-uncinata* and with presence of other moss species such as *Polytrichum piliferum* and *P. alpinum*. Vegetation cover is total, with a permanent water-saturated substrate, abundant in organic matter and N content of 40 ppm (Kozeretska et al., 2010; L. A. Bravo et al. unpublished data).
2. Dead moss carpet areas: dominated by *D. antarctica* with the presence of *C. quitensis* and *Usnea* spp. lichens, all of them occurring

above dead mosses. Vegetation cover is about 70%, with a permanent water-saturated substrate, abundant in organic matter and N content of 30 ppm (Kozeretska et al., 2010; L. A. Bravo et al. unpublished data).

3. Transition zone areas: these areas occur between dead moss carpets and fellfields, characterized by lower vegetation cover (<30%), dominated by *D. antarctica* with presence of some mosses, as well as fruticose and crustose lichens. Although the humidity of the substrate is always high, the organic matter content is low (15%) as is the N content of the soil (9 ppm; Kozeretska et al., 2010; L. A. Bravo et al. unpubl data).
4. Fellfields: characterized by very poor vegetation cover (<10%) and very scarce presence of both lichens and vascular plants. Soils are wet, rudimentary, with gravels and stones, and with very low organic matter content (<1%); N content of the soil is 4.3 ppm (Kozeretska et al., 2010; L. A. Bravo et al. unpubl data).

As the length of our stay in Antarctica is limited for logistical reasons, and appropriate weather conditions to work in the field (e.g., gentle chilly winds) are scarce and highly variable both within a single day and among days, we used high-resolution photographs to sample vegetation. A 50 cm × 50 cm quadrat was randomly laid out 50 times on each of the four different substrates previously identified according to the dominant vegetation. Each quadrat was photographed with a high-resolution digital camera (EK-CG100, Samsung) placed perpendicularly and at the same distance (1 m) to ground level. In the laboratory, the high-resolution images were used to generate a digital layer in shapefile spatial format in ArcGIS (v10.4.1) and with the aid of a digitizing table all the *D. antarctica* and *C. quitensis* individuals present on each shapefile were identified and delimited to obtain size (see Appendix S1: Figure S2). Subsequently, we counted the number of individuals of each species present in the quadrant either in isolation or spatially associated (i.e., growing together side-by-side or one inside the other) with the other vascular species. Finally, the size of those individuals growing associated or alone was obtained for each species.

## 2.4 | Foliar temperature

We used infrared thermal images to estimate whether growing associated with *D. antarctica* affected the foliar temperature of *C. quitensis* individuals. For this, on 27 Feb 2015, with partly clear sky conditions and a gentle breeze, 20 *C. quitensis* individuals growing alone and another 20 growing in association with *D. antarctica* were selected in the transition vegetation zone where plants were growing without surrounding mosses that can alter the temperature measurements. Selected individuals were photographed with an infrared thermal camera (Testo 875-2i; Testo, UK). Then each thermal image was processed with the software IRSofT (Testo) where four random points were marked on the foliage of each individual and the average temperature among these foliage points was recorded. In this way the foliar temperature of each photographed individual represents the average of four random points along their leaves (see Appendix S2: Figure S3). Then we used this single value per

individual to calculate the average foliar temperature of *C. quitensis* growing alone or associated with *D. antarctica*.

## 2.5 | Neighbour removal experiment

In Dec 2014, 40 healthy looking cushions of *C. quitensis* growing associated with *D. antarctica* in the transition vegetation zone were selected and marked. Then, a high-resolution photograph was taken for every marked individual. A total of 20 marked individuals were then randomly assigned to a neighbour removal experiment where each individual was isolated from its *D. antarctica* neighbours by carefully removing the above-ground part of every plant around it for a radius of 10 cm. To monitor the growth and survival of these isolated *C. quitensis* and of the control individuals, at the end of that growing season (Mar 2015) we recorded the survival of the experimental individuals, and new photographs were taken. Pictures were then analysed with the software ImageJ 1.42q (US National Institutes of Health, Bethesda, MD, USA) to obtain the growth of each experimental plant by estimating the difference in size between the two pictures. Survival of the experimental individuals was also recorded during the following growing season (Feb 2016).

## 2.6 | Photochemical efficiency

The photochemical efficiency of 15 isolated (neighbours removed) and 15 control individuals was assessed by means of chlorophyll *a* fluorescence measurements. The fluorescence of chlorophyll *a* associated with photosystem II (PSII) is a sensitive tool for probing the state of the photosynthetic apparatus *in vivo*, being useful to quantify stress on the photosynthetic performance through the photochemical efficiency of PSII under field conditions (Lambers, Chapin, & Ponds, 2008). Decreases in photochemical efficiency of PSII indicate restrictions or damage to the photosynthetic apparatus, compromising carbon gain, and considered one of the first manifestations of stress at the individual level (Maxwell & Johnson, 2000). The electron transport rate (ETR) is also a parameter derived from chlorophyll *a* fluorescence measurements that is directly related to quantum efficiency of PSII ( $\Phi$ PSII) and has the advantage of being directly correlated with carbon gain (Maxwell & Johnson, 2000). On 4 Mar 2015, we quantified the  $\Phi$ PSII and ETR at different light intensities as indicators of stress experienced by the *C. quitensis* individuals growing in the experimental conditions (with or without neighbours). Fully developed leaves on each *C. quitensis* individual were dark-adapted with leaf clips for 30 min before measurements to ensure maximum photochemical efficiency by fully opening the PSII centres. Fluorescence signals were generated with a pulse-amplitude modulated fluorometer (FMS 2; Hansatech, Instruments, Norfolk, UK). Minimum fluorescence ( $F_0$ ) with all PSII reaction centres in the open state was determined by applying a weak modulated light ( $0.4 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). Maximum fluorescence ( $F_m$ ) with all PSII reaction centres in the closed state was induced with a 0.8 s saturating pulse of white light ( $9,000 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). Then leaves were exposed for 5 min to

each of the following PPFD: 0, 131, 435, 665, 1,033, 1,292 and  $1,957 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ , to obtain steady state readings of  $\Phi$ PSII. From the  $\Phi$ PSII values at each PPFD level we estimated the ETR as follows:

$$\text{ETR} = \Phi\text{PSII} \times \text{PPFD} \times 0.84 \times 0.5$$

where 0.84 is assumed light absorption by the leaf, and 0.50 is the average ratio of PSII to PSI reaction centres (Maxwell & Johnson, 2000). Measurements were done at noon, with clear-sky conditions, so that all experimental individuals were exposed to similar solar radiation conditions.

## 2.7 | Data analyses

The abundances and individual size of *C. quitensis* associated and not associated with *D. antarctica* on the different substrate types were compared with a fully factorial two-way mixed ANOVA, where substrate type was a random factor, presence (or not) of neighbouring *D. antarctica* the fixed factor and number of *C. quitensis* individuals or their size (square root-transformed to achieve normality in distribution) the response variable. Analyses were done in R 3.1.1 statistical software (R Foundation for Statistical Computing, Vienna, AT) using the package lme4.

Differences in foliar temperature between alone and associated individuals were assessed with a Student's *t*-test. For control and neighbour-removed individuals we estimated intrinsic growth rate as the log ratio between final and initial sizes and the results were then compared with a Student's *t*-test.  $\Phi$ PSII and ETR measurements at different light intensities were compared among control and neighbour-removed plants with repeated measures ANOVAs, where presence of a neighbour was the independent factor, light intensity the within-subject factor and  $\Phi$ PSII and ETR the response variable. This analysis was performed with R 3.1.1 using the package car.

## 3 | RESULTS

### 3.1 | Abundance, survival and growth

We recorded a total of 24,155 vascular plant individuals, where 17,387 and 6,768 corresponded to *D. antarctica* and *C. quitensis*, respectively, and across the four substrate types *D. antarctica* was more abundant than *C. quitensis* (Appendix S2: Figure S4).

According to the two-way ANOVA, the substrate type, presence of neighbouring *D. antarctica* and the interaction between these factors significantly affected the number of *C. quitensis* individuals (Table 1). A higher amount of *C. quitensis* individuals occurred in the dead moss carpet and the transition zone (ca. 60 individuals/m<sup>2</sup>), while abundance of *C. quitensis* was very low (ca. 15 individuals/m<sup>2</sup>) in both the moss carpet and the fellfield. The number of *C. quitensis* individuals associated with *D. antarctica* was significantly higher than those growing alone in the moss carpet and the dead moss carpet,

**TABLE 1** Two-way ANOVA of the effect of substrate type, presence of neighbouring *Deschampsia antarctica* and the interaction between these factors on the number of *Colobanthus quitensis* individuals

	df	SS	MS	F value	p
Substrate	3	230.12	76.71	84.55	<0.001
Neighbour	1	17.18	17.18	18.94	<0.001
Substrate × Neighbour	3	17.49	5.83	6.43	<0.01
Error	304	0.91	0.91		

while in the transition zone there was a trend in the same direction but this was not statistically significant (Figure 1a). Overall, therefore, *C. quitensis* individuals were more frequent growing associated with *D. antarctica* than growing alone.

Interestingly, the analyses of individual size indicated that *C. quitensis* individuals growing associated with *D. antarctica* were bigger than those growing alone in three out of the four substrate types sampled (Figure 1b). Only in the fellfield site was there no significant differences in size of individuals when growing alone or associated with *D. antarctica* (Figure 1b). Thus, although the number of *C. quitensis* individuals associated with *D. antarctica* did not differ than the number growing alone in the transition zone, associated individuals were larger than non-associated individuals. This produced important differences in the total area covered by *C. quitensis* when grown associated with *D. antarctica* compared to when grown alone in most of the sampled habitats (Figure 1c).

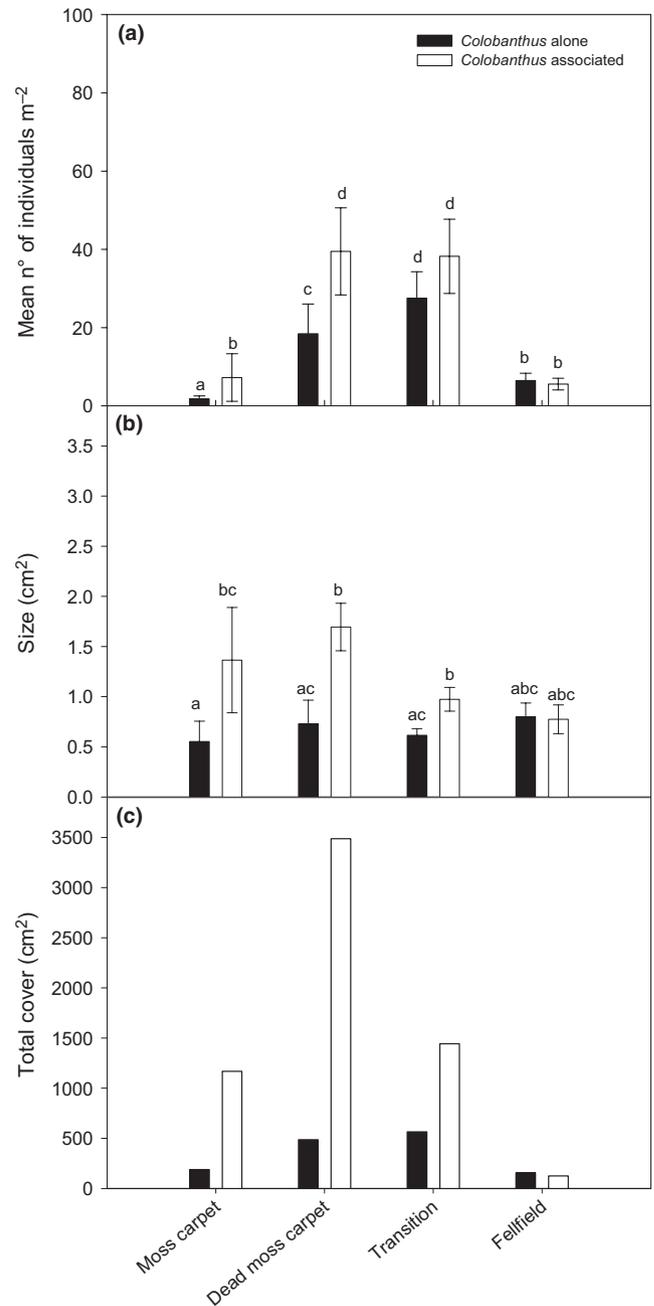
### 3.2 | Foliar temperature

While leaves of *C. quitensis* individuals growing alone had an average temperature of  $6.6 \pm 0.43^\circ\text{C}$  ( $\pm 2$  SE), the foliar temperature of *C. quitensis* individuals growing associated with *D. antarctica* was slightly but significantly higher ( $7.7 \pm 0.42^\circ\text{C}$ , Student's *t*-test = 0.21,  $p < 0.01$ ).

### 3.3 | Removal experiment

Overall, the growth and survival of control *C. quitensis* individuals (i.e., with neighbours) were higher than those individuals where neighbours were removed. At the end of the first season all *C. quitensis* individuals, both with and without neighbours, remained alive. On the contrary, at the end of the second season only 50% of the artificially isolated *C. quitensis* survived (Figure 2a), and those individuals had an average of ca. 10% of their surface still greenish and alive, being 90% already dry and dead.

Regarding growth, the intrinsic growth rate of control individuals was significantly higher than that of isolated individuals (log ratio 0.29 vs 0.17; *t*-test,  $p = 0.011$ ; Figure 2b). Isolated individuals registered an average increase in surface area of  $1.0 \pm 0.2 \text{ cm}^2$  (i.e., 1.1-cm diameter increase), which, considering their initial sizes, corresponded to an average percentage increase in surface of

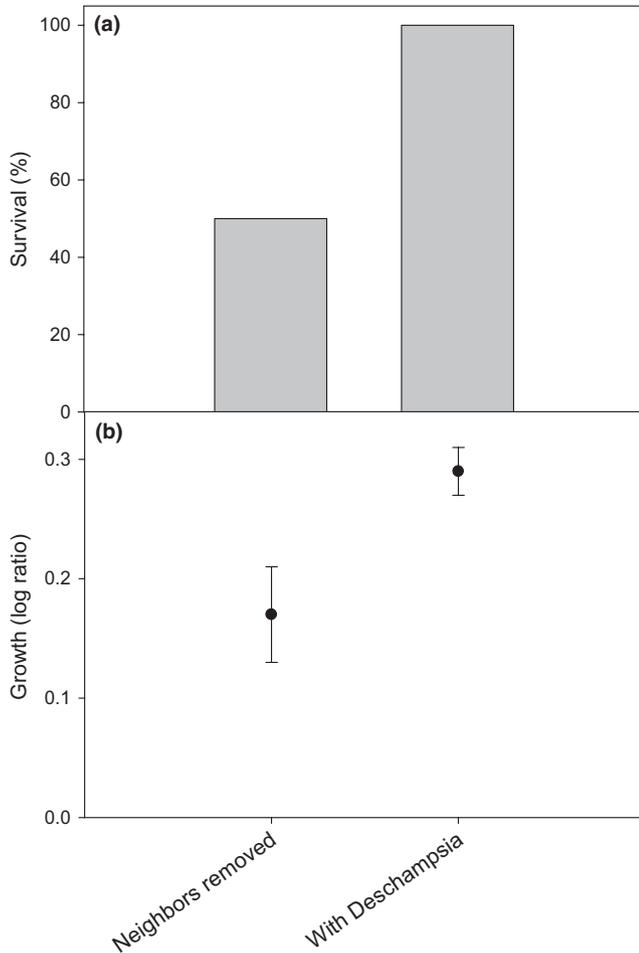


**FIGURE 1** Abundance (a), size (b) and total cover (c) of *Colobanthus quitensis* growing alone (black bars) or associated with *Deschampsia antarctica* (empty bars) in four different substrates in King Gorge Island, Maritime Antarctica. Different letters indicate significant differences according to Tukey HSD test

$19.8 \pm 5.2\%$  (average  $\pm$  SE). In contrast, control individuals had an increase in surface of  $1.9 \pm 0.3 \text{ cm}^2$  (1.6-cm diameter increase), which corresponded to an average percentage increase in surface area of  $34.0 \pm 2.9\%$ .

### 3.4 | Photochemical efficiency

Although the quantum efficiency of PSII ( $\Phi\text{PSII}$ ) in both control and isolated plants significantly decreased with light intensity (significant



**FIGURE 2** Survival after two growing seasons (a) and relative growth (b) of *Colobanthus quitensis* individuals growing associated with *Deschampsia antarctica* or with neighbours removed or in King Gorge Island, Maritime Antarctica

between-subject factor; Table 2, Figure 3), the overall quantum efficiency of control plants was significantly higher than that of isolated plants (Table 2, Figure 3). Likewise, in both control and isolated plants the ETR significantly increased with light intensity (significant between-subject factor; Table 2), saturating at light intensities  $>1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Figure 3). However, regardless of light intensity, ETR of control plants was always higher than in isolated plants (Figure 3), indicating that control plants are photochemically more efficient, and that at different light intensities they have the potential to achieve higher photosynthetic rates than isolated plants.

## 4 | DISCUSSION

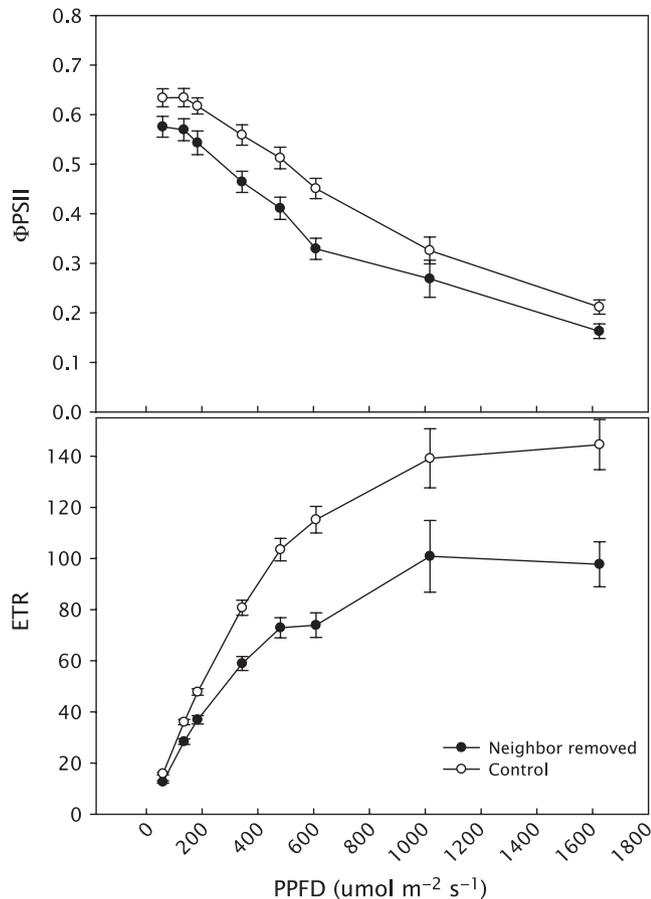
Very few studies have addressed interactions among Antarctic plants, with contrasting results. For instance, while Krna et al. (2009) reported negative effects of the presence of both mosses and *C. quitensis* on the growth of *D. antarctica*, Casanova-Katny and Cavieres (2012) reported that mosses facilitate growth of *D. antarctica*. The sign of interactions with *C. quitensis* as target species had

**TABLE 2** Repeated measures ANOVA of quantum efficiency of PSII ( $\Phi_{\text{PSII}}$ ) and electron transport rate (ETR) at different light intensities (within subject factor) in *Colobanthus quitensis* plants with *Deschampsia antarctica* neighbors (control) and with neighbours removed

	df	SS	MS	F	p
$\Phi_{\text{PSII}}$					
Neighbour	1	0.36	0.36	10.05	<0.01
Residuals	30	1.08	0.03		
Within-subject					
PAR	6	4.33	0.72	503.21	<0.001
Neighbour:PAR	6	0.03	0.01	3.81	<0.01
Residuals	180	0.26	0.001		
ETR					
Neighbour	1	30,030	30030	27.06	<0.001
Residuals	30	33,295	1110		
Within-subject					
PAR	6	27,9670	46612	244.58	<0.001
Neighbour:PAR	6	13,871	2312	12.13	<0.001
Residuals	180	34,305	191		

never been assessed before this study. We found that, in general, *C. quitensis* individuals grew more frequently associated with *D. antarctica* than alone, and that individuals growing close to *D. antarctica* (positively associated) were bigger than those non-associated with this species. The removal of *D. antarctica* neighbours around *C. quitensis* demonstrated that the presence of the grass was important for *C. quitensis* growth, survival and photochemical efficiency, as assessed by  $\Phi_{\text{PSII}}$  and ETR. Thus, our results clearly indicate that *D. antarctica* has a facilitative effect on *C. quitensis*, through promoting its growth and survival.

Although the substrate type affected the abundance of both *C. quitensis* and *D. antarctica* individuals, in general it was more frequent to observe *C. quitensis* individuals growing associated with *D. antarctica* than growing alone. Edwards (1972) reported the total number of joint occurrences of the major species within quadrats used in the vegetation sampling of Signy Island, and described that both *C. quitensis* and *D. antarctica* were positively associated with some bryophyte and lichen species (e.g., *Brachytecium* sp., *Cephaloziella varians*, *Marchantia berteroa*). Interestingly, Edwards (1972) did not mention the results for joint occurrences of *C. quitensis* and *D. antarctica*, but his Table IV clearly indicates that they were positively associated. In addition, he noted that *C. quitensis*, in contrast to *D. antarctica*, is not good in colonizing mosses, which is in line with our results, where higher abundances of *C. quitensis* occurred in the dead moss and the transition zone. Corner (1971) indicated that on Argentine Island in all the locations where *C. quitensis* was present it was associated with *D. antarctica*, and confined to the most sheltered positions. The fact that *C. quitensis* is frequently found in more sheltered habitats has also been highlighted in other studies (Greene & Holtom, 1971;



**FIGURE 3** Quantum efficiency of PSII ( $\Phi_{\text{PSII}}$ ) and electron transport rate (ETR) at different light intensities for *Colobanthus quitensis* individuals growing associated with *Deschampsia antarctica* (empty circles) or with neighbours removed (black circles) in King Gorge Island, Maritime Antarctica

Komárková et al., 1985; Vera, 2011), suggesting that this species requires some protection (see below).

In our study site individual sizes of *C. quitensis* varied from 8 to 20 mm in diameter (i.e., 0.5–2.0 cm<sup>2</sup> area) depending on the substrate and the association with *D. antarctica*. These values are similar to those reported in Vera (2011) for *C. quitensis* inhabiting gentle slopes and recently deglaciated habitats in Livingstone Island, but smaller than those reported by Xiong, Ruhland, and Day (1999) for Stepping Stones Islands (mean: 80 mm) and those reported by Fowbert and Smith (1994) in Argentine Island, where the majority of individuals were around 30–50-mm diameter. With the exception of the fellfield site, which has no development of an organic soil (L. A. Bravo et al., unpubl. results), *C. quitensis* individuals growing associated with *D. antarctica* were bigger than those growing alone, suggesting that the presence of this grass is relevant for growth. This was corroborated in our neighbour removal experiment, where the highest growth rates were observed in those individuals where the neighbouring *D. antarctica* individuals were not removed. We found that the increase in diameter of control individuals after 3 months was on average 1.5 cm (increase in area 1.9 cm<sup>2</sup>). Day, Ruhland, and Xiong (2001) found increases in diameter of 2.0–2.5 cm after 4 months in a 4-year study

conducted in Steeping Stone Islands. Day, Ruhland, Grobe, and Xiong (1999), also in Steeping Stone Islands, found increases in diameter for *C. quitensis* growing under natural conditions of 2.5 cm in 78 days. Hence, the average decrease in growth to 1.1-cm diameter increase (ca. 1 cm<sup>2</sup>) after 3 months found in the neighbour-removed individuals clearly indicates a departure from the normal growth rate of this species. This departure from normal conditions also affected survival as only 50% of the experimentally isolated individuals survived a second summer, suggesting again that the presence of *D. antarctica* as a neighbour is important for growth and survival.

In the Antarctic it has been shown that plants, especially mosses, substantially change the microclimatic conditions compared to bare ground (Block, Smith, & Kennedy, 2009). Edwards (1972), in a detailed study of temperature profiles on the canopy of different species on Signy Island, showed that temperature inside patches of *D. antarctica* and *C. quitensis* was as high as, and on sunny days, higher than that of moss carpets, and definitively higher than bare ground. An examination of the temperature profiles reported by Edwards (1972) for each Antarctic vascular plant shows that the canopy of *D. antarctica* reached higher temperatures than the canopy of *C. quitensis* both on sunny days and overcast conditions, with differences in temperature as high as 5°C. As a tussock grass, the canopy of *D. antarctica* is taller and denser than that of *C. quitensis*, which may explain the differences in temperature between them. But more importantly, in extremely cold and windy places such as Antarctica, the presence of a shelter that reduces the wind speed decreases the loss of heat and water (Nobel, 1981). In the Arctic it has been shown that plants sheltered by the canopy of other plants can increase their temperature 1–2°C above air temperatures (Carlsson & Callaghan, 1991). The infrared thermal images of *C. quitensis* individuals growing associated with *D. antarctica* indicated that their foliar temperature was on average 1.1°C higher than that of isolated individuals, in line with that expected from the shelter effect exerted. Although this increase might appear negligible, this small rise in temperature may nevertheless be of crucial importance when plants exist close to their lower temperature limit (Körner & Larcher, 1988). For instance, according to the leaf temperature–photosynthesis relationship described for *C. quitensis* in Xiong et al. (1999), increases in leaf temperature from 7°C to 8°C imply increases in photosynthesis rates from 5.0 to 6.5  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  of a maximum of 7.3  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ . According to the studies of Edwards and Smith (1988) and Sierra-Almeida, Casanova-Katny, Bravo, Corcuera, and Cavieres (2007), a 1°C increase in leaf temperature induced a 10%–20% increase in photosynthesis. Therefore, it seems likely that the presence of the taller and denser canopy of *D. antarctica* providing shelter to *C. quitensis* individuals may reduce their convective heat loss, allowing heat conservation and maintaining temperatures in the range of metabolic activity and biomass production (Smith, 1999, 2003). The fact that the quantum efficiency ( $\Phi_{\text{PSII}}$ ) of control plants was significantly higher than that of plants where the neighbours were removed supports the former argument. In addition, the higher ETR of plants with intact neighbours also supports the idea that the shelter provided by the canopy of *D. antarctica* allows *C. quitensis*

to maintain its temperature in a range where it can achieve higher photosynthesis than plants with no neighbours, thus accumulating more carbon to allocate to growth and survival.

Overall, our results clearly indicate that positive interactions are present and are important for the growth and survival of *C. quitensis* in the Antarctic tundra. Michalet et al. (2006), Michalet, Bagousse-Pinguet, Maalouf, and Lortie (2014) indicated a collapse of facilitative interactions under extremely harsh environmental conditions might be expected due to a decrease in the mitigating effect of nurse plant species. That is, the presence of a neighbour species does not generate milder conditions compared to the surrounding environment. In our study, the presence of *D. antarctica* seems to generate milder conditions for growth and survival of *C. quitensis* in most of the habitats evaluated. However, it is interesting to note that in the fellfield, a recently deglaciated terrain with no development of organic soil and hence very few available nutrients, there was no positive association between *C. quitensis* and *D. antarctica* and the sizes of individuals were very small, regardless of the presence of the nurse grass species. The size and abundance of *D. antarctica* individuals was also very small (data not shown), suggesting that the ability of *D. antarctica* to provide shelter depends on the nutrient availability of the site. However, further studies are needed to disentangle the mechanisms involved in the positive interactions between these two Antarctic vascular plants and under what conditions they may wane, generating a collapse in these positive interactions.

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## REFERENCES

- Aguirre, C. J., Rangel, C. O., Cleef, A. M., & Hooghiemstra, H. (1982). *Colobanthus quitensis* (Caryophyllaceae) en los andes colombianos. *Caldasia*, 13, 367–377.
- Alberdi, M., Bravo, L. A., Gutiérrez, A. H., Gidekel, M., & Corcuera, L. J. (2002). Ecophysiology of Antarctic vascular plants. *Physiologia Plantarum*, 115, 479–486. <https://doi.org/10.1034/j.1399-3054.2002.1150401.x>
- Angiel, P. J., Potocki, M., & Biszczuk-Jakubowska, J. (2010). Weather condition characteristics at the H. Arctowski Station (South Shetlands, Antarctica) for 2006, in comparison with multi-year research result. *Miscellanea Geographica*, 14, 5–11.
- Araźny, A., Kejna, M., & Sobota, I. (2013). Ground temperature at the Henry Arctowski station (King George island, Antarctic)—Case study from the Period January 2012 to February 2013. *Bulletin of Geography. Physical Geography Series*, 6, 59–80.
- Armas, C., & Pugnaire, F. I. (2005). Plant interactions govern population dynamics in a semi-arid plant community. *Journal of Ecology*, 93, 978–989. <https://doi.org/10.1111/j.1365-2745.2005.01033.x>
- Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology & Evolution*, 9, 191–193. [https://doi.org/10.1016/0169-5347\(94\)90088-4](https://doi.org/10.1016/0169-5347(94)90088-4)
- Block, W., Smith, R. I. L., & Kennedy, A. D. (2009). Strategies of survival and resource exploitation in the Antarctic fellfield ecosystem. *Biological Reviews*, 84, 449–484. <https://doi.org/10.1111/j.1469-185X.2009.00084.x>
- Brooker, R. W., & Callaghan, T. V. (1998). The balance between positive and negative plant interactions and its relationship to environmental gradients: A model. *Oikos*, 81, 196–207. <https://doi.org/10.2307/3546481>
- Brooker, R. W., Maestre, F. T., Callaway, R. M., Lortie, C. J., Cavieres, L. A., Kunstler, G., ... Michalet, R. (2008). Facilitation in plant communities: The past, the present and the future. *Journal of Ecology*, 96, 18–34.
- Callaway, R. M., Nadkarni, N. M., & Mahall, B. E. (1991). Facilitation and interference of *Quercus douglasii* on understory productivity in central California. *Ecology*, 72, 1484–1499. <https://doi.org/10.2307/1941122>
- Carlsson, B. A., & Callaghan, T. V. (1991). Positive plant interactions in tundra vegetation and the importance of shelter. *Journal of Ecology*, 79, 973–983. <https://doi.org/10.2307/2261092>
- Casanova-Katny, M. A., & Cavieres, L. A. (2012). Antarctic moss carpets facilitate growth of *Deschampsia antarctica* but not its survival. *Polar Biology*, 35, 1869–1878. <https://doi.org/10.1007/s00300-012-1229-9>
- Cavieres, L. A., Sáez, P., Sanhueza, C., Sierra-Almeida, A., Rabert, C., Corcuera, L. J., ... Bravo, L. A. (2016). Ecophysiological traits of Antarctic vascular plants: Their importance in the responses to climate change. *Plant Ecology*, 217, 343–358. <https://doi.org/10.1007/s11258-016-0585-x>
- Corner, R. W. M. (1971). Studies in *Colobanthus quitensis* (Kunth) Bartl. and *Deschampsia antarctica* Desv.: IV. Distribution and reproductive performance in the Argentine Islands. *British Antarctic Survey Bulletin*, 26, 41–50.
- Day, T. A., Ruhland, C. T., Grobe, C. W., & Xiong, F. (1999). Growth and reproduction of Antarctic vascular plants in response to warming and UV radiation reductions in the field. *Oecologia*, 119, 24–35. <https://doi.org/10.1007/s004420050757>
- Day, T. A., Ruhland, C. T., & Xiong, F. S. (2001). Influence of solar ultraviolet-B radiation on Antarctic terrestrial plants: Results from a 4-year field study. *Journal of Photochemistry and Photobiology B: Biology*, 62, 78–87. [https://doi.org/10.1016/S1011-1344\(01\)00161-0](https://doi.org/10.1016/S1011-1344(01)00161-0)
- de Bello, F., Doležal, J., Dvorský, M., Chlumská, Z., Řeháková, K., Klimešová, J., & Klimeš, L. (2011). Cushions of *Thylacospermum caespitosum* (Caryophyllaceae) do not facilitate other plants under extreme altitude and dry conditions in the north-west Himalayas. *Annals of Botany*, 108, 567–573. <https://doi.org/10.1093/aob/mcr183>
- Dvorský, M., Doležal, J., Kopecký, M., Chlumská, Z., Janatková, K., Altman, J., ... Řeháková, K. (2013). Testing the stress-gradient hypothesis at the roof of the world: Effects of the cushion plant *Thylacospermum caespitosum* on species assemblages. *PLoS ONE*, 8, e53514. <https://doi.org/10.1371/journal.pone.0053514>
- Edwards, J. A. (1972). Studies in *Colobanthus quitensis* (Kunth) Bartl. and *Deschampsia antarctica* Desv.: V. Distribution, ecology and vegetative performance on Signy Island. *British Antarctic Survey Bulletin*, 26, 41–50.
- Edwards, J. A., & Smith, L. R. (1988). Photosynthesis and respiration of *Colobanthus quitensis* and *Deschampsia antarctica*. *British Antarctic Survey Bulletin*, 81, 43–63.

- Fowbert, J. A., & Smith, R. I. L. (1994). Rapid population increases in native vascular plants in the Argentine Islands, Antarctic Peninsula. *Arctic and Alpine Research*, 26, 290–296. <https://doi.org/10.2307/1551941>
- Greene, D. M., & Holtom, A. (1971). Studies in *Colobanthus quitensis* (Kunth) Bartl. and *Deschampsia antarctica* Desv. III. Distribution, habitats and performance in the Antarctic botanical zone. *British Antarctic Survey Bulletin*, 26, 1–29.
- He, Q., & Bertness, M. D. (2014). Extreme stresses, niches, and positive species interactions along stress gradients. *Ecology*, 95, 437–444.
- Holmgren, M., & Scheffer, M. (2010). Strong facilitation in mild environments: The stress gradient hypothesis revisited. *Journal of Ecology*, 98, 1269–1275. <https://doi.org/10.1111/j.1365-2745.2010.01709.x>
- Kawai, T., & Tokeshi, M. (2007). Testing the facilitation–competition paradigm under the stress-gradient hypothesis: Decoupling multiple stress factors. *Proceedings of the Royal Society of London B: Biological Sciences*, 274, 2503–2508. <https://doi.org/10.1098/rspb.2007.0871>
- Kejna, M. (2008). Topoclimatic conditions in the vicinity of the Arctowski Station (King George Island, Antarctica) during the summer season of 2006/2007. *Polish Polar Research*, 29, 95–116.
- Komárková, V., Poncet, S., & Poncet, J. (1985). Two native Antarctic vascular plants, *Deschampsia antarctica* and *Colobanthus quitensis*: A new southernmost locality and other localities in the Antarctic Peninsula area. *Arctic and Alpine Research*, 17, 401–416. <https://doi.org/10.2307/1550865>
- Körner, C., & Larcher, W. (1988). Plant life in cold climates. *Symposia of the Society for Experimental Biology*, 42, 25–57.
- Kozeretska, I. A., Parnikoza, I. Y., Mustafa, O., Tyschenko, O. V., Korsun, S. G., & Convey, P. (2010). Development of Antarctic herb tundra vegetation near Arctowski station, King George Island. *Polar Science*, 3, 254–261. <https://doi.org/10.1016/j.polar.2009.10.001>
- Krna, M. A., Day, T. A., & Ruhland, C. T. (2009). Effects of neighboring plants on the growth and reproduction of *Deschampsia antarctica* in Antarctic tundra. *Polar Biology*, 32, 1487–1494. <https://doi.org/10.1007/s00300-009-0646-x>
- Lambers, H., Chapin III, F. S., & Ponds, T. (2008). *Plant physiological ecology*, 2nd ed (p. 623). New York, NY: Springer Science. <https://doi.org/10.1007/978-0-387-78341-3>
- Le Roux, P. C., & McGeoch, M. A. (2010). Interaction intensity and importance along two stress gradients: Adding shape to the stress-gradient hypothesis. *Oecologia*, 162, 733–745. <https://doi.org/10.1007/s00442-009-1484-9>
- Maxwell, K., & Johnson, G. N. (2000). Chlorophyll fluorescence: A practical guide. *Journal of Experimental Botany*, 51, 659–668. <https://doi.org/10.1093/jexbot/51.345.659>
- McIntire, E. J., & Fajardo, A. (2014). Facilitation as a ubiquitous driver of biodiversity. *New Phytologist*, 201, 403–416. <https://doi.org/10.1111/nph.12478>
- Méndez, E. (2007). La vegetación de los Altos Andes II: Las Vegas del flanco oriental del Cordón del Plata (Mendoza, Argentina). *Boletín de la Sociedad Argentina de Botánica*, 42, 273–294.
- Michalet, R., Bagousse-Pinguet, L., Maalouf, J. P., & Lortie, C. J. (2014). Two alternatives to the stress-gradient hypothesis at the edge of life: The collapse of facilitation and the switch from facilitation to competition. *Journal of Vegetation Science*, 25, 609–613. <https://doi.org/10.1111/jvs.12123>
- Michalet, R., Brooker, R. W., Cavieres, L. A., Kikvidze, Z., Lortie, C. J., Pugnaire, F. I., ... Callaway, R. M. (2006). Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecology Letters*, 9, 767–773. <https://doi.org/10.1111/j.1461-0248.2006.00935.x>
- Moore, D. M. (1979). Southern ocean heaths (incl. Magellanic Moorland). In R. L. Specht (Ed.), *Ecosystems of the World: Heathland and related Shrublands* (pp. 490–497). Amsterdam, NL: Elsevier.
- Moore, D. M. (1983). *The flora of Tierra del Fuego*. Shrewsbury, UK: Anthony Nelson.
- Nobel, P. (1981). Wind as an ecological factor. In O. L. Lange, P. S. Nobel, C. B. Osmond, & H. Ziegler (Eds.), *Physiological plant ecology I: Responses to the physical environment (vol 12)* (pp. 475–500). Heidelberg, Germany: Springer. <https://doi.org/10.1007/978-3-642-68090-8>
- Park, J. S., Ahn, I. Y., & Lee, E. L. (2012). Influence of soil properties on the distribution of *Deschampsia antarctica* on King George Island, maritime Antarctica. *Polar Biology*, 35, 1703–1711. <https://doi.org/10.1007/s00300-012-1213-4>
- Park, J. S., Ahn, I. Y., & Lee, E. J. (2013). Spatial distribution patterns of the Antarctic Hair grass *Deschampsia antarctica* in relation to environmental variables on Barton Peninsula, King George Island. *Arctic, Antarctic & Alpine Research*, 45, 563–574. <https://doi.org/10.1657/1938-4246-45.4.563>
- Pugnaire, F. I., Zhang, L., Li, R., & Luo, T. (2015). No evidence of facilitation collapse in the Tibetan plateau. *Journal of Vegetation Science*, 26, 233–242. <https://doi.org/10.1111/jvs.12233>
- Ruthsatz, B. (2012). Vegetación y ecología de los bofedales altoandinos de Bolivia. *Phytocoenologia*, 42, 133–179. <https://doi.org/10.1127/0340-269X/2012/0042-0535>
- Sierra-Almeida, A., Casanova-Katny, M. A., Bravo, L. A., Corcuera, L. J., & Cavieres, L. A. (2007). Photosynthetic responses to temperature and light of Antarctic and Andean populations of *Colobanthus quitensis* (Caryophyllaceae). *Revista Chilena de Historia Natural*, 80, 335–343.
- Smith, R. I. L. (1999). Biological and environmental characteristics of three cosmopolitan mosses dominant in continental Antarctica. *Journal of Vegetation Science*, 10, 231–242. <https://doi.org/10.2307/3237144>
- Smith, R. I. L. (2003). The enigma of *Colobanthus quitensis* and *Deschampsia antarctica* in Antarctica. In A. H. L. Huiskes, W. W. C. Gieskes, J. Rozema, R. M. L. Scorno, S. M. van der Vies, & W. J. Wolf (Eds.), *Antarctic biology in a global context* (pp. 178–196). Leiden, NL: Backhuys.
- Vera, M. L. (2011). Colonization and demographic structure of *Deschampsia antarctica* and *Colobanthus quitensis* along an altitudinal gradient on Livingston Island, South Shetland Islands, Antarctica. *Polar Research*, 30, 7146. <https://doi.org/10.3402/polar.v30i0.7146>
- Xiong, F. S., Ruhland, C. T., & Day, T. A. (1999). Photosynthetic temperature response of the Antarctic vascular plants *Colobanthus quitensis* and *Deschampsia antarctica*. *Physiologia Plantarum*, 106, 276–286. <https://doi.org/10.1034/j.1399-3054.1999.106304.x>

## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

**APPENDIX S1** Figures S1 and S2, High-resolution photographs of the different substrate type sampled and the cover of *D. antarctica* and *C. quitensis*, respectively

**APPENDIX S2** Figures S3 and S4. Infrared thermal images of *C. quitensis* and the abundance of *C. quitensis* and *D. antarctica*, respectively

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